Original Articles

Remote sensing of spectral diversity: A new methodological approach to account for spatio-temporal dissimilarities between plant communities

Christian Rossi [a,b,c,*], Mathias Kneubühler [a], Martin Schütz [b], Michael E. Schaepman [a], Rudolf M. Haller [c], Anita C. Risch [b]

[a] Remote Sensing Laboratories, Dept. of Geography, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland
[b] Research Unit Community Ecology, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
[c] Department of Geoinformation, Swiss National Park, Runatsch 124-Chastè Planta-Wildenberg, 7530 Zernez, Switzerland

ARTICLE INFO

ABSTRACT

The increasing availability of remote sensing data allows the quantification of biodiversity in space and time. In particular, spectral diversity, defined as the variability of electromagnetic radiation reflected from plants, can be assessed with remote sensing. Plant traits vary diurnally and seasonally due to plant phenology and land management. This results in strong temporal variation of spectral diversity, which cannot be accurately represented by remotely sensed data collected at a single point in time. However, knowledge of how datasets sampled at multiple points in time should best be used to quantify spectral diversity is scarce. To address this issue, we first introduced a new approach using spatio-temporal spectral diversity based on the dissimilarity measure Rao's quadratic entropy index (RaoQ). Thereby, we demonstrated how RaoQ can be used to partition the total spectral diversity of a region (γSD) into additive alpha (αSD, within communities) and spatio-temporal beta (βSD; between communities) components, allowing the calculation of βSD from community mean spectral features, independent from αSD. Second, we illustrated our methodological approach with a case study in which βSD is calculated from Sentinel-2 satellite data at high temporal resolution for managed grasslands which differ across a large gradient of environmental properties. We were able to show differences in βSD and separate its components into phenological and management effects. Furthermore, the contribution of different plant communities to βSD was assessed, and the results were validated against a dataset of *in-situ* measured β diversity from plant surveys. Compared to spatial dissimilarities from distinct stages of the growing season, using spatio-temporal dissimilarities between communities produced a more accurate estimation of the uniqueness of a community. This study shows how to account for temporal variations in the spectral diversity of plant communities and demonstrates that this improves the estimation of plant biodiversity through remote sensing. Spectral diversity in space and time makes it possible to assess mechanisms that drive biodiversity and identify plant communities relevant for conservation purposes.

1. Introduction

The worldwide loss of biodiversity (Barnosky et al., 2011; Ceballos et al., 2017) and the associated decline of ecosystem services call for a comprehensive monitoring of biodiversity (Gossner et al., 2016; Hautier et al., 2009; Newbold et al., 2016). In particular, plant biodiversity affects productivity and stability of an ecosystem, and plays a critical role in maintaining ecosystem functions (Díaz et al., 2006; Hautier et al., 2014; Tilman et al., 1996; Tilman et al., 2006). Yet, measuring plant diversity across large scales in the field requires a high investment of human and financial resources and suffers from biases due to environmental conditions and the person in charge (Jetz et al., 2016; Lõhmus et al., 2018). Seasonality of plants, observer experience and perceptions, as well as physical exhaustion in challenging working environments, are possible reasons for biases in botanical surveys (Burg et al., 2015; Rich and Woodruff, 1992).

New methods of assessing plant diversity via spectral diversity obtained from remote sensing (Wang and Gamon, 2019) can provide a straightforward large-scale continuous estimation of biodiversity at relatively high spatial and temporal resolution (Cawse-Nicholson et al.,

---

2021; Pettorelli et al., 2018). The variability in spectral reflectance from plant communities found in spectral data, known as the spectral diversity, is an expression of plant taxonomic, phylogenetic and functional diversity (Cavender-Bares et al., 2017; Gholizadeh et al., 2019; Oldeland et al., 2010; Ma et al., 2019; Rocchini et al., 2010; Rocchini et al., 2018a; Schweiger et al., 2018; Ustin and Gamon, 2010; Wang et al., 2018). Spectral diversity can be calculated from different spectral features such as the spectral reflectance at a certain wavelength, a combination of several wavelengths (Gholizadeh et al., 2019, Rocchini et al., 2004; Ma et al., 2019), vegetation indices (Rocchini et al., 2018b) or optical traits (Homolová et al., 2013; Ollinger, 2011; Rossi et al., 2020; Ustin et al., 2009). Thereby, the spatial resolution of the reflectance data (i.e., the pixel size) is a critical factor influencing the level of ecological organization (i.e., species, communities, ecosystems) that can be captured. Whittaker (1960) defined that the total diversity, gamma (γ) diversity, of a region includes two components: alpha (α) diversity (within community diversity), and beta (β) diversity (between community diversity). Partitioning plant diversity into α and β diversity provides deeper insights into plant assembly processes that generate and maintain plant biodiversity in ecosystems (Münkemüller et al., 2012). To quantify α diversity based on remote sensing data, the spatial resolution (pixel size) of these data needs to be equal to or smaller than the average size of a plant growing in that community (Hakkenberg et al., 2018). As a coarse pixel represents the spectral signal of multiple plant species, β diversity between plant communities can be quantified (Rocchini et al., 2018b; Rossi et al., 2020). However, spatial diversity and its partitioning into α and β describe only one part of the overall spectral variability of plants. Capturing the temporal variation of spectral data may be more important to distinguish between different plant development stages, functional groups or management types (Huang et al., 2019), which are important for species distribution patterns and their function (Schwinning et al., 2013). For example, spectral data collected over a time-period covering multiple flowering phases may allow co-occurring plant species to be better differentiated (Nagendra, 2001).

Similarly, spectral data with high temporal resolution may capture inter-annual differences in leaf properties (e.g., water content) that result from differences in soil microclimatic properties, phenology or nutrient availability over the course of the growing season (Anderegg, 2015; Chavana-Bryant et al., 2017; Gamon et al., 2019; Gholizadeh et al., 2020; McKown, et al., 2013; Wong and Gamon, 2015; Yang et al., 2016; Meireles et al., 2020). The same holds for capturing different ecosystem management states (anthropogenic stressors), such as grazing, mowing or fertilizing (Gómez Giménez et al., 2017; Homolová et al., 2014). Therefore, to fully capture spectral diversity and to understand which processes contribute to biodiversity dynamics, both spatial and temporal spectral variation need to be accounted for.

So far, indices to quantify spectral diversity have been used exclusively to capture spatial variation in reflectance data (Dahlin, 2016; Rocchini et al., 2017; Rocchini et al., 2010; Wang et al., 2018) and have mostly not considered the level of ecological organization (i.e., species, communities, ecosystems). Only recently, Laliberté et al. (2020) proposed an index that allows the partitioning of the total spectral variation of a region into independent within (α) and between (β) community diversity, and Rocchini et al. (2019) proposed a method to quantify the change of spectral diversity in space over time. Lopes et al. (2017) tried unsuccessfully to use spatio-temporal spectral diversity to quantify α diversity based on coarse spatial resolution data. To our knowledge, no study so far has assessed taxonomic diversity through spatio-temporal dissimilarities in spectral features between communities and quantified the importance of spectral variation over both space and time. In addition, none of the commonly used spectral diversity indices have been implemented in a way that allows spectral diversity to be partitioned into temporal and spatial components.

In order to fill this gap, we developed a new methodological approach and included the spatio-temporal spectral dissimilarity of plant communities when calculating Rao's quadratic entropy index (RaoQ) to obtain total γ spectral diversity of an area (γSD). Similar to the partitioning proposed by Laliberté et al. (2020), RaoQ was partitioned into space and time. Consequently, it was not only possible to quantify α spectral diversity (αSD) and β spectral diversity (βSD) separately, but also the contributions of space and time, as well as their interaction, to βSD.

We first introduce an implementation of RaoQ that allows spatio-temporal variations to be accounted for when quantifying spectral diversity (i.e., αSD, βSD and γSD). We then tested our new methodological approach specifically for βSD, based on a case study using Sentinel-2 multispectral and multi-temporal satellite data in grasslands. We (i) calculated βSD for differently managed grasslands and partitioned it into the contribution of space, time and their interaction, ii) compared how the contribution of a community to βSD over space and the entire growing season differs from the contribution of a community to βSD in space at different stages of the growing season (spatio-temporal versus mono-temporal spectral datasets) and (iii) validated the results using *in-situ* measured β diversity from plant surveys. We used our case-study to highlight the importance of assessing temporal in addition to spatial variations in spectral features when quantifying plant biodiversity.

2. Spectral diversity over space and time

Prior to introducing our new methodological approach, the definition of the term "plant community" as used in this study is explained. Here, a plant community is a group of interacting plant individuals representing multiple species occurring together in a spatially constrained unit (Stroud et al., 2015). The unit equals either; a pixel, an aggregation of pixels of remotely sensed data, or plots in field surveys. This definition is not free of debate and implies artificially bounded units with an overwhelming emphasis on localness (Ricklefs, 2008). However, instead of relying on a few individual pixels/plots covering the region of interest, remote sensing makes it possible to have the full region covered continuously by equally sized pixels/plots. Hence, the geographical area of interest can be divided into communities of a specific size and shape (e.g., pixel or an aggregation of pixels) depending on the spatial resolution of the remote sensing data and the ecosystem considered (Fig. 1). The extent of a community remains an artificial unit, but our approach allows us to vary the size of communities, which provides insights into scale dependencies of within and between community diversity (Gering and Crist, 2002; Laliberté et al., 2020). We assume the region of interest contains S plants spread over P communities recorded at D dates, and that each community includes the same number of plant individuals S_p ($S_p = S/P$).

