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Parcel level temporal variance of remotely sensed spectral reflectance predicts plant diversity

Christian Rossi[1,2,3,*] (ID), Nicholas A McMillan[4] (ID), Jan M Schweizer[1,3] (ID), Hamed Gholizadeh[2] (ID), Marvin Groen[5], Nikolaos Ioannidis[6] and Leon T Hauser[3] (ID)

1 Department of Geoinformation, Swiss National Park, Runatsch 124-Chastè Planta-Wildenberg, 7530 Zernez, Switzerland
2 Department of Geography, Oklahoma State University, Stillwater, OK, United States of America
3 Department of Geography, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
4 Department of Agronomy and Horticulture, School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE, United States of America
5 Institute of Environmental Sciences, Leiden University, Leiden, The Netherlands
6 Universität Bremen, 28199 Bremen, Germany
* Author to whom any correspondence should be addressed.

E-mail: christian.rossi@nationalpark.ch
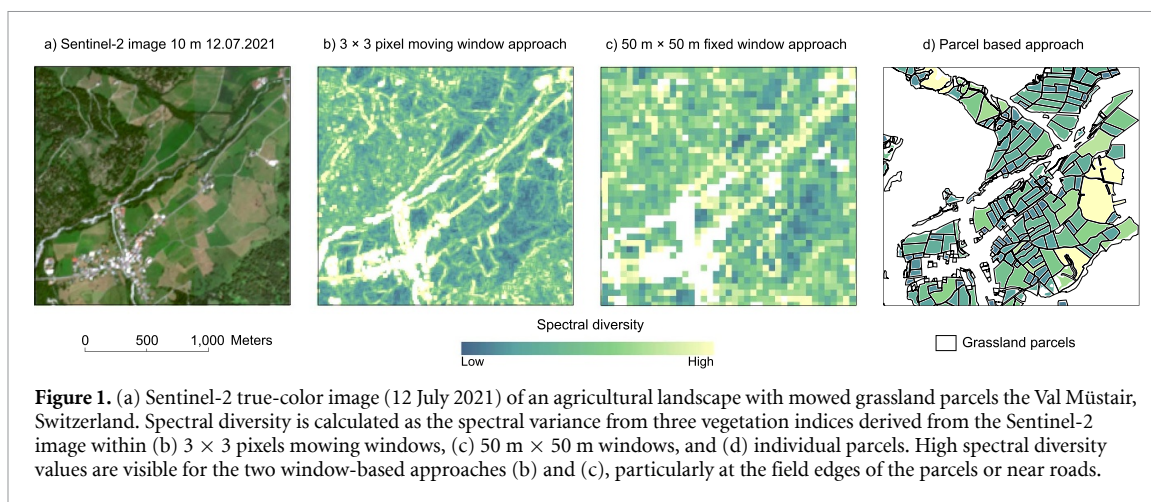
Abstract

Over the last two decades, considerable research has built on remote sensing of spectral diversity to assess plant diversity. The spectral variation hypothesis (SVH) proposes that spatial variation in reflectance data of an area is positively associated with plant diversity. While the SVH has exhibited validity in dense forests, it performs poorly in highly fragmented and temporally dynamic agricultural landscapes covered mainly by grasslands. Such underperformance can be attributed to the mosaic-like spatial structure of human-dominated landscapes with fields in varying phenological and management stages. Therefore, we argued for re-evaluating SVH's flawed window-based spatial analysis and underutilized temporal component. In particular, we captured the spatial and temporal variation in reflectance and assessed the relationships between spatial and temporal components of spectral diversity and plant diversity at the parcel level as a unit that relates to management patterns. Our investigation spanned three grasslands on two continents covering a wide spectrum of agricultural usage intensities. To calculate different components of spectral diversity, we used multi-temporal spaceborne Sentinel-2 data. We showed that plant diversity was negatively associated with the temporal component of spectral diversity across all sites. In contrast, the spatial component of spectral diversity was related to plant diversity in sites with larger parcels. Our findings highlighted that in agricultural landscapes, the temporal component of spectral diversity drives the spectral diversity-plant diversity associations. Consequently, our results offer a novel perspective for remote sensing of plant diversity globally.

1. Introduction

The expansion and intensification of agriculture to meet society's demand for soft commodities has emerged as a significant driver of biodiversity loss worldwide (Díaz *et al* 2019). Nearly half of the world's inhabitable terrestrial surface is under agricultural use and about 69% of the world's agricultural area is covered by grasslands for livestock production (O'Mara 2012, Ritchie and Roser 2020). Halting biodiversity losses in agricultural landscapes will therefore strongly depend on our ability to transform consumption and production systems to reduce our impacts on biodiversity (Leclère *et al* 2020). Achieving this goal would require monitoring biodiversity across large scales.

Ongoing advances in satellite remote sensing capabilities have spurred efforts to estimate biodiversity patterns across broad spatial scales. In particular, the analysis of spectral variation to infer plant diversity—known as the spectral variation hypothesis (SVH)—has gained traction as an intuitive approach.

Figure 1. (a) Sentinel-2 true-color image (12 July 2021) of an agricultural landscape with mowed grassland parcels the Val Müstair, Switzerland. Spectral diversity is calculated as the spectral variance from three vegetation indices derived from the Sentinel-2 image within (b) 3 × 3 pixels mowing windows, (c) 50 m × 50 m windows, and (d) individual parcels. High spectral diversity values are visible for the two window-based approaches (b) and (c), particularly at the field edges of the parcels or near roads.

