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Using airborne and DESIS imaging spectroscopy to map plant diversity across the largest contiguous tract of tallgrass prairie on earth

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ABSTRACT

Grassland ecosystems are under threat globally, primarily due to land-use and land-cover changes that have adversely affected their biodiversity. Given the negative ecological impacts of biodiversity loss in grasslands, there is an urgent need for developing an operational biodiversity monitoring system that functions in these ecosystems. In this paper, we assessed the capability of airborne and spaceborne imaging spectroscopy (also known as hyperspectral imaging) to capture plant α-diversity in a large naturally-assembled grassland while considering the impact of common management practices, specifically prescribed fire. We collected a robust in-situ plant diversity data set, including species composition and percent cover from 2500 sampling points with different burn ages, from recently-burned to transitional and pre-prescribed fire at the Joseph H. Williams Tallgrass Prairie Preserve in Oklahoma, USA. We expressed in-situ plant α-diversity using the first three Hill numbers, including species richness (number of observed species in a plant community), exponential Shannon entropy index (hereafter Shannon diversity; effective number of common species, where species are weighed proportional to their percent cover), and inverse Simpson concentration index (hereafter Simpson diversity; effective number of dominant species, where more weight is given to dominant species) at four different plot sizes, including 60 m × 60 m, 120 m × 120 m, 180 m × 180 m, and 240 m × 240 m. We collected full-range airborne hyperspectral data with fine spatial resolution (1 m) and visible and near-infrared spaceborne hyperspectral data from DESIS sensor with coarse spatial resolution (30 m), and used the spectral diversity hypothesis—i.e., that the variability in spectral data is largely driven by plant diversity—to estimate α-diversity remotely. In recently-burned plots and those at the transitional stage, both airborne and spaceborne data were capable of capturing Simpson diversity—a metric that calculates the effective number of dominant species by emphasizing abundant species and discounting rare species—but not species richness or Shannon diversity. Further, neither airborne nor spaceborne hyperspectral data sets were capable of capturing plant α-diversity of 60 m × 60 m or 120 m × 120 m plots. Based on these results, three main findings emerged: (1) management practices influence grassland biodiversity patterns that can be remotely detected, (2) both fine- and coarse-resolution remotely-sensed data can detect the effective number of dominant species (e.g., Simpson diversity), and (3) attention should be given to site-specific plant diversity field data collection to appropriately interpret remote sensing results. Findings of this study indicate the feasibility of estimating Simpson diversity in naturally-assembled grasslands using forthcoming spaceborne imagers such as National Aeronautics and Space Administration's Surface Biology and Geology mission.

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1. Introduction

1.1. Background

Grasslands are among the most threatened ecosystems globally, yet only a small portion of these biomes are protected (Bardgett et al., 2021; Carbutt et al., 2017; Scholtz and Twidwell, 2022). The transformation of grasslands to other cover types and their widespread degradation come with steep biodiversity and economic tradeoffs and erode ecosystem functions that underpin human well-being (Cavender-Bares et al., 2015; Purvis and Hector, 2000; Tilman et al., 1997). Given the widespread decline of grasslands and associated biodiversity, as well as the far-reaching negative impacts of land-management practices that do not consider biodiversity conservation (IPBES, 2018, 2019), developing monitoring systems to understand the status and patterns of biodiversity and inform progress towards biodiversity targets (CBD, 2021) will make critical contributions for managing these threatened ecosystems. Traditional field surveys are essential in research and management applications yet are unable to scale to the levels necessary to comprehensively monitor extensive grassland systems, which cover approximately 25–40% of the Earth land surface (Shantz, 1954; Strömberg et al., 2013). Remote sensing is a promising approach to monitor certain aspects of plant diversity across ecosystems (Lausch et al., 2016; Luque et al., 2018; Schimel et al., 2019; Turner, 2014), although details of how best to do this remain largely unanswered. In this study, we tested the effectiveness of imaging spectroscopy (also known as hyperspectral imaging) for mapping plant diversity at the Joseph H. Williams Tallgrass Prairie Preserve in Oklahoma, USA, the largest contiguous tract of tallgrass prairie on Earth.