2.1. Using Rao's quadratic entropy to calculate spectral diversity in space

Our new methodological approach is based on RaoQ, which is an index frequently used to estimate spectral diversity as it is sensitive to the number of pixels and their pairwise spectral differences (Khare et al., 2019; Rocchini et al., 2017; Rocchini et al., 2018a; Rocchini et al., 2018b; Torresani et al., 2019). Here, we use RaoQ to calculate γSD (Rao, 1982; Ricotta and Marignani, 2007), which equals the total spectral dissimilarity between all plants in the region of interest. We can then calculate γSD at a specific time t (γSD$_t$) in the region of interest. Thereby we i) assume that the dissimilarity between plants is calculated from the mean dissimilarity of spectral features (e.g., reflectance of specific band or standardized vegetation indices, Botta-Dukát, 2005), ii) use Euclidean distance between spectral features to calculate dissimilarity, and iii) assume that all communities and/or plants are equally important. These assumptions and the fact that the average of the squared pairwise differences of a random variable equals twice the variance of that variable (Champely and Chessel, 2002) reduces RaoQ to a spectral variance calculation between plant individuals (Eq. (1), Appendix S1 for a proof):
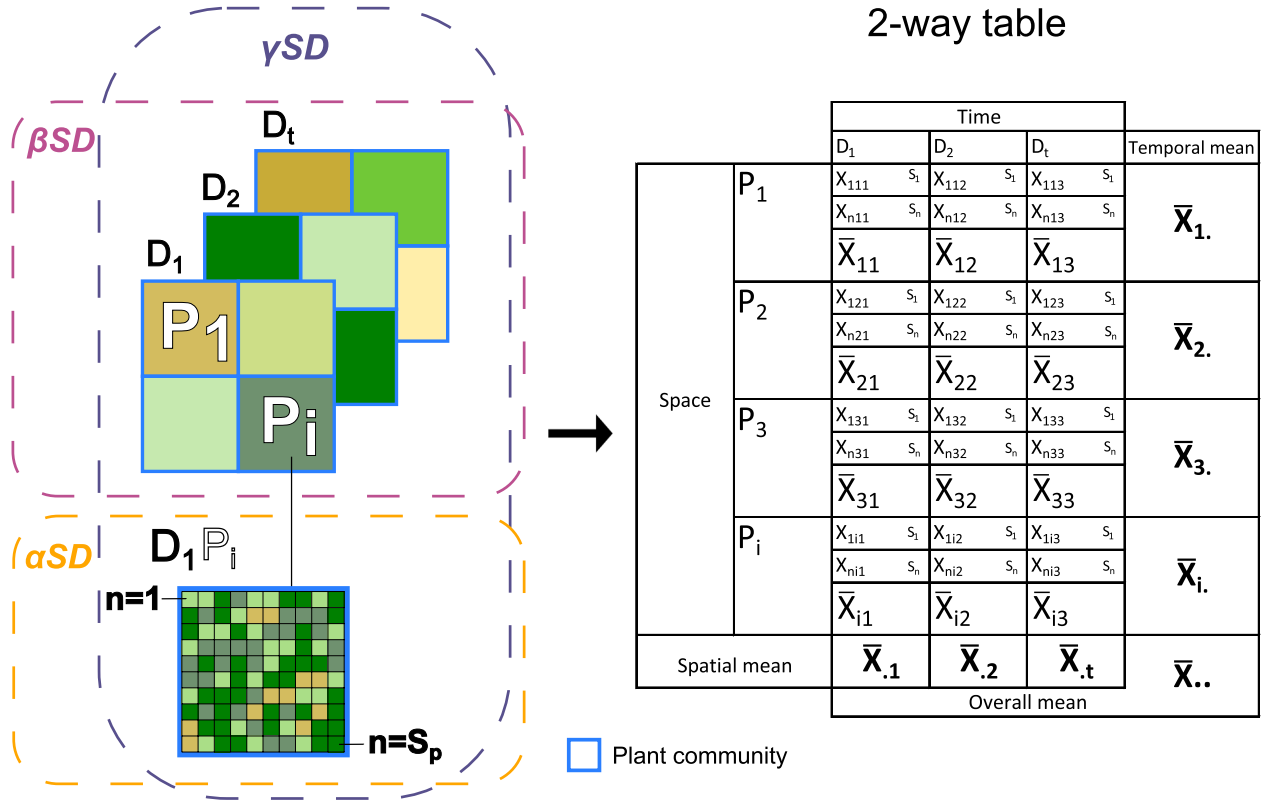
2-way table

Fig. 1. Each pixel or aggregation of pixels represents a plant community P_i with a community mean ($\bar{X}_{it}$) of a variable X (e.g., vegetation index, the reflectance at a certain wavelength or trait). In an ecosystem where an individual plant n matches or is larger than the pixel size (e.g., forests with a data resolution of a couple of meters), communities consist of an aggregation of S_p plant individuals and the community mean of X is calculated from the individual values (X_{nit}). Otherwise, when the pixel size matches the community size (e.g., grasslands with a data resolution of several meters), $\bar{X}_{it}$ is directly derived from remotely sensed values. In this case, only βSD can be derived. Adding temporal information from multiple datasets D in time results in a 2-way design with two explanatory variables (i.e., space and time), each consisting of different categories (i.e., communities and datasets, respectively), that can be studied with a two-way ANOVA, in conjunction with the response variable X.

$$\gamma SD_t = \frac{1}{NS} \sum_{k=1}^{N} \sum_{n=1}^{S} (X_{ntk} - \bar{X}_{.tk})^2 \quad (1)$$

where S is the number of plants in the area of interest, X_{ntk} is the spectral feature value k of the nth individual at time t, N is the number of spectral features and $\bar{X}_{.tk}$ is the mean value of spectral feature k across all individuals in the area of interest at time t. Apart from division by the number of observations (i.e., number of plants), the proposed index is equal to the spectral variance proposed by Laliberté et al. (2020).

2.2. Implementation of spectral diversity in time

So far, only γ spectral diversity in space at a specific time t (i.e., γSD_t) have been considered. Thus, in a next step we calculated γSD by adding the temporal variance of spectral features to Eq. (1), similar to what Chalmandrier et al. (2015) did with a multiplicative framework using Chao's index applied to functional and phylogenetic data. γSD represents the total dissimilarity in spectral information between individuals regardless of their space and time allocation (Eq. (2)).

$$\gamma SD = \frac{1}{NDS} \sum_{k=1}^{N} \sum_{t=1}^{D} \sum_{n=1}^{S} (X_{ntk} - \bar{X}_{..k})^2 \quad (2)$$

where D is the number of images in time, X_{ntk} is the value of spectral feature k of the nth individual at time t and $\bar{X}_{..k}$ is the mean value of spectral feature k across all individuals and images in time in the region of interest. Furthermore, γSD can be calculated if each single γSD_t is known; the total variance (i.e., γSD) is the pooled variance from mono-

temporal datasets (i.e., γSD_t, Rudmin, 2010).

2.3. Spatio-temporal components of γSD

Previous studies partitioned γSD, calculated as the sum of squares (SS), into different spatial components, i.e., αSD and βSD, analogous to an ANOVA (Laliberté et al., 2020). We propose calculating γSD as the spectral variance (Eq. (2)), which equals the average of the total sum of square (SS_{TOT} divided by the number of observations). ANOVA partitions SS_{TOT} into one component (βSD) capturing the variability between group means (e.g., communities), and the variability within a group (e. g., a community) into another component (αSD, Pavoine and Dolédec, 2005). In general, partitioning the SS_{TOT} allows the allocation of the overall variance of a dataset to different sources of variability in an additive manner (de Bello et al., 2011). Here, for the first time an extension of the SS partition to spectral data with a two-way ANOVA was applied, examining the influence of two different categorical independent variables (factors) on a continuous dependent variable. The factors consist of different categories. The combination of two categories belonging to different factors represents a group (e.g., community i at time t). The SS_{TOT} (Eq. (3)) is partitioned into the SS of the two factors SS_T and SS_S, and their interaction (SS_{TS}), as well as the within-group component (SS_W; Nayak, 1986; Pavoine, 2012). The sum of SS_T, SS_S and SS_{TS} equals the between-group SS (SS_B).

$$SS_{TOT} = SS_w + \overbrace{SS_S + SS_T + SS_{TS}}^{SS_B} \quad (3)$$

Here, the two factors of the two-way ANOVA are space and time with different categories, i.e., different plant communities and dates (Fig. 1).

The SS_{TOT} divided by the number of observations ($N * D * S$) equals γSD, and the categories of the two factors are composed of P communities and D repeated measurements in time (Eq. (4)). A group consists of a community with S_p plants at a certain point in time t (Eq. (4)):

$$\gamma SD = \frac{1}{N\,D\,S} \overbrace{\sum_{k=1}^{N} \sum_{t=1}^{D} \sum_{n=1}^{S} \left(X_{ntk} - \overline{X}_{..k} \right)^2}^{SS_{TOT}} = \frac{1}{N\,D\,S} \overbrace{\sum_{k=1}^{N} \sum_{t=1}^{D} \sum_{i=1}^{P} \sum_{n=1}^{S_p} \left(X_{nitk} - \overline{X}_{itk} \right)^2}^{SS_W} + \frac{1}{N\,D\,S} S_p \overbrace{\sum_{k=1}^{N} \sum_{t=1}^{D} \sum_{i=1}^{P} \left(\overline{X}_{itk} - \overline{X}_{..k} \right)^2}^{SS_B} \tag{4}$$

where X_{nitk}, is the value of spectral feature k of the nth individual of the ith community at time t and $\overline{X}_{itk}$ is the mean value of spectral feature k of the ith community and time t.

The within-group component SS_W divided by the number of observations corresponds to the average αSD (Eq. (4)), i.e., the mean spectral variance over all communities and timesteps. αSD may be quantified for datasets with high spatial resolution, where a pixel may represent an individual plant. In contrast to a mono-temporal approach, αSD is calculated as an average over multiple temporal datasets, yielding a more robust representation of the community diversity.