The SVH relates the spectral heterogeneity or variability of an image captured by an optical sensor to environmental heterogeneity, which can act as a proxy for species diversity (Palmer *et al* 2000, 2002). Simply put, regions with high spectral diversity are presumed to support a larger pool of species. Previous studies, particularly those utilizing fine spatial resolution data, have revealed a direct link between spectral diversity and plant diversity, presumably due to various biochemical, physiological, structural, and phenological characteristics of individual plant species that are detectable through remote sensing (Schweiger *et al* 2018, Frye *et al* 2021, Kothari and Schweiger 2022).

Although substantial progress has been made in assessing plant diversity using spaceborne remote sensing over the last two decades (Rocchini *et al* 2004, Khare *et al* 2019, Torresani *et al* 2019, Badourdine *et al* 2022, Gholizadeh *et al* 2022, Rossi and Gholizadeh 2023), there are still several unresolved challenges to developing an operational approach to map plant diversity (Hauser *et al* 2021). Of note is the weak performance of the SVH across highly-fragmented agricultural landscapes (Schmidtlein and Fassnacht 2017, Fassnacht *et al* 2022, Perrone *et al* 2023). Such poor performance is primarily due to the distinctive mosaic-like spatial structure of these landscapes characterized by complex arrangements of features, such as field edges, roads, and fields in varying phenological and management stages, all of which contribute to a significant increase in spectral diversity values not related to plant diversity (Garrigues *et al* 2006).

To address the weak SVH performance in agricultural landscapes, we propose quantifying spectral diversity within parcels, as opposed to fixed and regularly shaped boundaries (or windows; Laliberté *et al* 2020, Rocchini *et al* 2021), congruent with the mosaic-like and dynamic nature of these landscapes. We argue that a more suitable approach to quantify plant diversity in agricultural landscapes should be achieved by moving beyond a window-based approach to a parcel level one, where plant diversity is characterized for each parcel and not processing windows of arbitrary size (figure 1). In doing so, we not only eliminate edge effects but also avoid grouping different parcels at varying phenological and management stages with highly divergent reflectance characteristics into the same category. Ultimately, since parcels are core elements of agricultural landscapes, quantifying plant diversity at the parcel level and mirroring the delineations of ownership and management become essential for optimizing biodiversity-friendly management decisions.

From a temporal perspective, spectral diversity is often calculated at a single point in time and therefore offering only a snapshot of a dynamic environment (Thornley *et al* 2022) despite significant shifts in spectral responses over the growing season (Yang *et al* 2016, Chavana-Bryant *et al* 2017, Wu *et al* 2017). Furthermore, within an agricultural landscape, anthropogenic stressors such as burning, grazing, mowing, fertilizing, and harvesting significantly alter the spectral signature and hence spectral diversity over time within a growing season (Gholizadeh *et al* 2020). As a result, we argue that capturing spectral variations in time, in conjunction with spatial variations, becomes crucial within agricultural landscapes (Rossi *et al* 2021).

In this work, we assessed the association between spectral diversity and plant diversity at parcel level by decomposing the variability in spectral diversity into spatial, temporal, and spatio-temporal components, following the framework presented by Rossi *et al* (2021). In doing so, we capture the spectral variance over space and time and their interaction. We suggest that reconfiguring spectral diversity computation to a parcel level would substantially improve its utility for accurately estimating plant diversity across agricultural landscapes. Furthermore, we hypothesize that the temporal component of spectral diversity is closely related to the degree of land use intensity, such as mowing and grazing occurrences and intensities. Therefore, we anticipate high temporal spectral diversity to be associated with fewer species,

given the strong associations of land use intensity and related human disturbances with biodiversity (Klein *et al* 2020). To test our hypotheses, we defined two objectives: (1) calculate the spatial, temporal, and spatio-temporal components of spectral diversity within parcels with different management types and (2) assess whether the spatial and temporal spectral diversity of a parcel is associated with plant diversity. To achieve our first objective, we used large-scale management data available for grasslands in Switzerland and Sentinel-2 remote sensing data (spatial resolution of 10 m, 13 bands, Drusch *et al* 2012). To accomplish our second objective, we used Sentinel-2 data in combination with *in situ* species inventories from three grasslands utilized for agricultural production, two in Europe and one in the United States (U.S.). Our parcel-based remote sensing experiment is a necessary first step for assessing the capability of spectral diversity to detect plant diversity across agricultural landscapes.

2. Methods

2.1. *In situ* species inventories and parcels
Our study was conducted in three temperate grasslands in Switzerland, U.S., and the Netherlands. Our study sites spanned a wide spectrum of agricultural usage intensities, ranging from protected grassland grazed only by wild ungulates to artificial intensely used grasslands (table 1). For each study site, vector information on parcels was available (Switzerland and U.S.) or derived through image segmentation (Netherlands). To mitigate edge effects in the spectral diversity calculations, we negatively buffered all parcels (function *Buffer* ArcGIS Pro *v3.1.2*, Environmental Systems Research Institute, Redlands, California). We customized the buffer sizes based on the specific landscape characteristics of each study site, accounting for parcel size and the size of surrounding features such as dirt roads.

