


ORIGINAL RESEARCH

Spatial resolution, spectral metrics and biomass are key aspects in estimating plant species richness from spectral diversity in species-rich grasslands

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Abstract

Increasing evidence suggests that remotely sensed spectral diversity is linked to plant species richness. However, a conflicting spectral diversity–biodiversity relationship in grasslands has been found in previous studies. In particular, it remains unclear how well the spectral diversity–biodiversity relationship holds in naturally assembled species-rich grasslands. To address the linkage between spectral diversity and plant species richness in a species-rich alpine grassland ecosystem, we investigated (i) the trade-off between spectral and spatial resolution in remote sensing data; (ii) the suitability of three different spectral metrics to describe spectral diversity (coefficient of variation, convex hull volume and spectral species richness) and (iii) the importance of confounding effects of live plant biomass, dead plant biomass and plant life forms on the spectral diversity–biodiversity relationship. We addressed these questions using remote sensing data collected with consumer-grade cameras with four spectral bands and 10 cm spatial resolution on an unmanned aerial vehicle (UAV), airborne imaging spectrometer data (AVIRIS-NG) with 372 bands and 2.5 m spatial resolution, and a fused data product of both datasets. Our findings suggest that a fused dataset can cope with the requirement of both high spatial- and spectral resolution to remotely measure biodiversity. However, in contrast to several previous studies, we found a negative correlation between plant species richness and spectral metrics based on the spectral information content (i.e. spectral complexity). The spectral diversity calculated based on the spectral complexity was sensitive to live and dead plant biomass. Overall, our results suggest that remote sensing of plant species diversity requires a high spatial resolution, the use of classification-based spectral metrics, such as spectral species richness, and awareness of confounding factors (e.g. plant biomass), which may be ecosystem specific.

Introduction

Biodiversity is declining globally at rates unprecedented in human history (IPBES, 2019). In particular, grassland biodiversity is threatened by destruction, degradation and fragmentation due to urban development, agricultural land use such as grassland transformation into monocultures, eutrophication, overgrazing and climate change

(Clark & Tilman, 2008; Harrison et al., 2015; Hautier et al., 2014; Mooney et al., 2009). Grassland biodiversity provides a large range of ecosystem services (Hein et al., 2006; Lamarque et al., 2011) essential for the survival of plant and animal species (Dinnage et al., 2012) and vital in sustaining human life. Lower grassland biodiversity leads to lower stability in plant productivity over time (Hautier et al., 2014), limited carbon storage (Ward et al.,

2016) and reduced pollinator abundance (Batáry et al., 2010). Therefore, with the worldwide loss of grassland biodiversity and the associated decline of ecosystem services, comprehensive monitoring of grasslands remains a priority (Suding, 2011).

However, assessing grassland biodiversity based on field inventories is highly time-consuming, expensive and subjective (Bonar et al., 2011; Löhmus et al., 2018). In contrast, technological developments in passive remote sensing approaches, which measure the sunlight reflected by an object at a specific wavelength, allow for an efficient and relatively inexpensive collection of baseline data related to biodiversity (Cavender-Bares et al., 2017; Frye et al., 2021; Rocchini et al., 2018; Schweiger et al., 2018) across various spatial and temporal scales (Gholizadeh et al., 2020; Jetz et al., 2016; Pettoelli et al., 2018; Rossi et al., 2021). In particular, the approach known as the spectral variation hypothesis (Palmer et al., 2002) assumes that the remotely measured variation in spectral patterns, that is, spectral diversity, is related to biodiversity (i.e. plant species richness; Cavender-Bares et al., 2017; Dahlin, 2016; Oldeland et al., 2010; Rocchini et al., 2010). Spectral diversity represents a set of pixels recorded by remote sensing corresponding to the spatial heterogeneity of the environment, for example, vegetation, soil or topography. Vegetation spectral diversity may be based on specific spatial patterns in reflectance (hereinafter spectral metrics) of known vegetation indices (Rocchini et al., 2018), principal components (Rocchini et al., 2004) or the clustering and classification of reflectance spectra (Féret & Asner, 2014; Schäfer et al., 2016). The measured spectral diversity of vegetated areas is assumed to be shaped by morphological, physiological or phenological features that manifest the life history of a species, like plant leaf traits (e.g. pigments, leaf water content, leaf area and dry matter content), canopy structure, plant functional types and plant phenological state (Asner & Martin, 2008; Asner et al., 2011; Ollinger, 2011; Schweiger et al., 2017; Ustin & Gamon, 2010; Ustin et al., 2009; Wang et al., 2019). Some of these features represent different environmental adaptations or resource use strategies (Díaz et al., 2016). Therefore, variations in these features indicate the presence of different plant species and hence characterize plant species richness (Pavoine & Bonsall, 2011).

Nevertheless, using remote sensing techniques to estimate plant species richness in grasslands is more challenging than it appears to be (Gholizadeh et al., 2019; Rossi et al., 2020; Schmidlein & Fassnacht, 2017; Wang, Gamon, Cavender-Bares, et al., 2018). In general, grassland plants are much smaller than the pixel sizes of remotely sensed data. Several studies estimated grassland species diversities from spaceborne and airborne remote sensing data and spatial resolutions of several meters

(Gholizadeh et al., 2019; Lopes et al., 2017; Möckel et al., 2016; Rocchini et al., 2004). Such unfavourable spatial resolutions of the sensors may lead to pixels containing many individual plants, as well as many plant species. Therefore, it is likely that spectral diversity based on such an approach may only accurately reflect biodiversity at a regional level and between plant communities (Polley et al., 2019; Rossi et al., 2020), but not at a local level in an individual plant community (Lopatin et al., 2017) or an individual plot of an ecological experiment (Wang, Gamon, Cavender-Bares, et al., 2018).

Furthermore, a range of factors may confound the spectral diversity–biodiversity relationship. For instance, the fraction of bare soil (Gholizadeh et al., 2018), dead biomass (Schweiger et al., 2015), the size of plants (Conti et al., 2021), phenology, flowering patterns, short-term weather conditions and management (Gholizadeh et al., 2020; Rossi et al., 2021), as well as the amount of biomass (Villoslada et al., 2020) and the composition of the plant community (different life forms such as graminoids, forbs and legumes, Wang, Gamon, Schweiger, et al., 2018) affect spectral diversity and, thus, interfere with the estimation of plant species richness. Such confounding factors may in part be mitigated with an extensive use of spectral information. Using only limited spectral information, for example, only the Normalized Difference Vegetation Index (NDVI), can weaken the spectral diversity–biodiversity relationship or even result in a negative relationship between the two, due to strong correlations of NDVI with, for example, biomass (Goswami et al., 2015; Villoslada et al., 2020; Wang et al., 2016). In contrast, using imaging spectroscopy data (i.e. hundreds of spectral bands with a wavelength sensitivity in the range of a few nanometers) with a spatial resolution matching the object of investigation was found to result in a positive spectral diversity–biodiversity relationship (Wang, Gamon, Cavender-Bares, et al., 2018; Wang, Gamon, Schweiger, et al., 2018). Finally, to date, there is no consensus on the best spectral metrics to be used to quantify plant species richness in grasslands. Spectral metrics based on the information content in the spectral data (spectral complexity) heavily depend on the variance of spectral information, that is, extreme values that can confound the spectral diversity–biodiversity relationship (Lucas & Carter, 2008). Accordingly, spectral metrics based on classification algorithms (Féret & Asner, 2014) may be better suited to assess the high small-scale heterogeneity of grasslands. Whether the spectral variation hypothesis works for mapping plant species richness at small spatial scales is, therefore, likely to depend on (i) appropriate spatial and spectral resolution; (ii) the chosen spectral metrics and (iii) confounding factors such as bare soil, dead and live biomass.

