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The relationship between species and spectral diversity in grassland communities is mediated by their vertical complexity

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version:

Conti, L., Malavasi, M., Galland, T., Komárek, J., Lagner, O., Carmona, C.P., et al. (2021). The relationship between species and spectral diversity in grassland communities is mediated by their vertical complexity. *APPLIED VEGETATION SCIENCE*, 24(3), 1-8 [10.1111/avsc.12600].

Availability:

This version is available at: <https://hdl.handle.net/11585/829957> since: 2021-08-19

Published:

DOI: <http://doi.org/10.1111/avsc.12600>

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This is the final peer-reviewed accepted manuscript of:

Conti, Luisa; Malavasi, Marco; Galland, Thomas; Komárek, Jan; Lagner, Ondřej; Carmona, Carlos P.; Bello, Francesco; Rocchini, Duccio; Šimová, Petra: *The relationship between species and spectral diversity in grassland communities is mediated by their vertical complexity*

APPLIED VEGETATION SCIENCE VOL. 24 ISSN 1402-2001

DOI: 10.1111/avsc.12600

The final published version is available online at:

<https://dx.doi.org/10.1111/avsc.12600>

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The relationship between species and spectral diversity in grassland communities is mediated by their vertical complexity.

Running title: Spectral-species diversity in grasslands

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1

2 **Abstract**

3 *Aims*

4 The link between spectral diversity and **ground plant** biodiversity is one promising approach
5 for using remote sensing for biodiversity assessment. Nevertheless, there is little evidence to
6 whether this link is maintained at fine scales, as well as to how it is influenced by vegetation's
7 vertical complexity. Here we test, at community level in grasslands, the link between diversity

8 of the spectral signal (SDiv) and taxonomic diversity (TDiv), and the influence of vertical
9 complexity.

10 *Methods*

11 We used 196 1.5×1.5 m experimental communities with different biodiversity levels. To
12 measure vertical complexity, we quantified height diversity (HDiv) of the most abundant
13 species in the community. TDiv was calculated using Shannon index based on species cover.
14 Canopy spectral information was gathered using an UAV mounted with a multi-spectral sensor
15 providing spectral information via six 10 nm bands covering the visible and near-infrared region
16 at 3 cm spatial resolution. We measured SDiv in a core area of 1×1 m within the communities
17 as mean Euclidean distance of all pixels in a feature space spanned between the two first
18 components of a PCA calculated for the complete raster stack. We modelled SDiv through
19 mixed effect linear models, using TDiv in interaction with HDiv as fixed effect predictors.

20 *Results*

21 **Contrarily to our expectations, TDiv was negatively linked to SDiv.** The diversity in plant
22 height was positively related to SDiv. More importantly, diversity in plant height and TDiv had
23 a significant negative interaction, meaning the more complex the vegetation was in terms of
24 height, the more the SDiv-TDiv relationship became negative.

25 *Conclusions*

26 Our results suggest that in order to exploit the SDiv-TDiv link for monitoring purposes, it needs
27 to be contextualized. Moreover, they highlight that communities' functional characteristics (i.e.
28 plant height) mediate such link, calling for new insights on the relation between SDiv and
29 functional diversity.

30

31 **Keywords:** spectral diversity, grasslands, species diversity, community scale, vertical
32 stratification, height diversity, taxonomic diversity, mixed effect models, remote sensing, multi-
33 spectral sensor, UAV.

34 **Introduction**

35 Improving our ability to monitor biodiversity across scales is critical to understand its role in
36 shaping ecosystem functioning across the world, as well as to track ecological communities'
37 responses to rapid environmental changes. Despite a growing interest in biodiversity in recent
38 decades, the ability to measure and monitor biodiversity through traditional methods continues
39 to lag behind current global changes and its related challenges (Palmer et al. 2002; Wang and
40 Gamon 2019). National biodiversity monitoring programs differ widely, most data sets are
41 inconsistent, and few data are shared openly; further, measuring biodiversity on the ground is
42 laborious, requiring a lot of time, human, and financial resources, as well as being limited by a
43 lack of standardized procedures for reproducible data gathering (Rocchini, Marcantonio, and
44 Ricotta 2017; **but see also the GEOBON initiative, Scholes et al. 2018**). Recently, it has been
45 suggested that variation in plant diversity could be promptly monitored through remote sensing
46 (RS) techniques (Féret and Asner 2014; Jetz et al. 2016; Lausch et al. 2016; Skidmore et al.
47 2015; Wang and Gamon 2019), which provide a continuous source of information on different
48 facets of plant diversity on a wide range of scales in a consistent, borderless, and repeatable
49 manner (Turner 2014).

