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1 Measuring β -diversity by remote sensing: a
2 challenge for biodiversity monitoring

3 Duccio Rocchini ^{1,2,3,*}, Sandra Luque ⁴, Nathalie Pettorelli ⁵,
Lucy Bastin ^{6,7}, Daniel Doktor ⁸, Nicolás Faedi ^{3,9},
Hannes Feilhauer ¹⁰, Jean-Baptiste Féret ⁴, Giles M. Foody ¹¹,
Yoni Gavish ¹², Sergio Godinho ¹³, William E. Kunin ¹⁴,
Angela Lausch ⁸, Pedro J. Leitão ^{15,16}, Matteo Marcantonio ¹⁷,
Markus Neteler ¹⁸, Carlo Ricotta ¹⁹, Sebastian Schmidlein ²⁰,
Petteri Vihervaara²¹, Martin Wegmann ²²,
Harini Nagendra ²³

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5 ¹ Center Agriculture Food Environment, University of Trento, Via E.
6 Mach 1, 38010 S. Michele all'Adige (TN), Italy

7 ² Centre for Integrative Biology, University of Trento, Via Sommarive,
8 14, 38123 Povo (TN), Italy

9 ³ Fondazione Edmund Mach, Research and Innovation Centre, Depart-
10 ment of Biodiversity and Molecular Ecology, Via E. Mach 1, 38010 S. Michele
11 all'Adige (TN), Italy, corresponding author: ducciorocchini@gmail.com, duc-
12 cio.rocchini@fmach.it

13 ⁴ UMR-TETIS, IRSTEA Montpellier, Maison de la Télédétection, 500
14 rue JF Breton, 34093, Montpellier Cedex 5, France

15 ⁵ Institute of Zoology, The Zoological Society of London, Regent's Park,
16 London, United Kingdom

17 ⁶ School of Computer Science, Aston University, United Kingdom

18 ⁷ Currently on secondment to Knowledge Management Unit, Joint Re-
19 search Centre of the European Commission, Italy

20 ⁸ Helmholtz Centre for Environmental Research - UFZ, Department Com-
21 putational Landscape Ecology Permoserstrasse 15, 04318 Leipzig, Germany

22 ⁹ Department of Computer Science and Engineering, University of Bologna,
23 Mura Anteo Zamboni, 7, 40126 Bologna, Italy

24 ¹⁰ Institut für Geographie Friedrich-Alexander Universität Erlangen-Nürnberg
25 Wetterkreuz 15, 91058 Erlangen, Germany

26 ¹¹ School of Geography, University of Nottingham, Nottingham, NG7
27 2RD, United Kingdom

28 ¹² School of Biology, Faculty of biological Science, University of Leeds,
29 Leeds LS2 9JT, United Kingdom

30 ¹³ Universidade de Evora , Evora · Institute of Mediterranean Agricultural
31 and Environmental Sciences (ICAAM)

32 ¹⁴ School of Biology, University of Leeds, Leeds, UK

33 ¹⁵ Department Landscape Ecology and Environmental System Analy-
34 sis, Technische Universität Braunschweig, Langer Kamp 19c, 38106 Braun-
35 schweig, Germany

36 ¹⁶ Geography Department, Humboldt-Universität zu Berlin, Unter den
37 Linden 6, 10099 Berlin, Germany

38 ¹⁷ Department of Pathology, Microbiology, and Immunology, School of
39 Veterinary Medicine, University of California, Davis, USA

40 ¹⁸ Mundialis GmbH & Co. KG, Kölnstraße 99, 53111 Bonn, Germany

41 ¹⁹ Department of Environmental Biology, University of Rome “La Sapienza”,
42 00185 Rome, Italy

43 ²⁰ Karlsruher Institut für Technologie (KIT), Institut für Geographie und
44 Geoökologie, Kaiserstr. 12, 76131 Karlsruhe, Germany

45 ²¹ Finnish Environment Institute (SYKE), Natural Environment Centre
46 Mechelininkatu 34a,P.O.Box 140 FI-00251 Helsinki, Finland

47 ²² Department of Remote Sensing, Remote Sensing and Biodiversity Re-
48 search Group, University of Wuerzburg, Wuerzburg, Germany

49 ²³ Azim Premji University, PES Institute of Technology Campus, Pixel
50 Park, B Block, Electronics City, Hosur Road, Bangalore, 560100, India

51

Abstract

52 Biodiversity includes multiscalar and multitemporal structures and
53 processes, with different levels of functional organization, from genetic
54 to ecosystemic levels. One of the mostly used methods to infer bio-
55 diversity is based on taxonomic approaches and community ecology
56 theories. However, gathering extensive data in the field is difficult due
57 to logistic problems, [especially](#) when aiming at modelling biodiversity
58 changes in space and time, which assumes statistically sound sampling
59 schemes. In this [context](#), [airborne](#) or satellite remote sensing allow [in-](#)
60 [formation to be gathered](#) over wide areas in a reasonable time.

61 Most of the biodiversity maps obtained from remote sensing have
62 been based on the inference of species richness by regression analy-
63 sis. On the contrary, estimating compositional turnover (β -diversity)

64 might add crucial information related to relative abundance of dif-
65 ferent species instead of just richness. Presently, few studies have
66 addressed the measurement of species compositional turnover from
67 space.

68 Extending on previous work, in this manuscript we propose novel
69 techniques to measure β -diversity from airborne or satellite remote
70 sensing, mainly based on: i) multivariate statistical analysis, ii) the
71 spectral species concept, iii) self-organizing feature maps, iv) multi-
72 dimensional distance matrices, and the v) Rao's Q diversity. Each
73 of these measures addresses one or several issues related to turnover
74 measurement. This manuscript is the first methodological example
75 encompassing (and enhancing) most of the available methods for es-
76 timating β -diversity from remotely sensed imagery and potentially
77 relating them to species diversity in the field.