1.2. Remote sensing of plant diversity

Recent technological and methodological advances in optical remote sensing have improved our ability to estimate plant diversity remotely (Cavender-Bares et al., 2022; Kamoske et al., 2022; Lausch et al., 2016; Luque et al., 2018; Stavros et al., 2017). Specifically, imaging spectroscopy, with its capability to capture fine spectral resolution data, is a viable tool for mapping plant diversity (Schimel et al., 2020). The link between remotely-sensed data and plant diversity exists since spectral reflectance captures vegetation attributes associated with plant diversity (Kothari and Schweiger, 2022). One way to formally express the relationship between spectral data and plant diversity is through spectral diversity (Asner and Martin, 2009; Gholizadeh et al., 2019; Laliberté et al., 2020; Palmer et al., 2002; Rocchini et al., 2010; Rocchini et al., 2004; Wang et al., 2018a). The spectral diversity hypothesis states that variation in spectral data within a plant community is an indicator of plant diversity for that community. Specifically, individual plants species display different biochemical, physiological, structural, and phenological attributes. These traits, along with other environmental factors, influence remotely-sensed spectral data. As such, different plant species presumably display themselves differently in remotely-sensed data (Asner et al., 2015; Cavender-Bares et al., 2017; Ollinger, 2011; Schneider et al., 2017; Serbin and Townsend, 2020; Ustin and Gamon, 2010), and therefore a diverse plant community is expected to have higher spectral variability or diversity.

Previous studies have provided evidence that spectral diversity is capable of capturing different aspects of plant diversity, including functional (Schweiger et al., 2018), phylogenetic (Cavender-Bares et al., 2021), or taxonomic diversity (Laliberté et al., 2020; Rocchini et al., 2021). These previous studies all support the spectral diversity concept and provide critical evidence that remotely-sensed spectral data can be utilized as a proxy of different dimensions of biodiversity. However, most remote sensing studies of plant diversity have focused on vegetation types with large canopies such as forests (Féret and Asner, 2014; Hauser et al., 2021; Kalacska et al., 2007; Zheng et al., 2021). Remote sensing of plant diversity in grasslands is particularly challenging. First, grassland plants have much smaller canopies relative to the pixel size of typical remote sensing data, such as Landsat-8 or Sentinel-2 constellation with pixel sizes ranging from 10 m to 30 m. Therefore, there is a scale mismatch between the size of grassland plants and pixel size of most remote sensing data sets (Wang et al., 2018a). This scale-dependence of remote sensing of biodiversity–meaning the degree to which our ability to remotely estimate diversity varies as a function of spatial scale (e.g., pixel size, grain size, plot size)–has been reported in previous experiments, and largely influences whether biodiversity, as traditionally defined by ecologists, can be detected with remote sensing (Gamon et al., 2020). Second, management practices, such as prescribed fire or grazing, can promote spatial and temporal variability within and across grasslands ecosystems (Collins, 1992; Fuhlendorf et al., 2009; Knapp et al., 1999), which likely further influences biodiversity detection. Thus, we hypothesize that the impact of such management practices on grassland diversity and our ability to estimate plant diversity with remote sensing can also be highly scale-dependent, both in space and time (see Section 1.3 below and Dronova and Taddeo, 2022; Gholizadeh et al., 2020; Rossi et al., 2021a; Thornley et al., 2022).

1.3. Management practices in tallgrass prairies: implications for remote sensing of plant diversity

Biodiversity patterns in North America's scant remaining tallgrass prairies are driven to a large extent by management practices, particularly prescribed fire and grazing. There is strong evidence that these management practices have historically maintained grassland biodiversity, function, and structure (Collins, 1992; Collins et al., 1998; Knapp et al., 1999). Fire can suppress some invasive plants (e.g., woody plants) and therefore provide resource access to a more diverse set of persistent native species. By removing leaf litter, fire enhances the amount of light received at the soil surface. Fire also increases soil nutrients (e.g., nitrogen and phosphorous), which in turn improve vegetation growth (Frost, 1985; Frost and Robertson, 1985; Peterson and Reich, 2008; Rieske, 2002; Skidmore et al., 2010), and stimulates germination of certain species that may otherwise lie dormant (Ramos et al., 2019; Stone and Juhren, 1953). In addition, when coupled with other management practices, fire can further modify grassland ecosystems (Leonard et al., 2010). Grazing is a great example of an attendant management practice that is often applied in concert with fire (Fuhlendorf and Smeins, 1999). Plants in recently-burned grassland areas are more palatable and nutritious, attracting herbivores which further modify the plant community through grazing (Allred et al., 2011).

