Received: 8 December 2022 | Revised: 16 August 2023 | Accepted: 5 September 2023

DOI: 10.1111/geb.13759

Global Ecology and Biogeography | A Journal of Macroecology

WILEY

RESEARCH ARTICLE

Making remote sense of biodiversity: What grassland characteristics make spectral diversity a good proxy for taxonomic diversity?

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Funding information
Division of Environmental Biology, Grant/Award Number: 1637686; National Institute of Food and Agriculture, Grant/Award Number: 2018-68002-27923

Handling Editor: Lenore Fahrig

Abstract

Aim: The spectral variability hypothesis (SVH) predicts that spectral diversity, defined as the variability of radiation reflected from vegetation, increases with biodiversity. While confirmation of this hypothesis would pave the path for use of remote sensing to monitor biodiversity, support in herbaceous ecosystems is mixed. Methodological aspects related to scale have been the predominant explanation for the mixed support, yet biological characteristics that vary among herbaceous systems may also affect the strength of the relationship. Therefore, we examined the influence of three biological characteristics on the relationship between spectral and taxonomic diversity: vegetation density, spatial species turnover and invasion by non-native species. We aimed to understand when and why spectral diversity may serve as an indicator of taxonomic diversity and be useful for monitoring.

Location: Continental U.S.A.

Time Period: Peak greenness in 2017.

Major Taxa Studied: Grassland and herbaceous ecosystems.

Methods: For nine herbaceous sites in the National Ecological Observatory Network, we calculated taxonomic diversity from field surveys of 20 m × 20 m plots and derived spectral diversity for those same plots from airborne hyperspectral imagery with a spatial resolution of 1 m. The strength of the taxonomic diversity–spectral diversity relationship at each site was subsequently assessed against measurements of vegetation density, spatial species turnover and invasion.

Results: We found a significant relationship between taxonomic and spectral diversity at some, but not all, sites. Spectral diversity was more strongly related to taxonomic diversity in sites with high species turnover and low invasion, but vegetation density had no effect on the relationship.

Main Conclusions: Using spectral diversity as a proxy for taxonomic diversity in grasslands is possible in some circumstances but should not just be assumed based on the SVH. It is important to understand the biological characteristics of a community prior to considering spectral diversity to monitor taxonomic diversity.

KEYWORDS
beta diversity, biodiversity, hyperspectral imagery, invasion, remote sensing, species turnover, spectral variability hypothesis

1 | INTRODUCTION

Conserving and restoring biodiversity are among the major goals for society in the next decades (CBD, 2021). Achieving these goals is challenging, yet urgent, because biodiversity is changing rapidly across space and time (Blowes et al., 2019; Newbold et al., 2018). Monitoring programmes are crucial to detect biodiversity changes. However, field surveys are heavily limited by logistical and financial constraints. With the development of imaging spectrometers, complementary approaches are now arising to map biodiversity patterns (Lausch et al., 2016; Wang & Gamon, 2019). In fact, harnessing remote sensing technology is increasingly suggested as the way to move forward to realizing frequent and spatially explicit biodiversity observations (Besson et al., 2022; Jetz et al., 2016; Skidmore et al., 2015).

One approach to remotely sensing biodiversity is using spectral diversity, quantified as the variation in radiation reflected from a set of pixels across a set of wavelengths, as a proxy for taxonomic diversity, quantified as species numbers and variation in their abundance (Magurran, 1988; Wang & Gamon, 2019). The spectral variation hypothesis (SVH) predicts that spectral diversity increases as biodiversity increases because spectral signatures capture subtle differences in biochemical, physiological and structural characteristics across plant species (Palmer et al., 2000, 2002). Over the last two decades, the SVH has been tested in various ecosystems and conditions, with some studies supporting the hypothesis (see references in Rocchini et al., 2010 for older approaches; Hakkenberg et al., 2018; Frye et al., 2021), and others finding no or even negative relationships between spectral diversity and taxonomic diversity (e.g., Imran et al., 2021; Möckel et al., 2016; Rossi et al., 2022).

Across these cases, one intriguing pattern to emerge is that the SVH holds up more often in forests compared to herbaceous systems (Schweiger & Laliberté, 2022). This difference could be due to a scale mismatch between field sampling and remotely sensed data: individuals in grasslands and other herbaceous ecosystems are typically smaller than the pixel size of remotely sensed imagery (but see Lopatin et al., 2017; Wang et al., 2018). Nevertheless, there are some grassland studies where relatively coarse imagery was successfully employed to assess taxonomic diversity (e.g., Gholizadeh et al., 2020; Wang et al., 2016), raising the question why the SVH holds in some grasslands but not in others. Here, in addition to methodological issues of scale, we ask if biological characteristics might also be at play in affecting the strength of the relationship between taxonomic and spectral diversity.

We explore three potential moderators that may explain variation in the strength of the taxonomic diversity–spectral diversity relationship (Figure 1). First, vegetation density could impact the relationship between taxonomic and spectral diversity. Soil has a spectral signature that is very distinct from that of vegetation and may increase spectral diversity in areas with sparse vegetation cover, regardless of whether the plant community is highly diverse or not (Gholizadeh et al., 2018). Second, the spatial distribution of species in a community could influence the relationship between taxonomic and spectral diversity. Since one pixel likely represents a community rather than a plant individual in herbaceous systems, we expect that spectral diversity best picks up taxonomic diversity when species are heterogeneously distributed across the community, in other words, when spatial species turnover (beta diversity) is high (Wang & Gamon, 2019). For instance, spectral diversity was found to be a better proxy of taxonomic diversity in grasslands shortly after prescribed burning, presumably because this management action induced spatial heterogeneity in the community (Gholizadeh et al., 2020, 2022). Third, the relationship between taxonomic and spectral diversity could be affected by invasion of non-native species. This could be due to a variety of non-exclusive reasons. Invasion tends to reduce taxonomic diversity (Vilà et al., 2011), so in order for spectral diversity to be a good proxy of taxonomic diversity, it should also decrease with invasion. However, the addition of non-native species to a community may disproportionally increase spectral diversity compared to the addition of native species, because non-native species often exhibit biochemical and structural traits that are quite different from the native vegetation (Funk et al., 2008; Helsen et al., 2020; Van Cleemput et al., 2020). Alternatively, invasion may lead to biotic homogenization (Olden et al., 2004) and hence decreased species turnover, a pattern that we expect to weaken the relationship between taxonomic and spectral diversity (see Moderator 2 in Figure 1). Consequently, we expect spectral diversity to be less closely related to taxonomic diversity when a system is invaded.