78 *Keywords:* β -diversity, Kohonen self-organising feature maps, Rao's Q
79 diversity index, remote sensing, satellite imagery, Sparse Generalized Dis-
80 similarity Model, spectral species concept.

81 1 Introduction

82 Biodiversity cannot be fully investigated without considering the spatial com-
83 ponent of its variation. In fact, it is known that the dispersal of species over
84 wide areas is driven by spatial constraints directly related to the distance
85 among sites. A negative exponential dispersal kernel is usually adopted to
86 mathematically describe the occupancy of new sites by species, as:

$$F = \sum_{K=1}^N e^{\frac{-d_{ik}}{a}} \quad (1)$$

87 where d_{ik} = distance between two locations i and k and a is a parameter
88 regulating the dispersal from localized areas (low values of a) to widespread
89 ones (high values of a , Meentemeyer et al. (2008)).

90 In this sense, distance acquires a significant role in ecology to estimate bio-
91 diversity change. Hence, spatially explicit methods have been acknowledged
92 in ecology for providing robust estimates of diversity at different hierarchical
93 levels: from individuals (Tyre et al., 2001), to populations (Vernesi et al.,
94 2012), to communities (Rocchini et al., 2005).

95 When dealing with spatial explicit methods, remote sensing images repre-
96 sent a powerful tool, particularly when coupling information on compositional
97 properties of the landscape with its structure (Figure 1). Remote sensing has

98 widely been used for conservation practices including very different types of data
99 such as nighlights data (Mazor et al., 2013), Land Surface Temperature estimated
100 from MODIS data (Metz et al., 2014), spectral indices (Gillespie, 2005).

101 Most of the remote sensing applications for biodiversity estimation have relied
102 on the estimate of local diversity hotspots, considering land use diversity
103 (Wegmann et al., 2017) or continuous spatial variability of the spectral signal
104 (Rocchini et al., 2010). This is mainly grounded in the assumption that a higher
105 landscape heterogeneity is strictly related to a higher amount of species occupying
106 different niches. However, given two sites s_1 and s_2 , the final diversity is not only
107 related to the species / spectral richness of s_1 and s_2 , but overall to the amount of
108 shared species / spectral values. In other words, the lower the their intersection $s_1 \cap s_2$,
109 the higher will be the total diversity, while a low total diversity will be reached
110 when $s_1 \cap s_2 = s_1 \cup s_2$. Such intersection has been widely studied in ecology, after
111 the development of P-diversity theory (Whittaker, 1960).

112 Tuomisto et al. (2003) demonstrated the power of substituting distance in Eq. 1
113 by spectral distance to directly account for the distance between sites in an
114 environmental space, instead of a merely spatial one. However, while spectral
115 distance examples exist when measuring the P-diversity among pairs of sites (e.g.
116 Rocchini et al. (2015)), few studies have tested the possibility of measuring P-
117 diversity over wide areas considering several sites at the same time (however see
118 Alahuhta et al. (2017); Harris et al. (2015)). This is especially true when considering
119 the development of remote sensing tools for diversity estimate in which the concept
120 of P-diversity is still pioneering.

121 The aim of this paper is to present the most novel methods to measure P-
122 diversity from remotely sensed imagery based on the the most recently published
123 ecological models. In particular we will deal with: i) multivariate statistical
124 techniques, ii) the applicability of the spectral species concept, iii) multidimensional
125 distance matrices, iv) metrics coupling abundance and distance-based measures.

126 This manuscript is the first methodological example encompassing (and
127 enhancing) most of the available methods for estimating P-diversity from remotely
128 sensed imagery and potentially relate them to species diversity in the field.

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133 2 Multivariate statistical analysis for species diversity
134 estimate from remote sensing

135 Univariate statistics have been used to directly find relations between spectral and
136 species diversity. However, the amount of variability explained by single bands /
137 vegetation indices versus species diversity is generally relatively low, due to the fact
138 that different aspects related to the complexity of habitats might act in shaping
139 diversity, from disturbance and land use at local scales to climate and element fluxes
140 at global scales.

141 Ordination techniques are designed to quantitatively describe multivariate
142 gradual transitions in the species composition of sampled sites. Measuring the
143 distance between two sampling sites in the multi-dimensional ordination space is a
144 good proxy of the change in species composition. When this measure is related to
145 the geographical distance between the considered sites, the beta diversity at this
146 particular scale can be assessed.

147 Of the various available ordination techniques, Detrended Correspondence
148 Analysis (DCA, Hill and Gauch (1980)) is particularly suitable for such analyses. The
149 axes (i.e. gradients) of the DCA ordination space are scaled in standard deviation
150 (SD) units, where a distance of 4 SD is related to a full species turnover. This enables
151 a versatile analysis that easily reveals whether two sampled sites still have species in
152 common.

153 Several studies have mapped the ordination space using remote sensing data
154 (e.g., Schmidtlein and Sassini (2004); Schmidtlein et al. (2007); Feil-hauer et al. (2009,
155 2011, 2014); Gu et al. (2015); Harris et al. (2015); Leitao et al. (2015); Neumann et al.
156 (2015)). For this purpose, the axes scores of the sampled sites are regressed against
157 the corresponding canopy reflectance values extracted from air- or spaceborne
158 image data. The resulting multivariate regression models, one per ordination axis
159 and most often generated with machine learning regression techniques, are
160 subsequently applied on the image data for a spatial prediction of ordination scores.
161 Each pixel of the image data is assigned to a specific position in the ordination space
162 that indicates its species composition. The resulting gradient maps are a powerful
163 tool for analyses of beta diversity across different spatial scales (Feilhauer et al.,
164 2009; Hernandez-Stefanoni et al., 2012).

165 A simple analysis of the variability of the DCA scores in a defined pixel
166 neighborhood (i.e. a moving window) results in a efficient beta diversity assessment.
167 The spatial scale of this assessment can be varied either by resampling the gradient
168 map to a coarser spatial resolution (i.e. pixel size) or by changing the kernel size of
169 the considered pixel neighborhood. Such techniques have been further developed
170 e.g. for spatial conservation prioritization

171

172 programmes such as Zonation (Moilanen et al., 2005, 2009).