The between-group component SS_B divided by the number of observations represents βSD (Eqs. (4) and (5)). βSD is the variance of between-community mean spectral features over space and time and can be partitioned into the components for space (βSD_S), time (βSD_T) and their interaction (βSD_{TS}; Fig. 2, Eq. (5)).

$$\beta SD = \frac{1}{N\,D\,P} \sum_{k=1}^{N} \sum_{t=1}^{D} \sum_{i=1}^{P} \left(\overline{X}_{itk} - \overline{X}_{..k} \right)^2 = \overbrace{\frac{1}{NP} \sum_{k=1}^{N} \sum_{i=1}^{P} \left(\overline{X}_{i.k} - \overline{X}_{..k} \right)^2}^{\beta SD_S = SS_S/(NDS)} + \overbrace{\frac{1}{ND} \sum_{k=1}^{N} \sum_{t=1}^{D} \left(\overline{X}_{.tk} - \overline{X}_{..k} \right)^2}^{\beta SD_T = SS_T/(NDS)} + \overbrace{\frac{1}{NDP} \sum_{k=1}^{N} \sum_{t=1}^{D} \sum_{i=1}^{P} \left(\overline{X}_{itk} - \overline{X}_{i.k} - \overline{X}_{.tk} + \overline{X}_{..k} \right)^2}^{\beta SD_{TS} = SS_{TS}/(NDS)} \tag{5}$$
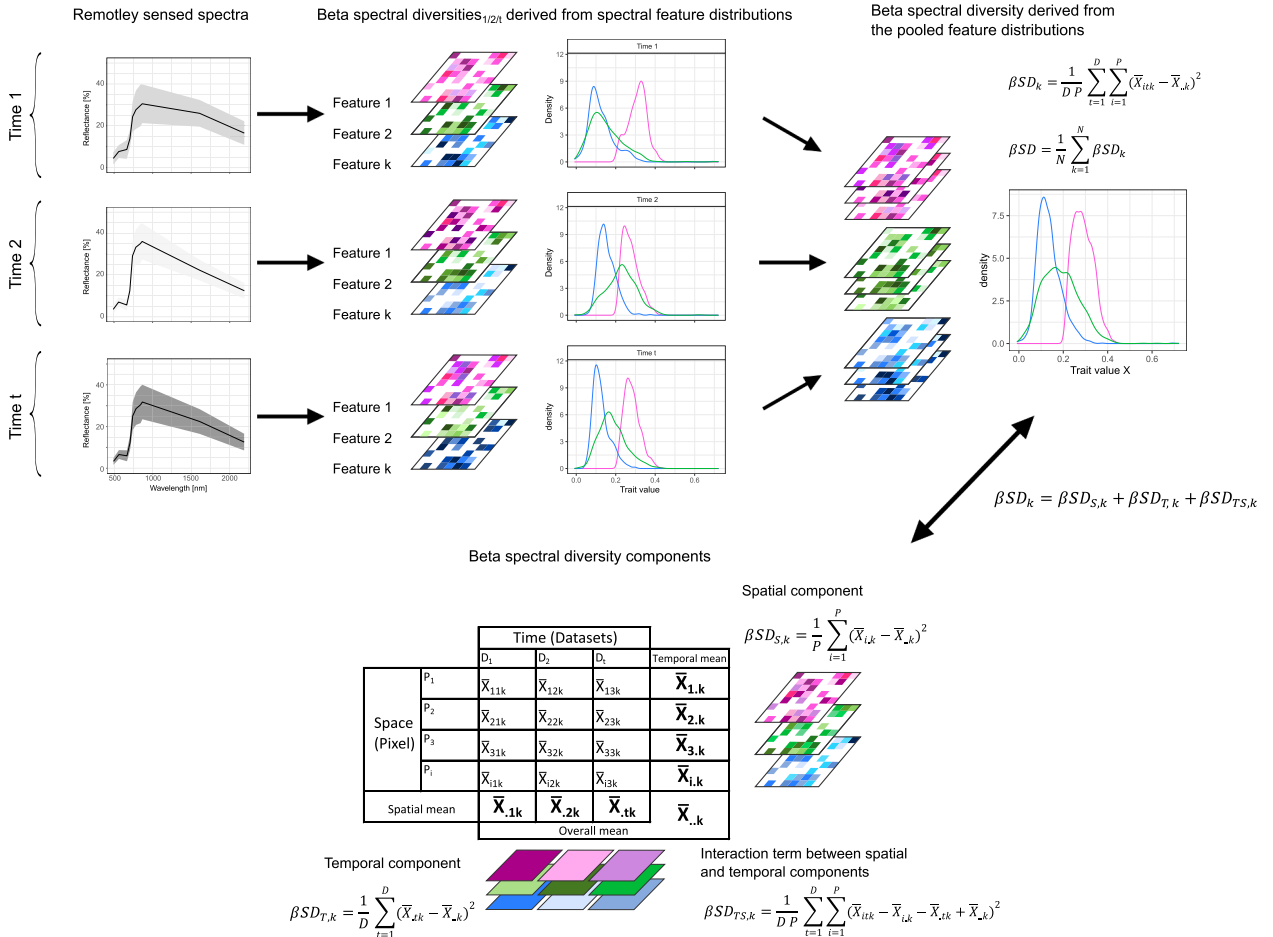

Fig. 2. Proposed approach for calculating β spectral diversity (βSD) of a region of interest, where a pixel or aggregation of pixels corresponds to a plant community P_i. Community mean spectral features for each dataset in time $\overline{X}_{itk}$ are derived from the measured reflectance spectra. βSD equals the variance of the community spectral features over space and time, which corresponds to the pooled spectral feature variance from the single datasets in time. From the partitioning similar to a two-way ANOVA of γSD (Eqs. (4) and (5)) three components of βSD emerge: βSD$_S$ (spatial), βSD$_T$ (temporal), and βSD$_{TS}$ (interaction term).
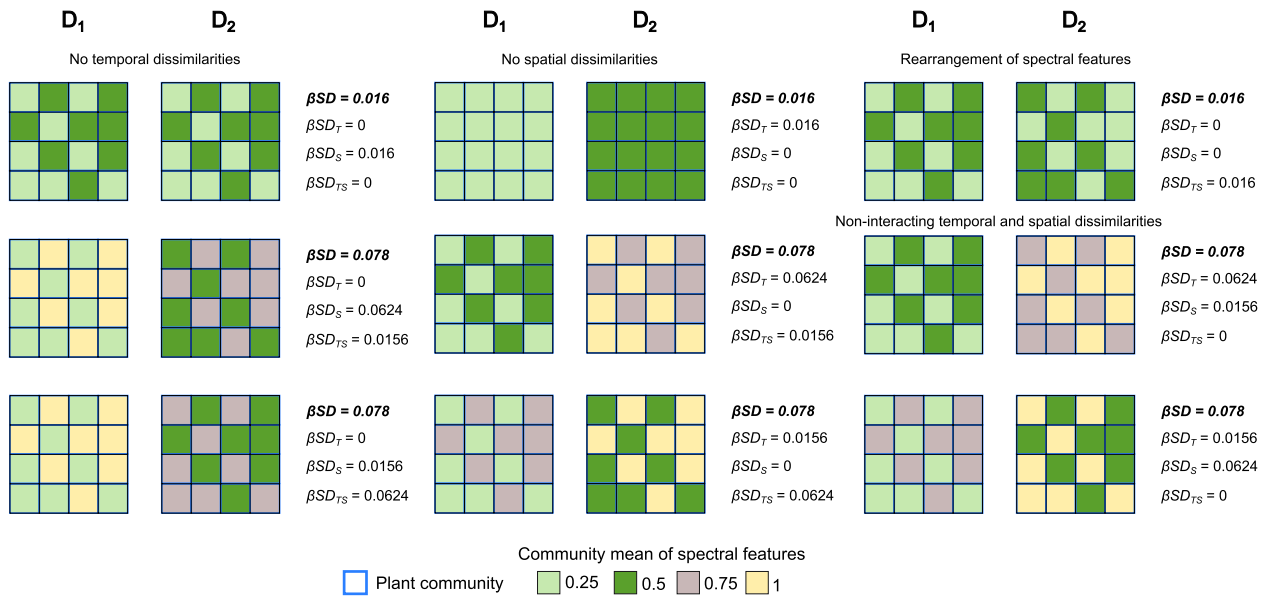
Fig. 3. Beta spectral diversity (βSD) and its components, i.e., βSD$_T$ (temporal), βSD$_S$ (spatial), and βSD$_{TS}$ (interaction term), calculated for simulated and simplified landscapes, consisting of 16 communities. Each community can display four possible community mean spectral features (0.25, 0.5, 0.75, 1) over two time periods D$_1$ and D$_2$. βSD$_S$ equals zero when no spatial or/and temporal dissimilarities between communities or no-interacting spatial and temporal spectral feature dissimilarities exist. The case where βSD$_{TS}$ equals zero indicates that there is an identical dissimilarity of spectral features across space and time between communities. βSD$_{TS}$ equals βSD (i.e., βSD$_S$ = βSD$_T$ = 0) when there is a rearrangement of spectral features between communities in time. It is possible to have a situation where βSD$_S$ or βSD$_T$ is zero, while βSD$_{TS}$ is not zero. This is the case when there is a spatial or temporal dissimilarity between communities; however, if averaged respectively over time or space, the spectral feature dissimilarities are zero.

where $\bar{X}_{i.k}$ is the mean value in time of spectral feature k of the ith community and $\bar{X}_{.tk}$ is the mean value in space of spectral feature k of the tth dataset and $S_p/S = 1/P$.

βSD$_S$ quantifies the diversity between communities after averaging their temporal variability. When using a mono-temporal dataset, βSD$_S$ is the only term that is not zero (βSD = βSD$_S$ for D = 1). When using a multi-temporal dataset βSD$_T$ quantifies the change in diversity between mono-temporal datasets, irrespective of the spatial patterns of diversity (i.e., averaging over communities). βSD$_{TS}$ can be used to quantify differences in spectral features between communities, which are not quantified by βSD$_S$ and βSD$_T$ (Fig. 3). βSD$_{TS}$ delivers additional information, because βSD$_S$ and βSD$_T$ are averaged out at larger spatial or temporal scales.

To summarize, γSD equals the average of αSD in space and time plus the three components of βSD (Eq. (6)).

$$\gamma SD = \overline{\alpha SD} + \overbrace{\beta SD_S + \beta SD_T + \beta SD_{TS}}^{\beta SD} \qquad (6)$$

To calculate αSD a spectral feature per individual plant (X_{ntk}) is required, while for βSD only the community mean spectral features for each dataset in time $\bar{X}_{itk}$ is needed.

3. Calculating βSD from spatio-temporal Sentinel-2 satellite data: A case study

To demonstrate how our new methodological approach works and to highlight the advantage of calculating spatio-temporal spectral diversity we conducted a case study using Sentinel-2 satellite data. Sentinel-2 data for an approximately 1300 km^2 area of south-eastern Switzerland (latitude 46°34′ to 46°54′N, longitude 9°58′ to 10°25′E, Figure Appendix S2.1a) were obtained. This area contains several grassland ecosystems under different management regimes (Appendix S2 and Rossi et al., 2020 for a detailed description of the study area). Detailed data processing procedures for the Sentinel-2 data are provided in Appendix S3.