To test these predictions about biological characteristics affecting the strength of the taxonomic diversity–spectral diversity relationship, we examine this relationship across sites while holding spatial extent (plot size) and resolution (pixel size) constant. Using standardized data from the National Ecological Observatory Network (NEON) on species presence and cover (1 m × 1 m quadrats nested in 20 m × 20 m plots) and airborne hyperspectral imagery with a spatial resolution of 1 m across nine herbaceous sites across the continental United States, we are able to test which biological characteristics influence the strength of the taxonomic diversity–spectral diversity relationship. We predict that this relationship is context dependent, and that spectral diversity is more closely related to taxonomic diversity when (i) vegetation density is high; (ii) species turnover (beta diversity) is high; and (iii) invasion is low.

2 | MATERIALS AND METHODS

2.1 | Sampling design

Our work is focused on terrestrial grassland and herbaceous ecosystems included in NEON. NEON is a US-based monitoring initiative, that collects information on terrestrial and aquatic ecosystems using field-based measurements as well as airborne observations (Thorpe et al., 2016). Within the NEON network, there are 81 sites organized within 20 ecoclimatic domains, of which 10 terrestrial sites have "grassland/herbaceous" listed as a dominant cover type (sometimes

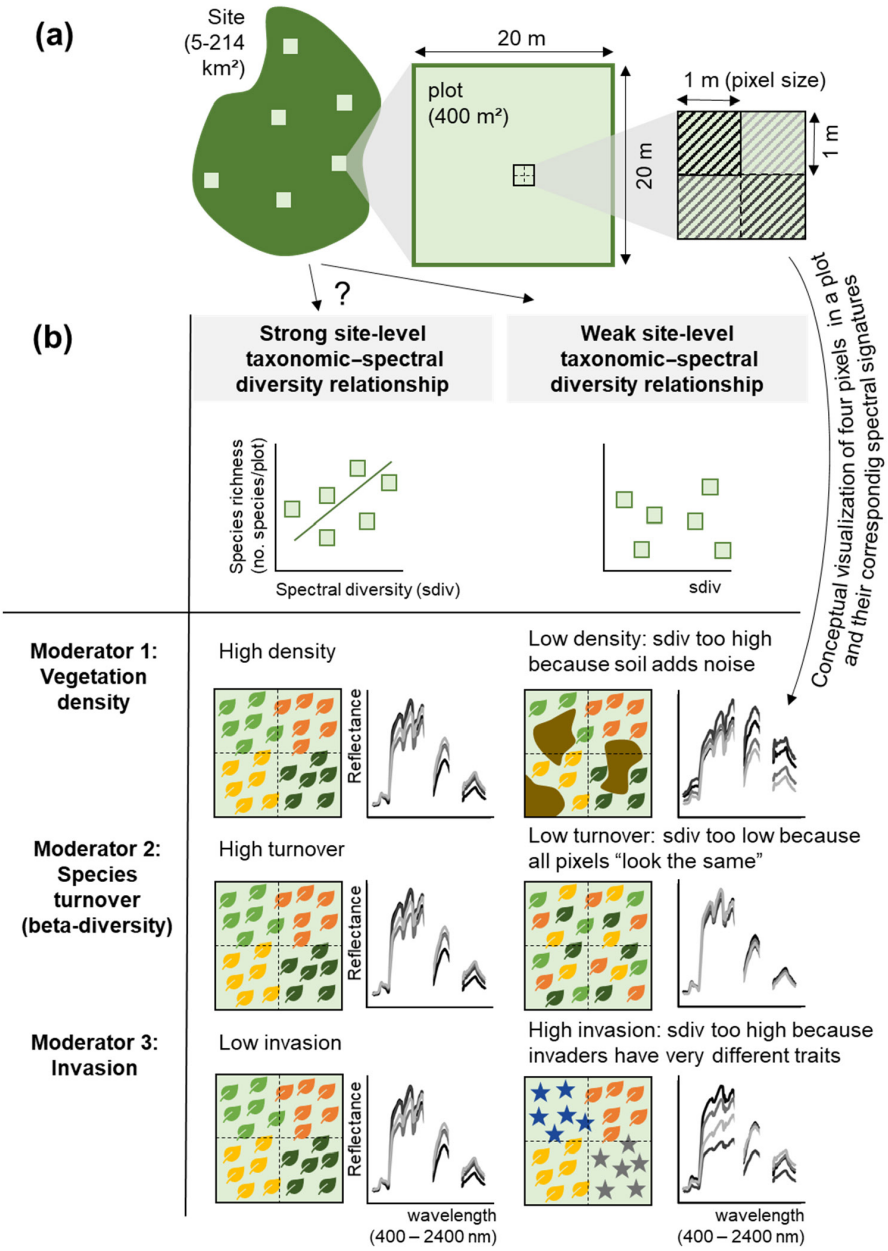

FIGURE 1 Conceptual figure of the sampling design (a) and the three proposed moderators that may affect the strength of the taxonomic diversity–spectral diversity relationship (b). At each site, the taxonomic diversity–spectral diversity relationship was fit using plot-level measurements (400 m^2) of taxonomic and spectral diversity (as exemplified in the first row of b). To conceptually clarify the three proposed moderators, we zoom in on four pixels covering equal species richness (four species, indicated by the coloured leaf and star symbols) and, next to that, visualize each pixel's hypothetical spectral signature with a different shade of grey. We expect a stronger link between taxonomic and spectral diversity when vegetation density is high (Moderator 1), species turnover is high (Moderator 2) and invasion is low (Moderator 3). The reasoning behind this is that we expect spectral diversity (sdiv; i.e., the variation across the spectral signatures) to be disproportionally higher when vegetation density is low, due to contributions of bare soil to a pixel's spectral signature (Moderator 1), and disproportionally lower when species turnover is low, because spectral signatures represent pixel-level communities and not single plant individuals (Moderator 2). Invasion may break the link between taxonomic and spectral diversity because it disproportionally increases spectral diversity, due to non-native species (star symbols) exhibiting distinctive functional traits (Moderator 3), or because of alternative pathways (e.g., through a decreased species turnover, as depicted in Moderator 2). The size of the individuals visualized in this figure is not representative of real plant sizes, but was chosen for the purpose of conceptually visualizing the moderators.

along with other dominant vegetation types). We further refer to these sites as herbaceous sites. We used data collected in 2017 since nine herbaceous sites were sampled with flights in that year (Figure 2, Table S1).

