

1 From local spectral species to global spectral
2 communities: a benchmark for ecosystem
3 diversity estimate by remote sensing

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5 November 2, 2020

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Abstract

In the light of unprecedented change in global biodiversity, real-time and accurate ecosystem and biodiversity assessments are becoming increasingly essential. Nevertheless, estimation of biodiversity using ecological field data can be difficult for several reasons. For instance, for very large areas, it is challenging to collect data that provide reliable information. Some of these restrictions in Earth observation can be avoided through the use of remote sensing approaches. Various studies have estimated biodiversity on the basis of the Spectral Variation Hypothesis (SVH). According to this hypothesis, spectral heterogeneity over the different pixel units of a spatial grid reflects a higher niche heterogeneity, allowing more organisms to coexist. Recently, the spectral species concept has been derived, following the consideration that spectral heterogeneity at a landscape scale corresponds to a combination of subspaces sharing a similar spectral signature. With the use of high resolution remote sensing data, on a local scale, these subspaces can be identified as separate spectral entities, the so called "spectral species". Our approach extends this concept over wide spatial extents and to a higher level of biological organization. We applied this method to MODIS imagery data across Europe. Obviously, in this case, a spectral species identified by MODIS is not associated to a single plant species in the field but rather to a species

64 assemblage, habitat, or ecosystem. Based on such spectral informa-
65 tion, we propose a straightforward method to derive α - (local relative
66 abundance and richness of spectral species) and β -diversity (turnover
67 of spectral species) maps over wide geographical areas.

68 *Keywords:* biodiversity; ecological informatics; modelling; remote sens-
69 ing; satellite imagery.

70 1 Introduction

71 1.1 A quest for robust and reproducible α - and β - 72 diversity measurement

73 The variability of life on Earth is heterogeneously distributed across the
74 planet; in fact, ecologists and biogeographers have long questioned the po-
75 tential causes of biodiversity distribution. Recently, the speed of change and
76 the uncertainty about possible consequences [on biodiversity](#) is concerning to
77 the global scientific community. The perception of these processes trans-
78 lates into the need to use standardized methods for biodiversity assessment
79 and monitoring in order to gain a better understanding and identify general
80 trends.

81 There is open debate as to the most reliable metrics for assessing biodiver-
82 sity (see Jurasinski et al. (2009); Tuomisto (2010)). Until now, no consistent
83 definition exists. Even the definition according to the Convention on Bi-
84 ological Diversity (CBD, 1992, <https://www.cbd.int/convention/text/>)
85 is more confusing than clear: “Biological Diversity means the variability
86 among living organisms from all sources, including, inter alia, terrestrial,
87 marine and other aquatic ecosystems and the ecological complexes of which
88 they are part; this includes diversity within species, between species and of
89 ecosystems.” Biodiversity obviously includes quantitative (number of species,
90 alpha-diversity, gamma-diversity), qualitative (turnover, composition, beta-
91 diversity) and functional (complexity, trophic levels, ecosystem services) as-
92 pects. To sum up our understanding on the term biodiversity (i.e. biological
93 diversity) and to base our study on a more general and consistent concept,
94 “biodiversity characterizes qualitative, quantitative and functional aspects of
95 biotic units at various levels of organization in a concrete or abstract con-
96 text, and at a given temporal or/and spatial scale” (Beierkuhnlein, 2003). In
97 consequence, species richness and metrics that are based on it are important,
98 but they represent just one aspect of biodiversity. In fact, the total number
99 of species co-occurring in a given community (α -diversity) is nested within

100 the total number of a species pools occurring for instance at the landscape
101 level (γ -diversity). But the reduction of biodiversity to the perspective of
102 inventory and proportion would not cover spatial gradients in composition
103 and species turnover (differentiation, β -diversity) (Jurasinski et al., 2009;
104 Baselga, 2012) and also ignores functional diversity (e.g. functional traits),
105 which is the main driver of ecosystem functioning.

106 In general, β -diversity is a crucial measure, since, given the same lo-
107 cal richness of different sites (α -diversity), it directly considers the turnover
108 among them. As an example, let A and B be two sampling sites with 10
109 different species each. If all 10 species are fully shared, the total γ -diversity
110 would equal 10 species, while if all 10 species are completely different from
111 one site to the other (high turnover, high β -diversity) the total diversity of
112 the whole area based on the two focal sites would double.

113 Therefore, it becomes particularly interesting to understand how β -diversity
114 originates, investigating how species composition differs among sites. In
115 fact, species composition could be related to environmental conditions, or
116 it could randomly fluctuate. A generally accepted hypothesis suggests that
117 β -diversity might change as a function of species types living in a certain
118 community. For instance, β -diversity should be small when communities are
119 dominated by a limited number of competitive species; this is recognized as
120 the null hypothesis and it entails a uniform distribution in species composi-
121 tion (Legendre et al., 2005).

122 The β -diversity concept reflects the environmental heterogeneity between
123 sites and thus within a given larger area that contains several of the focal
124 study sites. Heterogeneity is in fact highly associated with a high degree
125 of biological diversity since heterogeneous sites offer a diversity of ecological
126 niches (sensu Elton (1958)) that can be occupied if the species pool offers the
127 respective ecological diversity to address these niches (Gaston, 2000; Rocchini
128 et al., 2010). Furthermore, since β -diversity can be described as the spatial
129 turnover among sites within a given region, it captures a fundamental feature
130 of the spatial pattern of biodiversity.