173 Figure 2 shows an example of a DCA-based assessment of beta diversity on a
174 very local scale (10 m) following the approach described in Feilhauer et al. (2009).
175 The analyzed landscape is a mosaic of raised bogs, fens, transition mires and Molinia
176 meadows. For a detailed description of the data and site please refer to Feilhauer et
177 al. (2014, 2016).

178 Analyses like this require two different data sets: (1) a sample of field data that
179 is representative for the vegetation in the studied area and is used to generate the
180 ordination space; (2) image data with a sufficient spectral resolution to discriminate
181 the vegetation types within the ordination space and with a spatial resolution that is
182 in line with the sampling design of the field data (Feilhauer et al., 2013).

183 Using these data, the continuous spatial variability of the spectral signal in the
184 image pixels is translated into a spatially continuous measure of species
185 composition. The advantages of this approach are obvious: since the diversity
186 analyses are conducted in the floristic gradient space, the resulting measures
187 resemble field studies and are thus easier to interpret than spectral proxies and closer
188 to the point of view of many end-users. Furthermore, the analysis of ordination
189 scores in defined pixel neighborhoods is not restricted to a single spatial scale but
190 offers the opportunity to implement assessments of beta diversity on multiple scales.

191

192 3 The spectral species concept

193 The spectral species concept has been proposed by Feret and Asner (2014a) to map
194 both α and β component of the biodiversity using a unique framework. It is rooted in
195 the convergence between two other concepts, the spectral variation hypothesis
196 (SVH) proposed by Palmer et al. (2002), and the plant optical types proposed by Ustin
197 and Gamon (2010), sustained by the technological advances in the domain of high
198 spatial resolution imaging spectroscopy. The SVH states that the spatial variability
199 in the remotely sensed signal, that is the spectral heterogeneity, is related to
200 environmental heterogeneity and could therefore be used as a powerful proxy of
201 species diversity. SVH has been tested in different situations (Rocchini et al., 2010)
202 and conclusions show that the performance of this approach is very dependent on
203 several factors, including the instrument characteristics (spectral, spatial and
204 temporal resolution), the type of vegetation investigated, and the metrics derived
205 from remotely sensed information to estimate spectral heterogeneity. Plant optical
206 types refer to the capacity of sensors to measure signals that aggregate information
207 about vegetation structure, phenology, biochemistry

207

208

209

210 and physiology. Therefore, this concept is also tightly linked to the performances of
211 the sensor and finds particular echo with the increasing use of high spatial resolution
212 imaging spectroscopy for the estimation and identification of multiple vegetation
213 properties.

214 The details provided by high spatial resolution imaging spectroscopy are
215 sufficient to perform analyses of plant optical traits at the individual tree scale in
216 order to differentiate tree species, obtain information about leaf chemical traits and
217 estimate the α component of biodiversity (Asner et al., 2008, 2015; Chadwick and
218 Asner, 2016; Clark et al., 2005; Clark and Roberts, 2012; Feret and Asner, 2013;
219 Vaglio Laurin et al., 2014). These results illustrate that spectral information can be
220 related to taxonomic or functional information of the vegetation, which supports the
221 SVH under the hypothesis that the metrics used to compute spectral heterogeneity
222 and a given component of vegetation diversity are properly defined. However these
223 applications are currently limited by the important amount of field data required to
224 train regression or classification models, which is also directly linked to their low
225 generalization ability in time and space. Unsupervised approaches then appear as
226 valuable alternatives for the analysis of ecosystem heterogeneity (Baldeck and Asner
227, 2013; Baldeck et al., 2014; Feilhauer et al., 2011; Baldeck and Asner, 2013; Feret
228 and Asner, 2014b), as ecological indicators of α and β diversity at landscape scale
229 usually require one or several levels of abstraction beyond the correct taxonomic
230 identification (Tuomisto et al., 2006).

231 Clustering (properly pre-processed) spectral information should result in pixels
232 from the same species naturally grouping together rather than distributing randomly
233 among clusters, Feret and Asner (2014a) proposed a grouping method aiming at
234 assigning labels to pixels based on multiple clustering of spectroscopic data acquired
235 at landscape scale. These pixels, labeled with a set of so-called spectral species, can
236 then be used straightforwardly in order to compute various diversity metrics such as
237 Shannon index for α diversity, and Bray-Curtis dissimilarity for β diversity. The pre-
238 processing stage is divided into several stages. After masking all non-vegetated
239 pixels, a normalization based on continuous removal is applied to each pixel and
240 over the full spectral domain, then a principal component analysis is performed on
241 the continuously removed spectral data. The normalization reduces effects due to
242 changes in illumination, canopy geometry and other factors unrelated to vegetation,
243 while enhancing the signal corresponding to vegetation. The components including
244 individual-specific information are the components of interest. They can be
245 identified after visual inspection or automated routines, if initial data show sufficient
246 signal to noise ratio. Once a limited number of components have been selected, k-
247 means clustering is then applied to a certain number of subsets, and for each of these
248 subsets, centroids are com

249
250

251 puted and each pixel in the image is labeled based on the closest centroid. The
252 repetition of clustering based on various subsets of the image tends to minimize the
253 risk of assigning centroids to irrelevant groups of pixels. Experimental results
254 showed that the averaging of diversity indices computed from multiple centroid
255 maps can be seen as an analogous to signal averaging, which consists in increasing
256 signal to noise ratio by replicating measurements. For each repetition, the closest
257 centroid corresponds to the spectral species, and for each spatial unit of a given size,
258 the spectral species distribution is derived in order to compute any diversity metric
259 requiring either information at the local scale, or comparison of information across
260 spatially distant plots.