2.1.1. Switzerland
Our Swiss study site was located in southeastern Switzerland in the Canton of Grisons and encompassed approximately 800 km^2 and included the Swiss National Park (SNP), the Lower Engadine, and the Val Müstair (46°34′ to 46°54′N, 9°58′ to 10°25′E). The area is characterized by a dry inner-alpine climate with mean annual temperatures of 6 °C at the valley floor (1300 m asl), and mean annual precipitation of around 800 mm (MeteoSwiss 2018). The SNP is a category Ia nature reserve (highest protection level—strict nature reserve). Correspondingly, no agricultural management takes place within the park boundaries and grasslands are grazed by large populations of red deer, chamois, and ibex. Grasslands in the Lower Engadine and the Val Müstair are subject

to organic as well as traditional agricultural management, including fertilization, mowing, and grazing (Rossi *et al* 2020). Some grasslands are additionally irrigated. In total, we considered a dataset of 3574 parcels (https://geodienste.ch/services/lwb_nutzungsflaechen combined with parcels on subalpine meadows in the SNP), each with an area of at least 600 m^2 and an average size of 4472 m^2 after masking out forests (ESA WorldCover 10 m 2021 V200 product; Zanaga *et al* 2022) and negative buffering of 10 m. Each of these parcels was associated with one of seven distinct management types: (1) artificial meadows (6–10 species, $n = 301$), (2) permanent meadows (15–30 species, $n = 1638$), (3) low-intensity meadows (30–40 species, $n = 369$), (4) extensively used meadows (40–70 species, $n = 1007$), (5) pastures ($n = 35$), (6) extensively used pastures ($n = 201$), and (7) protected grasslands ($n = 23$). We derived indicative species counts for meadows from Bosshard (2016). In addition, to the management type information, we collected species inventories from 35 parcels distributed homogeneously across the Val Müstair. Specifically, we documented species composition within a 60 m^2 (6 m × 10 m) plot in each parcel in June 2021. Due to logistical constraints, we collected species data only in meadows (i.e. management types 1–4).

2.1.2. United States
Our U.S. study took place in the Nature Conservancy's Tallgrass Prairie Preserve (TGPP; 36°50′ N, 96°25′ W) in Oklahoma. The area under investigation consisted of a contiguous tallgrass prairie of ∼50 km^2 managed through the synergistic application of prescribed fire and cattle grazing. Mean annual air temperature is around 32 °C (summer) and 3 °C (winter) with mean annual precipitation around 960 mm (Sherrill *et al* 2022). The northern portion of the TGPP was subdivided into eight distinct pastures, each with three parcels, from which one is burned each year with prescribed fire to maintain a three-year fire-return interval (Fuhlendorf and Engle 2004). Parcels had an average size of 792 109 m^2 after masking out roads and forests and negative buffering of 50 m using parcel vector files provided by the Nature Conservancy. Pastures were moderately grazed (0.37 animal units ha^{-1}) from April to September. We collected species inventories every July for three years (2019–2021) in each of the 24 parcels. We removed parcels burned in the year of the survey from our analysis due to extended periods of elevated soil exposure (>50%), resulting in 48 parcel-based species counts over three years. The data collection in each parcel encompassed seven randomly positioned transect arrays, each consisting of two intersecting 60 m transects. For each intersecting set of 60 m transects, species composition was documented for 25 0.1 m^2 equidistant plots. For a detailed description of

Table 1. Overview of *in situ* and remote sensing data per study site.

	Spectral diversity-management type	Spectral diversity-plant diversity		
	Switzerland	Switzerland	United States	Netherlands
Number of Sentinel-2 images	7	13	21 (7 × 3)	7
Acquisition time	April to October, 2021	April to October, 2021	April to October, 2019–2021	April to October, 2020
Number of parcels	3574	35	48	20
Average parcel size (m^2)	4472	7042	792 109	11 600
Parcel buffer (m)	10	10	50	10
In situ species inventories	Management type	1 × 60 m^2/parcel	175 × 0.1 m^2/parcel	3 × 1 m^2/parcel
Management	Grazing, mowing, fertilizing, protecting	Grazing, mowing, fertilizing	Grazing, burning	Grazing, mowing, fertilizing

the species inventory sampling protocol, we refer to McMillan *et al* (2022).

2.1.3. Netherlands

The study area in the Netherlands covers three larger polders; the Boterhuispolder, Lakerpolder, and Vrouwe Vennepolder located northeast of Leiden, Zuid-Holland (52°11′ N, 4°33′ E). Mean annual air temperature is around 11 °C with an average annual precipitation of around 900 mm. The area consisted of meadows of peat grasslands that are managed for dairy farming. Within the area, both highly productive grasslands subject to intensive management regimes, as well as areas where management has transitioned to extensive practices, such as raised water levels, reduced mowing, grazing, and fertilization, existed. In September 2020, a baseline field campaign was conducted across 20 parcels covering 345 000 m^2 in total and averaging 11 600 m^2 after negative buffering of 10 m per parcel. Species inventories were collected in three 1 m × 1 m plots placed diagonally in transects 25 m apart within each parcel. Parcel data was acquired through unsupervised segmentation based on the pre-trained Segment Anything Model developed by Meta AI (Kirillov *et al* 2023) and implemented in ArcGIS Pro *v3.1.2*. Segments were delineated within the field edges, excluding ditches, waterways and banks, and included predominantly the vegetated grass surfaces only. We verified correspondence of the results with public governmental data on national agricultural land use in the Netherlands, the Agrarisch Areaal Nederland dataset (www.pdok.nl/-/dataset-agrarisch-areaal-nederland-is-referentiepercelen-geworden).