131 In some cases, spatial turnover can result from local extinction processes
132 that affect certain species more than others and enhance the dissimilarity
133 between sites without dispersal (Steinitz et al., 2006). This is the case in
134 highly fragmented landscapes where dispersal is limited (Hobbs et al., 2006).
135 Even stochastic processes (sensu Moran (1950) and Clark (2008)) may en-
136 hance β -diversity in previously homogeneous ecosystems. For instance, sud-
137 den fragmentation (Alados et al., 2009) can lead to disfunctional source-sink
138 metapopulations with intrinsic influences on the degree of spatial (and ge-
139 netic) connectivity of organisms (Waples and Gaggiotti, 2006), resulting in
140 the local loss of sink populations. However, in most situations, the spatial

141 turnover and therefore the dispersal of species between sites (metapopula-
142 tion and metacommunity dynamics) is linked to the distance among sites.
143 Strictly speaking, the similarity between two sites decays with increasing dis-
144 tance between them (Rocchini, 2007), a process also known as the distance
145 decay in similarity or the Tobler’s first law of geography (Tobler, 1970).

146 Hence, modelling the distribution of β -diversity in space is based on
147 softening the role of individual species, which are not even completely de-
148 scribed at wide geographical scales, for the sake of estimating a more ef-
149 ficient proxy for ecosystem patterns and processes. When these esti-
150 mates are available from remote sensing data, this process can lead to rapid,
151 large-scale monitoring and support management intervention aimed at pre-
152 serving entire ecosystems, as stipulated by the Aichi Biodiversity Targets
153 (<https://www.cbd.int/sp/>).

154 Field-based studies require an enormous investment in time in order
155 to collect reliable biodiversity data. A pioneering example is the public
156 database of the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>). GBIF is a network funded by the world’s governments
157 which contains almost 41,000 databases of species occurrences spread out
158 across the world. The large amount of publically accessible data and the
159 available techniques to analyze them will certainly facilitate biodiversity as-
160 sessment for the areas that it covers. Unfortunately, however, although it
161 would be possible in principle to use these data to make reasonable assump-
162 tions about biodiversity over larger areas, there are several limitations due
163 to their quality (Maldonado et al., 2015). The errors that usually arise from
164 field data are due to: (i) lack of or erroneous geographic coordinates of the
165 sampling sites; (ii) incorrect taxonomic identification with poor quality con-
166 trol; and (iii) difficulties in proving a reliable random sampling with large
167 areas being poorly covered. Furthermore, these data often appear as point
168 data, while grids are usually used in order to synthesize diversity metrics.
169 In addition, these data are mainly collected from presence-only data with-
170 out any link to relative abundance, dominance, biomass or cover, which in-
171 stead, is reflected in remote sensing. Finally, GBIF data are inadequate for
172 local estimates of biodiversity as they do not consider co-occurrence data.
173 Indeed, and contrary to recent databases at the community level such as
174 the European Vegetation Archive (EVA) (Chytry et al., 2016) or the sPlot
175 initiative (Bruehlheide et al., 2019), GBIF does not provide information on
176 species co-occurrence which is very problematic for biodiversity assessment
177 and monitoring. Despite the disadvantages that come from the use of public
178 databases, there is some benefits in the use of such data. First of all, there
179 is a huge amount of data collected and provided by citizens and research
180 institutions available in the GBIF database when compared to the data that
181

182 could be collected locally, resulting in a huge saving of time and costs. More-
183 over, GBIF data are standardized to the same format and therefore ready to
184 use.

185 To overcome the issues due to the collection and availability of in situ
186 ecological data, remote sensing imagery has become more and more impor-
187 tant and is now considered a reliable tool to assess and monitor biodiversity
188 (Tuanmu and Jetz, 2015).

189 1.2 The spectral species concept

190 Remote sensing based approaches have proven to be useful modelling tech-
191 niques to detect the variability of biodiversity in space and time across scales
192 of biological organisation, at different grains (spatial resolutions) and extents
193 (Rocchini et al., 2013). Airborne sensors have even been used to detect and
194 map single species distributions (Skorownek et al., 2017a), even the most
195 tiny and inconspicuous ones such as *Campylopus introflexus*, a moss species
196 which is highly invasive in Europe (Skorownek et al., 2017b).

197 Remote sensing techniques have been used to study the impact of land-
198 scape and environment on biodiversity, and to explore and visualize spatial
199 data and biodiversity change. Therefore, remote sensing data have become
200 among the most time and cost effective tools, allowing to make relevant con-
201 servation actions in a relatively short period of time. Furthermore, remote
202 sensing demonstrated the impact of biodiversity (including non-native inva-
203 sive species) on ecosystem functioning (Ewald et al., 2018).

204 In general, vegetation absorbs the blue and the red light, for photosyn-
205 thesis, while it reflects near infrared (hereafter, NIR) radiation due to the
206 physical structure of the cells composing the leaf mesophyllum (Wegmann
207 et al., 2016). The bands relative to RED and NIR are used as proxies for
208 photosynthetic activity of the vegetation. These bands are usually incor-
209 porated in a widely used index, the normalized difference vegetation index
210 (NDVI), which is calculated as $NDVI = (NIR - RED) / (NIR + RED)$. The higher
211 the relative abundance of photosynthetic vegetation, the higher would be the
212 reflectance in the NIR band and the absorption in the RED band. NDVI
213 ranges from -1 to 1, with 0 values usually associated with non vegetated
214 areas and negative values associated with water surfaces or snow.