50 Among the many approaches used to estimate plant diversity through RS (for a review
51 see Wang and Gamon 2019), “Spectral Diversity” (SDiv), has been gaining momentum
52 (Rocchini et al. 2021). SDiv, defined as the variation in spectral reflectance across a set of
53 neighbouring pixels (Palmer et al. 2002; Ustin and Gamon 2010), was originally proposed
54 under the framework of Spectral Variation Hypothesis (SVH; Palmer 1992). This framework
55 suggests that a higher spectral diversity can be interpreted as a higher ecosystem spatial
56 heterogeneity, thus as a potentially higher number of available niches and their related species.
57 However, this relationship also depends on the scale of the RS data. With the development of
58 RS techniques and the advances of instruments such as Unmanned Aerial Vehicles (UAV) it is
59 now possible to flexibly acquire data at very high spatial resolutions (Whitehead and
60 Hugenholtz 2014). Such high-resolution data can capture the direct link between the spectral
61 information at leaf and canopy level and the functional characteristics of the different plant
62 species in the analysed area (Asner and Martin 2009; Wang and Gamon 2019). It follows that
63 with a larger availability of fine spatial resolution images, SDiv can be used to directly estimate
64 plant species diversity, since a higher spectral diversity should relate to a higher number of
65 species with corresponding species-specific optical traits at leaf and canopy level (Asner and
66 Martin 2009; Wang and Gamon 2019). Several RS indices based on SDiv have been applied so

67 far to assess plant diversity and they have been recently grouped in three main categories (Wang
68 and Gamon 2019): metrics based on variation in vegetation indices (e.g. the Normalized
69 Difference Vegetation Index - NDVI) which often scales with species richness (Gillespie 2005);
70 metrics based on information theory (e.g. spectral entropy) providing information on the
71 “dimensionality” of a dataset for a given area, which can then be related to the number of
72 species present in that area (Rocchini et al. 2021); and metrics based on spectral species where
73 these are considered proxies or analogues for biological species, and spatial variation in spectral
74 species can be used to infer species richness (see Féret and Asner 2014). .

75 Nonetheless, while the link between SDiv and plant diversity has been confirmed in
76 several empirical studies (Rocchini et al. 2016; Wang et al. 2018; Wang and Gamon 2019), it
77 has also been criticized for being unstable and not reliable in every context (Schmidtlein and
78 Fassnacht 2017). These contradictory findings might be due to a lack of studies systematically
79 considering the most important factors influencing such relationship such as scale, phenology,
80 used metrics, and vertical structure of the observed ecosystems. In particular, the vertical
81 structure of the vegetation may hamper the optical detection of some of the plant species in the
82 area. In a closed vegetation with a complex vertical structure, taller species would tend to
83 obscure short species from RS detection (occlusion effect), which would lead to an
84 underestimation of ground plant diversity. However, a complex vertical structure could also
85 give rise to underexposed pixels or shadow patterns, which on the contrary could determine a
86 higher diversity of spectral values and lead to **an overestimation of** ground plant diversity. To
87 our knowledge, no studies have addressed the influence of the vertical complexity on the link
88 between SDiv and plant diversity. Moreover, no study has addressed this issue in herbaceous
89 communities, where despite having one single canopy level, species height variability can give
90 rise to an important gradient of vertical complexity (Brown and Cahill 2019).

91 Here, we focus on a grassland experiment situated on a mesic meadow in South
92 Bohemia (Czech Republic) to test the relationship between SDiv and communities’ taxonomic
93 plant diversity (TDiv) while accounting for the effect of the grassland vertical complexity. We
94 expect this relationship to be positive, although weaker in more vertically complex
95 communities, due to the occlusion effect. The unique settings of the experiment enabled us to
96 test this relationship by using a considerable **span of plant diversity** within grassland
97 ecosystems. Semi-natural meadows are considered to be one of the most important plant species
98 diversity hotspots worldwide (Dengler et al. 2014) and improving our ability of diversity

99 monitoring is essential to mitigate the loss of vascular plant species and associated ecosystem
100 services (Edwards and Kučera 2019).

101

102 **Methods**

103 To explore the relationship of SDiv and plant diversity at community level, we used **data from**
104 **a permanent** grassland experiment, established in 2015 and situated on a mesic meadow in
105 South Bohemia, Czech Republic (49.331N, 15.003E; for further details see Galland et al.,
106 2019). The experiment comprises 40 mesic grassland communities which cover independent
107 gradients of plant functional and phylogenetic diversity (Figure 1). Each sown community
108 comprised a combination of 6 species obtained from a pool of 19 species naturally present in
109 Czech mesic meadows. Each community was sown in two randomly situated 1.5×1.5 m plots
110 (fertilized and unfertilized), with a buffer zone of 0.5 m between each of them. Monoculture
111 plots were also sown in three replicates each, for a total of 196 plots. These represent the sown
112 communities, which are the basis for the actual communities present in each plot, composed by
113 sown and colonizer species (species present in the surroundings that invaded the experiment),
114 which were the communities actually sampled (see Supporting Information, Appendix S1).