Within the terrestrial ecosystems, NEON employs a permanent plot network that is monitored yearly. Species presence is surveyed in plots of 20 m × 20 m. Within those plots, there are eight quadrats of 1 m × 1 m for which species percent cover is noted on top of

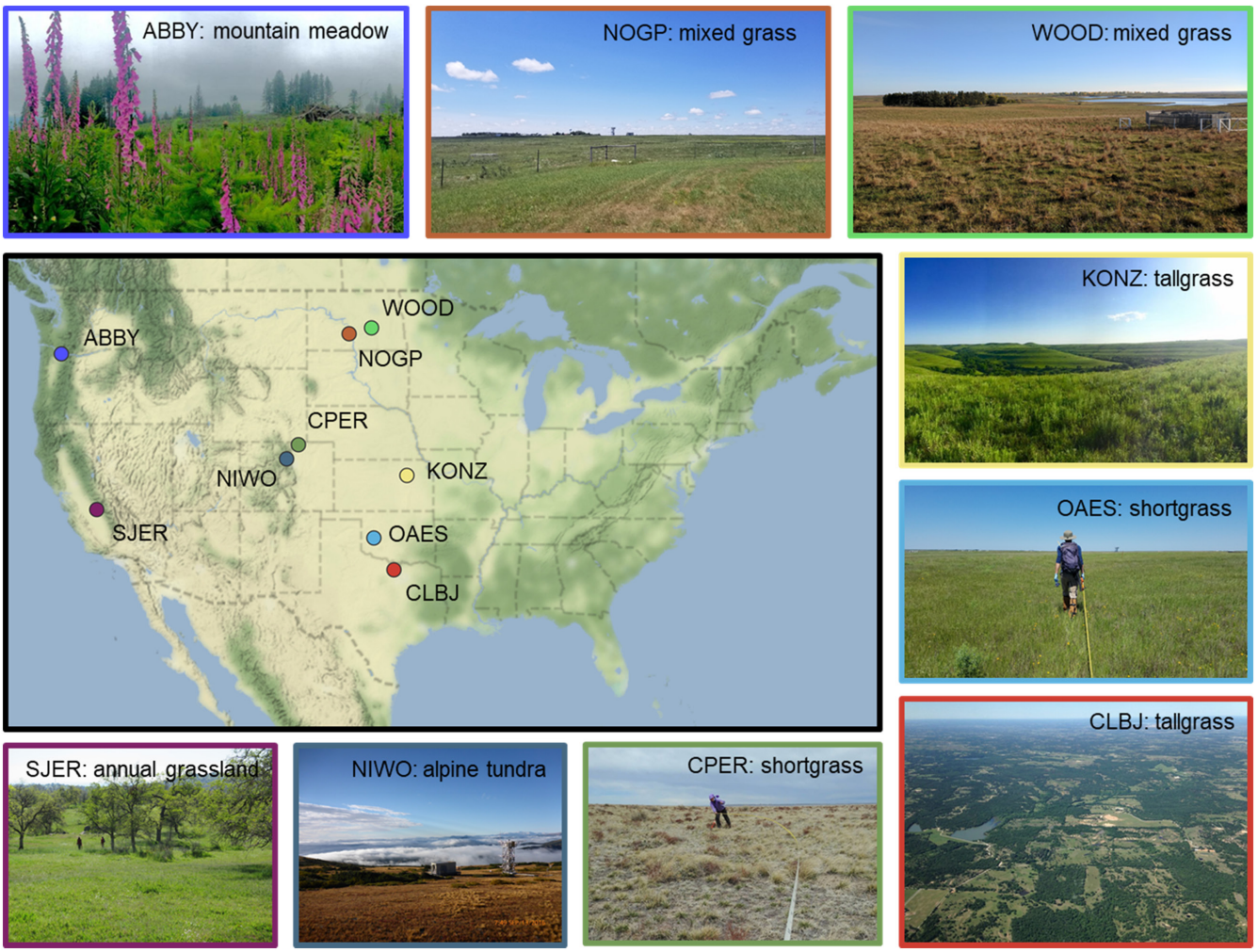

FIGURE 2 Location of NEON sites. We analysed data from grassland and herbaceous plots, extracted from nine sites: ABBY is Abby Road; CLBJ is Caddo—Lyndon B. Johnson National Grassland; CPER is Central Plains Experimental Range; KONZ is Konza Prairie Biological Station; NIWO is Niwot Ridge Mountain Research Station; NOGP is Northern Great Plains Research Laboratory; OAES is Marvin Klemme Range Research Station located on the Oklahoma Agricultural Experiment Station; SJER is San Joaquin Experimental Range; WOOD is Woodworth. Map tiles by Stamen Design, CC BY 3.0. Mat data: © OpenStreetMap contributors. All pictures are from NEON.

presence (number of quadrats changed to six from 2019 onwards) (NEON user guide DP1.10058.001) (Figure S1). Field-based observations of species presence and abundance are generally made in approximately a 1-2-month period around peak flowering (Table S1). We only considered "grassland/herbaceous" plots in this study (number of plots per site ranged between 6 and 33).

On a rotating basis, NEON sites are surveyed remotely, using a set of sensors mounted onto a De Havilland DHC-6 Twin Otter aircraft. NEON's Airborne Observations Platform operates a full waveform light detection and ranging (LiDAR) instrument and a push-broom hyperspectral imaging spectrometer. The LiDAR instrument is an Optech Incorporated Airborne Laser Terrain Mapper Gemini, emitting pulses of 1064 nm with a width on the order of 10 ns and nominal pulse repetition frequency of 100 kHz. The hyperspectral sensor operates in the electromagnetic spectral region between 0.38 and 2.5 microns with a spectral sampling of 0.5 nm (426 bands). NEON applies a series of in-house preprocessing algorithms to the LiDAR and spectrometer flight line data. Full waveforms measured by the LiDAR instrument are converted into discrete returns, which in turn are converted into a point cloud (NEON.DOC.001292). From this point, cloud several raster products are derived, including canopy height (NEON.DOC.002387). The raw radiance data from the spectrometer are first calibrated (NEON.DOC.001210), orthorectified and co-registered to the LiDAR data (NEON.DOC.001290), after which they are converted to reflectance, using the ATCOR-4 atmospheric correction algorithm (NEON.DOC.001288). Several spectral vegetation indices, including the normalized difference vegetation index (NDVI, NEON.DOC.002391), and other metrics, such as the leaf area index (LAI, NEON.DOC.002385), are subsequently computed from the reflectance cube and are readily available for download. Both the LiDAR and spectrometer data are processed and mosaicked in-house to 1-m spatial resolution products (NEON.DOC.004365). Most sites are flown around peak greenness, but the timing does not necessarily align well with that of field-based surveys, due to the sometimes-substantial temporal variation in the field data collection (Table S1). Therefore, we only retained plots

that were surveyed within 2 months (61 days) before or after the airborne data were collected.