Previous studies have been performed either in experimental grasslands like Cedar Creek (Gholizadeh et al., 2018; Wang, Gamon, Cavender-Bares, et al., 2018; Wang, Gamon, Schweiger, et al., 2018) with communities artificially composed of a limited species pool (i.e. 1, 2, 4, 8, or 16 species per plot) or in naturally assembled grasslands with spectrally (Villoslada et al., 2020) or spatially limited datasets (Möckel et al., 2016). Thus, the interdependencies of the relationship between spectral diversity and biodiversity, as well as possible trade-offs in natural settings still need to be explored. Hence, it is unclear whether the contradicting spectral diversity–biodiversity relationships reported between naturally and experimentally assembled grassland ecosystems result from differences in the spectral information used, or are instead driven more by confounding factors such as, for instance, biomass.

Due to technical constraints, remote sensing devices are usually designed as a trade-off between spatial and spectral resolution (Aiazzi et al., 2012). Unmanned aerial vehicles (UAVs) are remote sensing platforms that can provide imagery with high spatial resolution. Yet, UAVs are primarily used in combination with standard digital cameras providing low spectral resolution (Lu & He, 2017); and UAVs mounted imaging spectrometers of high spectral resolution are still rare, expensive and complex. Furthermore, they are frequently prone to radiometric noise and generally subject to lower spatial resolution in comparison to multispectral cameras with a limited number of wavelength bands (Aasen et al., 2018; Adão et al., 2017). In contrast, space- or airborne imaging spectrometers combine reduced spatial with high spectral resolution.

Here, we studied the controversial spectral diversity–biodiversity relationship in a naturally assembled grassland ecosystem above the timberline with high small-scale species richness of up to 35 plant species per square metre. We used plots from a long-term experiment (Nutrient Network; <https://nutnet.org>), in which small-scale plant species richness was manipulated by the application of fertilizers and the exclusion of plant-feeding animals (see e.g. Borer, Harpole, et al., 2014). Our objectives were to:

evaluate the trade-off between high spectral and high spatial resolution when estimating small-scale plant species richness using spectral diversity, in particular by testing image fusion methods (Zhang, 2004),
 compare three different spectral diversity metrics that have different sensitivities towards extreme values which potentially confound the spectral diversity–biodiversity relationship. Two of these three metrics are based on spectral complexity (convex hull volume and coefficient

of variation), and one on a clustering algorithm (spectral species richness)

to test how far confounding factors such as dead biomass, total biomass or plant life forms may influence the estimation of plant species richness from spectral diversity.

Materials and Methods

Study area

We collected our data in Val Mustair in south-eastern Switzerland in a naturally assembled grassland area above the timberline (2320 m above sea level, latitude 46°37'55" to 46°37'50" N, longitude 10°22'29" to 10°22'18" E, Fig. 1). Such alpine grasslands are characterized by high small-scale variability in topography and thus in edaphic conditions. This, in combination with generally nutrient-poor conditions due to low fine earth fractions in the soil, results in high small-scale plant species richness of up to 35 species per square metre on our control plots. The mean annual temperature is 0.3°C, and the mean annual precipitation amounts to 1098 mm. The parent material underlying the site is a mixture of dolomite and volcanic conglomerates. Soil organic carbon (C) concentration is roughly 4.5%, total soil nitrogen (N) is 0.3%; and the soil C:N ratio is 13.3 (Risch et al., 2019). Soil pH is around 5. The site is part of the globally distributed Nutrient Network (NutNet; Borer, Harpole, et al., 2014). The network aims to analyse global change effects such as fertilization and altered herbivore community composition on grassland productivity and biodiversity in a randomized-block design. Three replicate blocks with 10 treatment plots each were established. The 10 plots were randomly assigned to nutrient (seven plots) and fencing (two plots) treatments and control (one plot) without any experimental treatment. All plots are 5 × 5 m in size. Nutrient additions and herbivore removal treatments started in 2009, hence, were in place for nine years at the time of data sampling in 2018. For the nutrient additions, 10 g N m⁻² yr⁻¹ as time-release urea; 10 g P m⁻² yr⁻¹ as triple-super phosphate and 10 g K m⁻² yr⁻¹ as potassium sulphate are applied separately, as well as in all possible combinations in each block every year. The vertebrate herbivore removal treatments (fence) were established by fencing two plots, one with full fertilizer application (NPK) and one without fertilizer application. The fences were designed to effectively exclude above-ground mammalian herbivores with a body mass of over 50 g (i.e. ibex, chamois, red deer, marmots and snow hares, Borer, Harpole, et al., 2014). The fences at the Val Mustair site are 200 cm high and are covered with a 5-cm square mesh with extra cabling support to prevent