261 The concepts of spectral species and spectral species distribution have been
262 tested successfully on a limited number of situations and types of ecosystems (see
263 (Rocchini et al., 2016) for a review, and (Lausch et al., 2016) for an application to
264 similar concepts). As an example, Feret and Asner (2014a) showed ability to properly
265 estimate landscape heterogeneity at moderate spatial scale, up to few dozen square
266 kilometers over tropical forests, based on high spatial resolution imaging
267 spectroscopy (Figure 3). A generic parameterization of the method showed robust
268 performances for α diversity mapping across space and time, but mapping β diversity
269 across large spatial scales using images acquired during different airborne campaign
270 remains challenging, which leads to an unsolved problem when considering
271 operational regional mapping. In the perspective of global monitoring of
272 biodiversity, and given the unprecedented remote sensing capacity allowed by the
273 Copernicus program, including the Sentinel-2 multispectral satellites, several other
274 challenges are foreseen and currently investigated. The influence of decreased
275 spatial and spectral resolution on the ability to properly differentiate ecologically
276 meaningful spectral species across landscapes and over regions will need to be
277 investigated. The application of this concept beyond tropical forests and savanna
278 ecosystems should also be investigated, as it may not hold when applied on
279 moderately diverse ecosystems or systems with individuals whose individuals have
280 dimensions well below the resolving power of the instrument.

281

282 4 Self organizing feature maps

283 The Kohonen self-organising feature map (SOFM, Kohonen (1982)) is a neural
284 network that may be used to undertake unsupervised clustering of data. Critically,
285 the input to a SOFM can be a large multi-variate data set such as may be acquired on
286 species from quadrat based field surveys. The SOFM summarises the data in a low,
287 typically two, dimensional output (Figure

287

288

289 4). In this output space the data for individual quadrats are topologically
290 ordered – with sites that are similar close together while those of highly dif-
291 ferent species composition are more distant. Because the data sites in the
292 output space are arranged by relative similarity the output space may also
293 be used to aggregate or classify a data set. As such the SOFM is attrac-
294 tive as a non-parametric clustering analysis and as a means to undertake an
295 ordination (Chon et al., 1996).

296 A SOFM is, unlike some of the approaches used commonly in community
297 ecology, not constrained by assumptions relating the statistical distribution
298 of the data used. The SOFM uses unsupervised learning to produce a topo-
299 logically ordered output space in which the samples are arranged spatially
300 in relation to their relative similarity in species composition. The SOFM
301 thus performs a non-parametric ordination analysis (Foody, 1999). The pro-
302 duction of a classification by a SOFM comprises two main stages (Giraudel
303 and Lek, 2001). An iterative analysis, in which time-decaying parameters
304 that control network learning and the size of local neighbourhoods located
305 around output units, is used. For this, the user must specify a number of key
306 parameters such as the size and shape of the network, number of iterations of
307 the algorithm, the learning rate and its rate of decline and a neighbourhood
308 parameter. The need for such parameters can add some uncertainty to the
309 analysis. While there are no formal rules to follow in the design of a SOFM
310 there are recommendations for the determination of SOFM parameter set-
311 tings (Giraudel and Lek, 2001). A further concern is that as an unsupervised
312 classifier the classes defined may not always be the most useful for an in-
313 vestigation. In addition, the nature of the analysis means the direction of
314 the gradients cannot be controlled (Fritzke, 1995) but the analysis performs
315 well in comparison to popular ordination techniques such as PCA and DCA
316 (Foody and Cutler, 2003). The SOFM may also use a variety of different
317 data types such as presence/absence, abundance or importance values and
318 can solve complex non-linear problems (Giraudel and Lek, 2001).

319 **5 Multidimensional distance matrices: GDMs** 320 **and SGDMs**

321 One of the most widespread methods for assessing α -diversity is using distance
322 matrices (Legendre et al., 2005). Indeed, early work by Whittaker (1960) sug-
323 gested that β -diversity could be quantified by dissimilarity matrices among
324 (pairs of) sites. Furthermore, the Mantel test (Mantel and Valand, 2017),
325 designed to estimate the association between two independent dissimilarity

326 matrices, has been widely used to correlate a community composition dissim-
327 ilarity matrix with an environment dissimilarity one, thus providing useful
328 insights into community composition and turnover (Legendre et al., 2005;
329 Tahvanainen et al., 2011).

330 Generalized Dissimilarity Modelling (GDM; Ferrier (2007) can be con-
331 sidered as an extension of the Mantel test, which is able to accommodate
332 multidimensional environmental data, to be compared with the composi-
333 tional data. GDMs also allow for the prediction of compositional turnover
334 as well as for, e.g. environmental classification constrained to the compo-
335 sitional dissimilarity (Ferrier, 2007; Leathwick et al., 2011). In GDM, the
336 compositional dissimilarities between all pairs of samples are modelled as a
337 function of their respective environmental distances. This is done through a
338 linear combination of monotonic I-spline basis functions, under the assump-
339 tion that increasing environmental dissimilarity (e.g. along a gradient) can
340 only result in increasing compositional dissimilarity. This method is thus well
341 suited for measuring and mapping β -diversity, and is thus becoming widely
342 used in conservation science and macroecology, and recently been subject to
343 several developments as we describe below.

344 One such development is the phylogenetic GDM (phylo-GDM; Rosauer
345 et al. (2014)), which incorporates phylogenetic dissimilarities into GDM and
346 allows for analysing and predicting phylogenetic β -diversity, thus linking
347 ecological and evolutionary processes. This method can provide novel in-
348 sights into the mechanisms underlying current patterns of biological diversity
349 (Graham et al., 2008). Another recent development of GDM is the multi-
350 site GDM (MS-GDM; Latombe et al. (2017)), which extends GDMs from
351 pairwise to multi-site dissimilarity modelling. In such paper, the authors
352 tested MS-GDM by means of both constrained (monotonical) additive mod-
353 els and I-splines, although with no conclusive results relating to the best
354 method overall. They concluded, however, that when applying MS-GDM to
355 a high number of samples, they could better explain the drivers of species
356 turnover. Also, an important development of GDM is the Bayesian bootstrap
357 GDM (BBGDM; Woolley et al. (2017)) designed to characterize uncertainty
358 in generalized dissimilarity models. This approach allows better represent-
359 ing the underlying uncertainty in the data, by estimating the variance in
360 parameters based on the available data.