2.2. Plant diversity

In each study site, we used species richness to express the plant diversity of our parcels. Species richness reports the number of observed species within each sampling area regardless of their abundance and therefore places the same weight on rare and dominant species, providing a comparable and simple metric across different studies. The species richness per parcel corresponded to the total count of observed species within all the plots in the given parcel.

2.3. Remote sensing data

We used open-access Copernicus Sentinel-2 data to quantify the different components of spectral diversity on the parcel level. Pre-processing and downloading of Sentinel-2 Level-2 A images were performed in the Google Earth Engine (Gorelick *et al* 2017). Monthly collections from April to October were created for each study site aligning with the corresponding year of data collection. Only images with cloudy pixel percentage lower than 80% were considered. Pixels with a cloud probability higher than 35% were removed using the *s2cloudless* algorithm (Zupanc 2017). Furthermore, pixels not representing the class *vegetation* or *not vegetated* were masked out using the Scene Classification band provided in the Level-2A image product. The bidirectional reflectance distribution function correction implemented by Poortinga *et al* (2019) was applied. We then harmonized the spatial resolution of all bands to 10 m using bilinear interpolation, which takes the weighted average of the four nearest pixels. For each month, the image with the highest number of valid pixels was selected for the spectral diversity calculation (supplement: table S1). An exception was made for the data

utilized to investigate the relationship between spectral diversity and plant diversity in the Val Müstair region. Due to the relatively frequent revisit time of two to three days, resulting from the overlap of Sentinel-2 tiles, we used a subset of 13 images taken between April and October for the spectral diversity calculation.

2.4. Vegetation indices

To compute spectral diversity, we used three Sentinel-2 vegetation indices (VIs) across diverse spectral ranges instead of using reflectance values. Compared to the use of spectral bands, VIs offer a main advantage due to their inherent robustness in mitigating artifacts arising from atmospheric correction processes (Chraibi *et al* 2022). VIs are also easily derived, computed consistently across study sites and sensor (Steven *et al* 2003) and have been used in the context of mapping functional trait diversity of plant communities (Helfenstein *et al* 2022). Here, we used the triangular greenness index (TGI, Kong *et al* 2016), the MERIS terrestrial chlorophyll index (MTCI, Clevers and Gitelson 2013), and the cellulose absorption index (CAI, Guerschman *et al* 2009), each covering a different region of the spectra (i.e. visible, near infrared and short-wave infrared, respectively) and complementary information over time (see the supplement: figure S1). MTCI is mainly related to nitrogen content in grasslands (Clevers and Gitelson 2013). TGI is sensitive to the total pigment content such as chlorophylls, carotenoids, and anthocyanins in leaves. High CAI values occur for dry and non-photosynthetic vegetation (Verrelst *et al* 2023). All three indices were normalized (i.e. divided) by their potential index range, i.e. MTCI with a range from -1 to 15, TGI with a range from 0 to 10, and CAI with a range from 0 to 2. Any values that fell below zero or exceeded one after normalization were set to not available values. Finally, data gaps due to clouds in the VIs time series or values falling outside the valid range were filled using a linear interpolation between the datasets (function *approximate* of the package terra *v1.7-3* in R *4.2.0*).

2.5. Spectral diversity calculation

We calculated spectral diversity components, including temporal, spatial, and their interaction (i.e. spatio-temporal component), as well as their contribution to the overall spectral diversity in percentage for each parcel and each VI using the function *divcom* from the stdiversity *v1.1.0* package (Rossi *et al* 2021) in R *4.2.0* (R Core Team 2022). The resulting spectral diversity components on a parcel level were then averaged across the three VIs. In doing so, the spectral diversity components were calculated as the spectral variance accounting for temporal and/or spatial variations (supplement: equations (S1)–(S3)): (i) the

spatial component of a parcel accounted for the spectral variance between pixels after averaging their temporal variability, (ii) the temporal component calculated the spectral variance of the average parcel value over time and (iii) the spatio-temporal component quantified the spectral variance among pixels over both space and time within a parcel, encompassing the variance not captured by the other two components, thus serving as a measurement of spectral asynchrony (Mazzochini *et al* 2024). As a metric for spectral diversity that is normalized by the sample size, the spectral variance is less sensitive to the spatial extent of plant communities (Laliberté *et al* 2020), allowing for its applicability and comparability across parcels of differing sizes. For our three study sites, we demonstrated that the spectral variance was independent of the parcel size (see the supplement figure S2).