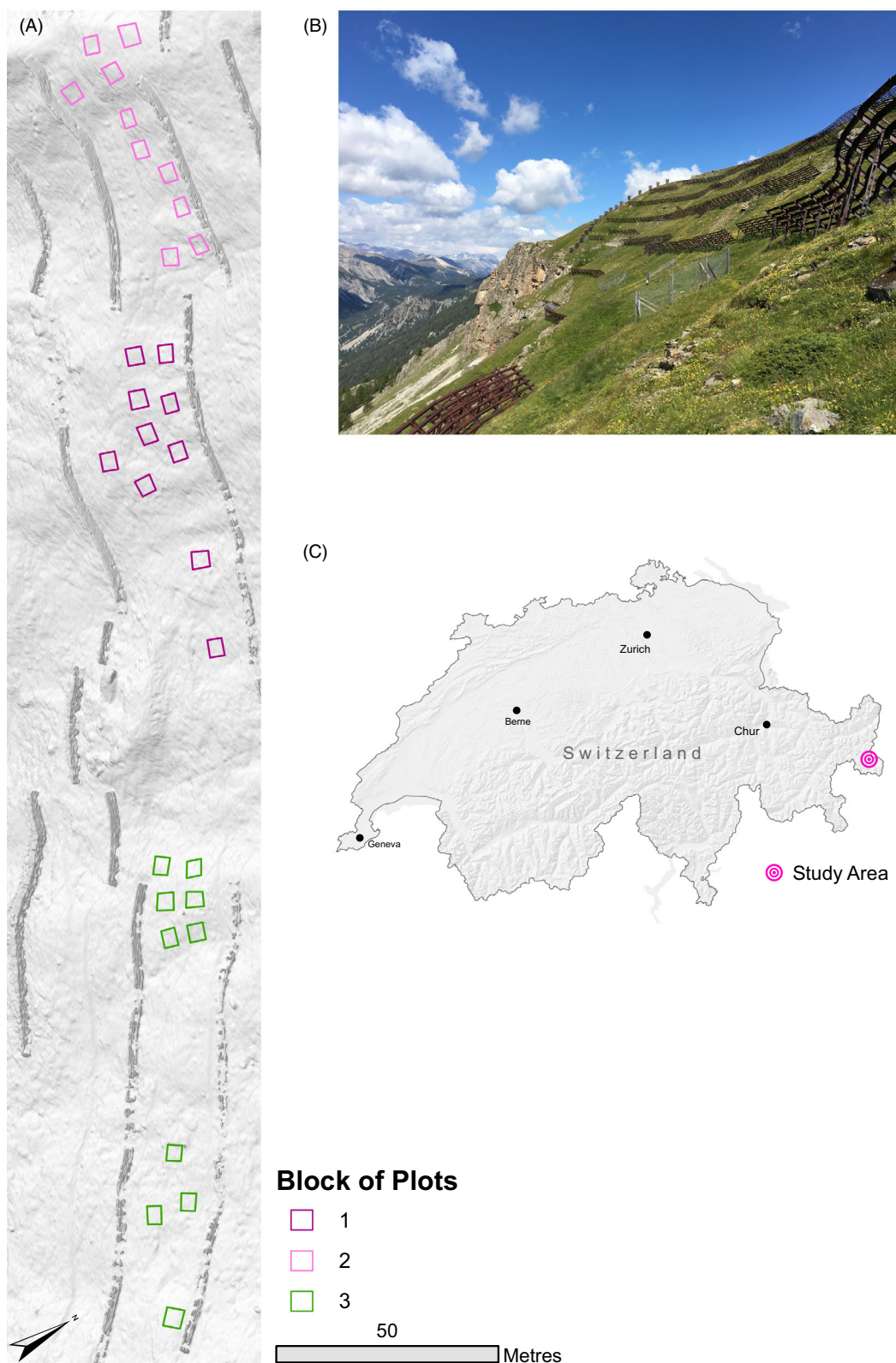


Figure 1. (A) Study area with location of field plots subdivided into blocks. (B) Photo of the study area. (C) Location of the study area in Val Mustair in south-eastern Switzerland.

snow damage. The treatments have, by now, resulted in significant differences in plant species richness and plant biomass. Thus, this experimental setup is well-suited for testing the spectral diversity–biodiversity relationship and possible confounding effects in a natural but still controlled setting.

Vegetation data

Plant species richness was assessed in early July 2018. For this purpose, all plant species within a permanently assigned 1×1 m square located within each 5×5 m plot were identified. Biomass was assessed by clipping two 0.1×1 m strips from a 1×1 m plot adjacent to each survey square. For each plot, the collected biomass was sorted into three life forms (graminoids, forbs and legumes) and dead biomass, afterwards oven-dried at 60°C and weighed.

Remote sensing data

UAV system, flight mission and image processing

We used a Falcon 8 octocopter (UAV; Ascending Technologies, Krailling, Germany) equipped with a Sony NEX-7 camera (total weigh 2.3 kg). Onboard navigation sensors (Global Navigation Satellite System GNSS, Inertial Measurement Unit, barometer, compass) and an adaptive control unit permitted high positional accuracy and stable flight characteristics. A laptop installed with a flight control system (AscTec Navigator Flight Planning Software v3.4.4) acted as the ground station to control the flight in real-time using communication devices.

We used two different Sony NEX-7 cameras, both with a 24 mega pixel complementary metal-oxide sensor and a small, lightweight Sony NEX 20 mm $F/2.8$ optical lens. One camera recorded red–green–blue (RGB) imagery, the other one had the internal NIR-blocking filter replaced with an 830-nm long-pass filter to record the NIR signal (Bühler et al., 2017; Holman et al., 2019; Lu & He, 2017). The cameras were connected to the Falcon 8 by a gimbal with active stabilization and vibration damping. Two flights were made over the study area, each collecting 98 images using either the RGB or NIR camera. Both flights were made between 11:03 and 11:33 local time on July 11, 2018 under stable light conditions, that is, sunny with no clouds and fixed camera settings. The UAV was operated at an altitude of approximately 40 m above ground and at a speed of about 4 m per second. The images had a spatial resolution of about 1.25 cm, an approximate 85% forward overlap and 60% side overlap. Twelve ground control points (GCPs, 15×15 cm in size) were evenly distributed over the entire test site for subsequent

georeferencing of the imagery. The locations of the GCPs were measured with a Trimble GeoXR real-time kinematic GNSS with an expected accuracy of <0.10 m.

Two of 98 images taken during each flight were eliminated manually due to blurring. The remaining images, that is, 96 RGB and 96 NIR images, were processed to remove Gaussian noise and optical vignetting by applying a linear filter (Wiener filter) and a flat-field correction, which uses Gaussian smoothing (Matlab *vR2020a* Image Processing Toolbox). The denoised images were subsequently processed in Pix4DMapper (Pix4D *v4.5.6*), which uses structure from motion techniques to generate a dense point cloud, a digital surface model and a mosaicked and rectified reflectance dataset. Detailed radiometric calibration procedures for the UAV data are provided in Appendix S1. During processing in Pix4D, the 12 GCPs were added for improved geo-rectification of the imagery (root mean square error of GCP localization around 2 cm). The resulting RGB mosaic and the blue band from the modified camera containing the NIR signal (Holman et al., 2019) were stacked together and resampled bilinearly, resulting in a reflectance dataset consisting of four bands and 10 cm spatial resolution. We chose to resample the original 1.25 cm resolution to 10 cm because of computational constraints and to better reflect an achievable resolution of UAV mounted hyperspectral sensors (Aasen et al., 2018).

Airborne imaging data

We used airborne imaging spectroscopy data that was acquired with the next generation airborne visible/infrared imaging spectrometer (AVIRIS-NG; Hamlin et al., 2011) on July 08, 2018 (11:3–1:36 local time). The AVIRIS-NG sensor collected reflected radiance at 5-nm intervals covering the spectral range from 380 to 2500 nm. The geometrically- and atmospherically corrected datasets are openly available via the AVIRIS-NG Data Portal 2014–2019 (Gao et al., 1993; Thompson et al., 2015). We used the mean reflectance values of two overlapping flight lines (CHNP 25 and CHNP 26) to reduce potential directional effects emerging from a different sun-target-sensor geometry. Due to inaccuracies in georeferencing according to standard data processing, we manually georeferenced the respective datasets using specific objects (e.g. avalanche protection structures) with known coordinates (ArcMap *v10.7.1* Georeferencing toolbar). Subsequently, we bilinearly resampled the data from 2.7 to 2.5 m spatial resolution and applied a mask to match the extent of the UAV data. We used 372 of the 425 AVIRIS-NG bands after removing bands showing low signal-to-noise ratios or strong water absorption (Appendix Fig S2.1).

Data fusion

The data fusion step combined the available high spatial resolution UAV data with the high spectral resolution airborne data. Since several data fusion techniques have been published that differ significantly in method and performance (Mookambiga & Gomathi, 2016; Yokoya et al., 2017), we tested seven different state-of-the-art fusion methods (Table 1). The goal was to find the best method for our application rather than making a general comparison of fusion methods. For a detailed description of the algorithms of the different methods and their code, we refer to Yokoya et al. (2017) and Appendix S4. The results of the seven different fusion approaches were compared (i) visually, (ii) using image entropies and (iii) using image standard deviations (Jagalingam & Hegde, 2015). A high standard deviation indicates high contrast. Similarly, high entropy represents high spectral information content. Furthermore, we assessed how the different methods were able to quantify plant species richness. Consequently, the best fused dataset was selected based on the highest standard deviation, the highest entropy and the strongest relationship with plant species richness.