115 In May 2018, at the peak of the growing season, species composition and percentage
116 cover were measured in each of the plots. Data regarding vegetative plant height was measured
117 on site for each species (sown or colonizer) that cumulatively covered 80% in at least one of
118 the plots, on fully developed individuals and following standardized protocols (Pérez-
119 Harguindeguy et al. 2013).

120 Shortly after the vegetation sampling, multi-spectral imagery at high spatial resolution
121 (~ 3 cm) was acquired over the grassland experiment by an Unmanned Aerial Vehicle.
122 Specifically, a hexacopter Kingfisher (Robodrone Industries) equipped with a Tetracam
123 μ MCA6 global shutter (Kelcey and Lucieer 2012), providing optical image data across six 10-
124 20 nm width bands ranging from 490 to 900 nm (Table 1). Acquired imagery was processed
125 using Structure from Motion and Multi-View Stereo algorithms in Photoscan image-matching
126 software (version 1.4, Agisoft LLC 2018). Orthomosaics were built and accurately
127 georeferenced using six Ground Control Points placed across the experimental site and
128 surveyed with a Leica GPS1200 GNSS aperture in RTK mode. The surface reflectance values
129 were calculated using a grey calibration target **for which the spectral properties were known**
130 **through** spectrometer **measurements** to produce radiometrically calibrated orthomosaics.

131

132 *Statistical analyses*

133 In each plot, first we determined vertical complexity, TDiv, and SDiv. Vertical complexity was
134 quantified through diversity in plant height (HDiv), measured as mean Euclidean distances
135 between the height values (normalized via log-transformation) of the species present in each of
136 the plots, weighted by the abundance of each species in terms of cover (de Bello et al. 2016).
137 TDiv was calculated using Shannon index based on species cover (Shannon and Weaver 1949).

138 To measure SDiv we used an index based on spectral entropy (Wang and Gamon 2019),
139 which is now the main approach used to quantify spectral diversity as a proxy for plant diversity
140 (see Schweiger et al. 2018, Wang et al 2018, Rocchini et al. 2021). We first performed a
141 standardized PCA (centered and scaled input image for equal weighting of all layers) to
142 summarize the values of the six bands (using ‘rasterPCA’ function in R package ‘RStoolbox’),
143 a common practice for spectral entropy metrics (Rocchini et al 2021). Then, for each plot, we
144 extracted the values of the first and second principal component axes derived from the PCA.
145 These values were extracted considering the pixels within a core area of 1×1 m inside the plot,
146 in order to avoid edge areas and thus avoid sampling bias due to potential overlap between
147 adjacent communities or between buffer zone and the actual sampled plot (Figure 1). We then
148 calculated the mean Euclidean distance of these two sets of values in each of the core areas. We
149 also quantified two separate SDiv measures, corresponding to the spectral diversity when
150 considering only the first axis (SDiv₁) or only the second axis (SDiv₂), results regarding these
151 indexes are in line with the results presented here and can be found in Supporting Information,
152 Appendix S2. We modelled the variation in SDiv through mixed effect linear models (R
153 package ‘nlme4’), using TDiv and HDiv (both scaled and centred), separately and in interaction,
154 as fixed effect predictors, and the combination of diversity level (type of community sowed)
155 and fertilization treatments as random effect. In addition, for each model we calculated marginal
156 and conditional R²s to assess the variance explained by fixed effect and both fixed and random
157 effects, respectively (function ‘r.squaredGLMM’ in R package ‘MuMIn’). A visual
158 representation of all the values used in the models on the study area is found in Appendix S3,
159 Supporting Information. Finally, we controlled for potential effect of visible flowerheads in our
160 images. We compared values of SDiv and HDiv in plots with or without flowers though
161 Kruskal-Wallis rank sum test. We did not find any effect of the flowers in either SDiv or HDiv
162 (see Supporting Information, Appendix S4). All analyses were performed in R statistical
163 software (version 3.5.2, Team R Core 2013)

164

165 **Results**

166 The two first principal components derived from the standardized PCA accounted for nearly
167 90% of the variance in the spectral signal of the communities (Table 2). When correlating these
168 components to the reflectance values in each of the bands, Pearson's correlation coefficients
169 showed that the first component is highly and positively correlated with bands 2, 4, and 6
170 (Green, Red Edge, and Near Infrared 2, respectively), while the second component is positively
171 correlated mainly with bands 1 and 3 (Blue and Red respectively), while negatively correlated
172 with bands 5 and 6 (Near Infrared 1 and 2; Table 3). Therefore, the higher variance in the
173 spectral signal of these communities is enclosed in the red edge, near infrared, and green
174 regions, which is represented in the first component axis. The rest of the spectral variance,
175 specially the one in the blue and red regions, is described mainly by the second component axis.