361 Finally, an implementation of GDM, which was created particularly for
362 dealing with high-dimensional (and potentially high-collinear) remote sensing
363 data as input in GDM is the Sparse Generalized Dissimilarity Model (SGDM,
364 Figure 5, Leitao et al. (2015)). This method is a two-stage approach that
365 consists of initially reducing the environmental space (e.g. reflectance data)
366 by means of a Sparse Canonical Correlation Analysis (SCCA, Figure 5; Wit-

367 ten et al. (2013)), and then fitting the resulting components with a GDM
 368 model. The SCCA is a form of penalized canonical correlation analysis based
 369 on the L1 (lasso) penalty function, and is thus designed to deal with high-
 370 dimensional data. The two algorithms are coupled in a way that the SCCA
 371 penalization is selected through a heuristic grid search manner, in order to
 372 minimize the cross-validate root mean square error in the dissimilarities pre-
 373 dicted by the GDM. In this procedure, the high-dimensional environmental
 374 data (such as coming from time series of multispectral or hyperspectral data)
 375 are subject to a supervised ordination approach that reduces their dimen-
 376 sion while capturing the axes of variation that most correlate to those of
 377 the community compositional matrix. SGDM has been successfully used for
 378 modelling and mapping the compositional turnover of both animal and plant
 379 species, using several different sources of remote sensing (and auxiliary) data
 380 (Leitao et al., 2015; Leitão et al., 2017).

381 **6 Rao’s Q diversity**

382 Most of the previously shown metrics are based on the distance among pixel
 383 values in a multidimensional spectral space. None of them considers the
 384 relative abundance of such pixel values in a neighbourhood.

385 By contrast, abundance-based metrics such as the Shannon entropy could
 386 output similar results despite a variable distance among pixel values. As an
 387 example, consider a 3x3 matrix of remotely sensed data:

$$\begin{pmatrix} x_{11} & x_{12} & x_{13} \\ x_{21} & x_{22} & x_{23} \\ x_{d1} & x_{d2} & x_{d3} \end{pmatrix} \quad (2)$$

388 composed by the following values:

$$\begin{pmatrix} 10 & 13 & 15 \\ 18 & 20 & 23 \\ 19 & 21 & 22 \end{pmatrix} \quad (3)$$

389 then consider a different matrix:

$$\begin{pmatrix} 10 & 121 & 227 \\ 1 & 40 & 251 \\ 7 & 100 & 149 \end{pmatrix} \quad (4)$$

390 From a Shannon’s entropy perspective, such matrices are equal in terms of
 391 heterogeneity. The Shannon’s entropy is indeed based on the relative abun-
 392 dance (and richness) of a sample, and its value is 2.197 for both the matrices.

393 This value, equalling the natural logarithm of the number of classes (pixel
394 values), is also Shannon’s maximum theoretical value given a 3x3 matrix,
395 due to the lack of identical numbers in the matrices. This example explicitly
396 shows that accounting for the distance among values and their relative abun-
397 dance is crucial to discriminate among areas in terms of measured (modeled)
398 heterogeneity.

399 One of the metrics accounting for both the abundance and the pairwise
400 spectral distance among pixels is the Rao’s Q diversity index, as:

$$Q = \sum \sum d_{ij} \times p_i \times p_j \quad (5)$$

401 where d_{ij} = spectral distance among pixels i and j and p = proportion of
402 occupied area.

403 Hence, Rao’s Q is capable of discriminating among the ecological diversity
404 of matrices 3 and 4, turning out to be 4.59 and 90.70, respectively. Appendix
405 1 provide an example spreadsheet to perform the calculation while the com-
406 plete R code is stored in the GitHub repository
407 <https://github.com/mattmar/spectralrao>.

408 We decided to make use of a case study to highlight the importance of
409 considering the distance among pixel values in remote sense ecological appli-
410 cation. The performance of Rao’s Q index in describing landscape diversity
411 was tested in a complex agro-forestry landscape located in southern Portu-
412 gal. A test site with an area of about 10 x 10km² (centroid located at 38°
413 39’ 10.74” N; 8° 12’ 52.30” W) was selected to conduct the analysis. In this
414 area, a savanna-like ecosystem called montado occupies about 40% of the test
415 site, followed by traditional olive groves, pastures, vineyards, and irrigated
416 monocultures (e.g. corn fields). Montado is spatially characterized by the
417 variability of its tree density (e.g. Godinho et al. (2016)), and the gradient
418 between low and high tree density over space can lead to different structural
419 heterogeneity and habitat diversity.

420 Within the test site, polyculture under small farming context (e.g. veg-
421 etable gardens, orchards, and cereal crops) is an important feature of this
422 landscape by generating a high compositional and configurational spatial
423 heterogeneity (Figure 6). The main goal in using this case study is to demon-
424 strate the potential and effectiveness of the Rao’s Q index in producing ac-
425 curately remote-sensing based maps of spatial diversity over such complex
426 landscape. For this study, a cloud-free Sentinel-2A (S2A) image acquired
427 on 8 of August 2016 was used to compute the NDVI at a 10 meters spatial
428 resolution. The S2A image download, as well as the atmospheric correction
429 (DOS method) were performed using the Semi-Automatic Classification plu-
430 gin (SCP) implemented in the QGIS software (QGIS Development Team ,
431 2016(@)).