Spectral diversity metrics

We calculated three different spectral diversity metrics for our datasets, namely for the UAV, airborne and the seven fused datasets for each plot (Table 2, Fig. 2). We chose three of the most commonly used diversity measures in current spectral diversity research (Gholizadeh et al., 2018; Wang, Gamon, Schweiger, et al., 2018), each with different sensitivities to extreme values. The convex hull volume (CHV) was derived from the first three principal components of the reflectance values (Fig. 2). CHV was standardized by subtracting the standard deviation for each dataset across all plots. The coefficient of variation (CV) was calculated as the ratio between the standard deviation and the mean of the reflectance value at a specific wavelength for each plot and was then averaged over

Table 2. Description of the three different spectral diversity metrics used in this study.

Spectral diversity metric	Description	References
Convex hull volume (CHV)	CHV calculates the volume of pixels forming a convex hull, using the first three principal components of the reflectance data.	Dahlin (2016)
Coefficient of variation (CV)	CV calculates the ratio between the standard deviation and the mean of the reflectance value at a specific wavelength, averaged over all wavelengths.	Wang, Gamon, Cavender-Bares, et al. (2018)
Spectral species richness	Defines the number of spectral species based on clustering of the reflectance signal.	Féret and Asner (2014)

all wavelengths. We quantified spectral species richness for the UAV and fused datasets, but not for the airborne dataset due to the limited number of pixels (four) per plot. The spectral species richness approach assumes that the spectral signature of one or several similar species is unique. Spectral species were defined based on the K-means clustering method of a random subset (2500 pixels, with NDVI values > 0.4 and 10 random starts) of the first four principal components of the reflectance image (i.e. UAV or fused dataset) collected across the entire scene (1.7 ha; package *randomForest v4.6-14* and *cluster v2.1.0* in R). The number of clusters was set to 50, which corresponds approximately to the number of plant species recorded in the area. To cluster the 2500 pixels, we used the K-means algorithm on the proximity matrix generated from Random Forest (RF) model (number of trees to grow = 500) applied on the first four principal components values of the 2500 pixels. The clusters obtained were used to train a subsequent RF model for spectral species classification. In other words, once the 50 spectral

Table 1. List of methods used for fusion of multispectral UAV data and AVIRIS-NG data.

Method	Category	Theory	References
Gram Schmidt adaptive algorithm (GSA)	Pansharpening-based methods	Component substitution	Aiazzi et al. (2007)
Generalized Laplacian pyramid (GLP)	Pansharpening-based methods	Multiresolution analysis	Aiazzi et al. (2006)
Smoothing filter-based intensity modulation (SFIM)	Pansharpening-based methods	Multiresolution analysis	Liu (2000)
Coupled non-negative matrix factorization (CNMF)	Subspace methods	Unmixing	Yokoya et al. (2011)
Maximum a posteriori with stochastic mixing model (MAP-SMM)	Subspace methods	Bayesian	Eismann & Hardie (2004)
Fast fusion based on Sylvester equation (FUSE)	Subspace methods	Bayesian	Wei et al. (2016)
Hyperspectral Superresolution (HySure)	Subspace methods	Bayesian and unmixing	Simoes et al. (2015)

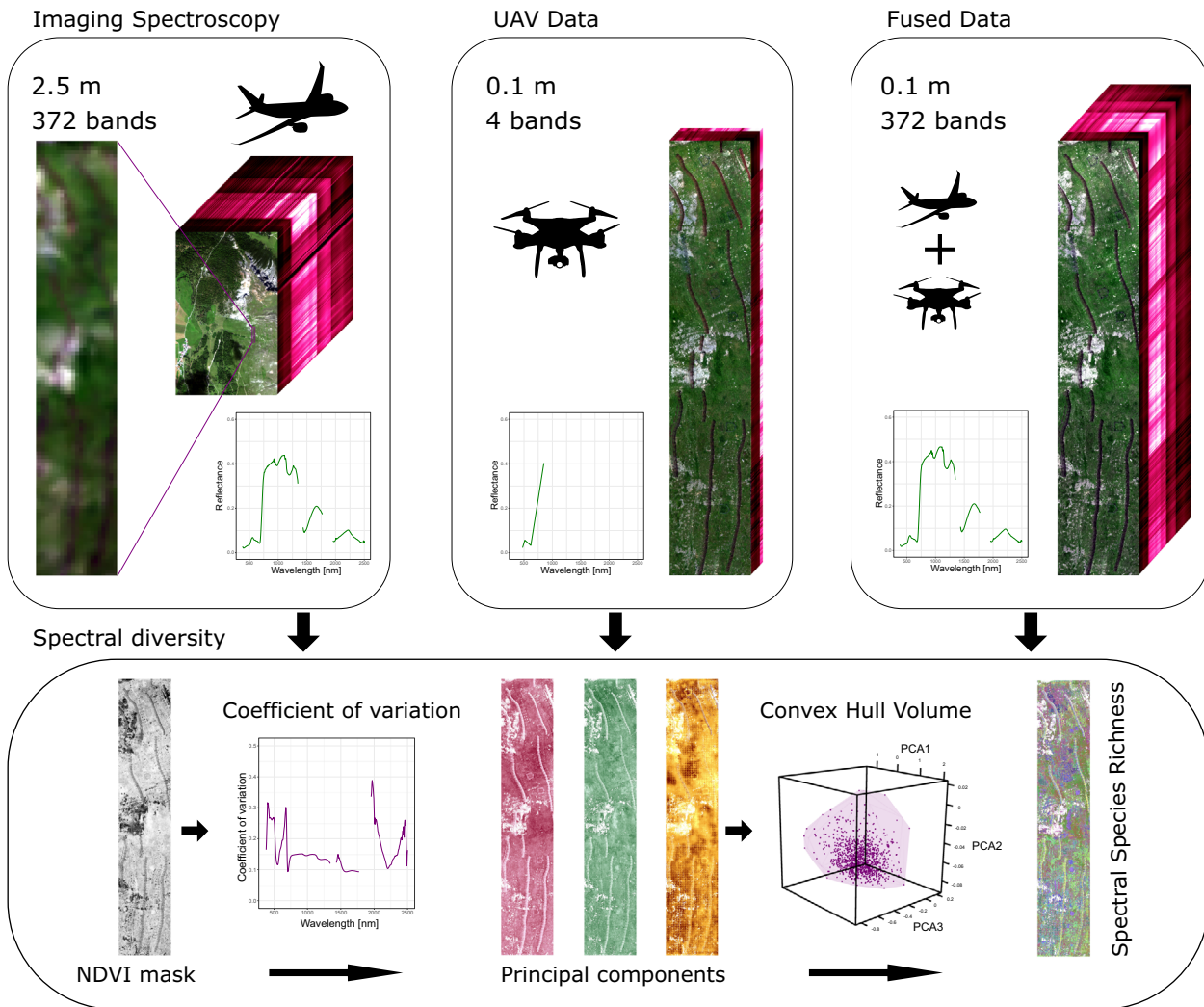


Figure 2. Overview of the workflow to calculate three spectral diversity metrics (coefficient of variation, convex hull volume and spectral species richness). Spectral diversity metrics were calculated from airborne imaging spectroscopy (AVIRIS-NG), UAV and fused datasets. We masked all pixels with NDVI values <0.4 . Convex hull volume was derived from the first three components of a principal component analysis (PCA). The first four PCA components of the reflectance image were used to classify spectral species. The spatial (m) and spectral (number of bands) resolutions of AVIRIS-NG, UAV and fused approach are indicated.

species were defined through clustering, each pixel contained in a plot was assigned to one of these spectral species with the trained RF classifier. Due to the random nature of clustering approaches, we repeated this process 20 times for each dataset and averaged the number of spectral species, that is, spectral species richness.