176 The mixed model showed that TDiv was significantly linked to SDiv, **although with a**
177 **negative coefficient (estimate = -0.26, standard error = 0.05, p-value < 0.001;** Figure 2). On the
178 contrary, HDiv, i.e. the vertical structure of the communities, was positively related to SDiv
179 **(estimate = 0.36, standard error = 0.05; p-value < 0.001** Fig. 2). More importantly, HDiv and
180 TDiv had a significant negative interaction **(estimate = -0.27, standard error = 0.06, p-value <**
181 **0.001;** Fig. 2), meaning that the more complex the vertical structure of the vegetation, the more
182 negative the relationship between TDiv and SDiv became (Fig. 2). The marginal R^2 calculated
183 was of 0.36, thus the fixed effects explained more than 30% of the variability. Together with
184 the random effects, the model explained 61% of the total variability (conditional $R^2 = 0.61$).

185

186 **Discussion**

187 Generally, our results show how the relationship between SDiv and communities' taxonomic
188 diversity (TDiv) is mediated by grasslands' vertical complexity. **The negative relationship**
189 **found between SDiv and TDiv is in contrast with previous empirical studies** (Rocchini et al.
190 2016; Wang et al. 2018; Wang and Gamon 2019). **This found relationship highlights that** SDiv
191 can't be used routinely to predict plant species diversity (e.g. Schmidtlein and Fasnacht 2017).
192 This is also suggested by the fact that in our models, the random effect (i.e. the fertility and
193 diversity treatment of each plot), explained nearly 30 percent of the variability in SDiv. Our
194 results do show both a relationship between SDiv and HDiv, and an interaction effect of HDiv

195 and TDiv. This means that herbaceous communities with a higher diversity in terms of height,
196 i.e. a more complex vertical structure, have a more diverse spectral signal. More importantly,
197 herbaceous communities with the most complex vertical structure manifest a **more** negative
198 relationship between SDiv and TDiv; meaning that these communities will express high SDiv
199 even when having low TDiv (probably because of taller species contributing to spectral
200 diversity by casting shadows and hence generating underexposed pixels) and will express low
201 SDiv even with high TDiv (due to potential occlusion effect). These relationships were also
202 confirmed when analysing the spectral variability using single PCA axes, meaning that they are
203 valid across different optical features of the communities (Supporting Information, Appendix
204 S2).

205 Results regarding the PCA highlighted that the highest variability in terms of spectral
206 signal is expressed in the wavelength range corresponding to the RE, G and NIR2 spectral
207 bands, while the rest of the spectral variability is expressed in the bands B and R but also
208 negatively through NRI1 and NRI2 (Table 2). The variability expressed in these ranges is linked
209 to species-specific differences in pigment content, leaf structure and canopy structural
210 components such as leaf area index (Jones and Vaughan 2010). The second principal
211 component linked mainly to R and B bands, which relate to pigments, including carotene and
212 xanthophylls. However, this axis is also expressing a negative correlation with NIR2, **in contrast**
213 **with the first axis being positively correlated to NIR2**. This variability could reflect the different
214 composition of the communities also in terms of phenological stage, e.g. flowers presence and
215 leaf senescence variability. These results show that despite the dimensionality reduction applied
216 to the spectral variance, SDiv metrics based on PC components, which belong to the
217 information theory type of metrics, are able to convey information across all bands as well as
218 important vegetation properties.

219 We observed an **overall negative** relationship between SDiv and TDiv, which suggests
220 that the inconsiderate use of spectral variation to quantify species diversity, **at this scale, might**
221 **be misleading** (Fig. 3). The use of spectral diversity as a surrogate of species diversity has been
222 indeed long debated, as this link is highly dependent on various factors that might be hard to
223 control (Schmidtlein and Fassnacht, 2017). Indeed, our results seem to confirm the context-
224 dependency of this method, with the relationship between SDiv and TDiv **in this case being**
225 **opposite to expectations, and generally driven by the diversity of heights, i.e. vertical**
226 **complexity, in the communities analysed (as seen in Fig. 3)**. Despite our results being
227 supposedly able to capture the direct spectral footprint of each plant individual given their high

228 spatial resolution, i.e. exploiting the known direct link between the spectral information at leaf
229 and canopy level and the characteristics of plant species (Asner and Martin 2009), the
230 relationship between SDiv and TDiv was actually **more negative** when analysing more
231 vertically complex communities. Reasons leading to the variation of the SDiv-TDiv
232 relationship may be connected partially to spatial grain effects, as well as to the effect **of the**
233 **spatial configuration of the vegetation** on the spectral diversity, as discussed below.