As a result of management practices, grasslands can be highly heterogeneous landscapes. Heterogeneity can have several definitions but in the context of grassland ecosystems, we define it as variability in vegetation and soil cover, vegetation composition, or stature in space and time (Coppedge and Shaw, 1998; Fuhlendorf and Engle, 2004; Fuhlendorf and Smeins, 1999). Although this heterogeneity has been suggested as the root of biodiversity at different levels of ecological organization (Wiens, 1997)–for example, through affecting niche availability for different species (Kisel et al., 2011)–it is highly variable both in space and time. Therefore, heterogeneity, and thereby its influence on biodiversity, are likely to be context and scale-dependent and both should be monitored across different spatial and temporal scales (Fuhlendorf and Smeins, 1999). We argue that spectral diversity is capable of capturing such spatial and temporal variations across multiple scales of observation.

There is substantial evidence to suggest that spectral diversity can capture grassland plant diversity, albeit with highly variable levels of uncertainty due to several confounding factors, such as soil exposure (Gholizadeh et al., 2018) and spatial resolution (Wang et al., 2018a). Previous studies have used spectral diversity to capture plant diversity for different grassland ecosystems, including small experimental grassland plots (Wang et al., 2018a), restored tallgrass prairies (Gholizadeh et al., 2019), semi-arid African savannahs (Oldeland et al., 2010), alpine

grasslands (Rossi et al., 2021b), subalpine semi-natural and experimental grasslands (Imran et al., 2021), European mesic meadows (Conti et al., 2021), or dry-grazed grasslands (Möckel et al., 2016). However, these studies have yet to fully address how and the degree to which grassland management practices affect remote sensing of plant diversity. Additionally, many previous remote sensing studies of grassland biodiversity have been conducted using small-scale, highly manipulated, experimental plots that by design cannot fully represent naturally-assembled heterogeneous grasslands. We address critical knowledge gap concerning the viability of using remote sensing to capture plant diversity in naturally-assembled heterogeneous grasslands, as opposed to small or experimental grassland plots, and the dependence of the spectral diversity-plant diversity relationship on spatial scale. Such studies are essential for broadening understanding of the response of grassland ecosystems to various environmental changes and identifying strategies to maintain their biodiversity.

In this paper, we seek to understand whether imaging spectroscopy can be used to measure plant diversity in naturally-assembled heterogeneous grasslands subject to common management practices. We hypothesized that (1) management practices–focusing on prescribed fire–influence grassland heterogeneity (variability in vegetation and soil cover, vegetation composition, or stature) and affect spectral reflectance patterns and thereby spectral diversity and (2) hyperspectral remote sensing can detect such changes across multiple levels of spatial resolution as suggested by the optical surrogacy concept (Gamon, 2008). We have based these central hypotheses upon previous proof-of-concept studies (e.g., Oldeland et al., 2010; Wang et al., 2018a) that have shown promise in estimating grassland plant diversity remotely at different grassland types. To test our central hypotheses, we defined two objectives: (1) determine the effect of prescribed fire–expressed as time since fire–on grassland plant α-diversity–expressed as species richness (number of observed species), exponential Shannon entropy index (effective number of common species, where species are weighed proportional to their percent cover), and inverse Simpson concentration index (effective number of dominant species, where more weight is given to dominant species)–and (2) assess how time since fire affects our ability to remotely estimate grassland plant α-diversity across different spatial scales. To achieve our specific objectives, we collected airborne hyperspectral data (spatial resolution of 1 m; covering the 400–2450 nm range) and spaceborne hyperspectral data from the German Aerospace Center (DLR) Earth Sensing Imaging Spectrometer (DESIS; spatial resolution of 30 m; covering the 400–1000 nm range; Krutz et al., 2019) in summer 2021. While airborne data were used to test the capability of spectral diversity to detect grassland plant diversity at a fine spatial resolution, DESIS data were used for remote sensing of grassland diversity at coarse spatial resolution, comparable to that of planned missions, such as the National Aeronautics and Space Administration's (NASA) Surface Biology and Geology (SBG) mission (Cawse-Nicholson et al., 2021; Schneider et al., 2019) or the European Space Agency's (ESA) Copernicus Hyperspectral Imaging Mission (CHIME) (Nieke and Rast, 2019). For validation, we collected in-situ species inventories, including species composition and percent cover from 2500 sampling locations at The Nature Conservancy's Tallgrass Prairie Preserve (TGPP; also known as the Joseph H. Williams Tallgrass Prairie Preserve), the largest contiguous tract of tallgrass prairie on Earth, located in northeastern Oklahoma, USA (TNC, 2022). Our multiscale remote sensing experiment is a necessary first step for assessing the capability of spectral diversity to detect grassland plant diversity across large spatial extents. Such an experiment informs how grassland management practices affect plant diversity and to what extent remote sensing can capture plant diversity under different grassland management regimes. Further, through using fine-resolution airborne and coarse-resolution spaceborne hyperspectral data, our multiscale study can inform the effectiveness of hyperspectral data with coarse spatial resolution to map grassland plant diversity and contribute to the development of operational biodiversity monitoring approaches applicable to forthcoming imagers, such as NASA's SBG mission.