432 The NDVI was used as input data for Rao's Q index computation using a window
433 size of 3 x 3 pixels. The performance of the Rao's Q was compared to the Shannon
434 Entropy index (Shannon's H), which is one of the simplest, and widely used, remote
435 sensing-based diversity measures for landscape heterogeneity assessment (Rocchini
436 et al., 2016). To investigate whether both diversity indices differ between land cover
437 types, one-way ANOVA tests were performed. This approach was used for
438 analysing the degree of dissimilarity between Rao's Q and Shannon H index across
439 two high complex land cover types; i) montado, and ii) polyculture. To do so, a
440 sample of 60 squares with 250 x 250 meters size was randomly selected over these
441 two land cover types. Each square represents a sample of 625 S2A NDVI pixels, thus
442 corresponding to a total of 37,500 pixels over the 60 squares. For the comparison
443 between both indices, the coefficient of variation (CV) was calculated for each 250 x
444 250 m squares. Regarding the Rao's Q performance, Figure 6 clearly points to the
445 significant improvements shown by Rao's Q index compared to the Shannon H
446 index in describing the spatial diversity. In particular, it can be seen through the
447 Figure 6, that Rao's Q index can highlight different gradients of spatial diversity of
448 montado areas, which present high tree density variability (Figure 6), and thus high
449 spatial heterogeneity. One-way ANOVA tests revealed that both indices values were
450 significantly different between the two land cover types (montado: $F = 503.3$,
451 $p < 0.001$; polyculture: $F = 889.8$, $p < 0.001$). Overall, the obtained results demonstrate
452 the capability of Rao's Q index in producing accurate landscape diversity maps in a
453 complex landscape such as the Mediterranean agro-forestry systems.

454

455 7 Conclusion

456 In this paper, we showed several methods based on ecological 0-diversity, which can
457 be investigated by remote sensing through the calculation of ecosystem
458 heterogeneity, to estimate the spatial variability of biodiversity. When there is a wide
459 range of heterogeneity, for example when the data include homogeneous and
460 heterogeneous zones, no single measure might capture all the different aspects of 0-
461 diversity (e.g. Baselga (2013)). That is why we suggested in this manuscript
462 multivariate and multidimensional methods (e.g. multivariate statistics and
463 multidimensional distance matrices) based on the spectral signal and its variability
464 over space to account for different aspects of diversity, also including distance- and
465 abundance-based methods (e.g. the Rao's Q).

466 Biodiversity measured as species richness is often used for conservation
467 purposes, hence the importance of avoiding an under- or over-estimate has

467

468

469

470 been highlighted (Chiarucci et al., 2009). Furthermore, pairwise distance- based
471 methods might be profitably used to detect not only diversity hotspots in an area but
472 also the variation of biodiversity over space, and potentially over time, once
473 multitemporal sets of images are used.

474 In this paper we focused on optimising measures of q -diversity based on remote
475 sensing data. Such measures might be used to regress species diversity against
476 remotely sensed heterogeneity, based on new regression techniques which maximise
477 the possibility of predicting the zones in a study area, or at larger spatial scales, of
478 peculiar conservation value. As an example, shrinkage regression, recently applied
479 in biodiversity conservation (Authier et al., 2017) could allow a direct focus on habitat
480 modelling, which is one of the major strengths of remote sensing (Gillespie et al.,
481 2008). Moreover, such analysis might be performed in a Bayesian framework
482 allowing to i) model multidimensional covariates with non-stationary variation over
483 space (Randel et al., 2016), such as the bands of satellite images, and ii) model the
484 errors in the output and their variation over space (Rocchini et al., 2017).

485 As previously stated, the suggested methods for 0 -diversity estimation from
486 remote sensing are mainly based on distances, but they could be effectively
487 translated to relative abundance-based methods. As an example Rocchini et al. (2013)
488 introduced the possibility of applying generalized entropy theory to satellite images
489 with one single formula representing a continuum of diversity measures changing
490 one parameter. One of the best examples in this framework could be the use of Hill
491 numbers, in which diversity is expressed as:

$$492 \quad * D = \frac{1}{\sum p^q} \quad (6)$$

493

494 where S = number of samples / pixels and p = relative abundance of a species /
495 spectral value. Varying the parameter q , qD varies accordingly in several diversity
496 indices, e.g. for $q = 0$ qD is the simple number of species, for $\lim(q) = 1$ qD equals
497 Shannon's entropy, etc. (Hsieh et al., 2016).

498 Furthermore, connectivity analysis might also be taken into account (Moilanen
499 et al., 2005, 2009). For instance, a remote sensing based connectivity network among
500 different sites, based on 0 -diversity measures, could be applied for the estimate of
501 landscape connectivity and consequent genetic flow, as demonstrated by Vernesi et al.
502 (2012). It has also been shown that community related biodiversity indicators are often
503 missing from current monitoring programmes (Vihervaara et al., 2017); thus methods
504 such as remote sensing based Rao's Q diversity applied for various ecosystems might
505 improve otherwise challenging monitoring of biological communities.

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505
506

507 With this manuscript we hope to stimulate discussion on the available
508 methods for estimating β -diversity from remotely sensed imagery by propos-
509 ing innovative techniques grounded on ecological theory.

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513 manuscript

514 Authors' contribution statement

515 All authors contributed to the development and writing of the manuscript.

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- 773 Figures

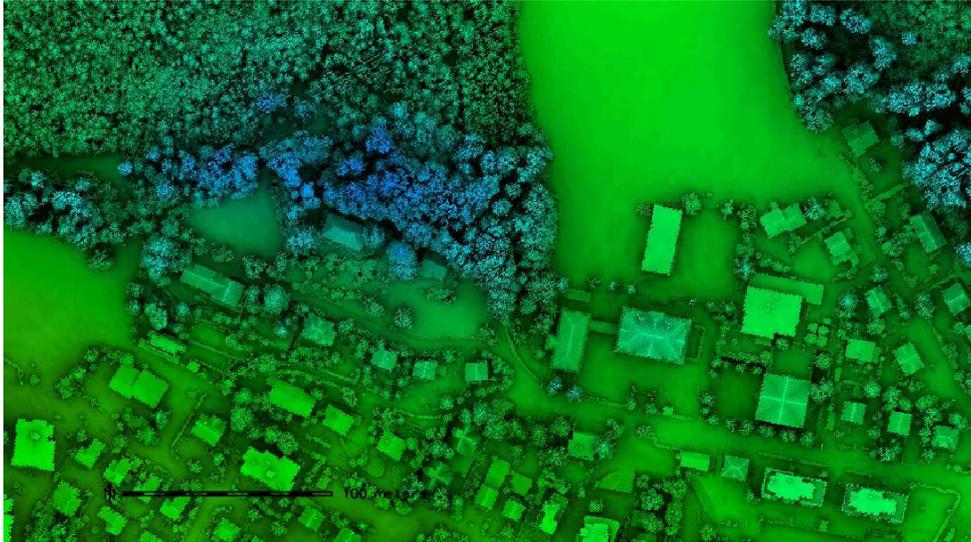


Figure 1: An example of how to couple information on compositional properties of the landscape by optical data together with structural (3D) properties by laser scanning LiDAR data.