2.2 | Taxonomic and spectral diversity

For each "grassland/herbaceous" plot, we quantified three metrics of taxonomic diversity. First, we calculated species richness based on species presence observations recorded for the full extent (400 m^2) of the plots. Because species abundance is another important aspect of taxonomic diversity, we also calculated two abundance-weighted metrics of taxonomic diversity. Using species cover data from the eight 1-m^2 quadrats within a plot, we derived the exponentiated Shannon entropy and inverse Simpson concentration for each plot with the "vegan" R package (Oksanen et al., 2019). We used exponentiated Shannon entropy and inverse Simpson concentration rather than their raw forms because they represent the "effective number of species" rather than "the uncertainty in species identity" in a plot (Jost, 2006). Given the sampling incompleteness of the abundance-based metrics and the more widespread use of species richness in ecosystem assessments, we use species richness as our primary taxonomic diversity metric and report results of the abundance-weighted metrics in the Supplementary Information.

For each plot, we computed three metrics of spectral diversity that are commonly used in spectral diversity studies (Frye et al., 2021; Gholizadeh et al., 2018). First, the coefficient of variation (CV; Wang et al., 2016) is a metric of the spectral "complexity" of a plot. It was computed by calculating the CV for each band across all pixels (1 m × 1 m) in a plot (20 m × 20 m) and then taking the average of all band-specific CVs. Second, the spectral angle mapper (SAM; Kruse et al., 1993) quantifies the dissimilarity between two spectral signatures as the angle in multidimensional spectral space. For each plot, we calculated the angle between each individual pixels' spectral signature and the plot's average spectral signature. These angles were subsequently averaged across all pixels in a plot to retrieve the average SAM of a plot (script adapted from Frye et al., 2021). Third, we calculated the convex hull volume (CHV; Dahlin, 2016) encompassed by all pixels within a plot. We calculated this volume using the first three principal components derived from the hyperspectral data. For all three spectral diversity metrics, higher values indicate higher diversity. Because these three spectral diversity metrics were strongly correlated (Pearson $r = 0.78–0.91$, Figure S2), we focus on CV and include results for SAM and CHV in the Supplementary Information.

Prior to calculating plot-level spectral diversity metrics, we applied some standard preprocessing steps to the spectral signatures. This custom spectral preprocessing consisted of removing noise (350–400 nm and 2400–2550 nm) and atmospheric absorption bands (1325–1455 nm and 1775–1970 nm), rendering a total of 333 bands for analysis. We also applied the Savitzky–Golay spectral smoothing algorithm with a window of seven bands. Preprocessing steps were performed using the "hsdar" R package (Lehnert et al., 2019). Finally, we masked all pixels with an NDVI ≤ 0.2 and a canopy height ≥ 2 m (detection limit of the airborne LiDAR sensor) to retain only pixels that are dominated by live herbaceous vegetation (Figure S3).

2.3 | Evaluating the spectral variability hypothesis

To evaluate the validity of the SVH and strength of the taxonomic diversity–spectral diversity relationship, we fit linear regression models with taxonomic diversity as the response variable and log-transformed spectral diversity as the explanatory variable. We fit this model structure on the full dataset, containing taxonomic and spectral measurements of all sites combined, and on data of each site separately, to obtain site-specific taxonomic diversity–spectral diversity relationships. To more directly assess the context specificity of the SVH, we also fit linear regression models with taxonomic diversity as the response variable, log-transformed spectral diversity, site and the interaction between log-transformed spectral diversity and site as explanatory variables on the pooled dataset. We fit a separate model for each metric of taxonomic diversity (species richness, exponentiated Shannon entropy and inverse Simpson concentration) and each metric of spectral diversity (CV, SAM and CHV). To assess the strength of the taxonomic diversity–spectral diversity relationships, we determined the coefficient of determination (R^2) and slope of the relationships. Both of these metrics are used in the SVH literature (e.g., Gholizadeh et al., 2020; Wang et al., 2018).

2.4 | Evaluating the effect of biological characteristics on the strength of the taxonomic–spectral diversity relationship

We determined three types of site-level characteristics to test our three potential moderators. First, we used measures of productivity as a proxy for vegetation density. These included NDVI and LAI derived by NEON from the hyperspectral airborne imagery, and herbaceous net primary productivity (NPP, g carbon m^{-2} $year^{-1}$), calculated as the sum of annual and perennial forbs and grasses NPP which is provided by the Rangeland Analysis Platform (https://rangelands.app/, version 2 of the dataset). These NPP products are model-based predictions based on Landsat imagery (30-m spatial resolution) (Robinson et al., 2019) and were accessed using the Google Earth Engine. From the detailed cover surveys of the 1-m^2 quadrats within each plot, we also calculated the average percentage soil cover per plot, as a more direct, but inverse, measure of vegetation density. Site-level plant density was computed as the average NDVI, LAI, herbaceous NPP and soil cover across all plots.

To test our second moderator, we determined within-plot spatial species turnover or beta diversity as the slope of the semilogarithmic species–area relationship (SAR; Ricotta et al., 2002). For each plot, a SAR was fit using the "sars" R package (Matthews et al., 2019), as

$$S_N = k + h\,log(N); \quad (1)$$

where S_N is the total number of species recorded within an area of N (m^2). The paired information on S_N and N was obtained from the individual quadrat surveys (8 times 1 m^2) and computing all quadrat combinations (2–8 m^2; 247 combinations per plot). The slope h of this relationship measures the (linear) rate of accumulation of species with increasing area sampled, and therefore is an indication of the average magnitude of species turnover within a plot. Site-level species turnover was determined as the average slope across plots (Figure S4).

To evaluate our third moderator, for each plot, we determined the percentage of recorded species that are non-native, based on species presence/absence surveys of the entire plot, and the percentage vegetation cover of non-natives, based on abundance data observed in the quadrats. Again, site-level metrics were obtained by averaging across plots.