2. Methods

2.1. Study site

The Nature Conservancy's TGPP is a ~160 km^2 contiguous grassland, located 20 km north of Pawhuska, Oklahoma (36° 50′ N, 96° 25′ W) within the Flint Hills Ecoregion (Coppedge et al., 1998; TNC, 2022). Mean annual rainfall at TGPP is 960 mm. This site has hot summers with average high temperature of 32 °C and relatively cold winters with average low temperature of 3 °C, respectively (Sherrill et al., 2022). About 90% of TGPP consists of tallgrass prairie and the remaining landcover is mainly oak woodland (Hamilton, 2007). Dominant grasses at TGPP include little bluestem (*Schizachyrium scoparium* (Michx.) Nash), big bluestem (*Andropogon gerardii* Vitman), switchgrass (*Panicum virgatum* L.), and hairy wild rye (*Elymus villosus* Muhl. ex Willd.). Dominant forbs include western ragweed (*Ambrosia psilostachya* DC.) and Canada goldenrod (*Solidago Canadensis* L.).

Our site is managed through synergistic application of prescribed fire and grazing where grazers are freely able to interact with patches that vary with time-since-fire (Fuhlendorf and Engle, 2004). In this approach, which mimics the pre-European settlement management practices, fire is applied to different patches of the landscape. Following this prescribed fire regime, herbivores are attracted to recently-burned patches presumably because of the higher forage quality in these areas (Allred et al., 2011). This means that grazing animals are distributed in a non-uniform manner across the landscape. The result is a "shifting mosaic" landscape characterized by high spatio-temporal variability, where the recently-burned patch is heavily grazed and the remaining landscape is largely ungrazed (Fuhlendorf and Engle, 2004). Please see Section 4.4.4 for more discussion on grassland management practices.

In our site, about one-third of the TGPP is burned each year with prescribed fire to maintain a three-year fire-return interval. Following this prescribed-fire regime, grassland units at different stages, including recently-burned, transitional, and pre-prescribed fire exist at any given time. For our study, about one-third of the grassland units were burned less than one year before 2021 remote sensing data collection (i.e., recently-burned stage), approximately one-third of the grassland units were burned within 1–2 years before remote sensing data collection (i.e., transitional stage), and the remaining units were burned >2 years before remote sensing data collection (i.e., pre-prescribed fire stage).

About 47 km^2 of TGPP is managed by fire-cattle grazing, 110 km^2 is managed by fire-bison grazing with American bison (*Bison bison* L.), and a very small portion (~3 km^2) is managed with fire only (Sherrill, 2019). We limited our experiment to 67 km^2 of TGPP (Fig. 1a). Out of this 67 km^2, 47 km^2 (approximately 70%) was managed with prescribed fire and cattle grazing, 17 km^2 (approximately 25%) was managed with prescribed fire and bison grazing, and 3 km^2 (approximately 4%) was managed with prescribed fire-only (i.e., grazers were excluded).

2.2. Field-based data collection

2.2.1. Species inventories

We designed our species inventory sampling protocol with three goals in mind: (1) the dimensions of a sampling plot, which we used to estimate plant diversity across a fixed extent, must be large enough to match the pixel size of our airborne and spaceborne remotely-sensed data to reduce the uncertainty associated with small sample size (i.e., small number of pixels within each plot), (2) in-situ data must be high-quality and accompanied with ancillary data (e.g., soil percent cover), and (3) to minimize the impact of plant phenology on our results, the length of the field campaign must reasonably correspond to the date of remote sensing data collection. With these criteria in mind, we defined our plots as 240 m × 240 m squares. Before the field campaign, we randomly selected 100 plots, avoiding roads or surface water (Fig. 1a).