2.6. Statistical analyses to assess the performance of spectral diversity components to estimate plant diversity
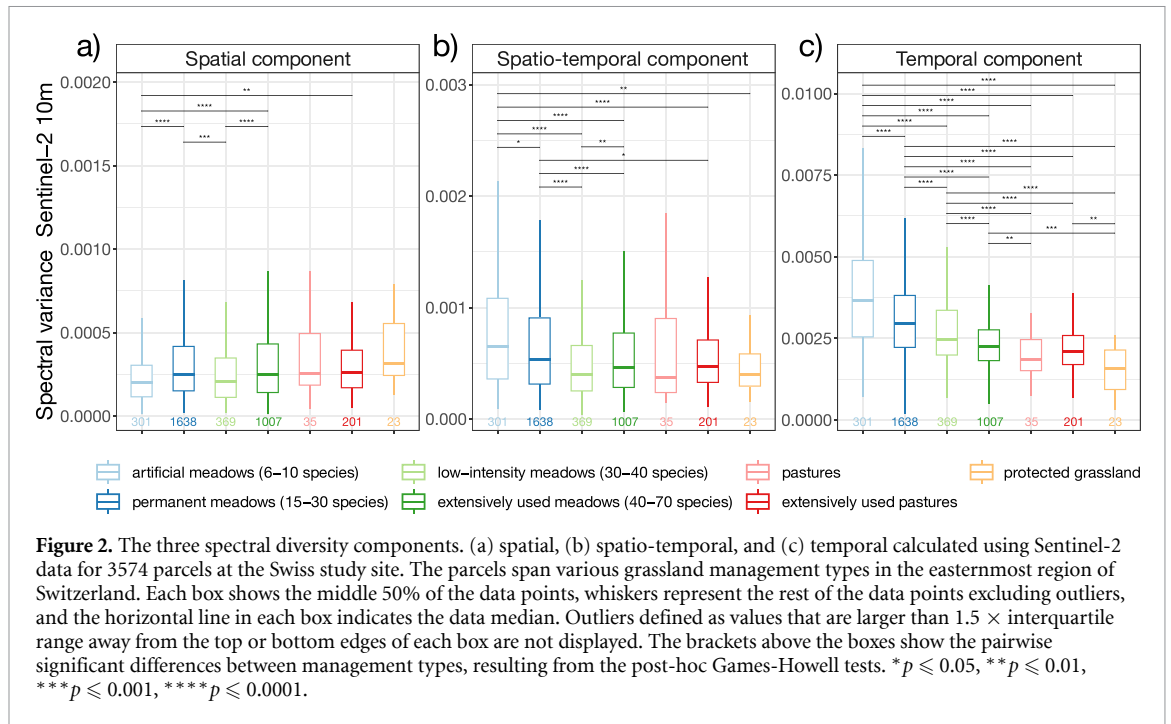
For the Swiss site only, we assessed if each spectral diversity component on a parcel level differed between our seven management types with a Welch's ANOVA test (package *onewaytests v2.7* in R). A post-hoc Games-Howell test, which does not assume equal variances and sample sizes, was conducted when significant differences between management types were detected to investigate specific pairwise comparisons among management types (package *userfriendlyscience v0.7.2* in R).

Moving beyond the lens of management types, we assessed the direct association between plant species richness and the components of spectral diversity at the parcel level. In particular, we compared the spatial and temporal spectral diversity of parcels distributed over the three grassland sites with their species richness using the Pearson correlation coefficient (*R*; package *stats v3.6.2* in R).

3. Results

3.1. Assessing the spectral diversity components for different management types

For the Swiss site, we found that each of the three components of spectral diversity differed between management types (Welch's ANOVA, $p < 0.01$, $n = 3574$; figure 2). The spatial and temporal components displayed conspicuous trends that aligned with land use intensity. Specifically, we observed a gradient ranging from areas with the most intense human intervention to those with minimal human influence (figures 2(a) and (c)). Higher land use intensity was associated with lower spatial diversity but contributed to elevated temporal diversity of spectral signals. Notably, the protected grasslands showed a highly distinguishable spectral diversity profile compared to the agricultural parcels. Another