A pixel size of 10 × 10 m was used. Hence, based on our earlier definition, a pixel represents a grassland community, and spectral features of a pixel are representative of the community mean ($\bar{X}_{itk}$). The coarse spatial resolution of the Sentinel-2 data does not allow a direct quantification of αSD and γSD in grasslands (see explanation above), thus, we specifically calculated βSD and its components.

The two-way ANOVA partitioning requires a balanced design, i.e., the same number of individuals per community. We therefore assumed that each grassland community (i.e., a pixel) contained the same number of individual plants. βSD based on pixel values ($\bar{X}_{itk}$) was calculated of three spectral features, i.e., three vegetation indices (TGI, MTCI, CAI, Appendix S4), obtained from ten temporal Sentinel-2 datasets that covered the entire growing season (Table 1).

3.1. βSD and its components for different grassland management types

We calculated βSD and its components, i.e., time, space and their interaction (Eq. (5)) for four grassland management types separately; namely, grassland that was 1) mown and fertilized multiple times a year with organic or mineral fertilizer (henceforth referred to as "intensive

Table 1

List of Sentinel-2 datasets used in this study, sorted by growing degree days (GDD). All images or composite products show low cloud cover for the study area (<20%). DOY = day of year (Appendix S3 for details).

Acquisition date	Sensor	DOY	GDD [°C-days]	Acquisition year
27 May	Sentinel-2A	147	53	2017
16 June	Sentinel-2B	167	195	2018
26 June	Sentinel-2A	177	287	2017
06 July and 03 July	Sentinel-2A	187	343	2017
16 July	Sentinel-2A	197	419	2017
31 July and 26 July	Sentinel-2A and 2B	212	516	2018
15 August	Sentinel-2A	227	646	2017
27 and 20 August	Sentinel-2A	239	736	2018
09 September	Sentinel-2A	252	797	2018
14 October	Sentinel-2A	287	811	2017

meadows"), 2) mown with either no fertilization or slightly fertilized (once per year or every two years with organic fertilizer; "extensive meadows"), 3) protected and not managed (Swiss National Park SNP, "protected grassland"), and 4) summer grazing by cattle and/or sheep ("summer pasture"; Figure Appendix S2.1b). Mowing takes place between mid-June and mid-September in all meadows, but the exact timing depends on the location and type of meadow. Wild ungulates follow high-quality forage at the upper edge of spring green-up in the protected areas and stay within the SNP borders until the end of the hunting season (beginning of October; Rempfler, 2017). Livestock graze on alpine pastures for roughly three months, from mid-June to mid-September, with spatial constraints established by shepherds moving the animals from one grazing paddock to another. All available grassland pixels (i.e., communities) over the entire study area belonging to one of the four management types and the magnitude, as well as the contribution (in %) of the different spatial and temporal components to βSD of each management type were reported. We assumed that management events (e.g., mowing and grazing) and phenology alter the spectral response of a community (Wellmann et al., 2018). Thus, a particular community composition of plants, which for its part is stable in time, is characterized by multiple spectral responses in time. The differences between spectral responses in space and time are responsible for βSD and most likely reflect the diversity between communities in terms of species composition.

We found that the spatio-temporal βSD, calculated following our proposed approach, varied between management types across the study area (Fig. 4). Substantial differences were found in the magnitude and contribution of the different components (in %) to βSD between the management types (Fig. 4). Protected grasslands had the highest (59%) spatial component βSD$_S$, being responsible for an overall high βSD (Fig. 4). In contrast, when averaged over time, both extensive and intensive meadows had low spatial variances in spectral features, i.e., lowest βSD$_S$ values.

The temporal component βSD$_T$ was highest for extensive meadows and summer pastures (Fig. 4). In particular the datasets obtained late (GDD = 811) and early (GDD = 53) in the growing season differed strongly from the other datasets (Appendix S4.1) and contributed most to βSD (Appendix S6). Phenological differences in spectral features increase βSD$_T$ and therefore βSD. In contrary, management events (e.g., mowing) that occur heterogeneously in space and time keep the average spectral features in space almost even over time, reducing βSD$_T$.

In the case of heterogeneous management in space and time, a rearrangement of spectral features occurs (example in Fig. 3), increasing βSD$_{TS}$. Therefore, it is not a surprise that βSD$_{TS}$ was highest in both meadow types experiencing mowing (Fig. 4). In intensive meadows, βSD$_{TS}$ contributed most (63%) to the high βSD value, indicating that communities changed more in spectral features than expected from the averaged temporal trend over the entire study area (βSD$_T$). This indicates potential for including βSD$_{TS}$ as a spatio-temporal component in the differentiation between communities. Although βSD$_{TS}$ is sensitive to the diversification of management practices, spatio-temporal variations could potentially lead to an overestimation of taxonomic or functional β diversity through βSD in managed grasslands. The extent to which heterogeneity of management in space and time increases biodiversity is debatable (Socolar et al., 2016). Nevertheless, compared to the highest mono-temporal βSD$_{t|D=1}$ (D = 1 Eq. (1); Appendix S5), spatio-temporal βSD mitigates the effect of high spectral variance occurring just once per growing season due to an even spatial distribution of mown and unmown meadows. The unmown areas could be mown just a couple of days later. The spectral variance captured at an individual date is therefore most likely not representative of differences between plant communities, since mowing date differences of a few days will not result in a diversified plant community composition.

Although spatio-temporal βSD seems to offer a more consistent representation of biodiversity compared to mono-temporal spectral variance (βSD$_{t|D=1}$), quantifying the overall value of βSD could be of marginal interest for an ecological application. Quantifying the contribution of individual communities to βSD is, however, of much greater interest. Plant communities can contribute to βSD to varying degrees. Being able to correctly identify unique communities in an ecosystem is of great value for nature conservation. Using our new methodological approach, spatial–temporal dissimilarities between communities can increase (e.g., unique spectral values in time and space) or decrease (e. g., similar spectral values in time and space) the contribution of a community to βSD. The following considerations seek to demonstrate that our proposed spatio-temporal approach to calculate βSD improved the estimation of the community contributions to taxonomic β diversity.

3.2. Community contributions to βSD: Comparing mono-temporal to the proposed spatio-temporal approach

A main advantage of the proposed methodological approach is its ability to assign the overall βSD to different sources of variability, e.g., the three components space, time and their interaction. Furthermore, βSD may be partitioned into the contributions of specific communities as done by Laliberté et al. (2020) for a single dataset in time, which we here refer to as the community contribution to βSD of the ith community at time t (CCβSD$_{i,t|D=1}$). We compared community contribution to βSD calculated with our spatio-temporal approach, i.e., the contribution in space and time of the ith community (CCβSD$_i$, Eq. (7)), to a reference contribution to β diversity measured from *in-situ* plant surveys. Similarly, community contribution to βSD at a specific and thus different stage of the growing season (i.e., from a mono-temporal dataset, Eq. (7) with D = 1 and βSD = βSD$_{t|D=1}$) was compared with the *in-situ* reference. In doing so, only spatial dissimilarities between communities were considered.

$$CC\beta SD_i = \frac{1}{\beta SD \, NDP} \sum_{k=1}^{N} \sum_{t=1}^{D} \left(\bar{X}_{itk} - \bar{X}_{..k} \right)^2 \qquad (7)$$

We calculated βSD on 38 locations (i.e., pixels) distributed across the study area (Appendix Fig. S2.1), independently of the management type (βSD$_{N=38}$). Each of these 38 pixels corresponds to the location of an *in-situ* reference plot and was 10 × 10 m in size. The plots were chosen to be located in a homogeneous area (i.e., same management type, high fractional vegetation cover) of at least 1 ha to avoid edge effects in the remotely sensed data. For each pixel, we calculated the community contribution to βSD$_{N=38}$ for the spatio-temporal dataset (CCβSD$_i$, Eq.
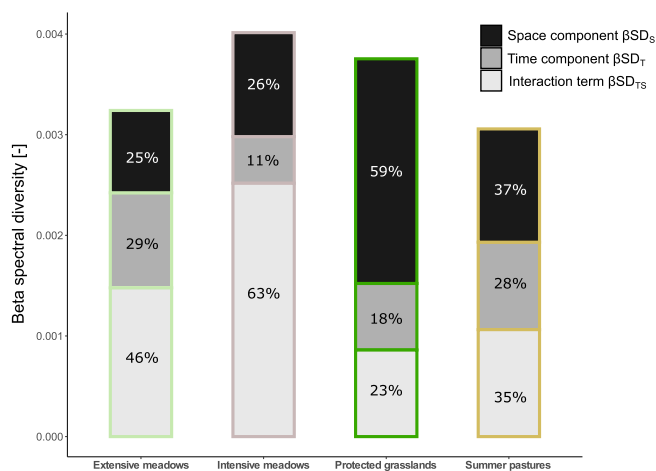

Fig. 4. Barplots representing β spectral diversity (βSD) divided by components (Eq. (5)) in different grassland management types (i.e., extensively used meadows, intensively used meadows, protected grasslands, summer pastures). The contributions percentage of space, time and their interaction to βSD spectral diversity are reported.

(7)) and for each of the mono-temporal datasets ($CC\beta SD_{i,t|D=1}$).

The *in-situ* plant surveys were conducted during summer 2016 and 2017 along 10 m-long transects in each of the 38 reference plots. We calculated the community contribution of each plot to taxonomic β diversity ($CC\beta D_i$; Legendre et al., 2013). In this case, β diversity was estimated by the Bray–Curtis dissimilarity (function beta.div, package adespatial *v0.3–10* in R) using species abundance data (Appendix S8), as the Euclidean distance is not appropriate for the analysis of community composition data (Legendre et al., 2013).

To quantify the degree of correlation between the *in-situ* measured $CC\beta D_i$ and the remotely sensed $CC\beta SD_i$ and $CC\beta SD_{i,t|D=1}$, the Spearman correlation coefficient (ρ) and the root mean square error (RMSE) were used.