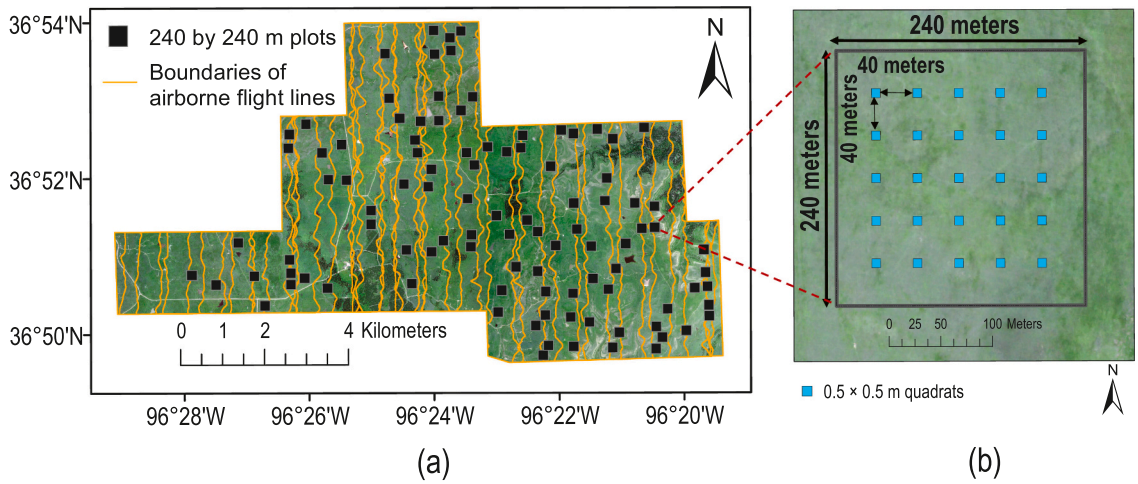

Fig. 1. (a) True colour composite of the study area at The Nature Conservancy's Tallgrass Prairie Preserve (also known as the Joseph H. Williams Tallgrass Prairie Preserve) in Oklahoma, USA. Each black square represents a 240 m × 240 m sampling plot. Orange lines show the boundaries of airborne flight lines. Date of imagery: July 31, 2021. (b) Schematic diagram of a single plot showing species inventory sampling design. Blue squares in Fig. 1b represent 0.5 m × 0.5 m quadrats. There are 100 plots in total (Fig. 1a) and within each plot, we sampled species composition and percent cover in 25 quadrats (Fig. 1b). In other words, we sampled species composition and percent cover in a total of 2500 quadrats. Quadrats are not drawn to scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Out of 100 plots, 39 plots were at the recently-burned stage (i.e., burned less than one year before remote sensing data collection), 28 plots were at the transitional stage (i.e., burned within 1–2 years before remote sensing data collection), and 33 plots were at the pre-prescribed fire stage (i.e., burned >2 years before remote sensing data collection). Within each plot, we documented species composition and percent cover in 25 equally-spaced 0.5 m × 0.5 m quadrats (Fig. 1b; 25 sampling quadrats per plot × 100 plots = 2500 sampling quadrats in total). While a total of 2500 sampling quadrats is remarkably high, this sampling was still constrained in that it might not fully capture plant diversity in diverse and heterogeneous communities. See also Sections 4.2.2 and 4.4.1 for further discussion on in-situ data collection. In addition, although other sampling protocols (e.g., nested plots, parallel or perpendicular transects) have their own advantages, we opted for this regular grid sampling as the field data collected following this protocol are more compatible with the raster and gridded nature of remotely-sensed data.

The locations of all 2500 sampling quadrats were imported to handheld GPS units (Trimble Geo 7X, Trimble, Sunnyvale, CA, USA) before the field campaign; using this handheld GPS unit, the field crew navigated to each plot with an all-terrain vehicle (Kawasaki KAF620R; Kawasaki Heavy Industries, Kobe, Japan) and started data collection from the Northwestern sampling quadrat in each plot (Fig. 1b). Collecting species inventories started in early-July and concluded in approximately four weeks, in early-August 2021.