234 The effect of spatial grain on the link between SDiv and TDiv has been highlighted by
235 several authors (Rocchini et al. 2016; Wang et al. 2018). In particular, Wang et al. (2018), using
236 central-European experimental grasslands, highlighted that in order to observe a positive
237 relationship, the used pixel size should reflect the individual plant size. Despite the use of a fine
238 spatial grain (~3 cm, corresponding to the average size of the individuals found in our
239 communities), the SDiv measure used presented a **negative** link to TDiv. **In our system and at**
240 **this scale, more taxonomically diverse communities were less diverse in terms of spectra, and**
241 **less taxonomically diverse species had higher spectral diversity.** One explanation might be that
242 within this particular setting species' taxonomic identity doesn't correspond to the species'
243 spectral identity. On the one hand individuals of the same species might have slightly different
244 spectral signals, because of intra-specific variability or different phenological stages; on the
245 other hand, different species might have similar spectral signals, as they might possess similar
246 plant functional traits. In order to better discriminate between species specific signals, a
247 hyperspectral sensor could be preferred over the here adopted multi-spectral sensor (e.g.
248 Lopatin et al. 2017; Möckel et al. 2014). In any case, plant functional types (defined by plant
249 traits), are more closely and more mechanistically linked to the spectral identity of species.
250 Therefore, functional diversity would be more strongly related to spectral variability (as seen
251 in Schweiger et al. 2018; and Ustin and Gamon 2010), compared to species or taxonomic
252 diversity. Which is also highlighted by the direct link we found between diversity in spectral
253 variability and plant height diversity.

254 Our findings show that SDiv was linked more strongly to the vertical structure of the
255 sampled communities, compared to TDiv (Figs. 1 and 3). While the link between vegetation
256 structure and different remote sensing indicators has been highlighted by previous studies,
257 especially in woody vegetation (Campos et al. 2018; Wood et al. 2012), the present work is the
258 first work assessing this link using optical data within grasslands. Spatial configuration of
259 vegetation is an important functional characteristic, tightly linked with different ecosystem
260 functions such as biomass production and ecological niche availability (Zuppinger-Dingley et

261 al. 2014). Indeed, remote sensing techniques have been employed to quantify spatial
262 configuration of vegetation and its spatial variability. In particular, regarding optical data, a
263 series of textural indices have been linked to vegetation vertical structure (Campos et al. 2018;
264 Wood et al. 2012). These studies have been performed at wide extent and coarse spatial
265 resolution, as they focus mainly on differences in the vertical structure of different vegetation
266 types. Our results suggest that, when using the proper resolution, communities' spatial structure
267 can be quantified even within a seemingly homogeneous vegetation type, with diversity of plant
268 height being directly related to the diversity of reflectance within a certain area.

269 Finally, not only HDiv was directly linked to SDiv, it mediated the relationship between
270 SDiv and TDiv, **and thus provided an explanation for the found negative link between the two**
271 **variables**. For highly structured communities in terms of their vertical configuration, we found
272 a **more negative** relationship between the diversity of species measured at ground level and the
273 diversity of the spectral signal (negative interaction, Fig. 2 and 3). **Moreover**, communities with
274 a low species diversity but high HDiv showed a high spectral diversity. This may depend on
275 the horizontal configuration of the communities, which is constrained by the pre-established
276 size of the experimental plot. At high HDiv, the species-poor communities might have more
277 space compared to species-rich communities which express a low SDiv. That is to say that
278 wherever in our experimental plots we observe a species-rich community with high HDiv, its
279 species, in order to populate the plot, may be squeezed in a relatively small area, overlapping
280 one another in the vertical and horizontal space. In this case, fewer species would be able to
281 lean out in the higher strata and mask the lower layers, which results in a more homogeneous
282 canopy sensed and therefore lower SDiv (i.e., occlusion effect).

283

284 **Conclusions**

285 Ultimately, our results show that the link between SDiv and species diversity in grasslands is
286 mediated by vegetation's vertical complexity. In particular, they suggest that in order to exploit
287 the link for monitoring purposes, it needs to be contextualized. Despite recent evidence pointing
288 at the use of remote sensing data for estimating species richness and diversity (Rocchini et al.
289 2016; Wang et al. 2018; Wang and Gamon 2019), this approach is not straightforward,
290 especially when focusing on grassland systems on community scale. However, the relationship
291 between SDiv and structural characteristics of the communities found here calls for more

292 insights regarding the link between SDiv and functional diversity (as seen in Schweiger et al.
293 2018).

294 Finally, although our findings **partly reject the** theorized link between SDiv and plant species
295 diversity, this does not mean that spectral diversity cannot be useful for biodiversity monitoring.
296 Besides the promising usefulness of its link with functional diversity (e.g. Schweiger et al.
297 2018), our results indicate that spectral diversity can be used when appropriately calibrated to
298 the context analysed. In particular, our work highlights the importance of considering
299 vegetation structural characteristics affecting the relationship between spectral diversity and
300 plant diversity.