Finally, we evaluated the link between these site-level biological characteristics and the strength of the taxonomic diversity–spectral diversity relationship by fitting linear models. We fit a simple univariate model for each of the biological characteristics, linking them individually to the site-specific R^2 values and slope parameters extracted from the taxonomic diversity–spectral diversity models. If our first proposed moderating effect holds, we should observe a positive relation between the strength of the taxonomic diversity–spectral diversity relationships (R^2 and slope) and metrics of vegetation density. The same pattern should be observed with the SAR slopes (indicating species turnover) to confirm our second moderating effect. In contrast, for our third moderating effect to be true, the link between taxonomic diversity and spectral diversity should weaken with increasing presence of non-native species.

3 | RESULTS

3.1 | Spectral diversity as a proxy for taxonomic diversity

There was considerable variation in taxonomic and spectral diversity across sites (Figure 3a,b). Some sites with high species richness ranked high on spectral diversity (e.g., CLBJ), though some sites with low richness also had high spectral diversity (e.g., SJER).

When combining data across all sites, spectral diversity significantly increased with taxonomic diversity ($p<0.001$), yet only explained a small amount of the total variation in taxonomic diversity ($R^2=0.08$) (Figure 4a, Table 1). The fit improved considerably when including site as an additional explanatory variable ($R^2=0.65$), indicating that the relationship between taxonomic and spectral diversity is context-specific (Table 1). These patterns were observed when linking species richness to CV, but also for the other taxonomic and spectral diversity metrics (Tables S2 and S3). Site-specific models, linking taxonomic and spectral diversity at each site separately, had an R^2 ranging between 0.0002 and 0.38 (Table 1). We found a (marginally) significant positive relationship between species richness and spectral CV at some sites (CLBJ: $p=0.02$, CPER: $p=0.09$, NOGP: $p=0.06$, OAES: $p=0.01$), but not at others ($p>0.10$ for ABBY, SJER, KONZ, NIWO, SJER and

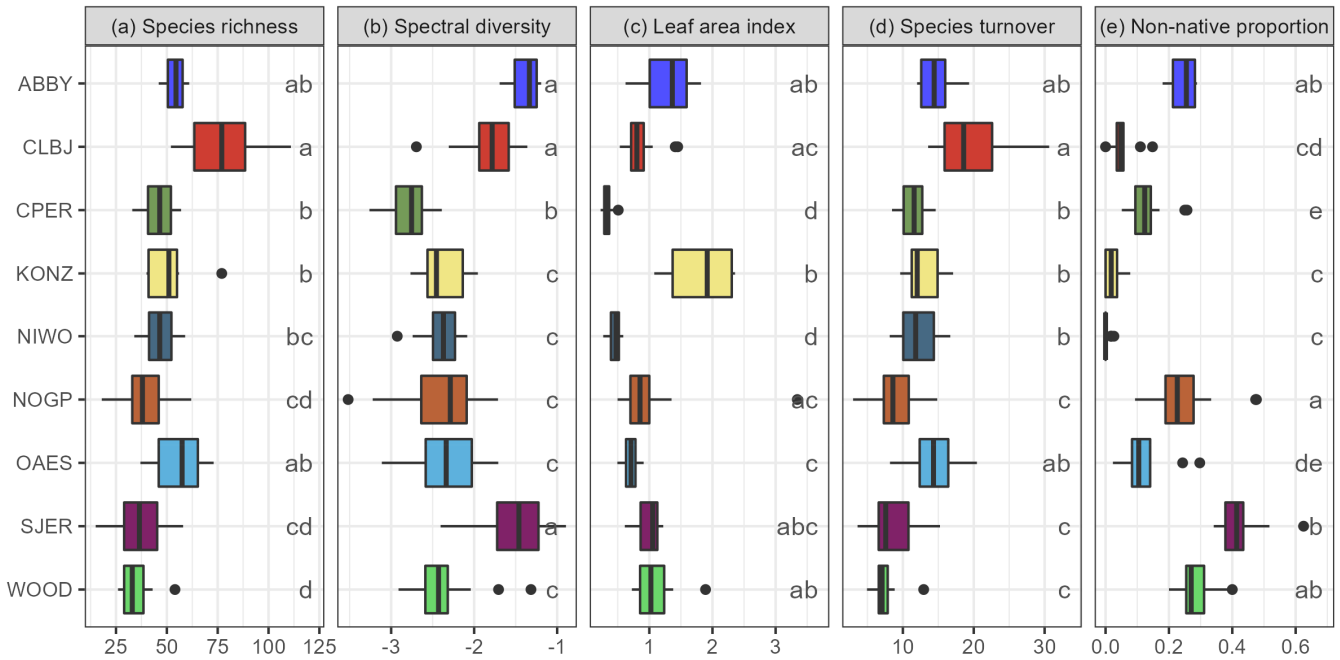

FIGURE 3 Boxplots of species richness (a), spectral diversity (b; here represented by the log-transformed spectral coefficient of variation; CV), vegetation density (c; represented as leaf area index), species turnover (d) and invasion (e; represented as the proportion of the total species richness that is non-native). Pairwise group comparisons were performed via Dunn's tests with Benjamini–Hochberg adjusted p-values (code adapted from Van Cleemput et al., 2021). Groups that share a letter were not significantly different (0.95 confidence level). For site abbreviations, see Figure 2.

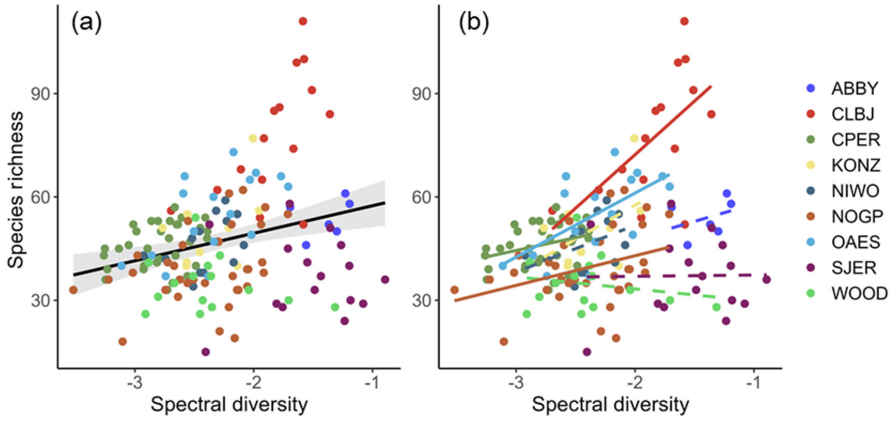

FIGURE 4 Relationships between taxonomic diversity, here represented by species richness, and spectral diversity, here represented by the log-transformed spectral coefficient of variation. Each point represents a plot for which taxonomic and spectral diversity were calculated. Taxonomic diversity–spectral diversity relationships were fit for all plots of all sites combined (a) and for each site separately (b). Full and dashed lines indicate sites for which the *p*-value of the slope was ≤0.1 and >0.1 respectively (Table 1). See Tables S2 and S4 for model statistics and model results based on other taxonomic and spectral diversity metrics. For site abbreviations, see Figure 2.