215 This index has widely been used to discriminate different vegetation types
216 over an area. In fact, in several studies, NDVI is positively correlated to the
217 net primary productivity (NPP, e.g. Gillespie et al. (2008)). Therefore, it
218 can be used as a proxy to quantify species richness and diversity, based on the
219 species-energy theory, proposed by Currie (1991), namely a relation between
220 species richness and energy, that would depend mainly on annual potential

221 evapotranspiration and actual evapotranspiration. Another hypothesis re-
222 lated to the variability in space of the spectral signal has been proposed
223 by Palmer et al. (2002). The so called spectral variation hypothesis (SVH)
224 states that the higher the environmental heterogeneity the higher would be
225 the species diversity of an area, due to a higher number of available ecological
226 niches.

227 Hence, based on the SVH, spectral variability can effectively be related to
228 environmental heterogeneity and therefore it could be used to assess species
229 biodiversity of an area. In this sense, since the spectral variability is derived
230 from the information present in the pixels of an acquired image, it is im-
231 portant that the pixels, describing the area of study, would have a spatial
232 resolution coherent with the ecological assumptions taken into account and
233 such that predictions on biodiversity can be made.

234 Among the most novel methods to estimate diversity by remote sensing,
235 described in Rocchini et al. (2018), the spectral species concept (Féret and
236 Asner, 2014) is one of the most powerful, since it allows to couple k-means
237 approaches to the gridded data obtained from remote sensing technologies
238 as a mean to derive α - and β -diversity 2D-matrices. The spectral species al-
239 gorithm allows the separation of the spectral space in subunits identified as
240 spectral species. Its root theory is built upon two major founding principles.
241 The first is the aforementioned Spectral Variation Hypothesis, relating spec-
242 tral to environmental heterogeneity. The second is based on the plant optical
243 types proposed by Ustin and Gamon (2010). This concept is mainly related
244 to the use of particular sensors providing high spatial resolution images and
245 able to measure different signals about the phenology, the biochemistry and
246 the structure of vegetation. Such sensors can obtain information at the in-
247 dividual plant scale level.

248 The method is based on an unsupervised clustering algorithm, first rely-
249 ing on dimensionality reduction obtained after running a principal component
250 analysis (PCA) and then on the actual clustering of the pixels, with the sub-
251 sequent assignment to spectral species, based on a k-means approach. PCA
252 and similar clustering methods have already been shown to reliably reduce
253 the multidimensional spectral sets for models on species and biodiversity
254 distribution (Rocchini et al., 2010). Furthermore, the method provides an
255 interesting visual inspection of diversity building α - and β -diversity maps.

256 As far as we know, the spectral species concept has been applied so far
257 only at the local scale (Féret and Asner, 2014). Hence, the aim of this
258 manuscript is to extend this concept over wider spatial extents passing to a
259 spectral community concept, by generating a heterogeneity map at a wide
260 geographical scale to estimate α - and β -diversity across Europe.

261 2 The algorithm

262 The spectral species algorithm was originally developed to map tropical forest
 263 canopy diversity using imaging spectroscopy with a spatial resolution up to
 264 2 meters (F  ret and Asner (2014), Figure 1). Following the hypothesis that
 265 species are spectrally separable (Asner and Martin, 2009), the approach is
 266 based on the segmentation of the spectral space defined by the remote sensing
 267 data. In fact the spectral space is assumed to be a combination of several
 268 subspaces, reflecting the “signature” of one or several species. Therefore
 269 these subspaces would be the expression of a more general “spectral species”.
 270 From the resultant “spectral community”, it would be possible to derive the
 271 diversity of an area. Therefore, the output of this algorithm is not a list of
 272 the actual species of an area, but rather a map of the distribution of the
 273 spectral communities available within the area that may be used to calculate
 274 several diversity indices. In particular we focused here on α - and β -diversity
 275 metrics. Both introduced by Whittaker (1972), the first reflects the mean
 276 species diversity in sites at a local scale whereas the second is an indicator
 277 of the spatial (or temporal) heterogeneity at a relatively larger scale. In the
 278 algorithm, α -diversity is calculated in a neighbourhood (plot) of $n \times n$ pixels
 279 by the Shannon diversity index (Shannon, 1948) calculated as follow:

$$H' = -\sum_{s=1}^N p_s \ln p_s \quad (1)$$

280 where p_s is the proportion of each spectral species s in each plot.

281 The β -diversity indicator is instead computed by the Bray-Curtis (here-
 282 after BC) dissimilarity metric (Bray and Curtis, 1957):

$$BC_{ij} = \frac{\sum_{s=1}^N |x_{is} - x_{js}|}{\sum_{s=1}^N (x_{is} + x_{js})} \quad (2)$$

283 where BC_{ij} is the dissimilarity between plots i and j and x_{is} and x_{js} are the
 284 abundances of spectral species s in plots i and j .

285 In the spectral species algorithm, once the BC dissimilarity matrix be-
 286 tween all pairs of plots is computed, a multidimensional scaling is performed
 287 in order to translate information about the pairwise dissimilarity among P
 288 plots into a configuration of P points mapped in a 3-dimensional Cartesian
 289 space such as NMDS or PCoA (Mead, 1992). This simplified translation of
 290 the BC dissimilarity matrix can then be displayed as a colored map. More
 291 details can be found in F  ret and de Boissieu (in press).