301

302 **Acknowledgements:** We want to acknowledge the people involved in maintenance and data
303 sampling of the experimental communities, particularly Miroslav Šrůtek who gave access to his
304 land.

305 **Author contributions:** LC and MM conceived the idea, CC designed the experimental
306 communities, TG, FdB, and CC sampled and/or analysed ground data, JK and OL sampled and
307 cleaned the drone images, DR and PS helped analyse spectral data, LC analysed the complete
308 dataset and wrote the first draft of the manuscript. All authors contributed to the writing.

309 **Data availability statement:** Aggregated data (metrics) used in this manuscript is available in
310 Supporting Information Appendix S1, Table S1.1.

311

312

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411 **Appendix S1:** Ground diversity values for the communities sampled and spectral diversity values
412 measured at each plot are presented in a separate file “[TableS1.1.txt](#)”

413 **Appendix S2:** Linear mixed models using SDiv₁ and SDiv₂.

414 **Appendix S3:** Visual representation of SDiv, TDiv, and HDiv values in the study area.

415 **Appendix S4:** Flowers effect on SDiv and HDiv

416

417 **Table 1.** Spectral bands measured and their corresponding range.

Band	Band peak (nm)	Band full width at half maximum (nm)	Corresponding range	Abbreviation
Band 1	490	485 - 495	Blue	B
Band 2	550	545 - 555	Green	G
Band 3	680	675 - 685	Red	R
Band 4	720	715 - 725	Red edge	RE
Band 5	800	795 - 805	Near infra-red	NIR1
Band 6	900	890 - 910	Near infra-red	NIR2

418

419 **Table 2.** Variability explained by the principal components derived from the standardized PCA
 420 (centered and scaled input layers) performed over the 6 spectral bands.

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6
Standard deviation	2.0532060	1.0874347	0.54525290	0.38164219	0.3254505	0.230133368
Proportion of Variance	0.7026091	0.1970857	0.04955012	0.02427513	0.0176530	0.008826895
Cumulative Proportion	0.7026091	0.8996949	0.94924497	0.97352010	0.9911731	1.00000000