When estimating percent canopy cover, we considered all individuals that were rooted inside the quadrat. The total percent canopy cover for all vegetation in each quadrat or plot was not necessarily equal to 100% as plant species could overlap (therefore making the total canopy cover >100%) or the surface could be partially covered with soil (in which case the total vegetation percent cover could be <100%). We acknowledge that other measures, such as proportional biomass or the number of individuals from each species (to calculate relative abundance), could be used in lieu of percent canopy cover. We used percent canopy cover as it is well-documented in the plant ecology literature (Daubenmire, 1959; McMillan et al., 2019; Peet et al., 1998) and because counting the number of individuals from each grassland species is rarely feasible.

Since previous work has shown the confounding impact of soil and vertical heterogeneity on remote sensing of grassland diversity (Conti et al., 2021; Gholizadeh et al., 2018), we also documented percent cover of soil, rocks, and other non-vegetation surface cover types for each quadrat. To assist with interpreting our results and provide further ancillary data, we also took an RGB image from each quadrat in near-nadir mode using tablet computers.

2.3. Remote sensing data collection

2.3.1. Airborne hyperspectral data

We collected airborne hyperspectral data between 14:12 and 17:12 GMT on July 31, 2021 using a Twin Commander 500-B aircraft (Aero Commander, Oklahoma City, OK) during clear sky conditions. Airborne hyperspectral imagery was captured in 21 flight lines with minimum side overlap of 25% using a full-range pushbroom imaging spectrometer (AISA Fenix 1K, Specim, Oulu, Finland) covering the 400–2450 nm range in 323 bands and spectral resolution of approximately 4.5 nm in the 400–970 nm range and 14 nm in the 970–2450 nm range. With 1024 spatial pixels, field of view of 40°, and operational altitude of approximately 1400 m above ground level, the resulting airborne imagery had spatial resolution (i.e., pixel size) of 1 m. To increase the geometric accuracy of the imagery, the hyperspectral sensor and the navigation system of the aircraft were boresight-calibrated, and TerraStar® real-time differential corrections were used to maximize the accuracy of navigation data. All 21 flight lines were geometrically and radiometrically corrected (i.e., converting raw data to at-sensor radiance) in the CaliGeoPRO software (Specim, Oulu, Finland). We used 1 m digital elevation model (from USGS 3DEP) for ortho-correction of hyperspectral data. ATCOR-4 package based on MODTRAN-5 radiative transfer model was used for atmospheric correction of the airborne data (Berk et al., 2006; Richter and Schläpfer, 2002). Finally, we removed noisy bands or those affected by atmospheric water vapor absorption. Final airborne hyperspectral data had 238 bands that included wavelengths between 431.10 and 1299.36 nm, 1487.71–1775.03 nm, and 1998.23–2353.76 nm. We also established 15 ground control points (GCPs) throughout the study area for post-hoc geometric correction of our hyperspectral data. However, since we did not detect any major systematic or visual misalignments in our remotely-sensed data, and the deviation between measured GCP coordinates and their image coordinates was less than a pixel, we did not deem post-hoc geometric correction necessary and therefore did not apply it. Processed full-range 1-m airborne

hyperspectral data can be downloaded from the NASA Earth Observing System Data and Information System (EOSDIS) Land Processes Distributed Active Archive Center (Gholizadeh, 2022).

2.3.2. Spaceborne hyperspectral data

Spaceborne DESIS hyperspectral data (Krutz et al., 2019) were collected six days after our airborne data collection on August 06, 2021 at 17:48 GMT. We used the Level 2A DESIS product with no spectral binning applied. DESIS Level 2A product is the surface reflectance data generated using DLR's Python Atmospheric Correction (PACO) library based on the ATCOR package (de los Reyes et al., 2020). The data covered the 401.9–999.5 nm range in 235 spectral bands with spectral resolution of approximately 3 nm and spatial resolution of 30 m. Due to manufacturing defects in the first 10 DESIS bands, etaloning effect, and uncertainties associated with water vapor correction for longer wavelengths, especially for bands around 940 nm, we used 195 DESIS bands between ~430 and 927.1 nm (Alonso et al., 2019; Hu et al., 2018).