To consider only vegetated pixels, pixels with NDVI values <0.4 , which were assumed to represent bare soil, were excluded from the UAV and fused imagery analysis for all three spectral diversity metrics. After excluding bare soil, we took a random subsample of 1000 pixels from the centre of each plot to avoid edge effects when calculating the metrics for the UAV and fused datasets.

Statistical analysis of spectral diversity and plant species richness

First, we assessed the relationship between spectral diversity (i.e. spectral metrics), and *in situ* plant species richness for each experimental plot for each fused, UAV and airborne dataset using bivariate Spearman correlations (ρ). In addition, we calculated the root mean square error (RMSE) between spectral species richness and plant species richness for each fused (Appendix S4) and UAV dataset. To further investigate differences between the datasets in estimating plant species richness, we used an analysis of covariance (ANCOVA). An ANCOVA allows testing

for differences in slopes and intercepts between different regression lines. We compared those linear regressions between plant species richness and spectral diversity derived for the different datasets and spectral metrics that showed a significant relationship.

Second, we modelled the plot wise relationship between spectral diversity and possible confounding factors of the spectral diversity–biodiversity relationship using linear models without interactions (package `stats` in R 4.0.2). Each spectral diversity metric derived from the three datasets (i.e. UAV, airborne only CHV and CV, fusion) served as a response variable (i.e. eight linear models). The response variables were log-transformed to improve normality of the residuals. The explanatory variables were (i) total biomass (live plus dead), (ii) the ratio of dead biomass to total biomass and (iii) the ratio of different life forms (grass, forb and legume) to live biomass. We assessed the independence of the explanatory variables, that is, multicollinearity, by computing the variance inflation factor (R package `car` v3.0-10). For each model, residuals were inspected visually for their randomness and normal distribution. Note that two plots in block 2 (see

Fig. 1A) had to be removed from the datasets due to blurred UAV images, resulting in 28 of 30 experimental plots.

Results

HySure was found to be the best performing fusion algorithm in terms of standard deviation and entropy (Appendix S4). It led to the visually most convincing results when inspecting the colour composite images (Fig. 3). HySure also showed significant correlations between spectral diversity and plant species richness (Appendix Figure S4.1), together with one of the lowest RMSE between the number of spectral species and plant species.

Spectral diversity versus plant species richness

Comparing our three spectral diversity metrics calculated for the different datasets with plant species richness, we found a wide range of relationships. Overall, no

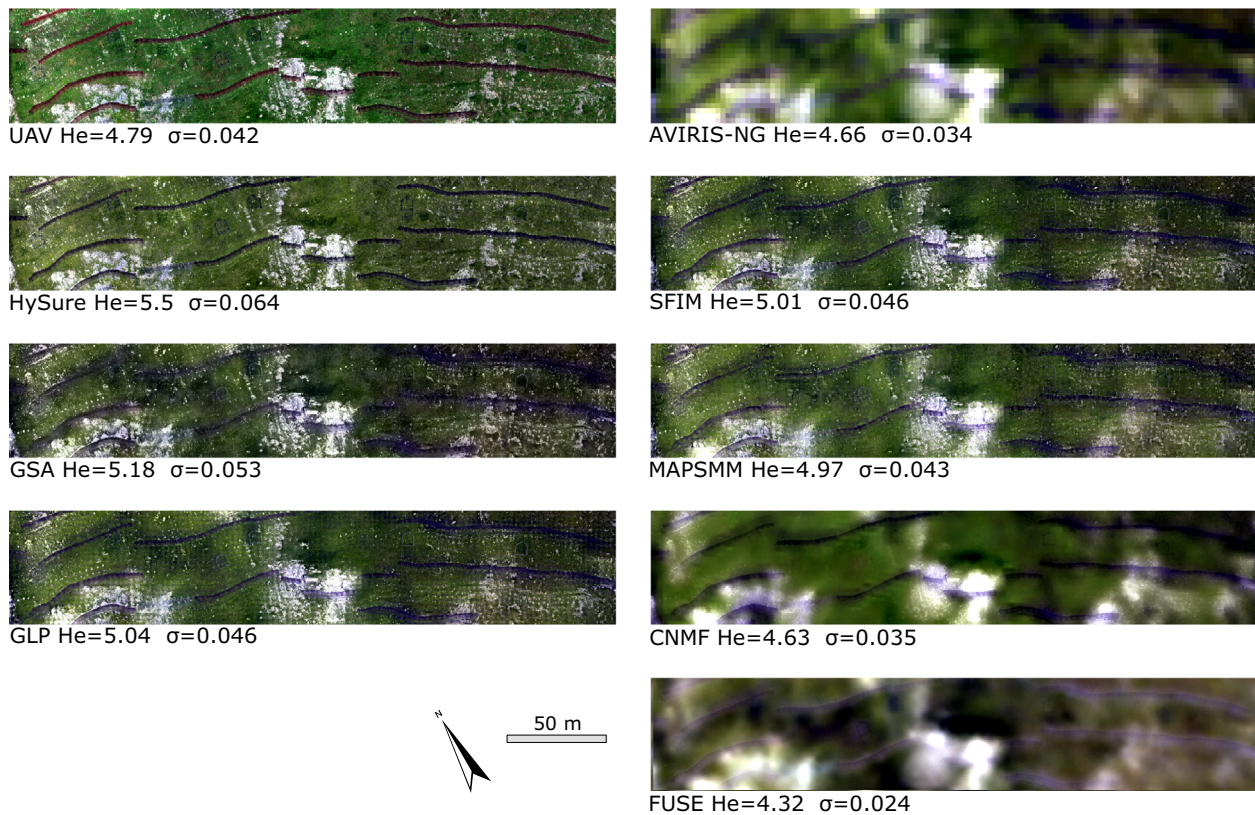


Figure 3. True colour composites of the study area acquired by the UAV camera, the AVIRIS-NG sensor, and processed from fused datasets with seven different fusion methods (HySure, GSA, GLP, SFIM, MAP-SSM, CNMF and Fuse). High entropy (He) values indicate rich information content in the image. High standard deviation (σ) indicates high image contrast.

correlations ($p > 0.05$) were found for the three metrics when using airborne AVIRIS-NG data, indicating an inappropriate spatial resolution for this dataset (Fig. 4). Both UAV and fused datasets did not allow the prediction of plant species richness based on CHV either (Fig. 4A). However, for CV, we found a significant negative relationship with plant species richness for both the UAV and fused datasets (Fig. 4B). The high values of spectral information content in plots with low species richness suggested that other factors like biomass or intraspecific spectral variability may affect spectral diversity. The spectral species richness derived from the UAV dataset and the fused data product (Appendix Fig S5.1) showed, in contrast, significant positive relationships with plant species richness (Fig. 4C).