Figure 2. The three spectral diversity components. (a) spatial, (b) spatio-temporal, and (c) temporal calculated using Sentinel-2 data for 3574 parcels at the Swiss study site. The parcels span various grassland management types in the easternmost region of Switzerland. Each box shows the middle 50% of the data points, whiskers represent the rest of the data points excluding outliers, and the horizontal line in each box indicates the data median. Outliers defined as values that are larger than $1.5 \times$ interquartile range away from the top or bottom edges of each box are not displayed. The brackets above the boxes show the pairwise significant differences between management types, resulting from the post-hoc Games-Howell tests. $^*p \leqslant 0.05$, $^{**}p \leqslant 0.01$, $^{***}p \leqslant 0.001$, $^{****}p \leqslant 0.0001$.
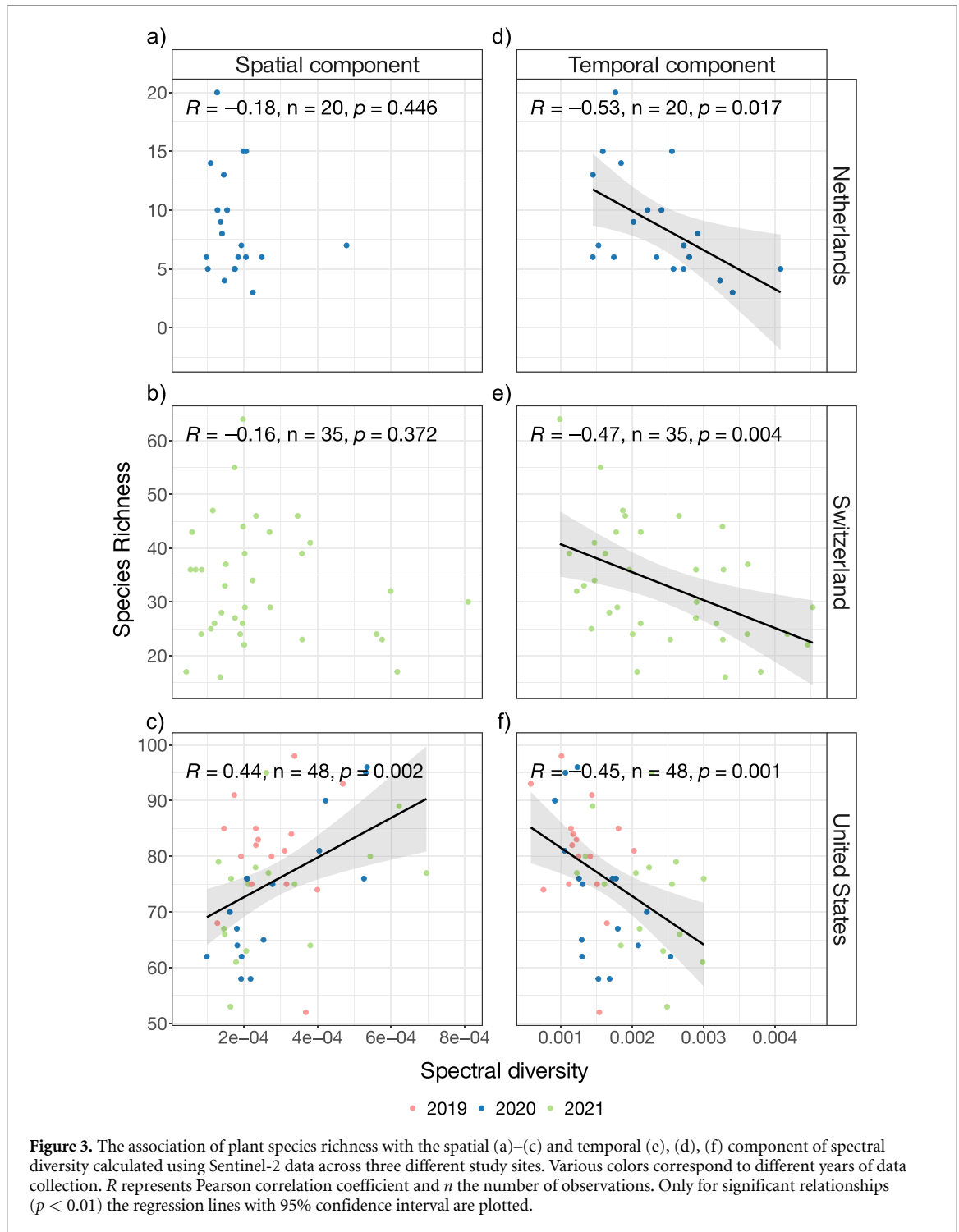
notable finding was the distinct magnitudes observed among the components of spectral diversity. The predominant source of variance within the spectral signals was attributed to the temporal component, accounting for an average of 74% of the total spectral variability across all parcels and management types. Furthermore, approximately 17% of the total spectral variability was attributed to the spatio-temporal, while a mere 9% could be ascribed to the spatial component. These findings underpin the significant contribution of temporal variation to the spectral signal within a highly fragmented agricultural landscape.

The post-hoc tests revealed a more pronounced differentiation between management types in the temporal component contrary to the spatial component (figure 2, supplement: table S2). For the spatial component, only artificial and low-intensity meadows showed statistically significant differences from the other management types ($p < 0.01$). In line with this result, we found a wide range of spatial diversity values within the same management (figure 2(a)). The variation within management categories can arise from irregular management practices within individual parcels, which caveats the parcel-based approach where substantial within-parcel heterogeneity in management occurs. This was evident in parcels displaying a relatively high spatio-temporal component, such as artificial and permanent meadows (figure 2(b)). In particular, upon visual inspection of the satellite data, high spatio-temporal values were systematically found in parcels where mowing occurred at distinct times within specific parcel segments. In other words, the entire parcel did not undergo simultaneous mowing.

3.2. Capability of spatial and temporal spectral diversity data as proxies for grassland plant diversity

When comparing the species richness with the spatial component of spectral diversity at the parcel level across three distinct study sites, there was a significant relationship only for the U.S. site ($R = 0.44$; $p < 0.01$; figures 3(a)–(c)). Notably, the U.S. study site had the largest parcel sizes (table 1) and the highest average percentage of total spectral variability explained by the spatial component over all parcels (14% compared to 6% for the Netherlands and 9% for Switzerland). However, all sites showed very similar ranges of spectral diversity in space. These findings suggest that parcel size may not alter the magnitude of spectral variance, but it does affect the ability to estimate species diversity. Hence, it appears that having only a few pixels for each parcel may be insufficient for capturing robust plant diversity estimates via the spatial component of spectral diversity.

In contrast, the temporal component of spectral diversity was strongly associated with species richness across all sites ($R = -0.45$ to -0.53; $p < 0.01$; figure 3), displaying consistent significant negative correlations. The temporal component of spectral diversity accounted for an average of 78% of the total spectral variability in the Netherlands and Switzerland. In the U.S. (figure 3(f)), where only grazing and no mowing occurred and recently burned patches were excluded from the analysis, we found lower maximal values in temporal variance compared to the other sites (figures 3(d) and (e)) and only 73% of the spectral variance was explained by the temporal component.

Figure 3. The association of plant species richness with the spatial (a)–(c) and temporal (e), (d), (f) component of spectral diversity calculated using Sentinel-2 data across three different study sites. Various colors correspond to different years of data collection. *R* represents Pearson correlation coefficient and *n* the number of observations. Only for significant relationships ($p < 0.01$) the regression lines with 95% confidence interval are plotted.