TABLE 1 Regression results of models relating taxonomic diversity (here species richness) to spectral diversity (sdiv; here log-transformed spectral coefficient of variation).

	R^2	Slope sdiv	*p*-value sdiv	*p*-value site	*p*-value interaction
All sites combined ($n=156$)					
Species richness ~ sdiv	0.08	7.99	<0.001		
Species richness ~ sdiv + site + sdiv:site	0.65	Ranges between −3.49 and 31.08	<0.001	<0.001	0.029
Individual sites					
Species richness ~ sdiv at					
ABBY ($n=6$)	0.12	10.1	0.49		
CLBJ ($n=15$)	0.35	31.08	0.02		
CPER ($n=32$)	0.09	7.46	0.09		
KONZ ($n=9$)	0.23	19.65	0.19		
NIWO ($n=14$)	0.18	13.61	0.13		
NOGP ($n=33$)	0.11	8.61	0.06		
OAES ($n=16$)	0.38	18.57	0.01		
SJER ($n=16$)	0.0002	0.37	0.96		
WOOD ($n=15$)	0.04	3.49	0.49		

Note: Models were fit for data pooled across sites and for each site separately. Results for other taxonomic and spectral diversity metrics can be found in the Supplementary Information (Tables S2–S4). For site abbreviations, see Figure 2.

WOOD) (Figure 4b, Table 1). For some sites, the significance of the taxonomic diversity–spectral diversity relationship changed when using other metrics of taxonomic and spectral diversity (Table S4).

3.2 | Which biological variables explain variation in the taxonomic diversity–spectral diversity relationship?

We found mixed support for our proposed biological characteristics moderating the strength of the taxonomic diversity–spectral diversity relationship.

First, there was no general support for a moderating effect of vegetation density on the strength of the taxonomic–spectral diversity relationship. We did not find significant effects of LAI, nor NDVI, herbaceous NPP or soil cover, on the strength (R^2 and slope) of the species richness–spectral diversity relationships (Figure 5a, Table 2). This was also observed for the models using abundance-weighted taxonomic diversity metrics, with a few exceptions (Tables S5 and S6).

We found evidence for our second proposed moderating effect: Spectral diversity was a better proxy for taxonomic diversity in sites with higher within-plot species turnover (beta diversity). Both the slope and the R^2 of the species richness–spectral diversity

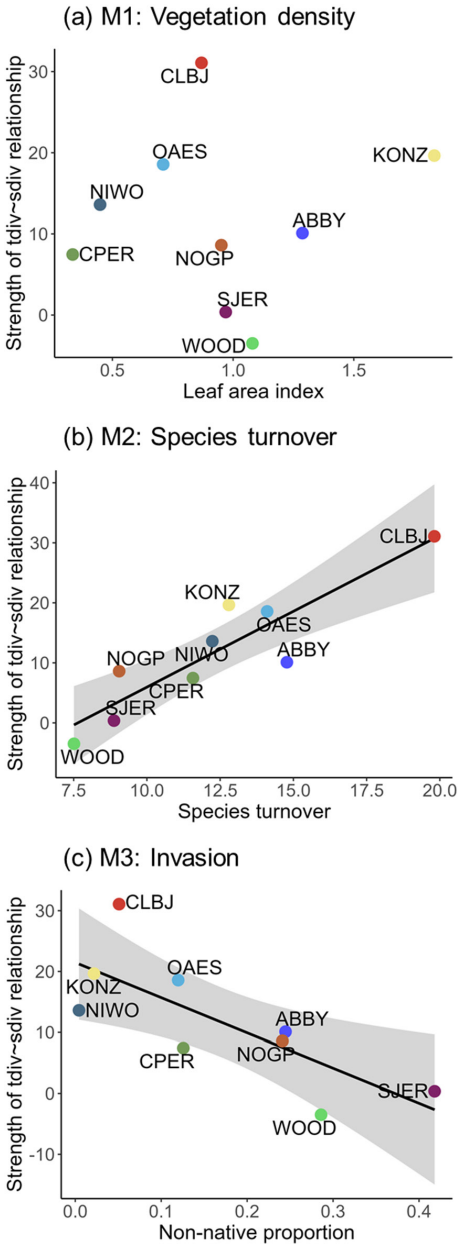

FIGURE 5 Variation in the strength of the taxonomic diversity–spectral diversity relationship (quantified as the slope of the tdiv~sdiv relationship at each site) as a function of vegetation density, represented as leaf area index (a); within-plot beta diversity, represented as spatial species turnover (b); and invasion, represented as the proportion of species that are non-native (c). Taxonomic diversity and spectral diversity are represented by species richness and the log-transformed spectral coefficient of variation respectively. For site abbreviations, see Figure 2.

relationships increased with beta diversity (Figure 5b, Table 2). Similarly, the slope of the relationship between abundance-weighted taxonomic diversity metrics and spectral diversity increased with beta diversity (Tables S5 and S6). Variation in species turnover was independent of variation in vegetation density, as indicated by low pairwise correlations (*r* ranging between −0.06 and 0.17; Figure S2). Species turnover positively correlated to both taxonomic diversity

TABLE 2 Regression results of models relating the strength (slope and R^2) of the taxonomic diversity–spectral diversity relationship to biological characteristics, to test our three proposed moderators (M).