We found that the proposed spatio-temporal approach was very effective in estimating the measured local taxonomic contribution to β diversity (ρ = 0.51, p = 0.0013, RMSE = 0.011, n = 38, Fig. 5a). More precisely, we were able to reduce the RMSE by 48% (RMSE from 0.021 to 0.011) when accounting for spatio-temporal dissimilarities between communities over the entire growing season compared to the best mono-temporal dataset (Fig. 5). No significant correlation between remotely sensed $CC\beta SD_{i,t|D=1}$ and locally measured $CC\beta D_i$ was found for six of the 10 mono-temporal datasets (Fig. 5b, p > 0.05). These results together with the high variability observed between mono-temporal spectral variances (Figure Appendix S5.1) suggest that spectral dissimilarities calculated over both space and time (in contrast to dissimilarities over space at a single point in time) offer a better representation of differences between communities experiencing management types and distributed over a large elevation gradient inducing high temporal phenological variation.

4. Discussion

In this study we developed a new methodological approach which extended RaoQ to include both spatial and temporal spectral variations of remotely sensed data. RaoQ can be used to partition γSD, the spectral diversity of a region, into αSD (within community) and βSD (between community) components via a two-way ANOVA when using multi-temporal data. Partitioning of γSD in space and time can help to reveal the scale and extent of a spectral feature, trait convergence and divergence (de Bello et al., 2009) and allows βSD to be calculated independently as done in the study case. Thereby, we included an interaction term between temporal and spatial βSD, unique for a remote sensing application, which allowed the quantification of differences in plant communities between two individual remote sensing datasets obtained at different times. By adding this spatio-temporal perspective, our approach can be seen as an extension to the spectral diversity approach proposed by Laliberté et al. (2020).

4.1. βSD and its components

It is assumed that variation in spectral reflectance is associated with differences in plant traits. Plant traits indicate how plants exploit resources and interact with one another (Díaz et al., 2016; Garnier and Navas, 2012; Wright et al., 2004). Spectral diversity may therefore originate from interactions among co-occurring plants, e.g., by resource partitioning (Schoener, 1974). The partitioning of resources may change in time as suggested by the theory of temporal variability of the niche (Loreau, 2000). The quantification of βSD_T and βSD_{TS} is in line with this niche concept, which states that temporal niche separation can be estimated by the variance of plant variables in time (i.e., traits and phenology; Kearney et al., 2010; Terradas et al., 2009). Furthermore, βSD_T and βSD_{TS} are compatible with a metric-based measurement of phenology (Yan et al., 2015), i.e., the differences in phenology as pairwise distances between species or communities (Sapijanskas et al., 2014). Capturing variation on spectral features across time may therefore highlight distinct plant strategies, which determine species

distribution patterns and their function (Huang et al., 2019; Pesaresi et al., 2020; Schwinning et al., 2013).

If spectral variation in time may highlight the temporal niche separation, spectral variation in space (βSD_S) reflects the environmental heterogeneity, i.e., the number of available niches (Rocchini et al., 2010). The calculation of βSD_S is consistent with the calculation of spectral variance proposed by Laliberté et al. (2020), or RaoQ with spectral features by Rocchini et al. (2018b). The difference is that βSD_S is calculated after averaging the spectral features over multiple datasets, yielding a more robust spatial diversity quantification.

Our results suggest that the total βSD is likely related to divergence in spectral feature composition resulting from management type or environmental properties (e.g., elevation). Management, such as mowing, impacts βSD by altering plant traits (Bouchet et al., 2017; McIntyre, 2008; Pakeman, 2011), or in some systems by accelerating flowering (Ollerton and Lack, 1992). In particular, heterogeneous mowing or grazing in space and time strongly promotes different life-history traits (e.g., time of flowering) and plant structural properties, i.e., short- vs. tall-growing plants (Johansen et al., 2019; Klimešová et al., 2010; Schütz et al., 2006). In grasslands with low anthropogenic disturbance, traits and therefore spectral features reflect conservative resource allocation strategies of plants (Louault et al., 2005; Peco et al., 2005; Rossi et al., 2020). Like traits, species composition is strongly dependent on the management type (Moog et al., 2002). Essentially, communities with similar management or/and environmental properties usually contain similar species and trait compositions. Compositional differences will become larger with increasing differences in management. As a result, management differences drive β diversity (Socolar et al., 2016). As the proposed βSD metric is sensitive to management differences in space and time, it is suitable for taxonomic or functional β diversity estimations.

In comparison to Rossi et al. (2020), where a mono-temporal approach was used, differences between certain management types (i. e., protected grasslands versus summer pasture) were more pronounced when accounting for spatio-temporal dissimilarities between communities. These results reflect the enhanced classification of different ecosystems and management types using multi-temporal remote sensing as reported by previous studies (Alcantara et al., 2012; Immitzer et al., 2019; Mousivand et al., 2015; Vuolo et al., 2018). However, the degree to which temporal variation in spectral features due to management reflects taxonomic or functional β diversity needs further investigation. In particular, heavily managed systems display high spatio-temporal variations in spectral features, which could inflate biodiversity estimates (Gholizadeh et al., 2020). The method proposed here allows spatial and temporal variation in βSD to be disentangled, and the increasing availability of multi-temporal datasets, this provides an opportunity to conduct these studies.

4.2. Mono- versus multi-temporal approach to quantify community contributions to βSD

Our approach further allows the partitioning of βSD into the contributions of individual plant communities (CCβSD). We consider this as one of the major strengths of the presented approach. Such an approach could, for example, help conservationists identify areas of particular importance for biodiversity.

The approach, which accounts for spatio-temporal dissimilarities, accurately predicted community contributions to taxonomic β diversity. In fact, we showed that the RMSE can be reduced by up to 74% (RMSE from 0.043 to 0.011, Fig. 5) when estimating *in-situ* measured community contributions to taxonomic β diversity (CCβD) from space by using multi-temporal datasets that cover the entire growing season compared to using mono-temporal datasets. Accounting for spatio-temporal dissimilarities between communities was crucial, since spatial dissimilarities between communities calculated by averaging the datasets over time only weakly predicted CCβSD (Appendix S7).

A spatio-temporal approach efficiently mitigates negative effects

a)

b)
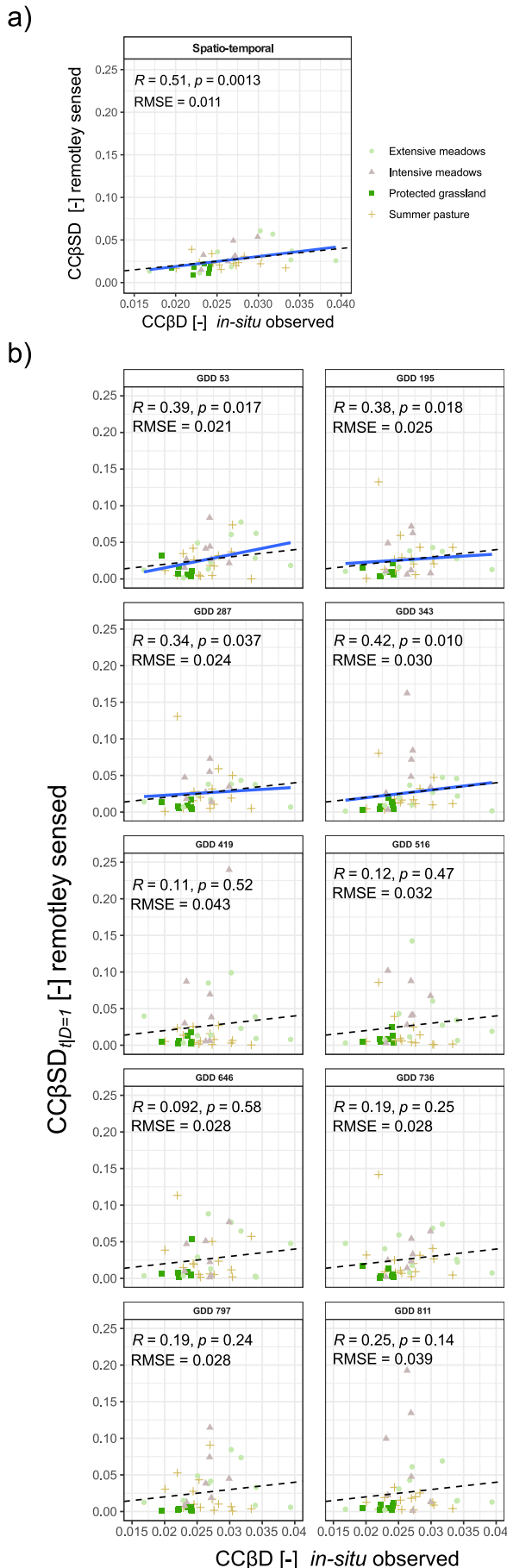
Fig. 5. a) Relationship between remotely sensed community contributions to β spectral diversity for our newly proposed approach (CCβSD$_i$), accounting for spatio-temporal spectral dissimilarities, and the contribution of the 38 field plots to β diversity calculated from species abundance (CCβD$_i$). b) Relationship between the remotely sensed community (i.e., plot) contribution to β spectral diversity for each mono-temporal dataset (CCβSD$_{i,t|D=1}$), accounting only for spatial dissimilarities, and CCβD$_i$. ρ = Spearman correlation, RMSE = root mean square error, GDD = growing degree days; the dashed line represents the 1:1 line. Linear regression lines were plotted only for significant relations (p < 0.05).

observed when using mono-temporal datasets, such as i) sub-optimal temporal windows not capturing key phenological indicators (i.e., flowering or end of season; Cole et al., 2014; Mannel and Price, 2012), or ii) the inability to compare the spectral signature of plants at the same phenological or management stage in large study areas. Finally, building on multiple datasets of differing angular sampling (i.e., solar zenith, azimuth angle) may offer a source of complementary reflectance information (Huber et al., 2010; Mousivand et al., 2015).