292 While the Shannon index has a theoretical maximum limit corresponding
 293 to the $\ln(\text{richness})$, the Bray-Curtis index ranges from 0 to 1, where 0 is

294 indicating that the two sites are identical whereas 1 indicates that the two
 295 sites do not share species. Hence, BC can be considered as an estimate of
 296 the heterogeneity of a certain area. The final aim of the method was to gener-
 297 ate an heterogeneity map across the study region. Strictly speaking, the
 298 method is a clustering approach which (i) divides the subspaces in spectral
 299 units and (ii) assigns it to spectral species from which (iii) different diver-
 300 sity maps can be obtained. Box 1 focuses in detail on the main steps of
 301 the algorithm, while the dedicated R package `biodivMapR` is now available
 302 (<https://github.com/jbferet/biodivMapR>) and fully described in F  ret and
 303 de Boissieu (in press).

304 2.1 Application of the algorithm

305 Remote sensing data are usually provided as raster objects with a geographic
 306 coordinate system information, namely regular grids (matrices) or stacks of
 307 raster layers (e.g. one raster layer per band for multispectral or hyperspectral
 308 data), in which each cell represents a pixel with the corresponding reflectance
 309 value associated to a specific band. Such data have been manipulated with
 310 the Software R Development Core Team (2019). R can be used for remote
 311 sensing data analysis since it includes spatial functionalities throughout a
 312 suite of R packages like the `rgdal` and `raster` packages (see Box 2 for more
 313 information).

314 Our main purpose was to apply the spectral species algorithm to a continental-
 315 scale geographical region such as Europe. Hence, Moderate Resolution Imag-
 316 ing Spectroradiometer (MODIS) data, with a spatial resolution of 500m cov-
 317 ering Europe, were downloaded from the United States Geological Survey
 318 (USGS) site (<https://lpdaac.usgs.gov/products/mod09a1v006/>). After
 319 a visual check of the images, in order to guarantee i) the coverage of a com-
 320 plete phenological period and to ii) avoid noise related to clouds, we referred
 321 to the RED and NIR bands from 2018 from January to December ([one im-
 322 age per month](#)), to calculate NDVI, by generating a sample set of 12 NDVI
 323 images (Figure 2).

324 Due to the coarse spatial resolution of MODIS images (500m), the re-
 325 flectance related to a single plant species is averaged and mixed with the
 326 reflectance of other species within a single pixel. In other words, the direct
 327 relationship between spectral species detected in the spectral space versus
 328 the number of plant species does not hold true. However, in any case, from a
 329 diversity measurement perspective, this is just a matter of terms being used,
 330 with spectral species being actually more related to field plant communities,
 331 habitats or other ecological entities.

332 For the derivation of spectral species, in order to define the number of

clusters, we relied on the highest number of clusters with stable results after a trial and error procedure, reaching 200 clusters, i.e. spectral species. Once pixels with similar NDVI values in 12 dimensions were clumped together, Shannon's H' was calculated with a window size of 10x10 pixels and an output resolution of 5km. The attained α -diversity map quantitatively showed the local spectral diversity distribution over Europe (Figure 3), with a higher heterogeneity found in i) more topographically complex regions, mainly due to strong local differences induced by elevation gradients (passing from forests to grasslands, to rocks and snow), and/or differences in terms of seasonality in relation with elevation, as in Rocchini et al. (2019), and in ii) more contrasted agricultural areas in both the spatial and temporal dimensions (Hobbs et al., 2006; Vihervaara et al., 2017). Concerning topographical complexity, the higher variability in areas with a marked topographical gradient might be related to shadows. Local field work in such areas will be needed to validate the measurements in such areas.

β -diversity (Figure 3) showed a clear differentiation among different areas over Europe. The attained map was in line with the European Environmental Agency (EEA) map of ecoregions (Figure 4, see Mucher et al. (2009)). The correspondence of the achieved patterns in the two maps was apparent, with a similar contour of the major ecoregions such as the mediterranean, the atlantic, the continental, the boreal and the alpin regions. This demonstrates an intrinsic ability of the spectral species approach to capture differences in the physiological and functional properties of vegetation even at wide spatial scales, starting from spectral reflectance or spectral indices. Minor differences were mainly related to the biogeographical (i.e., purely spatial) differentiation of ecoregions in the EEA map. As an example, north and south alpine ecoregions could not be distinguished by the spectral species approach, since they both have very similar conifer species composition, with the same physiological, phenological and thus spectral pattern.

3 Discussion

In this paper, for the first time, the spectral species concept has been extended from the consideration of a single species to an entire community. We demonstrated that the combined use of the novel unsupervised clustering method proposed by Féret and Asner (2014) with NDVI time series at European scale, allows the derivation of local (α) diversity and turnover (β) relying on free to use and operationally available satellite data.

With regards to a potential validation with in-situ data, the uncertainty of wide-scale datasets hampers a spatial overlap. In this case, in-situ datasets

371 meet all five major concerns recently raised by Hobohm et al. (2019), i.e.:
 372 i) there is insufficient data coverage across Europe to make an unbiased
 373 comparison between predicted and actual distributions, ii) taxonomic stan-
 374 dards differ across sampled regions, iii) there are generally different shapes
 375 of areas being sampled, iv) political borders often define sampling areas and
 376 aggregated sampling areas, and v) data are not aggregated in the same way
 377 in all areas. Furthermore, spatial information has an intrinsic varying de-
 378 gree of relevance mainly due to the fact that, rather than species lists, it is
 379 composed of geometrical precision, attributes robustness and temporal con-
 380 sistency (Hobona et al., 2006). Finally, different models and approaches to
 381 measuring diversity inevitably provide different outputs, as pointed out in the
 382 generalised entropy theory put forward by Rényi (1961). Given the above
 383 validation difficulties, we decided to qualitatively compare our generated out-
 384 put, in particular the β -diversity map, with existing ecoregion maps, which
 385 are expected to discriminate different spatial areas based on natural bor-
 386 ders defined by biological diversity (<https://ecoregions2017.appspot.com/>)
 387 and thus are intrinsically related to differences in the species and spectral
 388 turnover of communities.