	Slope of species richness ~ sdiv relationship		R^2 of species richness ~ sdiv relationship	
	ß (*p*-value)	R^2	ß (*p*-value)	R^2
M1: vegetation density				
LAI	1.70 (0.85)	0.01	−0.002 (0.98)	0.0001
NDVI	2.90 (0.92)	0.002	−0.002 (0.996)	0.000004
Herbaceous NPP	0.32 (0.29)	0.16	0.004 (0.23)	0.20
Soil cover	0. (040)	0.11	−0.0 (0.71)	0.02
M2: beta diversity				
Species turnover	**2.53 (<0.001)**	**0.81**	**0.03 (0.01)**	**0.63**
M3: invasion				
%SR invaded	**−57.72 (0.02)**	**0.58**	**−0.67 (0.03)**	**0.51**
% cover invaded	**−0.21 (0.03)**	**0.51**	−0.002 (0.07)	0.39

Note: Taxonomic diversity and spectral diversity (sdiv) are represented by species richness and the log-transformed coefficient of variation respectively. Models were fit for each biological characteristic separately to test each moderator. ß denotes the slope of the models. LAI is leaf area index; NDVI is the normalized difference vegetation index; NPP is net primary production. Significant relations ($p \leq 0.05$) are indicated in bold. Results for other spectral diversity metrics and other metrics of vegetation density and invasion can be found in the Supplementary Information (Tables S5 and S6).

(*r* ranging between 0.65 and 0.94) and spectral diversity (*r* ranging between 0.23 and 0.34) (Figure S2).

Third, we found support for our last proposed moderator, invasion, weakening the relationship between taxonomic and spectral diversity. The slope of the species richness–spectral diversity relationship decreased as the percentage of total species richness and vegetation cover that was non-native increased (Figure 5c, Table 2). Likewise, the R^2 of the link between species richness and spectral diversity decreased with an increasing proportion of species that are non-native (Table 2). The slope of the relationship between abundance-weighted taxonomic diversity metrics and spectral diversity also declined with invasion (Table S5). Highly invaded plots were associated with higher vegetation density (*r* ranging between −0.0004 and 0.44) and lower species turnover ($r = -0.55$ and $r = -0.56$) (Figure S2). Invaded plots showed lower taxonomic diversity (*r* ranging between −0.37 and −0.54), but, despite the lower species turnover, also exhibited higher spectral diversity (*r* ranging between 0.07 and 0.32) (Figure S2).

4 | DISCUSSION

Across grassland and herbaceous ecosystems in NEON, we found mixed support for the spectral variability hypothesis, which assumes that spectral diversity is positively related to taxonomic diversity.

Our results demonstrate that spectral diversity represents relative variation in taxonomic diversity at some sites, even when the spatial resolution of pixels does not match the spatial scale of plant individuals, and we identified biological factors that moderate the strength of the relationship between taxonomic and spectral diversity.

4.1 | Species turnover and invasion, but not vegetation density, influence the strength of the taxonomic diversity–spectral diversity relationship

We assessed the influence of three biological characteristics on the strength of the taxonomic diversity–spectral diversity relationship. First, contrary to Schweiger and Laliberté (2022), spectral diversity was not a better proxy of species richness at sites with higher vegetation density. Despite restricting our analysis to herbaceous sites, there was a considerable range of vegetation density across our plots and study sites: Mean LAI ranged between 0.34 and 1.83, NDVI ranged between 0.30 and 0.78, herbaceous NPP ranged between 107.1 and 517.5 g carbon m^{-2} $year^{-1}$ and percentage soil cover ranged between 2.0 and 48.1%. Yet, this variation was not associated with a variation in the strength of the taxonomic diversity–spectral diversity relationship. While we masked out pixels that were purely soil (based on an NDVI threshold of 0.2), we expected vegetation density to still be a moderating variable because it "contaminates" spectral signatures of sparsely (but unmasked) vegetated pixels. One explanation for the lack of support for this moderator could be related to plant community characteristics other than soil that confound the relationship between taxonomic and spectral diversity at both low and high vegetation densities. At densely vegetated sites, structural complexity of the canopy may be influential. With increasing complexity of the vertical structure of a community, spectral diversity may overestimate taxonomic diversity due to shadow effects, but it could also underestimate taxonomic diversity when short species get obscured by taller species and hence are not picked up by the sensor (Conti et al., 2021). Alternatively, especially at lower densities, mosses and lichens may contribute to spectral variation but are typically not included in metrics of taxonomic diversity because they are not identified to the species level during field surveys. Second, higher within-plot spatial species turnover (beta diversity) improved the relationship between taxonomic and spectral diversity. This finding may explain the mixed support for the SVH in grassland studies using imagery with a similar spatial resolution as we use here (1 m × 1 m pixels) but different spatial extents or plot sizes: Spectral diversity has been linked to taxonomic diversity when plot sizes are rather large (e.g., Gholizadeh et al., 2020; Wang et al., 2016), but not when using smaller plots (e.g., Möckel et al., 2016; Wang et al., 2018). With increasing plot size, compositional change within a plot (spatial species turnover) becomes more prominent. Species turnover may be related to spatial heterogeneity in environmental variables, which influence the ecological niches available to different species (Soberón, 2007), and can be shaped by management. For instance, grazing and prescribed burns can modify the spatial heterogeneity of vegetation (Adler et al., 2001; Collins & Smith, 2006; Werner et al., 2021), which in turn could affect the link between taxonomic and spectral diversity (e.g., Gholizadeh et al., 2020, 2022).While it has been suggested that beta diversity may promote a positive taxonomic diversity–spectral diversity relationship (Wang & Gamon, 2019), to our knowledge our study is the first to explicitly demonstrate this.

Third, we found a weakened link between taxonomic diversity and spectral diversity with increasing invasion. This was also observed in an experimental grassland setting by Gholizadeh et al. (2019), but has so far not been demonstrated using observational data. Highly invaded plots exhibited lower taxonomic diversity, which is consistent with previous studies (Vilà et al., 2011), yet also had higher spectral diversity, which could be due to the introduction of distinct plant characteristics (Funk et al., 2008; Helsen et al., 2020; Van Cleemput et al., 2020). Big changes in the biochemical or structural composition following invasion may disproportionally increase spectral diversity and this could explain the disconnect between taxonomic and spectral diversity when non-native abundance is high. However, some highly invaded sites (e.g., WOOD, NOGP) did not show higher spectral diversity compared to less invaded sites. Instead, these sites exhibited lower species turnover, suggesting that the weaker relationship between taxonomic and spectral diversity at highly invaded sites might be partly explained by a biotic homogenization effect (Olden et al., 2004), or in other words through the second moderator. There could be other community changes related to invasion that explain the disconnect between taxonomic and spectral diversity at more invaded sites (e.g., patchiness, structural complexity), and these pathways require further exploration to fully understand the mechanisms driving our results. For instance, while we noticed that highly invaded plots also had lower species evenness (Figure S2), evenness was not correlated with the strength of the taxonomic–spectral diversity relationship (Table S7). Fusing data from multiple remote sensing instruments can help unravel these mechanisms. Invasion is substantial at some of our study sites (e.g., at SJER on average 42% of a plot's species richness was non-native), and our results suggest that monitoring biodiversity changes from hyperspectral imagery in these circumstances is challenging.