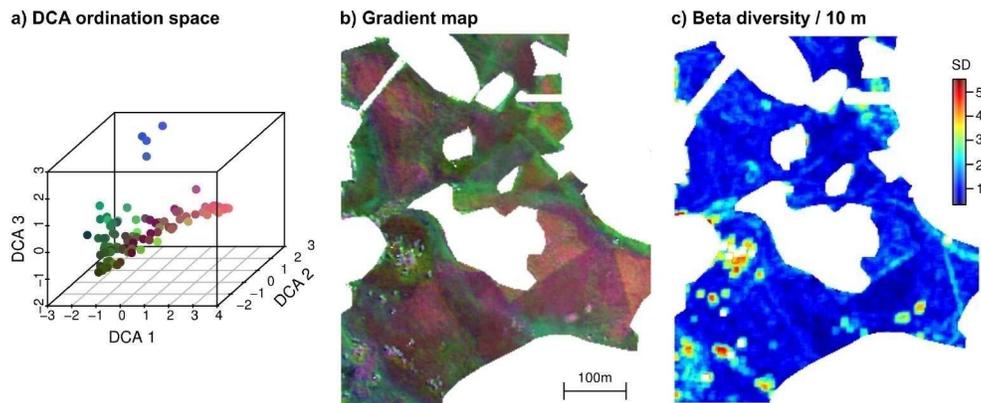


Figure 2: β -diversity assessment with a combination of ordination techniques and remote sensing. a) Three dimensional DCA ordination space of $n=100$ vegetation plots sampled in raised bogs, fens, transition mires and *Molinia* meadows in the alpine foothills of Southern Germany. An inter-plot distance of 4 SD corresponds to a full species turnover. b) Maps of the ordination axes resulting from a spatial prediction based on canopy reflectance. Each pixel has a predicted position in the ordination space that is indicated by its color. The color scheme corresponds to a). The map has a spatial resolution of 2 m x 2 m, which is in line with the sampled plot size. c) Cumulative change rates along the three DCA axes in a 5 x 5 pixel neighborhood. A high change rate indicates a high beta diversity.

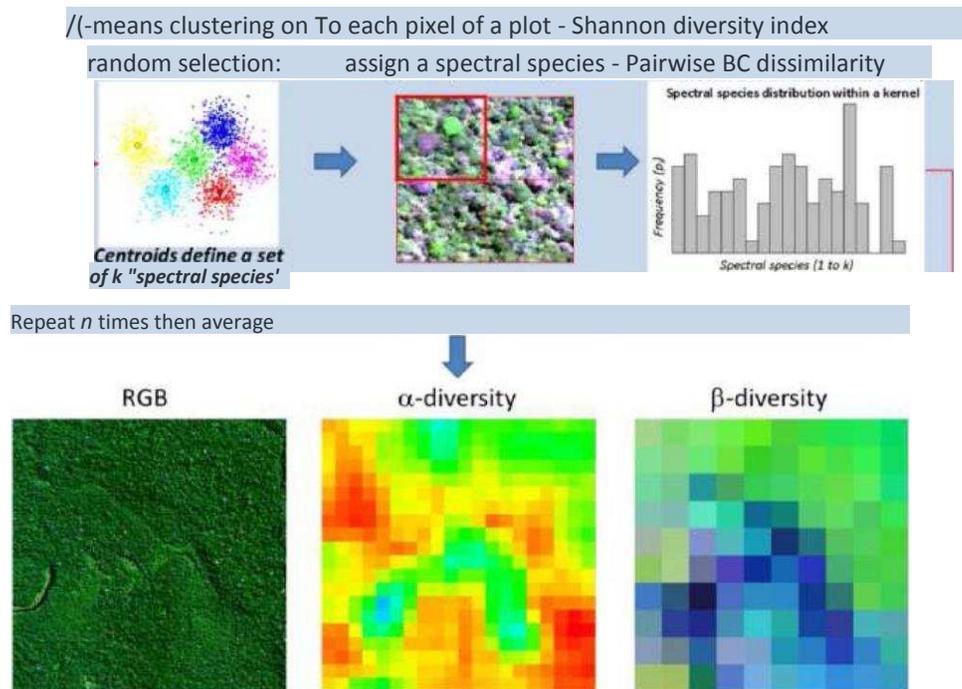


Figure 3: Spectral species can be identified in a hyper- or multi-spectral image by spatial clustering method and their distribution can be mapped. Such maps can further be used to apply local-based heterogeneity measurements (α -diversity) as well as iterative distance based methods to build β -diversity maps. Reproduced from Feret and Asner (2014a).