389 Since the output of the algorithm represents the variation of the pixel
 390 values in space and time, the most diverse pixels were those with the highest
 391 turnover among the neighborhood areas and most affected by seasonality.
 392 The importance of accounting for turnover instead of simple richness has
 393 been widely discussed in the ecological literature (Tuomisto, 2010), since
 394 environmental variability over spatial gradients is one of the major drivers
 395 of the structure and composition of diversity (Legendre et al., 2005). In this
 396 view, the use of the “spectral species concept”, defined as the variation of
 397 clustered pixel values, represents a powerful approach for the investigation
 398 of gradient variation of diversity in space and, potentially, in time.

399 In general, the measure of variability in space has been demonstrated
 400 to follow scale-based differentiation. In other words, results are expected
 401 to change with spatial scale in terms of both grain (spatial resolution) and
 402 extent (extent of geographical area of interest, Palmer et al. (2002)). Re-
 403 garding extent, one of the major weaknesses of the proposed algorithm in
 404 β -diversity quantification (although this applies in general to all measure-
 405 ments of turnover) is that by increasing the extent of an observation area,
 406 the estimated values for an individual comparison between sites are modified
 407 by the increasing spectral species pool.

408 Additional drawbacks at the current stage of the algorithm include: i)
 409 the use of remotely sensed data which are not necessarily related to the main
 410 drivers of species distributions and of diversity, ii) the general multicollinear-
 411 ity found in most of the remotely sensed sets, iii) the unsupervised clustering

412 process being adopted.

413 Concerning climate, a solution might be found in the use of remotely
414 sensed derived climate data adding climate change as an additional layer
415 of complexity as in Rocchini et al. (2015a) and in (Zellweger et al., 2019).
416 Also in this case multicollinearity of climate variables should be seriously
417 taken into account, as we did for the original remote sensing data, by ap-
418 plying a PCA to reduce the noise in the data and detect potential artifacts;
419 consequently, PCA components might also be visualized to find potential
420 congruence between spectral species and real species patterns. Finally, the
421 process for grouping pixels in spectral species is based on an unsupervised
422 clustering, where the definition of the number of clusters should be done a-
423 priori. In this case, we hypothesized that the diversity of types of landscapes
424 and gradient of climates across Europe may require a large number of clusters
425 to correctly differentiate among them, relying on a fuzzy view of ecosystems
426 (Rocchini and Ricotta, 2007). Hence, we decided to adopt a trial and error
427 procedure until a threshold was reached in which no significant changes were
428 found. Such a threshold resulted in 200 clusters. In the near future, it would
429 be interesting to make a sensitivity analysis to demonstrate the impact of
430 the number of clusters on the final analysis.

431 Considering the use of remote sensing for species diversity estimates, cor-
432 relation and determination coefficients are generally statistically significant
433 but low, hampering the direct use of remotely sensed diversity in simple uni-
434 variate models (Rocchini et al., 2018). In fact, the relationship between α -
435 or β -diversity and habitat heterogeneity, which is the founding principle for
436 the use of remote sensing data for these analyses, is rarely linear (Ferrier et
437 al., 2007), mainly because of variation in the rate of species turnover along
438 an environmental gradient. However, remotely sensed variables are generally
439 well suited in more complex multivariate models accounting for part of the
440 diversity explained for species communities (Rocchini et al., 2018). This is es-
441 pecially true considering that environmental turnover generally explains more
442 variation in species diversity rather than mere spatial structure (Hernandez-
443 Stefanoni et al., 2012). Moreover, based on their high temporal resolution,
444 remote sensing data might be useful to detect drastic changes of diversity
445 in space and time, e.g. related to catastrophic events, overall considering
446 the intrinsic difficulties in relying on in-situ data for wide geographical scales
447 (Cord and Rödder, 2011; Hobohm et al., 2019).

448 From an ecological perspective, remote sensing imagery bands (dimen-
449 sions) show a high affinity with the hypervolume axes proposed by Hutchin-
450 son (1957) for modelling species niches. In the Hutchinson's theory, an hy-
451 pervolume is represented by a space defined by a set of n independent axes
452 which could be related to the final variables driving the realised niche of a

species (see also Blonder (2017) and Ricotta et al. (2010) on the niche differentiation concept). In our case, such axes would be the original satellite sensor bands being strictly related to the identification of a spectral species and the resulting spectral community in a site, instead of a niche. From this point of view, spectral species and communities are in line with joint species distribution models (JSDMs), which explicitly take into account biotic interactions among species in a community, while in our model the “interaction” among pixel values is ruled out in general by their proximity both from a spatial and from a spectral point of view. In this paper, the final aim was not to model single spectral species or spectral communities but rather to estimate diversity and its change over space and time, following the mathematical principles described in Liu et al. (2014) and Rocchini et al. (2015b), for which the distribution of diversity over space is actually a particular case of the so-called switched systems, i.e. hybrid systems resulting from both continuous and discrete dynamics with a high number of different potential variables acting as main drivers of diversity response. In our view we succeeded here to fill a previous gap in spatio-ecological analysis, i.e. the translation of what in remote sensing science is known as “spectral mixture modeling” (Jensen, 2015) into an ecological diversity theory approach. In spectral mixture modeling the measured spectral reflectance is decomposed as a mixture of endmembers. In our case, such a mixture was used to directly compute alpha- and beta-diversity over wide spatial areas in a very short time.