Using the fused product instead of the UAV dataset, the relationship between spectral species richness and plant species richness improved in terms of ρ , and the number of spectral species was closer to the number of observed plant species (RMSE = 8.47 against 12.37, Fig. 4C). The result of the ANCOVA, however, suggested that the slopes of the regressions between both CV or spectral species richness and plant species richness did not differ between the UAV and the fused dataset ($F_{1,52} = 0.40/0.57$, $p = 0.53/0.45$, CV/spectral species richness). Similarly, the intercepts did not statistically differ between the two approaches ($F_{1,53} = 1.14/3.676$, $p = 0.29/0.065$).

Confounding effects of the spectral diversity–biodiversity relationship

To study confounding effects of the spectral diversity–biodiversity relationship, we used linear models to examine

the relationship between spectral diversity and (i) total biomass, (ii) the ratio of dead to total biomass and (iii) the ratio of life forms (i.e. graminoids, forbs and legumes) to live biomass. In these models, the explanatory variables, represented by the different biomass metrics, were independent (i.e. no multicollinearity, variance inflation factor < 3.5).

As for the previous analysis, we found no significant relationship between the spectral diversity and biomass metrics when using airborne AVIRIS-NG data (Appendix Table S3.1). The relationships between spectral diversity and biomass metrics were, in contrast, significant and very similar for the UAV and the fused dataset (Appendix Table S3.1). We, therefore, show the results for the fused dataset only (Fig. 5): Total biomass was found to have a significant positive relationship with CV (slope = 0.001, CI (0, 0.002)) and seemed to be the most confounding factor of the spectral diversity–biodiversity relationship. This result may be explained by a significant negative correlation between total biomass and species richness in the study area ($\rho = -0.40$, $p = 0.035$), where nutrient additions lead to more biomass but a decrease in species richness. Furthermore, plots with high total biomass displayed a high percentage of accumulated dead biomass ($\rho = 0.73$, $p < 0.001$).

However, we found a negative relationship between CV and dead:total biomass (slope = -1.42 , CI (-2.56 , -0.283)). These results suggest that dead biomass played a crucial role in shaping the spectral information content only in the presence of low to intermediate total biomass. Therefore, there must be other factors influencing the spectral information content in high biomass plots. Contrary to the findings obtained for CV, we found no significant relationship between CHV and any of our biomass

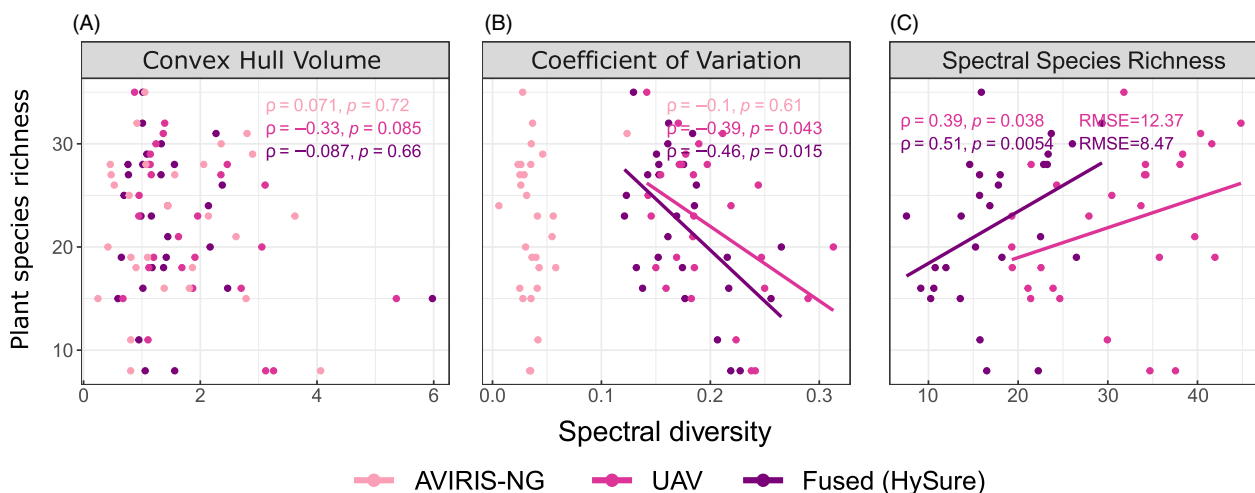


Figure 4. Spectral diversity metrics (A–C) derived from AVIRIS-NG, UAV and the HySure fused dataset versus *in situ* plant species richness. ρ = Spearman correlation. Linear regression lines were plotted only for significant relationships ($p < 0.05$).

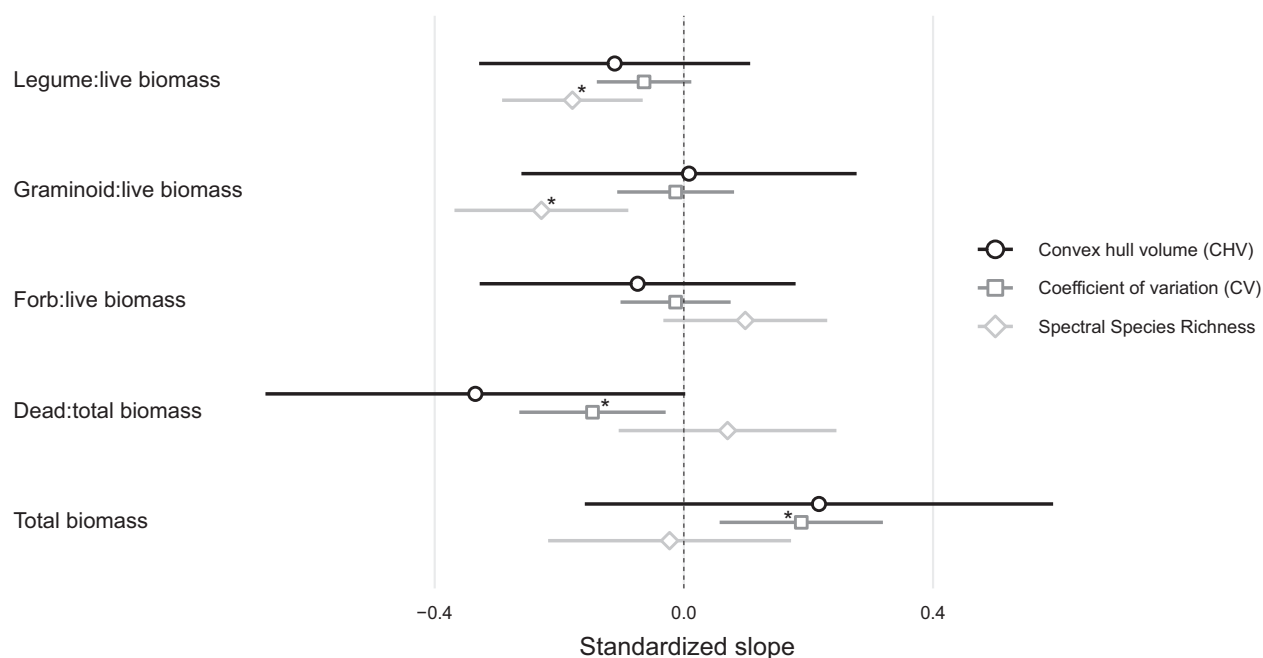


Figure 5. Standardized slope with 95% confidence intervals of the linear regression models between the three spectral metrics convex hull volume (CHV), coefficient of variation (CV) and spectral species richness and total biomass, the ratio of dead biomass to the total biomass and life forms (i.e. graminoids, forbs and legumes) to live biomass. Spectral metrics are calculated from the best fused product, that is, obtained from UAV and airborne data applying the HySure fusion method. *Significant relationships.

metrics. The main reason might be that the CHV metric is highly susceptible to extreme values, which do not reflect the overall characteristics of a community.