4.3. Methodological considerations

4.3.1. Spectral features

Our approach to calculating spectral diversity is compatible with a range of input data, e.g., original spectral bands, a set of vegetation indices, as well as spectral or trait features extracted via principal component analysis. The selected spectral features depend on the research question and available data. The determination of features that most effectively highlight differences between species and/or communities at a certain stage of the growing season is of importance for the estimation of biodiversity. Thereby, the composition of a community is a key factor. Species or communities displaying similar traits may not be distinguishable spectrally. The problem is magnified when only a low number of spectral features – or features that are not representative of species differences – are used (Rocchini, 2007). In contrast, species with highly contrasting evolutionary histories, genetic backgrounds and/or environmental conditions, for example species belonging to different plant functional types (Schweiger et al., 2017), are distinguishable with a much higher success rate (Bahrami and Mobasheri, 2020). Depending on the feature type, a standardization (as proposed in the study case) should be applied to avoid the disproportionate contribution of certain features. Moreover, our method is not limited to remotely sensed data, but could also be applied to multi-temporal *in-situ* plant trait data (Kattge et al., 2020).

4.3.2. Number of datasets

Plant trait studies recommend that traits are sampled at least three times during the growing season (early, middle, late; Fajardo and Siefert, 2016; McKown et al., 2013), allowing sufficient trait variation to be captured in order to properly characterize species and communities. This recommendation is in line with our results in which spectral datasets from early, peak and late in the growing season captured a high percentage of variance. However, to better distinguish between communities with different species composition, spectral signatures in time covering phenological variations as well as management events are needed (Dudley et al., 2015; Pasquarella et al., 2018).

4.3.3. Spatial resolution

The availability of higher spatial resolution data than those used in our case study (e.g., drone data) would allow the calculation of αSD and thus γSD in grasslands. For data with coarser spatial resolution than that provided by Sentinel-2, e.g., from the Landsat and MODIS missions, we see potential for using our approach to quantify βSD. However, for plant ecological applications, plant communities or individual species need to be represented by "homogeneous" pixels (i.e., spectral signal) in terms of

(caption on next column)

vegetation cover and management types. Otherwise, spectral unmixing techniques may be needed to extract a pure spectral signal (Malenovský et al., 2007). Spatial sampling units, such as those provided by MODIS, are often only partly covered by vegetation and therefore most likely violate the underlying assumption of equally distributed individual plants. An uneven spectral representation of individuals per community also occurs when shadows or soil fractions are masked out within a community. In such cases, SS_S and SS_T overlap (i.e., space and time are not independent of each other), and the proposed partitioning would not equate to γSD ($SS_S + SS_T + SS_{TS} + SS_W \neq S_{TOT}$ in Eq. (3)). Similarly, with an unbalanced design, the partitioning into α and β components, as proposed in our approach, may lead to average αSD exceeding γSD, as demonstrated by de Bello et al. (2010). To prevent this, the contribution of αSD within each community can be weighted by a factor that includes the contribution of individuals to γSD (Villéger and Mouillot, 2008). In order to partition βSD into its components, different types of adjusted SS exist for an unbalanced ANOVA (Hector et al., 2010). However, an implementation would not be straightforward. Alternatively, a workaround consisting of a rarefaction procedure to standardise the number of pixels per community could be used (Laliberté et al., 2020). Ultimately, if the number of individuals between communities does not differ much, partitioning as proposed in in this study (i.e., without using a workaround or adjusting SS) remains a good approximation (Hector et al., 2010).

4.3.4. Community size

When quantifying spectral diversity, important methodological considerations should include not only the number of individuals per community and the community composition, but also the community size. The size of a community influences how much of γSD can be explained by αSD and βSD. Small communities with a low number of individuals will have a high contribution of βSD and a low contribution of αSD to γSD. Laliberté et al. (2020) found that there is a specific community size above which the relative importance of β versus α components stabilizes. However, this size is most likely dependent on the ecosystem and the available spatial resolution of the remotely sensed datasets. Using an adjusted SS would allow the application of our proposed method to communities with different shapes and sizes, e.g., those derived from image segmentation (sets of pixels, also known as superpixels, Ren and Malik, 2003) or by clustering the region of interest into communities based on environmental variables. In addition, the concepts of α and β diversity were developed for ecological studies with discrete plot data and may be less obvious and discernible on continuous scales as provided by remote sensing data. Finally, as pointed out by other studies, temporal components as well as spatial components of biodiversity can vary with community size (Korhonen et al., 2010; Soininen, 2010). Further research is therefore necessary to investigate the relationship between α and β diversity on the continuous scales provided by remote sensing in space and time.

5. Conclusions

The era of openly available satellite data at a high revisit time and high spectral resolution offers new opportunities for measuring biodiversity from space. In particular, temporal variation in remotely sensed spectral features can cast light on ecological processes, including species coexistence, environmental filtering and ecosystem functioning. Here, a new spatio-temporal approach based on RaoQ that accounts for the dissimilarity in spectral features between plants or communities over space and time was presented. Our approach allows the quantification of βSD in space and time by including differences in phenology and management practices, which is crucial when assessing biodiversity, especially in light of on-going global change. As such, it has the potential to identify communities of unique species composition and therefore high conservation value which could support ecosystem conservation and restoration decision-making processes. The approach is not limited to satellite data, but can be used with multi-temporal datasets collected from platforms carrying flexible spectral imaging devices for small-scale applications, i.e., drones. Although more work is required in understanding the effect of temporal variation of βSD, we believe that the properties of our methodology open up promising avenues for evaluating and testing ecosystem diversity changes across space and time. In addition, increased knowledge about temporal variation of spectral diversity helps to contextualise and compare a wider range of ecological large-scale studies.

Data availability

An R package was built to calculate the proposed β spectral diversity metrics and the contributions of their components from a stack of raster files (R package stdiversity v0.1; https://github.com/RossiBz/stdiversity). The lcd function of the package allows to map the contribution of each pixel in a dataset to β spectral diversity.

CRediT authorship contribution statement

Christian Rossi: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Project administration. **Mathias Kneubühler:** Conceptualization, Validation, Writing - review & editing. **Martin Schütz:** Conceptualization, Writing - review & editing. **Michael E. Schaepman:** Conceptualization, Writing - review & editing, Supervision. **Rudolf M. Haller:** Conceptualization, Funding acquisition. **Anita C. Risch:** Conceptualization, Validation, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108106.

References

Alcantara, C., Kuemmerle, T., Prishchepov, A.V., Radeloff, V.C., 2012. Mapping abandoned agriculture with multi-temporal MODIS satellite data. Remote Sens. Environ. 124, 334–347.

Anderegg, W.R.L., 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. New Phytol. 205 (3), 1008–1014.

Bahrami, M., Mobasheri, M.R., 2020. Plant species determination by coding leaf reflectance spectrum and its derivatives. Eur. J. Rem. Sens. 53 (1), 258–273.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., et al., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471 (7336), 51.

Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Veg. Sci. 16 (5), 533–540.

Bouchet, D.C., Cheptou, P.-O., Munoz, F., Overbeck, G., 2017. Mowing influences community-level variation in resource-use strategies and flowering phenology along an ecological succession on Mediterranean road slopes. Appl. Veg. Sci. 20 (3), 376–387.

Burg, S., Rixen, C., Stöckli, V., Wipf, S., Acosta, A., 2015. Observation bias and its causes in botanical surveys on high-alpine summits. J. Veg. Sci. 26 (1), 191–200.

Cavender-Bares, J., Gamon, J.A., Hobbie, S.E., Madritch, M.D., Meireles, J.E., Schweiger, A.K., Townsend, P.A., 2017. Harnessing plant spectra to integrate the biodiversity sciences across biological and spatial scales. Am. J. Bot. 104 (7), 966–969.

Cawse-Nicholson, K., Townsend, P.A., Schimel, D., Assiri, A.M., Blake, P.L., Buongiorno, M.F., Campbell, P., Carmon, N., Casey, K.A., Correa-Pabón, R.E., Dahlin, K.M., Dashti, H., Dennison, P.E., Dierssen, H., Erickson, A., Fisher, J.B., Frouin, R., Gatebe, C.K., Gholizadeh, H., Gierach, M., Glenn, N.F., Goodman, J.A., Griffith, D.M., Guild, L., Hakkenberg, C.R., Hochberg, E.J., Holmes, T.R.H., Hu, C., Hulley, G., Huemmrich, K.F., Kudela, R.M., Kokaly, R.F., Lee, C.M., Martin, R., Miller, C.E., Moses, W.J., Muller-Karger, F.E., Ortiz, J.D., Otis, D.B., Pahlevan, N., Painter, T.H., Pavlick, R., Poulter, B., Qi, Y.i., Realmuto, V.J., Roberts, D., Schaepman, M.E., Schneider, F.D., Schwandner, F.M., Serbin, S.P., Shiklomanov, A. N., Stavros, E.N., Thompson, D.R., Torres-Perez, J.L., Turpie, K.R., Tzortziou, M., Ustin, S., Yu, Q., Yusup, Y., Zhang, Q., 2021. NASA's surface biology and geology designated observable: a perspective on surface imaging algorithms. Remote Sens. Environ. 257, 112349. https://doi.org/10.1016/j.rse.2021.112349.

Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc. Natl. Acad. Sci. 114 (30), E6089–E6096.

Chalmandrier, L., Münkemüller, T., Devictor, V., Lavergne, S., Thuiller, W., Chisholm, R., 2015. Decomposing changes in phylogenetic and functional diversity over space and time. Methods Ecol. Evol. 6 (1), 109–118.

Champely, S., Chessel, D., 2002. Measuring biological diversity using Euclidean metrics. Environ. Ecol. Stat. 9 (2), 167–177.

Chavana-Bryant, C., Malhi, Y., Wu, J., Asner, G.P., Anastasiou, A., Enquist, B.J., Cosio Caravasi, E.G., Doughty, C.E., Saleska, S.R., Martin, R.E., Gerard, F.F., 2017. Leaf aging of Amazonian canopy trees as revealed by spectral and physiochemical measurements. New Phytol. 214 (3), 1049–1063.

Cole, B., McMorrow, J., Evans, M., 2014. Spectral monitoring of moorland plant phenology to identify a temporal window for hyperspectral remote sensing of peatland. ISPRS J. Photogramm. Remote Sens. 90, 49–58.