4 Conclusion

Predicting and mapping α - and β -diversity using remotely sensed images acquired over large areas is currently a key topic in ecology, and could provide landscape managers with rapid and effective tools to estimate and monitor global change. In this paper, we proposed a novel method based on preliminary unsupervised clustering of spectral data (NDVI time series derived from MODIS data), assigning each pixel to a “spectral species” and then calculating diversity based on a dissimilarity metric. At the scale of this study, the one-to-one relationship between spectral species and in-situ plant species is not achieved, but the spectral species concept still holds true once considering that the detected spectral species in the spectral space are related to higher-order plant hierarchies (assemblages, entire habitats, etc.). That is, from an algorithmic point of view, the bulk of the calculations are unaltered.

Based on the results presented here, the use of the spectral species and communities concept would appear to promote more effective planning and

491 policies related to the conservation of wild species, by improving our under-
492 standing of the dynamics of local and global biodiversity at various spatial
493 and temporal scales.

494 **5 Acknowledgements**

495 DR was partially supported by the H2020 project SHOWCASE and by the
496 H2020 COST Action CA17134 “Optical synergies for spatiotemporal sensing
497 of scalable ecophysiological traits (SENSECO)”. This paper has been par-
498 tially developed during a Short Term Scientific Mission supported by the
499 H2020 COST Action CA15212 “Citizen Science to promote creativity, scien-
500 tific literacy, and innovation throughout Europe”.

501 JBF and FdB acknowledge financial support from Agence Nationale de
502 la Recherche (BioCop project—ANR-17-CE32-0001) and TOSCA program
503 grant of the French Space Agency (CNES) (HyperTropik/HyperBIO project).

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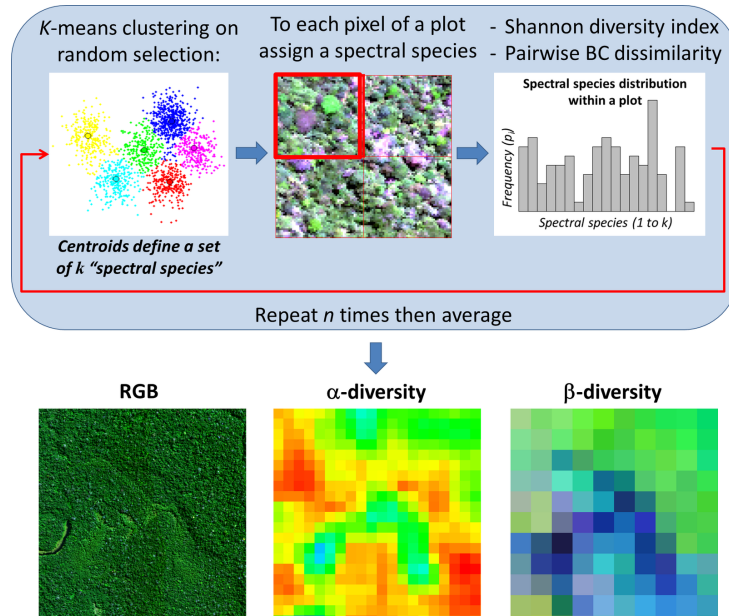


Figure 1: Diagrammatic representation of the steps of the algorithm used to achieve α - and β -diversities, redrawn from (Féret and Asner, 2014). Pixels are clumped in a spectral species and spectral community diversity is calculated. We refer to the main text and to Box 1 for additional information.

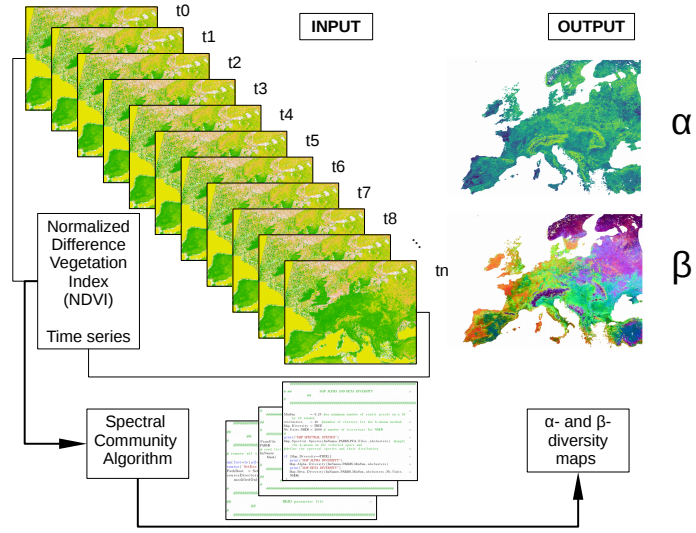


Figure 2: An input set of n images can be handled to create a time series and use the stack to further calculate the spectral community diversity. In our paper, a stack of 12 NDVI images of 2018 from the MODIS sensor was processed by the spectral species algorithm, by producing α - and β -diversity maps.