2.4. Data analysis

2.4.1. Calculating α-diversity from species inventories

We used Hill numbers (Hill, 1973) to express α-diversity of our sampling plots, which provide a generalized approach to calculating species diversity, instead of focusing on one metric. Specifically, we focused on the first three Hill numbers, including species richness, exponential Shannon entropy index (e^H; hereafter referred to as Shannon diversity), and inverse Simpson concentration index (D^{-1}; hereafter referred to as Simpson diversity) (Chao et al., 2014). Species richness reports the number of observed species within each sampling plot regardless of their abundance and therefore places the same weight on rare and dominant species. Shannon and Simpson indices, on the other hand, both consider the abundance of all species. The main difference between Shannon and Simpson diversity is their sensitivity to rare species. Shannon diversity places weight on species based on their frequency and is an indicator of common species in a plant community, whereas Simpson diversity puts more weight on dominant species. By including three measures of α-diversity, we do not argue which of these three metrics are more suitable to express diversity, but rather we wanted to interpret what a remote sensing instrument can see from above (see Interpretation column in Table 1 below). We acknowledge that other modified versions of Shannon and Simpson indices also exist.

2.4.2. Calculating spectral diversity to map α-diversity

We used coefficient of variation (CV; Lucas and Carter, 2008) in MATLAB 2020b (Mathworks Inc., Natick, Massachusetts, USA) to calculate spectral diversity. We calculated the average coefficient of variation of the pixels inside each 240 m × 240 m plot using bands between 431.10 and 2353.76 nm, while excluding water vapor absorption bands, for airborne data and bands between ~430 and 927.1 nm for DESIS data. Larger CV values correspond to higher spectral diversity whereas smaller CV values correspond to lower spectral diversity. More details on CV calculation, including its formula are provided in Appendix A in Supplementary material. To assess the agreement between field-based and remotely-sensed α-diversity values, we used the proportion of explained variance (R^2) between measured plant diversity (Section 2.4.1) and spectral diversity. There is no perfect spectral diversity metric (Fassnacht et al., 2022; Gholizadeh et al., 2018; Schmidtlein and Fassnacht, 2017). Consequently, in addition to CV, we also tested two others metrics of spectral diversity, including convex hull volume (CHV) (Dahlin, 2016) and spectral angle mapper (Kruse et al., 1993). Our preliminary results showed that CV and SAM had comparable performance while CHV underperformed (results not shown here). To improve the readability of the manuscript, we used CV as our primary spectral diversity metric in this paper.

To determine how soil exposure affects the capability of spectral diversity to capture plant α-diversity, we used a partial correlation analysis (Erb, 2020). Specifically, we assessed the association between spectral diversity (from airborne and DESIS data) and three metrics of plant diversity, including species richness, Shannon diversity, and Simpson diversity whilst controlling for the effect of soil cover.

2.4.3. Impact of time since fire on measured and remotely-sensed plant diversity

To determine the impact of time since fire on measured and remotely-sensed plant diversity, we compared plots at recently-burned, transitional, and pre-prescribed fire stages. Specifically, we assessed the impact of time since fire on measured plant diversity–including species richness, Shannon diversity, and Simpson diversity–as well as remotely-sensed plant diversity (i.e., spectral diversity) using one-way analysis of variance (ANOVA; at significance level of 0.05 or 5%) followed by pairwise group comparisons using the Tukey's honestly significant difference procedure (Tukey, 1949).

To provide further context to whether the impact of time since fire on measured and remotely-sensed plant diversity varied across space, we looked at the species richness-area relationship (hereafter referred to as species-area relationship) and spectral diversity-area relationship. The species-area relationship shows the general pattern of observed species versus sampled area (Preston, 1960). Although several mechanisms have been identified to explain the species-area relationship (see Hill et al., 1994; Rosenzweig, 1995), the shape of species-area curve–particularly, its slope–has been associated with heterogeneity and species turn-over (β-diversity; Connor and McCoy, 1979). Based on a similar premise, the spectral diversity-area relationship describes the spectral diversity values as a function of sampled area, and has been adapted to elucidate patterns of plant diversity across space using remotely-sensed data in the absence of in-situ species diversity measurements (Dahlin, 2016).