We found a negative relationship between spectral species richness and the ratio of graminoids to live biomass (slope = -1.04 , CI (-1.68 , -0.41)). Most plots with a high percentage of graminoids, mainly *Festuca rubra*, displayed low plant species richness due to the individual plants growing in clumps occupying a relatively large area. Similarly, the ratio of legumes to live biomass displayed a negative relationship with spectral species richness (slope = -3.62 , CI (-5.90 , -1.34)). In plots with high nutrient addition, legumes were suppressed, promoting the dominance of graminoids and a reduced plant species richness.

Discussion

The results obtained from UAV or fusing UAV data with airborne imaging spectroscopy data proved to be useful for quantifying plant species richness. In addition, we showed that a fused dataset can cope with the requirement of both high spatial and spectral resolution to remotely measure biodiversity (Wang, Gamon, Cavender-Bares, et al., 2018), a prerequisite, which is still challenging to obtain from a single sensor. Nevertheless, the

results of this study confirm that remote sensing of plant species diversity remains challenging and that spatial resolution, choice of appropriate spectral metrics and awareness of confounding factors – which might be ecosystem specific – are essential when leveraging the spectral diversity–biodiversity relationship in species-rich grassland ecosystems.

Trade-off between spectral and spatial resolution

Due to technical constraints, a trade-off between spatial and spectral resolution determines sensor design. Our results underpin the overwhelming importance of the spatial resolution in estimating plant species richness in grasslands. Grassland plants are relatively small compared to the grain size of remotely sensed data, decreasing our ability to quantify diversity. As previous studies in experimental settings demonstrated, a decreasing spatial resolution weakened the spectral diversity–biodiversity relationship (Gholizadeh et al., 2019; Wang, Gamon, Cavender-Bares, et al., 2018). At coarse spatial resolution, such as in our airborne data where the number of pixels per plot or community was limited, it becomes difficult to establish any relationship between spectral and plant diversity. In addition, the difference in size and life forms

between plant species in grasslands presents a challenge. The optimal spatial resolution may be very specific for a species and is often unknown *a priori*. Even with spatial resolutions of less than one centimetre, the detection of individual plants may only be possible under favourable conditions such as low structural complexity, low spatial overlap and a low number of species (Lopatin et al., 2017). Very high spatial resolution may, on the other hand, enhance within-species variation and increase noise, that is, mutual shading, making it difficult to establish a significant spectral diversity–biodiversity relationship.

While the choice of spatial resolution is key to establishing a significant spectral diversity–biodiversity relationship, the same cannot be said for spectral resolution in our study. Although spectral resolution is known to affect the spectral diversity–biodiversity relationship (Rocchini, 2007; Wang, Gamon, Schweiger, et al., 2018), it could not replace a high spatial resolution and was weaker than expected from other studies (Ollinger, 2011; Ustin & Gamon, 2010). We are aware that our fused product cannot replace an imaging spectrometer with high spatial resolution since it is synthetic. Nevertheless, our findings partly correspond with findings in other studies: Gholizadeh et al. (2019) showed, for example, that the standard deviation of NDVI performs well among other spectral diversity metrics. Wang, Gamon, Schweiger, et al. (2018) found no additional benefit of using full-range spectrometer data in quantifying plant diversity. Spatial resolution was the limiting factor in both studies.

We suggest two major reasons for the subordinate importance of high spectral resolution in comparison to high spatial resolution:

- 1 The combined effect of correlated bands and how spectral metrics condense the spectral information make the full information highly redundant and biased towards some spectral features (Rocchini, 2007). A bias is generated because the numbers of bands that capture different spectral features are not equal and some bands provide more information than others. For instance, if several bands capture the same spectral feature, that is, if they are correlated, the contribution of this feature to the spectral diversity will be misleadingly high. In contrast, the contribution of single bands that capture a distinct spectral feature will contribute insufficiently to spectral diversity. Using principal component analysis (PCA) to reduce data dimensionality may not resolve this issue since the first PCA axes will reflect the set of the most correlated bands among those with a larger contribution. Some specific spectral bands capture the relevant species information that is necessary to successfully apply the spectral variation hypothesis. For example, Schweiger et al. (2018) showed that only

the local maxima of the coefficient of variation that corresponded to known absorption features of plant pigments, water content and carbon-based leaf constituents were required to estimate plant diversity. Nevertheless, the choice of spectral features to best represent plant species richness remains an issue of future research. In particular, different spectral regions display contrasting responses to plant species richness. Möckel et al. (2016), for example, reported positive correlations between reflectance and plant diversity for chlorophyll absorption bands, and a negative one for the NIR region of the electromagnetic spectrum.

- 2 The spectral diversity approach does not decouple leaf-from canopy effects. The measured reflectance may include canopy structure as well as different leaf traits and their interactions. Canopy structure, rather than leaf traits, may thus drive the majority of the reflectance signal (Kattenborn, Fassnacht, et al., 2019; Yao et al., 2015). Grassland canopy variables, such as total biomass, are highly related to the VIS and NIR region of the electromagnetic spectrum (Tucker, 1977). Thus, the reflectance of a few bands in the VIS and NIR region of the spectrum may capture most of the remotely sensed variance between plants. In general, the spectral diversity–biodiversity relationship studied at leaf level (Frye et al., 2021; Schweiger et al., 2018) cannot be easily upscaled to the plant or community level. Thus, it is crucial to understand the effect of canopy structure on spectral diversity and its impact on the relationship between spectral diversity and plant species richness. In this light, it is surprising that spectral metrics from UAV data are rarely used (Conti et al., 2021; Villoslada et al., 2020), despite increasing data availability, high spatial resolution and the potential of the onboard sensors to quantify the VIS and NIR part of the spectrum. Despite the relatively small areas covered, UAVs are very beneficial for studying the spectral diversity–biodiversity relationship and assessing the capabilities of other platforms. Moreover, the results of this study encourage the use of UAVs to operationally estimate plot-scale plant diversity. As such, our study can be considered a valuable contribution to monitoring and conservation/protection efforts at small to medium spatial scales. Taking into account that commercially available spaceborne data at 30 cm spatial resolution already exist today (e.g. WorldView-3) and an increasing number of commercial companies have started to operate in the sector of readily available, very high spatial resolution multispectral datasets, it is likely that operational monitoring of biodiversity should also be possible at larger scales. However, it remains to be investigated what the impact of a reduction of spatial

resolution from 10 cm (UAV data in this study) to, for example, 30 cm would be on the performance of our proposed method to monitor grassland biodiversity.