Díaz, S., Fargione, J., Chapin, F.S., Tilman, D., 2006. Biodiversity loss threatens human well-being. PLoS Biol. 4 (8), e277. https://doi.org/10.1371/journal. pbio.004027710.1371/journal.pbio.0040277.g00110.1371/journal.pbio.0040277. g00210.1371/journal.pbio.0040277.g00310.1371/journal.pbio.0040277.t001.

Dahlin, K.M., 2016. Spectral diversity area relationships for assessing biodiversity in a wildland–agriculture matrix. Ecol. Appl. 26 (8), 2758–2768.

de Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., Janeček, Š., Lepš, J., 2011. Quantifying the relevance of intraspecific trait variability for functional diversity. Methods Ecol. Evol. 2 (2), 163–174.

de Bello, F., Thuiller, W., Lepš, J., Choler, P., Clément, J.-C., Macek, P., Sebastià, M.-T., Lavorel, S., 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. J. Veg. Sci. 20 (3), 475–486.

de Bello, F., Lavergne, S., Meynard, C.N., Lepš, J., Thuiller, W., 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. J. Veg. Sci., 21, 992–1000.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529 (7585), 167–171.

Dudley, K.L., Dennison, P.E., Roth, K.L., Roberts, D.A., Coates, A.R., 2015. A multi-temporal spectral library approach for mapping vegetation species across spatial and temporal phenological gradients. Remote Sens. Environ. 167, 121–134.

Fajardo, A., Siefert, A., 2016. Phenological variation of leaf functional traits within species. Oecologia 180 (4), 951–959.

Gamon, J.A., Somers, B., Malenovský, Z., Middleton, E.M., Rascher, U., Schaepman, M. E., 2019. Assessing vegetation function with imaging spectroscopy. Surv. Geophys. 40 (3), 489–513.

Garnier, E., Navas, M.-L., 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. Agron. Sustain. Dev. 32 (2), 365–399.

Gering, J.C., Crist, T.O., 2002. The alpha–beta–regional relationship: providing new insights into local–regional patterns of species richness and scale dependence of diversity components. Ecol. Lett. 5 (3), 433–444.

Gholizadeh, H., Gamon, J.A., Townsend, P.A., Zygielbaum, A.I., Helzer, C.J., Hmimina, G.Y., Yu, R., Moore, R.M., Schweiger, A.K., Cavender-Bares, J., 2019. Detecting prairie biodiversity with airborne remote sensing. Remote Sens. Environ., 221(June 2018), 38–49.

Gholizadeh, H., Gamon, J.A., Helzer, C.J., Cavender-Bares, J., 2020. Multi-temporal assessment of grassland α- and β-diversity using hyperspectral imaging. Ecol. Appl. 1–13. https://doi.org/10.1002/eap.2145.

Gómez Giménez, M., de Jong, R., Della Peruta, R., Keller, A., Schaepman, M.E., 2017. Determination of grassland use intensity based on multi-temporal remote sensing data and ecological indicators. Remote Sens. Environ. 198, 126–139.

Gossner, M.M., Lewinsohn, T.M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S.C., Sikorski, J., Wubet, T., et al., 2016. Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540 (7632), 266–269.

Hakkenberg, C.R., Zhu, K., Peet, R.K., Song, C., 2018. Mapping multi-scale vascular plant richness in a forest landscape with integrated Li DAR and hyperspectral remote-sensing. Ecology 99 (2), 474–487.

Hautier, Y., Niklaus, P.A., Hector, A., 2009. Competition for light causes plant biodiversity loss after eutrophication. Science 324 (5927), 636–638.

Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H., Lind, E.M., MacDougall, A.S., Stevens, C.J., Bakker, J.D., et al., 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. Nature 508 (7497), 521–525.

Hector, A., von Felten, S., Schmid, B., 2010. Analysis of variance with unbalanced data: An update for ecology & evolution. J. Anim. Ecol. 79 (2), 308–316.

Homolová, L., Schaepman, M.E., Lamarque, P., Clevers, J.G.P.W., de Bello, F., Thuiller, W., Lavorel, S., 2014. Comparison of remote sensing and plant trait-based modelling to predict ecosystem services in subalpine grasslands. Ecosphere 5 (8), 1–29.

Homolová, L., Malenovský, Z., Clevers, J.G.P.W., García-Santos, G., Schaepman, M.E., 2013. Review of optical-based remote sensing for plant trait mapping. Ecol. Complexity 15, 1–16.

Huang, J., Xue, W., Herben, T., Roxburgh, S., 2019. Temporal niche differentiation among species changes with habitat productivity and light conditions. J. Veg. Sci. 30 (3), 438–447.

Huber, S., Koetz, B., Psomas, A., Kneubuehler, M., Schopfer, J.T., Itten, K.I., Zimmermann, N., 2010. Impact of multiangular information on empirical models to estimate canopy nitrogen concentration in mixed forest. J. Appl. Remote Sens. 4 (1), 43530.

Immitzer, M., Neuwirth, M., Böck, S., Brenner, H., Vuolo, F., Atzberger, C., 2019. Optimal Input Features for Tree Species Classification in Central Europe Based on Multi-Temporal Sentinel-2 Data. Remote Sens. 11 (22), 2599.

Jetz, W., Cavender-Bares, J., Pavlick, R., Schimel, D., Davis, F.W., Asner, G.P., Guralnick, R., Kattge, J., Latimer, A.M., Moorcroft, P., 2016. Monitoring plant functional diversity from space. Nature Plants 2, 16024.

Johansen, L., Westin, A., Wehn, S., Iuga, A., Ivascu, C.M., Kallioniemi, E., Lennartsson, T., 2019. Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes. Global Ecol. Conserv. 18, e00619. https://doi.org/10.1016/j.gecco.2019.e00619.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., et al., 2020. TRY plant trait database – enhanced coverage and open access. Glob. Change Biol. 26 (1), 119–188.

Kearney, M., Simpson, S.J., Raubenheimer, D., Helmuth, B., 2010. Modelling the ecological niche from functional traits. Philos. Trans. Royal Soc. B: Biol. Sci. 365 (1557), 3469–3483.

Khare, S., Latifi, H., Rossi, S., 2019. Forest beta-diversity analysis by remote sensing: How scale and sensors affect the Rao's Q index. Ecol. Ind. 106, 105520. https://doi.org/10.1016/j.ecolind.2019.105520.

Klimešová, J., Janeček, Š., Bartušková, A., Lanta, V., Doležal, J., 2010. How is Regeneration of Plants after Mowing Affected by Shoot Size in Two Species-Rich Meadows with Different Water Supply? Folia Geobotanica 45 (3), 225–238.

Korhonen, J.J., Soininen, J., Hillebrand, H., 2010. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. Ecology 91 (2), 508–517.

Laliberté, E., Schweiger, A.K., Legendre, P., He, F., 2020. Partitioning plant spectral diversity into alpha and beta components. Ecol. Lett. 23 (2), 370–380.

Legendre, P., De Cáceres, M., Morlon, H., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16 (8), 951–963.

Lõhmus, A., Lõhmus, P., Runnel, K., 2018. A simple survey protocol for assessing terrestrial biodiversity in a broad range of ecosystems. PloS One 13 (12), e0208535.

Lopes, M., Fauvel, M., Ouin, A., Girard, S., 2017. Spectro-temporal heterogeneity measures from dense high spatial resolution satellite image time series: Application to grassland species diversity estimation. Remote Sens. 9 (10), 993. https://doi.org/10.3390/rs9100993.

Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91 (1), 3–17.

Louault, F., Pillar, V.D., Aufrère, J., Garnier, E., Soussana, J.-F., 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. J. Veg. Sci. 16 (2), 151–160.

Ma, X., Mahecha, M.D., Migliavacca, M., van der Plas, F., Benavides, R., Ratcliffe, S., Kattge, J., Richter, R., Musavi, T., Baeten, L., Barnoaiea, I., Bohn, F.J., Bouriaud, O.,

Bussotti, F., Coppi, A., Domisch, T., Huth, A., Jaroszewicz, B., Joswig, J., Pabon-Moreno, D.E., Papale, D., Selvi, F., Laurin, G.V., Valladares, F., Reichstein, M., Wirth, C., 2019. Inferring plant functional diversity from space: the potential of Sentinel-2. Remote Sens. Environ. 233, 111368. https://doi.org/10.1016/j.rse.2019.111368.

Malenovský, Z., Bartholomeus, H.M., Acerbi-Junior, F.W., Schopfer, J.T., Painter, T.H., Epema, G.F., Bregt, A.K., 2007. Scaling dimensions in spectroscopy of soil and vegetation. Int. J. Appl. Earth Obs. Geoinf. 9 (2), 137–164.

Mannel, S., Price, M., 2012. Comparing Classification Results of Multi-Seasonal TM against AVIRIS Imagery - Seasonality more Important than Number of Bands. Photogrammetrie - Fernerkundung - Geoinformation 2012 (5), 603–612.

McIntyre, S., 2008. The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. Agric. Ecosyst. Environ. 128 (4), 251–258.

McKown, A.D., Guy, R.D., Azam, M.S., Drewes, E.C., Quamme, L.K., 2013. Seasonality and phenology alter functional leaf traits. Oecologia 172 (3), 653–665.

Meireles, J.E., Cavender-Bares, J., Townsend, P.A., Ustin, S., Gamon, J.A., Schweiger, A. K., Schaepman, M.E., Asner, G.P., Martin, R.E., Singh, A., Schrodt, F., Chlus, A., O'Meara, B.C., 2020. Leaf reflectance spectra capture the evolutionary history of seed plants. New Phytol. 228 (2), 485–493.

Moog, D., Poschlod, P., Kahmen, S., Schreiber, K.-F., 2002. Comparison of species composition between different grassland management treatments after 25 years. Appl. Veg. Sci. 5 (1), 99–106.

Mousivand, A., Menenti, M., Gorte, B., Verhoef, W., 2015. Multi-temporal, multi-sensor retrieval of terrestrial vegetation properties from spectral–directional radiometric data. Remote Sens. Environ. 158, 311–330.

Münkemüller, T., de Bello, F., Meynard, C.N., Gravel, D., Lavergne, S., Mouillot, D., Mouquet, N., Thuiller, W., 2012. From diversity indices to community assembly processes: a test with simulated data. Ecography 35 (5), 468–480.