4.2 | Important caveats and future steps

Surprisingly, Schweiger and Laliberté (2022) found a negative taxonomic diversity–spectral diversity relationship for Lyndon B. Johnson National Grassland (CLBJ) and Niwot Ridge (NIWO), for which we found positive associations. It is important to note that both of these sites contain forested plots, which we excluded from our analyses, but likely influenced the site-level patterns observed by Schweiger and Laliberté (2022). This illustrates that the taxonomic diversity–spectral diversity relationship can be biome-specific and adds to recent work warning researchers to not assume the general

validity of the SVH based on theory (Fassnacht et al., 2022). Since a biome's LAI is more or less correlated with the size of the plant individuals it hosts (trees > grasses, forbs and small shrubs; Asner et al., 2003), it is difficult to disentangle scale and vegetation density effects on the taxonomic diversity–spectral diversity relationship when looking across biomes.

In this study, we sought to obtain insights into the biological conditions under which spectral variation could be a good indicator of biodiversity, and tackled this from the perspective of taxonomic diversity as it is the most widely used aspect of biodiversity. Obviously, this work can be extended to other dimensions of biodiversity. Although spectral diversity was linked to taxonomic diversity in some sites, it does not mean that spectral diversity represents species richness directly or that spectral signatures reflect species identity, per se. Instead, it is more likely that spectral diversity represents the variation in biochemical and structural properties (functional traits) of the vegetation, which presumably is related to species richness to some extent (Flynn et al., 2011; Petchey & Gaston, 2002), dictated by evolutionary history (phylogeny; Meireles et al., 2020) and adaptations to environmental and resource limitations (e.g., light, water, nutrients). Given that plant biochemical and structural properties have specific light absorption and scattering characteristics (Curran, 1989; Ollinger, 2011; Ustin et al., 2009), variation in these properties can lead to variation in spectral signatures, and thus drive spectral diversity. The idea that spectral diversity links to different aspects of biodiversity is also referred to as the "surrogacy hypothesis" (Wang et al., 2018; Wang & Gamon, 2019). Future research could explore the moderators identified here in the context of functional and phylogenetic diversity.

Our results are only valid for the spatial scale and grain of our study, calculating diversity for 20 m × 20 m plots and using spectral imagery acquired with a 1-m spatial resolution. While investigating the scale dependence of the taxonomic diversity–spectral diversity relationship is important for designing future combined field and remote sensing data collection campaigns, there is limited room to tweak operational settings of airborne (and spaceborne) missions. Sensors on drones often offer a finer spatial resolution compared to sensors on aircrafts, but this currently comes at a cost of reduced spectral resolution and total area flown. Today, advanced technology allows us to obtain hyperspectral airborne imagery with a spatial resolution of 1 m. For example, other airborne imaging spectrometers, such as the National Aeronautics and Space Administration's AVIRIS (Airborne Visible/Infrared Imaging Spectrometer, https://aviris.jpl.nasa.gov/) and the European Space Agency's APEX (Airborne PRISM Experiment, https://apex-esa.org/en/apex), operate at settings offering a similar or often coarser spatial resolution compared to NEON's hyperspectral imaging spectrometer. Therefore, evaluating biological moderating effects on the SVH is extremely relevant for grassland research and management, where the size of plant individuals typically does not match the grain/pixel size of remote sensing observations. As airborne spectral campaigns are becoming more common, we hope that intercontinental comparisons of sites become possible using data collected with the same standardized design.

5 | CONCLUSION

Monitoring biodiversity patterns is an essential part of restoration and management practices. However, because traditional field methods are extremely time and labour intensive, field surveys are often restricted in space and time. Consequently, remote sensing is increasingly suggested as a complementary tool to measure diversity, capitalizing on the idea that species have unique spectral signatures. Yet, remotely sensing biodiversity remains challenging, especially in grasslands and herbaceous systems, where individual plants are often smaller than the size of a pixel. Given that the operational settings of most remote sensing collection campaigns are set, or have limited room to be adjusted, there will be many circumstances for which the spatial resolution of the imagery does not correspond with the spatial scale of plant individuals. In this study, we started from the idea that operational settings are predetermined and sought to obtain insights into when and why a strong relationship between taxonomic and spectral diversity can be expected. Altogether, our results show that in low stature vegetation, spectral diversity can be a proxy of taxonomic diversity, if within-plot spatial species turnover is high and invasion is low. These results demand careful consideration of the actual use of remote sensing technology to follow up restoration and management efforts over large spatial scales, map biodiversity hotspots to guide conservation and tackle sampling incompleteness of field-based surveys in grasslands and herbaceous ecosystems.

ACKNOWLEDGEMENTS

This work was supported by the U.S. Department of Agriculture (NIFA 2018-68002-27923) and the National Science Foundation (DEB 1637686). The National Ecological Observatory Network is a program sponsored by the National Science Foundation and operated under cooperative agreement by Battelle. This study is based in part upon work supported by the National Science Foundation through the NEON Program. We thank the numerous scientists, ecologists and staff at NEON who collected plant community data, contributed to the acquisition and preprocessing of the airborne imagery and managed the NEON database and portal.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Species composition surveys, hyperspectral and LiDAR imagery, as well as raster products derived from the imagery (NDVI, LAI, canopy height), are available in the NEON data portal at https://data.neonscience.org/. NPP images are available in the Rangeland Analysis Platform at https://rangelands.app/. Code supporting this paper can be accessed via https://github.com/elisa-vancleemput/NEON_tdiv_sdiv.git.

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BIOSKETCHES

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SUPPORTING INFORMATION

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

How to cite this article: Van Cleemput, E., Adler, P., & Suding, K. N. (2023). Making remote sense of biodiversity: What grassland characteristics make spectral diversity a good proxy for taxonomic diversity? *Global Ecology and Biogeography*, *32*, 2177–2188. https://doi.org/10.1111/geb.13759