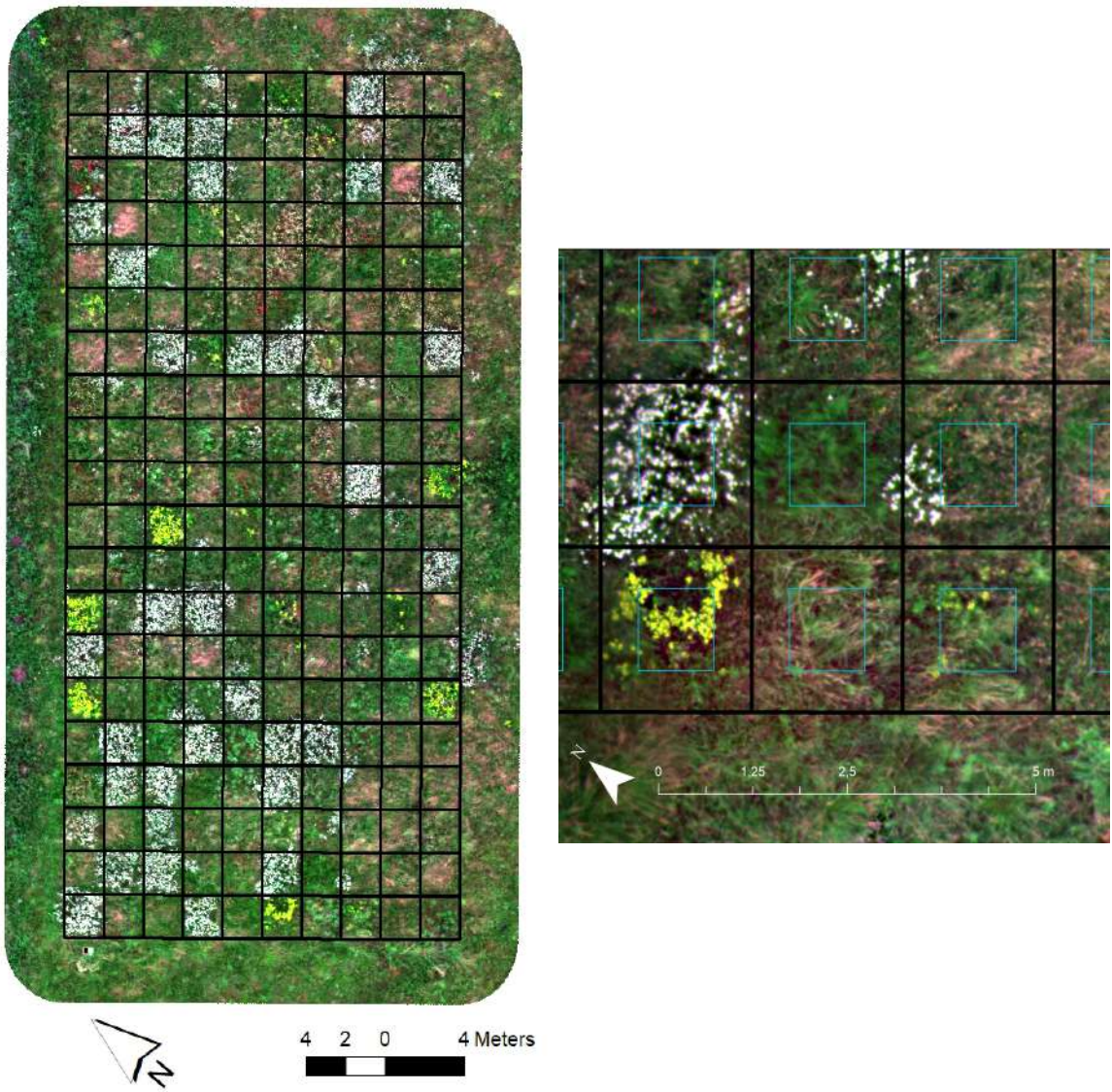
421

422 **Table 3.** Pearsons' correlation estimates between principal components 1 and 2, and spectral
 423 bands

	Band.1 (B)	Band.2 (G)	Band.3 (R)	Band.4 (RE)	Band.5 (NIR1)	Band.6 (NIR2)
Comp.1	0.7725979	0.9039081	0.8194706	0.91142	0.7912322	0.8206282
Comp.2	0.5090558	0.2589284	0.5005981	-0.1966337	-0.5297212	-0.535224