Selection of the spectral diversity metrics

Our results also suggest that selecting appropriate spectral metrics plays an important role in quantifying plant species richness and may not be compensated by using additional spectral information. A successful spectral metric reflects species richness rather than extreme values in the spectral data that originate from different sources, which do not reflect the overall characteristics of the community. These extreme values may represent spectral noise, bare ground reflectance (Gholizadeh et al., 2018), illumination geometry (Weyermann et al., 2014) or dead biomass. Metrics that are heavily influenced by extreme values, that is, CHV and CV should, therefore, be used with care (Gholizadeh et al., 2018). In our case, the presence of dead biomass and its spectral contrast to live biomass (Beerli et al., 2007; Numata et al., 2007; Schweiger et al., 2015) was partially responsible for the high spectral diversity calculated by the CHV and CV metrics. Removing the spectral signal for dead biomass from the data would theoretically be possible by using spectral unmixing techniques. However, this requires an additional processing step. It might be easier to tackle this problem by using metrics such as spectral species richness, which are less sensitive to extreme values (Rocchini et al., 2016). Such a classification-based approach can be less sensitive to pixels corresponding to dead biomass. In particular, dead biomass may be classified as a distinct spectral species, minimizing its effect upon spectral diversity. Yet, this metric is only suitable if the spectral differences between plant species are large enough to identify single species (Wang, Gamon, Schweiger, et al., 2018) or at least different plant life forms (Polley et al., 2019; Schweiger et al., 2017). The good performance of the spectral species richness metric in our study is in line with similar plant life form or plant community type classifications used in previous studies with UAV data (Fraser et al., 2016; Kattenborn, Eichel, et al., 2019; Lu & He, 2018; Villoslada et al., 2020). The better performance of the spectral species richness metric has also been found in large-scale satellite applications (Schmidtlein & Fassnacht, 2017).

In addition to the selection of the spectral metric, also the way in which plant diversity was measured may affect the spectral diversity–biodiversity relationship. We used the number of plant species (richness) as a measure of plant diversity. However, Wang, Gamon, Schweiger, et al. (2018) found an improved relationship between spectral diversity and plant diversity in experimental grasslands when adding species evenness to species richness. In

particular, species evenness combined with species traits may better represent the complexity of the canopy structure (Rossi et al., 2020), which can drive spectral diversity. Overall, to maximize the spectral diversity–biodiversity relationship, we suggest testing and comparing various plant diversity indices that incorporate both the relative abundances of species and a measure of differences (e.g. in traits or phylogeny) between them.

Confounding effects of biomass in the spectral diversity–biodiversity relationship

In contrast to the studies of Gholizadeh et al. (2018, 2019), Schweiger et al. (2018), Wang, Gamon, Cavender-Bares, et al. (2018) and Wang, Gamon, Schweiger, et al. (2018), spectral information (i.e. spectral complexity) was negatively correlated with plant diversity in our study, independent of the number of spectral bands considered. We hypothesize that plant biomass was the strongest confounding factor since increasing biomass is assumed to cause higher canopy structure complexity and consequently higher spectral complexity. Our hypothesis partly reflects the spectral diversity–biodiversity relationship found by Villoslada et al. (2020), which turned negative in communities with high plant biomass. In our grassland ecosystems, fertilized plots produced high amounts of plant biomass, which in turn led to a steep decrease in plant species richness (Borer, Seabloom, et al., 2014). In contrast, in the grasslands artificially composed of a limited species pool studied by Gholizadeh et al. (2018), Schweiger et al. (2018), Wang, Gamon, Cavender-Bares, et al. (2018) and Wang, Gamon, Schweiger, et al. (2018), plant biomass was positively correlated with species richness (Wang et al., 2016). Overall, a positive relationship between biomass and plant species richness reported from experimental grasslands (Tilman et al., 1996), does not necessarily hold for naturally assembled or fertilized grasslands (Borer, Seabloom, et al., 2014; Fraser et al., 2015) with major consequences for deriving plant species richness from spectral diversity.

A first possible explanation for the positive spectral diversity–biomass relationship in high biomass communities is the presence of large amounts of dead biomass (Gavazov, 2010). However, the spectral response of dead biomass is relatively homogeneous. Therefore, in communities where dead biomass is more abundant than live biomass, the homogeneity of dead biomass could lead to a decrease in the spectral information content. High biomass can also lead to high canopy complexity and a diverse spectral response (Zhang et al., 2015), for example, due to shadowing. Hence, in high biomass plots with only a few plant species, these species may cause heterogeneous patterns of light extinction and scattering of

radiant flux as described by canopy reflectance models (Verhoef, 1985), which can lead to high spectral information despite low plant species richness. Similarly, varying observation geometries between the sun, target pixel and sensor, the so-called bidirectional reflectance distribution function (BRDF), can heavily affect the measured spectral information (Müller et al., 1998; Schaepman-Strub et al., 2006), which can result in a few species causing high spectral diversity. We tried to reduce BRDF effects by using a high amount of image overlap, which produces near-nadir view geometries (Assmann et al., 2019) but did not further minimize BRDF effects (Li et al., 2012; Vögtli et al., 2021; Wierzbicki et al., 2018). Yet, we think that it may be valuable to address these issues in future studies. For example, the local illumination and observation geometry for each pixel could be calculated based on the characteristics of the sensor, the solar angle and the local orientation of the canopy (Jia et al., 2020). In particular, canopy orientation information could be obtained from a digital surface model generated through photogrammetry from the UAV imagery. Sensor view zenith and azimuth angles may be calculated using the projection vectors from the camera to each pixel (Tu et al., 2018). Alternatively, a recent study (Arroyo-Mora et al., 2021) showed that BRDF effects of vegetation could be mitigated under diffuse light conditions (i.e. clouds). Obtaining spectral data under different light conditions is possible with UAVs and should therefore be used to further investigate the impact of diffuse light conditions on spectral diversity measurements. Confounding effects on the spectral diversity–biodiversity relationship not considered in this study are, for example, the temporal variability of spectral diversity due to phenology, management and weather conditions (Gholizadeh et al., 2020; Rossi et al., 2021; Schmidlein & Fassnacht, 2017). Furthermore, bare soil removed from our analysis could also be a good proxy for species richness, either because it indicates sparsely vegetated areas with many unique species or areas with generally low species numbers. Therefore, investigating the spectral diversity–biodiversity relationship at multiple temporal stages and in different ecosystems exhibits a valid direction for future research suitable for UAV applications.

Conclusions

Spectral diversity–biodiversity relationships depend on the grassland ecosystems studied. The correlation between plant biomass and plant species richness, which can be positive or negative, can confound this relationship. We found that spectral metrics that rely on spectral complexity are much more strongly influenced by the correlation between species richness and plant biomass than

classification-based spectral metrics. Classification-based spectral metrics, such as spectral species richness, can mitigate confounding effects and lead to satisfactory results in species-rich grasslands, that is, a positive correlation between plant species richness and spectral diversity. In addition, we were able to show that fusion techniques that combine the high spatial resolution of UAV-mounted cameras with the high spectral resolution of airborne imaging spectroscopy improved the small-scale estimation of plant species richness in grasslands. Hence, data fusion represents a powerful way to achieve adequate spatial and spectral resolution for quantifying biodiversity using remote sensing techniques. Nevertheless, a high spatial resolution from UAV data proved to be more important than high spectral resolution from airborne imaging spectroscopy.

Our results suggest that spatial resolution should be prioritized in future satellite missions aiming to quantify species richness in grasslands. We are aware that obtaining spatial resolutions in which an individual plant corresponds to a pixel will not be feasible. Therefore, investigations to compensate spatial resolution by spectral or even temporal resolution should be a future goal. To our knowledge, no study has simultaneously analysed the trade-offs between the spatial, spectral and temporal dimensions of remote sensing data for quantifying biodiversity to date.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Radiometric calibration of UAV data.

Appendix S2. Average AVIRIS-NG spectra.

Appendix S3. Results of linear regression models.

Appendix S4. Data fusion.

Appendix S5. Spectral species map.