4. Discussion

Our finding presents a novel perspective on the relationship between spectral diversity and plant species richness, marking the first multi-country assessment of spectral diversity in space and time across agricultural grasslands. In particular, we showed that calculating spectral diversity from Sentinel-2 data at the parcel level proved to be useful for quantifying plant species richness. Interestingly, our findings

highlight the significance of the temporal component of spectral diversity, rather than the spatial component. Specifically, we observed that decreased temporal variance calculated over a growing season corresponds to greater plant diversity. We also noted that the different components of spectral diversity can exhibit contrasting relationships with plant diversity. Consistent with previous studies (Lopes *et al* 2017, Rossi *et al* 2021), not differentiating between temporal and spatial components of spectral diversity

may result in a weak relationship between spectral diversity and plant diversity within grasslands. Therefore, we recommend utilizing both temporal and spatial components of spectral diversity to predict plant diversity from space. Moreover, the spatio-temporal component offers an avenue for identifying non-uniformly managed parcels, thus facilitating a more precise interpretation of spectral diversity patterns.

4.1. Temporal component of spectral diversity offers a pathway to biodiversity estimations

Our findings across multiple grassland sites suggest significant negative correlation between the temporal component of spectral diversity and plant diversity, reflecting the biodiversity decline as land use intensifies (Weiner *et al* 2011, Allan *et al* 2014) and the stability of an ecosystem decreases (Radeloff *et al* 2019). In line with previous studies, land use intensity of grasslands can be estimated from temporal variations in a spectral signal (Franke *et al* 2012, Gómez Giménez *et al* 2017, Reinermann *et al* 2020, Lange *et al* 2022, Weber *et al* 2023). The highlighted connections between the temporal component of spectral diversity, land use intensity, and plant species richness introduce an intriguing concept: spectral variance in time can be a versatile and adaptable approach for biodiversity monitoring across diverse sites. Quantifying plant diversity using spectral variance has low computation cost, which further bolsters its appeal and potential for global applicability. Additionally, spectral variance can provide a valuable input variable for machine learning-based geospatial biodiversity modeling.

While other spaceborne estimations of land use intensity in grasslands often only encompass the number of mowing events and rely on one VI (Griffiths *et al* 2020, Schwieder *et al* 2022), the temporal facet of spectral diversity emerges as a viable solution that responds to another range of management practices too, such as tilling, grazing, and irrigation. Furthermore, the calculation of the spectral variance in time is not constrained solely to specific spectral indices as including the full spectral signature of remotely-sensed data to calculate spectral diversity is straightforward. Accounting for the full spectral signature may capture a wider extent of relevant grassland management practices, reduce uncertainties (Hank *et al* 2019), and take advantage of the increased spectral coverage of future spaceborne missions such as ESA's CHIME (Copernicus Hyperspectral Imaging Mission for the Environment, Rast *et al* 2021) and NASA's SBG (Surface Biology and Geology, Cawse-Nicholson *et al* 2021). The increased availability of spectral information should also stimulate investigating the contribution of different spectral features (e.g. spectral bands, VIs, and optical

traits) to the spectral diversity over time, an aspect not explored in our study.

While our findings underpin the significance of considering the temporal dimension of spectral data, using it to estimate plant species richness can also present several potential challenges. For example, in our Swiss study site, abandoned grasslands were subject to grazing by wild ungulates which fosters a rich mosaic of plant communities (Schütz *et al* 2003, Rossi *et al* 2020). Yet, abandoned grasslands elsewhere, despite displaying a low temporal variance in remotely sensed signals, might also exhibit diminished plant diversity with some species becoming dominant, forcing others to recede (Niedrist *et al* 2009). Other discording scenarios might involve systems that exhibit pronounced temporal variance in the spectral signatures due to natural or prescribed disturbances such as flooding or fires, that can increase plant diversity (e.g. Johnson *et al* 2016, Pausas and Ribeiro 2017). To address these issues, we excluded recently burned parcels in the U.S. from our analysis due to their disproportionately high spectral variance. Finally, changes in land use intensity often correspond to subtle spectral changes, complicating their distinction from phenological changes or various stressors such as drought (Kuemmerle *et al* 2013, De Vroey *et al* 2022). These issues could by particularly pronounced in tropical grasslands, having a distinct wet and dry season (Ma *et al* 2013). Therefore, further investigations and validation against phenological cycles and anthropogenic stressors such as mowing, grazing, tilling and irrigation in different grasslands are needed to comprehend the precise interactions between spectral diversity in time, agricultural practices and ecological dynamics. To that end, having access to spaceborne data with a high revisit time (e.g. every few days) becomes crucial for capturing all spectral fluctuations within grassland parcels.