424

425

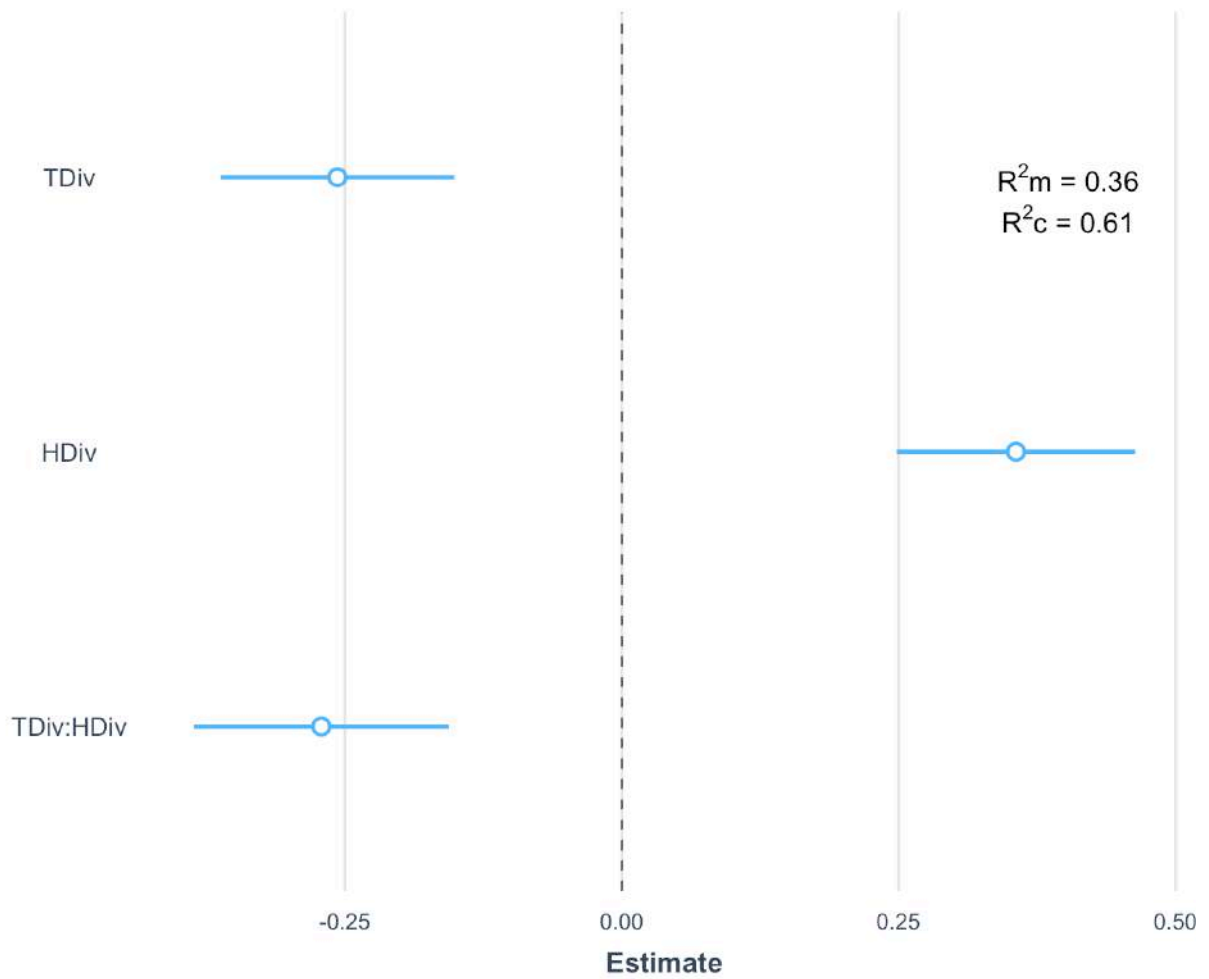


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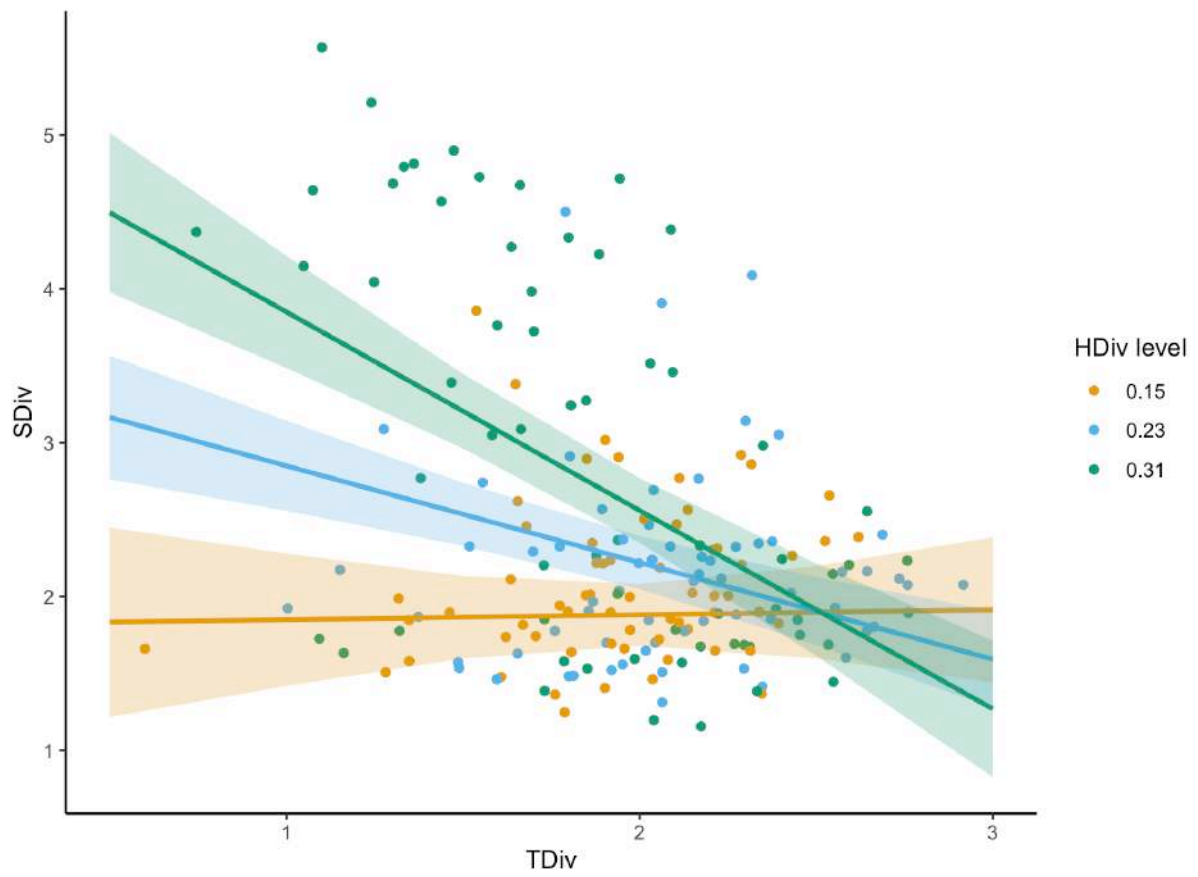
429 **Figure 1.** RGB image of the multi-spectral image sampled. Whole area in the left panel, zoom-
430 in on the single plots in the right panel. Community plots are shown with black lines while the
431 core areas considered in the analyses are delineated in cyan.

432



433

434 **Figure 2.** Coefficient plot of the mixed model showing estimate values for each explanatory
 435 variable and their interaction, as well as their 95% confidence interval. R^2 marginal and
 436 conditional are shown in-graph.



437

438 **Figure 3.** Predicted relationships between SDiv and TDiv derived from the mixed effect model,
439 when setting different values of HDiv (in legend).

440