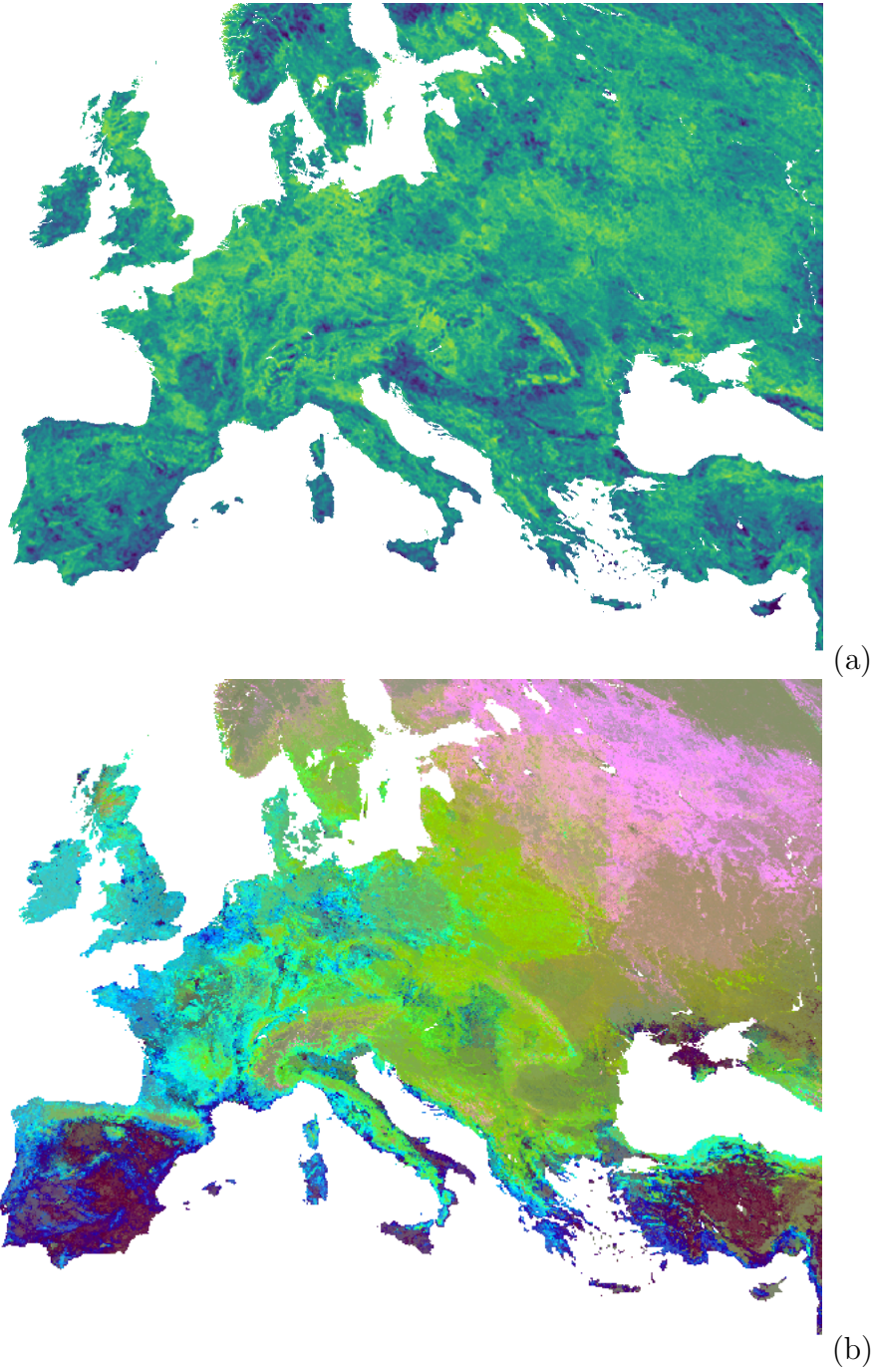


Figure 3: α - (a) and β -diversity (b) maps obtained by the spectral species algorithm. (a) The α -diversity map, based on Shannon's H' index (ranging from blue [low values] to light green [high values]) calculated in a 10x10 pixels local neighbourhood, corresponds to the local entropy of clusters, so that each location is independent from the others; (b) The β -diversity map - Bray-Curtis dissimilarity reduced to 3 dimensions with NMDS - provides information about the dissimilarity along any location in the image. Here, the distance between pairs of spatial units is expressed as a 3 colour code.