4.2. The spatial perspective on the plant diversity-spectral diversity relationship

Contrary to the temporal component, the spatial component of spectral diversity exhibited only partial association with plant species richness. This result is not surprising given the conflicting spectral diversity-plant diversity relationship found in other studies (Thornley *et al* 2023). In particular, the spectral diversity-plant diversity relationship can be confounded by several factors, such as vegetation cover, soil exposure, and canopy structure (Gholizadeh *et al* 2018, Conti *et al* 2021, Hauser *et al* 2021, Rossi *et al* 2022). Previous studies have suggested that higher spatial resolution could enhance the relationship between the spatial component of spectral diversity and plant diversity (Wang *et al* 2018, Pacheco-Labrador *et al* 2022). We also suggest that another aspect of spatial scale—that is plot size, or in our case, parcel size—influenced our results (Anderson

2018, Gholizadeh *et al* 2022, Rossi and Gholizadeh 2023). We found that the spatial resolution provided by spaceborne sensors similar to Sentinel-2 was inadequate for effectively employing the SVH in smaller parcels of the Dutch and Swiss sites, but was sufficient for the larger parcels in the U.S. site. A moderate number of pixels per parcel not only hampers capturing fine-scale features but also results in an unstable spectral variance (Piovesana and Senior 2018), increasing the susceptibility of spectral diversity to artifacts and noise. Our results align with Robertson *et al* (2023), which showed that mapping spectral diversity depends on both the spatial resolution and dimensions of the mapping windows. Therefore, we believe that the parcel to pixel size ratio is critical for accurate estimation of plant diversity from space. For example, in the U.S. study site, the parcel to pixel size ratio was in the order of 1:10 000, indicating that a successful application of the SVH for parcels in the Dutch and Swiss sites might require pixel sizes of approximately 10–30 cm. Future research should continue to explore the idea of an optimal ratio between parcel and pixel size to inform ongoing sensor development. Additionally, *in situ* data collection protocol differences among our study sites (plot size, type and number) may have influenced the results. Despite, the relationship between species richness and area sampled in all study site may have reached an inflection point (see species area curves in supplement figure S3), the sampling of the U.S. site, with its high number and spatially well distributed plots, may be more adequate to capture the majority of the plant richness in a parcel. These findings highlight the challenge of designing a representative field sampling protocol which is achievable within a reasonable time frame, aligns with the scale of remote sensing data and captures all species—an issue that is to some extent a paradox, as remote sensing data are typically touted for its potential to overcome such limitations. Future studies could try to match satellite data with *in situ* data more effectively through methods like spatial interpolation of *in situ* data (Rossi and Gholizadeh 2023), extrapolation of species-area curves and the use of drone data (Alvarez-Vanhard *et al* 2021).

4.3. Spectral diversity at the parcel level

Our results at the parcel level and the previous weak performance found by window-based approaches in agricultural landscapes (Schmidtlein and Fassnacht 2017, Perrone *et al* 2023), heavily influenced by factors such as field edges and varying management stages (figure 1), suggest the potential of parcel-based spectral diversity for remote sensing of plant diversity. A parcel-based approach is feasible only when the necessary information is accessible or when parcels are easily distinguishable using segmentation algorithms (Ez-zahouani *et al* 2023). However, in the latter case, the spectral diversity of a parcel might be constrained, as the pixel values of a generated segment display comparable spectral values in space (Hossain and Chen 2019). A possible solution could involve segmenting ecosystems into patches based on environmental variables instead. If feasible, the parcel or object-based approaches could be extended beyond agricultural systems (White *et al* 2010, Zheng *et al* 2022), providing a solution to the arbitrariness associated with selecting window sizes that may not represent meaningful geographical and ecological objects or units (Fisher 1997, Ricklefs 2008). Moreover, the adoption of a parcel-based approach offers distinct advantages compared to regular-sized windows or pixels, particularly within the framework of multi-temporal methods. By averaging data at the parcel level, we mitigate misregistration problems (Skakun *et al* 2017) while also reducing the impact of factors such as cloud edges that are challenging to remove. Nevertheless, a systematic comparison between window-based and parcel level approaches is still missing, leaving room for future studies to explore the efficacy and applicability of the different approaches.

5. Conclusions

In this study, we re-evaluated the SVH to include the temporal dimension and calculated spectral diversity on a parcel level as opposed to processing windows with arbitrary sizes. Across three sites, we found that the plant diversity of a given area is negatively associated with the spectral variation in time and that considering the temporal dimension of the SVH is necessary for mapping plant diversity. As such, the temporal SVH may offer a framework for studying plant diversity which can be further integrated into different modeling pipelines aiming to estimate biodiversity dynamics from space. Additionally, within agricultural landscapes, it is imperative to account for spectral variation in time, as fluctuations over time have been identified as the primary driver of spectral variance. Consequently, relying solely on mono-temporal remote sensing methods to estimate plant diversity can yield both limited and potentially misleading results and leave out valuable information on land use intensity.

Estimating plant diversity based on regular-sized windows can be problematic when applied to heterogeneous human-dominated landscapes because such regular-sized units do not represent actual spatial entities of real-world phenomena and are rather arbitrary. In contrast, parcel-based approaches better delineate observable management units that directly affect biodiversity. Through remote estimation of plant diversity at scales relevant for human decision-making, we can provide a more accurate assessment of plant diversity in agricultural landscapes.

Data availability statement

Acknowledgments

Author contributions

C R and L T H designed the study, analyzed the data and acquired funding. N A M, H G, M G and N I designed and collected *in situ* data. J M S preprocessed the remote sensing data. C R led the writing of the manuscript. All authors contributed to reviewing previous drafts and gave their final approval for publication.

ORCID iDs

Christian Rossi ⓘ https://orcid.org/0000-0001-9983-8898
Nicholas A McMillan ⓘ https://orcid.org/0000-0003-2817-9762
Jan M Schweizer ⓘ https://orcid.org/0009-0003-1931-0981
Hamed Gholizadeh ⓘ https://orcid.org/0000-0002-4770-7893
Leon T Hauser ⓘ https://orcid.org/0000-0003-1408-9942

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