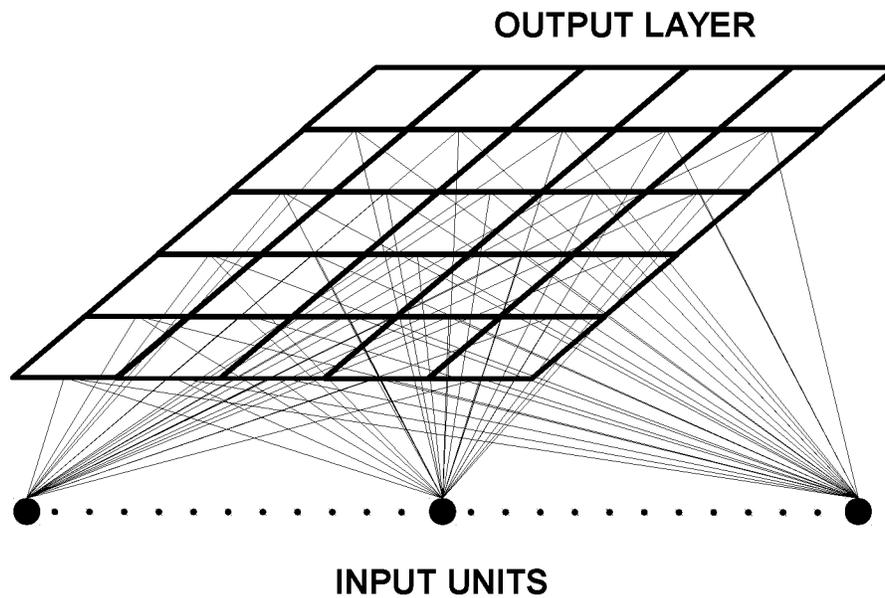


Figure 4: A self-organising feature map can be built starting from an input layer, e.g. the presence absence of a tree species or of a peculiar spectral value) which is connected to every unit in the output layer by a weighted connection. The self organising feature map uses unsupervised learning to map the location of field sites within the output space on the basis of their relative similarity in species or spectral composition. [Redrawn](#) from Foody and Cutler (2003).

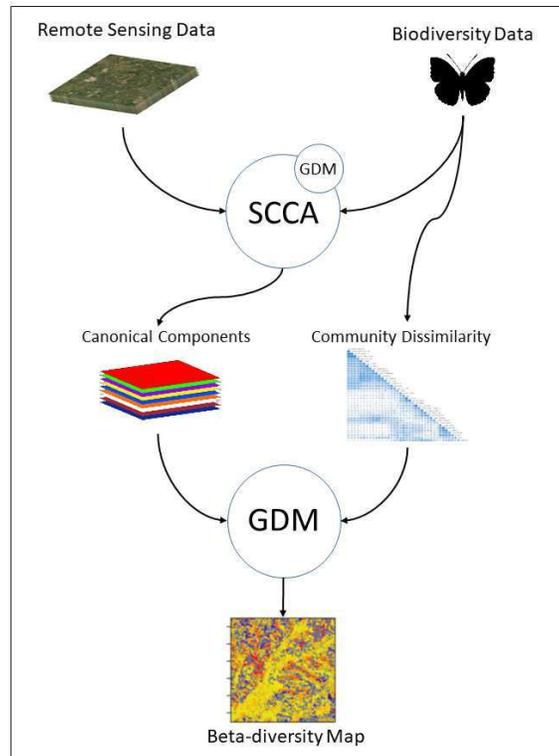


Figure 5: An example of the Sparse Generalized Dissimilarity Model (SGDM) approach. Remote sensing data and biodiversity data in the field can be coupled by Sparse Canonical Correlation Analysis to produce canonical components and a community dissimilarity matrix, which are then used to build a Generalized Dissimilarity Model to finally derived a β -diversity map.

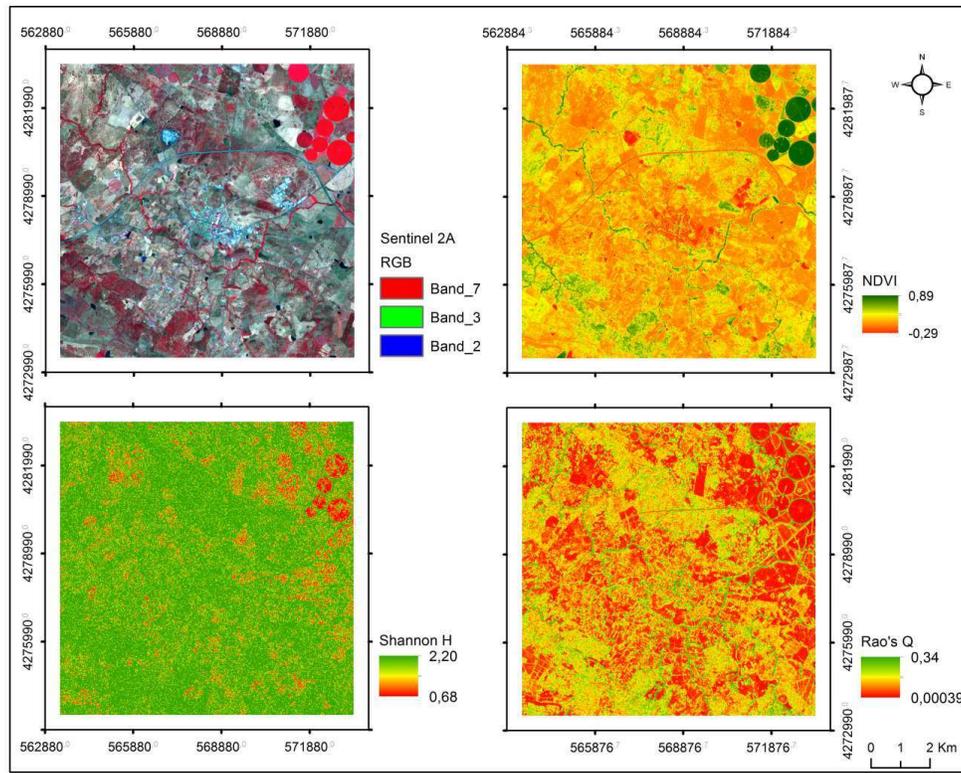


Figure 6: Upper panels: Sentinel-2A scene (8 August 2016) and derived NDVI for the agro-forestry systems test site located in southern Portugal. Lower panels: results from Shannon's H and Rao's Q indices computation. Shannon index tends to overestimate the landscape diversity when compared to the Rao's Q index.