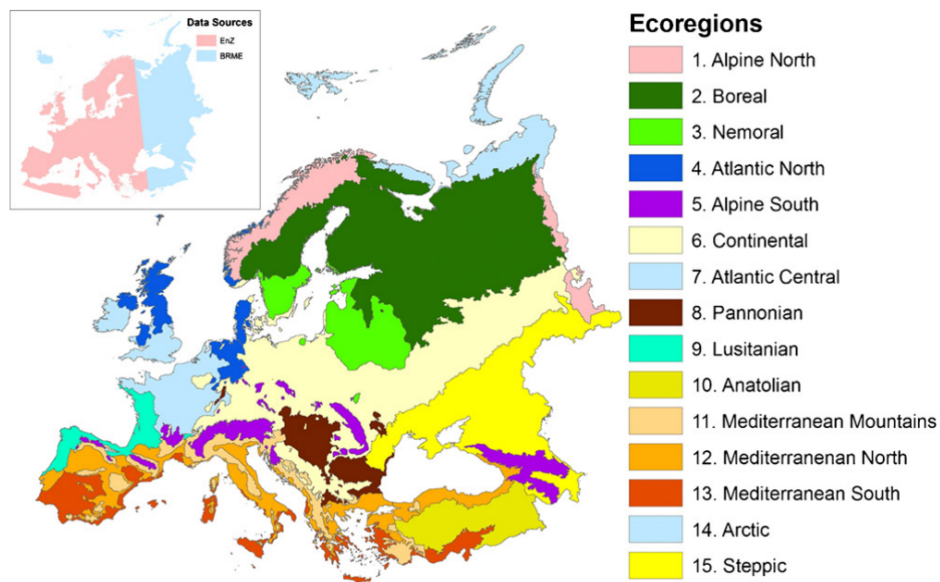


Figure 4: European Environmental Agency ecoregions map redrawn by Mucher et al. (2009). Similar maps at a coarser grain are provided by Mouchet et al. (2015) and Dinerstein et al. (2017).

771 **Box 1 - Steps composing the spectral species** 772 **algorithm**

- 773 1. A Principal Component Analysis (PCA) is applied to the spectral data.
774 PCA is not performed on the whole image, but only on a large subset
775 of pixels randomly selected from the image. Due to the high dimen-
776 sionality of the data, the reduction of the dataset is not altering the
777 result. Those principal components explaining most of the variance of
778 the original set are then retained for further steps.
- 779 2. A subset of pixels is then randomly selected across the entire map and
780 the spectral space containing such a subset is partitioned into spectral
781 species using k-means clustering with the number of k clusters being
782 decided a priori. Then the centroids defining the spectral species are
783 located.
- 784 3. The spectral dataset is divided into final mapping units. Each pixel
785 is assigned to a given spectral species based on the minimal Euclidean
786 distance between pixels (Peuquet, 1992) and the previously defined
787 centroids.
- 788 4. A spectral species distribution is obtained for each mapping unit from
789 which the α - and β -diversity indices are computed as previously stated.
- 790 5. Since the spectral species distribution is obtained by a subset of pixels,
791 in order to avoid under-representation of some small-scaled ecological
792 classes (e.g. small scale vegetation patterns), steps 4 and 5 are repeated
793 100 times, and the indicators obtained for each repetition are averaged.
794 In particular the Bray-Curtis dissimilarity matrix is computed for each
795 pair of spatial units, based on their spectral species distribution at each
796 iteration; then the final matrix corresponds to the BC dissimilarity
797 averaged over all the iterations.
- 798 6. Non metric Multidimensional Scaling (NMDS) (e.g. Borg and Groenen
799 (2005)) is applied to the matrices in order to obtain a visual representa-
800 tion of the results. NMDS is an ordination technique usually applied in
801 ecology that differs from other ordination techniques as PCA, since in
802 NMDS a small number of axes are chosen prior to the analysis and then
803 the data are fitted into the chosen dimensions. Furthermore, NMDS

is not an analytical but numerical technique, seeking for the right solution (convergence) iteratively. Finally, NMDS is not an eigenvector-eigenvalue technique, hence a NMDS ordination can be rotated among the axes. NMDS is mostly used in ecology for its versatility since it accepts any distance measure of the samples. In this case the Bray-Curtis matrix was used. In the applied NMDS approach, the first step is generally to decide the number of reduced dimensions; in this case 3 dimensions were chosen. The algorithm starts with the construction of initial random arrangements of the pixels. Then the Euclidean distances among the samples is calculated in this first configuration; those distances are regressed against the original distance matrix, and the predicted ordination distances are calculated. Finally, the regression is fitted by the least-squares method. The goodness of fit is measured by the sum of squared differences between ordination-based distances and the predicted distances. The goodness of fit is calculated through the Kruskal's Stress index:

$$Stress = \sqrt{\frac{[r]\sum_{h,i}(d_{hi} - \hat{d}_{hi})^2}{[r]\sum_{h,i}d_{hi}^2}} \quad (3)$$

where d_{hi} is the ordinated distance between pixels h and i , and \hat{d}_{hi} is the distance predicted from the regression. Then, a new configuration is computed moving in the direction in which stress changes most rapidly. The entire procedure is repeated until convergence. A *Stress* value that provides an excellent representation in the reduced dimensions is considered to be lower than 0.05; nevertheless a value of *Stress* < 0.2 is still considered a good representation Borg and Groenen (2005).

Basically, the algorithm provides both single spectral species maps and the α - and β -diversity maps. The algorithm input file needs to be in ENVI binary format with the corresponding header file. The file should be in Band Interleave by Line (BIL) format and 2-byte signed integer, and should not have extension. A further masking file in the same format is necessary in order to mask clouds and water surfaces.

833 **Box 2 - Packages used in this manuscript to**
834 **handle and analyse spatial data in R**

- 835 • **raster**: It provides classes and functions to manipulate geographic
836 data in raster format. Raster data divides space into cells (as pixels) of
837 equal size (in units of the coordinate reference system). Along with the
838 **raster** package, the **sp** package is also loaded, which provides spatial
839 object classes and methods to retrieve coordinates.
 - 840 • **rgdal**: It provides functions to import and export spatial data in differ-
841 ent formats.
 - 842 • **RStoolbox**: A toolbox for remote sensing image processing and analy-
843 sis.
 - 844 • **rasterdiv**: It provides algorithms for measuring diversity from spatial
845 matrices.
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