Nagendra, H., 2001. Using remote sensing to assess biodiversity. Int. J. Remote Sens. 22 (12), 2377–2400.

Nayak, T.K., 1986. An analysis of diversity using Rao's quadratic entropy. Sankhyā: Indian J. Stat. Ser. B 315–330.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., et al., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353 (6296), 288–291.

Oldeland, J., Wesuls, D., Rocchini, D., Schmidt, M., Jürgens, N., 2010. Does using species abundance data improve estimates of species diversity from remotely sensed spectral heterogeneity? Ecol. Ind. 10 (2), 390–396.

Ollerton, J., Lack, A.J., 1992. Flowering phenology: an example of relaxation of natural selection? Trends Ecol. Evol. 7 (8), 274–276.

Ollinger, S.V., 2011. Sources of variability in canopy reflectance and the convergent properties of plants. New Phytol. 189 (2), 375–394.

Pakeman, R.J., 2011. Multivariate identification of plant functional response and effect traits in an agricultural landscape. Ecology 92 (6), 1353–1365.

Pasquarella, V.J., Holden, C.E., Woodcock, C.E., 2018. Improved mapping of forest type using spectral-temporal Landsat features. Remote Sens. Environ. 210, 193–207.

Pavoine, S., 2012. Clarifying and developing analyses of biodiversity: towards a generalisation of current approaches. Methods Ecol. Evol. 3 (3), 509–518.

Pavoine, S., Dolédec, S., 2005. The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. Environ. Ecol. Stat. 12 (2), 125–138.

Peco, B., de Pablos, I., Traba, J., Levassor, C., 2005. The effect of grazing abandonment on species composition and functional traits: the case of dehesa grasslands. Basic Appl. Ecol. 6 (2), 175–183.

Pesaresi, S., Mancini, A., Casavecchia, S., 2020. Recognition and Characterization of Forest Plant Communities through Remote-Sensing NDVI Time Series. Diversity 12 (8), 313.

Pettorelli, N., Schulte to Bühne, H., Tulloch, A., Dubois, G., Macinnis-Ng, C., Queirós, A. M., Keith, D.A., Wegmann, M., Schrodt, F., Stellmes, M., Sonnenschein, R., Geller, G. N., Roy, S., Somers, B., Murray, N., Bland, L., Geijzendorffer, I., Kerr, J.T., Broszeit, S., Leitão, P.J., Duncan, C., El Serafy, G., He, K.S., Blanchard, J.L., Lucas, R., Mairota, P., Webb, T.J., Nicholson, E., Rowcliffe, M., Disney, M., 2018. Satellite remote sensing of ecosystem functions: opportunities, challenges and way forward. Remote Sens. Ecol. Conserv. 4 (2), 71–93.

Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. Theor. Popul Biol. 21 (1), 24–43.

Rempfler, T., 2017. Where do red deer come from and where do they go?. In: 6th Symposium for Research in Protected Areas, pp. 530–539.

Ren, X., Malik, J., 2003. Learning a classification model for segmentation. In: Computer Vision, IEEE International Conference On, 2, 10.

Rich, T.C.G., Woodruff, E.R., 1992. Recording bias in botanical surveys. Watsonia 19 (2), 73–95.

Ricklefs, R., 2008. Disintegration of the ecological community: American Society of Naturalists Sewall Wright award winner address. Am. Nat. 172 (6), 741–750.

Ricotta, C., Marignani, M., 2007. Computing β-diversity with Rao's quadratic entropy: a change of perspective. Divers. Distrib. 13 (2), 237–241.

Rocchini, D., Bacaro, G., Chirici, G., Da Re, D., Feilhauer, H., Foody, G.M., Galluzzi, M., Garzon-Lopez, C.X., Gillespie, T.W., He, K.S., et al., 2018a. Remotely sensed spatial heterogeneity as an exploratory tool for taxonomic and functional diversity study. Ecol. Ind. 85, 983–990.

Rocchini, D., Balkenhol, N., Carter, G.A., Foody, G.M., Gillespie, T.W., He, K.S., Kark, S., Levin, N., Lucas, K., Luoto, M., Nagendra, H., Oldeland, J., Ricotta, C., Southworth, J., Neteler, M., 2010. Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. Ecol. Inf. 5 (5), 318–329.

Rocchini, D., Chiarucci, A., Loiselle, S.A., 2004. Testing the spectral variation hypothesis by using satellite multispectral images. Acta Oecol. 26 (2), 117–120.

Rocchini, D., Luque, S., Pettorelli, N., Bastin, L., Doktor, D., Faedi, N., Feilhauer, H., Féret, J.-B., Foody, G.M., Gavish, Y., et al., 2018b. Measuring β-diversity by remote sensing: A challenge for biodiversity monitoring. Methods Ecol. Evol. 9 (8), 1787–1798.

Rocchini, D., Marcantonio, M., Da Re, D., Chirici, G., Galluzzi, M., Lenoir, J., Ricotta, C., Torresani, M., Ziv, G., 2019. Time-lapsing biodiversity: An open source method for measuring diversity changes by remote sensing. Remote Sens. Environ. 231, 111192. https://doi.org/10.1016/j.rse.2019.05.011.

Rocchini, D., Marcantonio, M., Ricotta, C., 2017. Measuring Rao's Q diversity index from remote sensing: an open source solution. Ecol. Ind. 72, 234–238.

Rocchini, D., 2007. Effects of spatial and spectral resolution in estimating ecosystem α-diversity by satellite imagery. Remote Sens. Environ. 111 (4), 423–434.

Rossi, C., Kneubühler, M., Schütz, M., Schaepman, M.E., Haller, R.M., Risch, A.C., 2020. From local to regional: Functional diversity in differently managed alpine grasslands. Remote Sens. Environ. 236, 111415. https://doi.org/10.1016/j.rse.2019.111415.

Rudmin, J.W., 2010. Calculating the Exact Pooled Variance. 1–4. http://arxiv.org/abs/1007.1012.

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., Loreau, M., 2014. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. Ecology 95 (9), 2479–2492.

Schoener, T.W., 1974. Resouce partitioning in ecological communities: Research on how similar species divide resources helps. Science 185 (4145), 27–39.

Schütz, M., Risch, A.C., Achermann, G., Thiel-Egenter, C., Page-Dumroese, D.S., Jurgensen, M.F., Edwards, P.J., 2006. Phosphorus translocation by red deer on a subalpine grassland in the Central European Alps. Ecosystems 9 (4), 624–633.

Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., Madritch, M.D., Wang, R., Tilman, D., Gamon, J.A., 2018. Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. Nat. Ecol. Evol. 2 (6), 976–982.

Schweiger, A.K., Schütz, M., Risch, A.C., Kneubühler, M., Haller, R., Schaepman, M.E., Chisholm, R., 2017. How to predict plant functional types using imaging spectroscopy: linking vegetation community traits, plant functional types and spectral response. Methods Ecol. Evol. 8 (1), 86–95.

Schwinning, S., Kelly, C.K., Robinson, D., 2013. Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments. Funct. Ecol. 27 (4), 886–897.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? Trends Ecol. Evol. 31 (1), 67–80.

Soininen, J., 2010. Species turnover along abiotic and biotic gradients: Patterns in space equal patterns in time? Bioscience 60 (6), 433–439.

Stroud, J.T., Bush, M.R., Ladd, M.C., Nowicki, R.J., Shantz, A.A., Sweatman, J., 2015. Is a community still a community? Reviewing definitions of key terms in community ecology. Ecol. Evol. 5 (21), 4757–4765.

Terradas, J., Peñuelas, J., Lloret, F., 2009. The fluctuation niche in plants. Int. J. Ecol., 2009.

Tilman, D., Reich, P.B., Knops, J.M.H., 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441 (7093), 629–632.

Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379 (6567), 718–720.

Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Marcantonio, M., Ricotta, C., Tonon, G., 2019. Estimating tree species diversity from space in an alpine conifer forest: The Rao's Q diversity index meets the spectral variation hypothesis. Ecol. Inf. 52 (March), 26–34.

Ustin, S.L., Gamon, J.A., 2010. Remote sensing of plant functional types. New Phytol. 186 (4), 795–816.

Ustin, S.L., Gitelson, A.A., Jacquemoud, S., Schaepman, M., Asner, G.P., Gamon, J.A., Zarco-Tejada, P., 2009. Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. Remote Sens. Environ. 113, S67–S77.

Villéger, S., Mouillot, D., 2008. Additive partitioning of diversity including species differences: a comment on Hardy & Senterre (2007). J. Ecol. 845–848.

Vuolo, F., Neuwirth, M., Immitzer, M., Atzberger, C., Ng, W.-T., 2018. How much does multi-temporal Sentinel-2 data improve crop type classification? Int. J. Appl. Earth Obs. Geoinf. 72, 122–130.

Wang, R., Gamon, J.A., 2019. Remote sensing of terrestrial plant biodiversity. Remote Sens. Environ. 231, 111218. https://doi.org/10.1016/j.rse.2019.111218.

Wang, R., Gamon, J.A., Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Zygielbaum, A.I., Kothari, S., 2018. Influence of species richness, evenness, and composition on optical diversity: a simulation study. Remote Sens. Environ. 211, 218–228.

Wellmann, T., Haase, D., Knapp, S., Salbach, C., Selsam, P., Lausch, A., 2018. Urban land use intensity assessment: The potential of spatio-temporal spectral traits with remote sensing. Ecol. Ind. 85, 190–203.

Whittaker, R.H., 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecol. Monogr. 30 (3), 279–338.

Wong, C.Y.S., Gamon, J.A., 2015. Three causes of variation in the photochemical reflectance index (PRI) in evergreen conifers. New Phytol. 206 (1), 187–195.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G.,

Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428 (6985), 821–827.

Yan, E., Wang, G., Lin, H., Xia, C., Sun, H., 2015. Phenology-based classification of vegetation cover types in Northeast China using MODIS NDVI and EVI time series. Int. J. Remote Sens. 36 (2), 489–512.

Yang, X.i., Tang, J., Mustard, J.F., Wu, J., Zhao, K., Serbin, S., Lee, J.-E., 2016. Seasonal variability of multiple leaf traits captured by leaf spectroscopy at two temperate deciduous forests. Remote Sens. Environ. 179, 1–12.