Our expectation was that grassland communities with shorter time since fire are more heterogeneous and have higher species and spectral variability across space. We expect this pattern to manifest itself as species- and spectral diversity-area curves with steeper slopes in recently-burned communities. To test this hypothesis, we used the

Table 1
Metrics used to express α-diversity in our in-situ data (Chao et al., 2014). In these equations, N is the total number of species observed by the botanist in a plot, p is the vegetation cover of the ith species in a plot calculated by taking the average of measured percent cover in 25 quadrats within each plot divided by 100%, and ln is natural logarithm.

Index	Hill number	Equation	Interpretation
Species richness	0	N	Number of observed species in a plant community.
Exponential Shannon entropy index (referred to as Shannon diversity in the manuscript)	1	$\exp(-\Sigma p_i \ln p_i)$	Effective number of common species in a plant community. Gives weight to species proportional to their abundance.
Inverse Simpson concentration index (referred to as Simpson diversity in the manuscript)	2	$1/\Sigma p_i^2$	Effective number of dominant species in a plant community. Gives more weight to dominant species in a plant community.

analysis of covariance on the species- and spectral diversity-area regression lines in the ln-ln space (natural logarithm) with the time since fire category as the treatment effect.

To develop our species- and spectral diversity-area curves, we followed a non-contiguous and non-spatially explicit category IIIB approach (Scheiner, 2003) similar to Dahlin (2016). Specifically, we randomly selected one plot, calculated diversity (both species richness and spectral diversity), and incrementally added additional randomly-selected plots up to 25 plots. We repeated this process 100 times for recently-burned ($n = 39$), transitional ($n = 28$), pre-prescribed fire ($n = 33$), and all plots combined ($n = 100$) and used the average and 95% confidence interval from 100 runs to show variability in our species- and spectral diversity-area relationships.

2.4.4. Capability of spectral diversity to map plant diversity across spatial scales

To test the capability of spectral diversity to detect grassland α-diversity across multiple spatial resolutions, we used airborne data (spatial resolution of 1 m) and DESIS data (spatial resolution of 30 m) collected at almost the same time of the year (only six days apart). Additionally, we used airborne imagery to generate additional data sets with coarser spatial resolutions (5 m, 10 m, 15 m, 20 m, 25 m, and 30 m pixel sizes) through resampling original images in MATLAB 2020b. Unlike our airborne sensor, the DESIS sensor does not cover the shortwave infrared (SWIR) region of the electromagnetic spectrum. Therefore, to assess the added value of SWIR region for remote sensing of plant diversity, we repeated this resampling experiment two times: using the full-range airborne data–that included the visible, near-infrared (NIR) and SWIR regions–and then for the airborne data using the visible and near-infrared (VNIR) regions (up to 927 nm) but without the SWIR region. This multiscale analysis assisted us to assess (1) the performance of spectral diversity across different spatial resolutions in naturally-assembled heterogeneous grasslands and (2) the capability of forthcoming spaceborne imagers, such as NASA's SBG mission–which will have comparable spatial resolution to DESIS data and include the SWIR region–for mapping grassland plant diversity.

Another less-studied component of spatial scale in remote sensing of plant diversity is plot size, which is a construct used to estimate plant diversity across a fixed extent. We selected plot size of 240 m × 240 m in our study, yet it was unclear how this choice of plot size would affect our results. To fill this knowledge gap, in addition to our native plot size of 240 m × 240 m, we defined additional 60 m × 60 m, 120 m × 120 m, and 180 m × 180 m plot sizes (see Fig. 2) and revisited the plant diversity-spectral diversity relationship. Through this analysis, we were particularly interested to find out whether remote sensing is more suitable to capture plant diversity for small or large herbaceous plant communities.

3. Results

3.1. Impact of time since fire on measured and remotely-sensed plant diversity

Time since fire did not affect plant diversity expressed as species richness or Shannon diversity according to our ANOVA analysis (Fig. 3a-b), although Simpson diversity was significantly higher directly following fire (Fig. 3c). Results also showed that the average and range of spectral diversity values–calculated using CV–from airborne and DESIS data were significantly higher for recently-burned plots (Fig. 4a-b), due to significantly higher heterogeneity (i.e., variability in vegetation and soil cover, vegetation composition, or stature) in recently-burned plots compared to those at the pre-prescribed fire stage (Fig. 4c and 5a-b; see also Fig. S1 in Supplementary material for the spectral diversity-soil percent cover relationship). Since soil has strikingly different spectral signature from green vegetation, we expected higher spectral variability, and thereby higher spectral diversity in

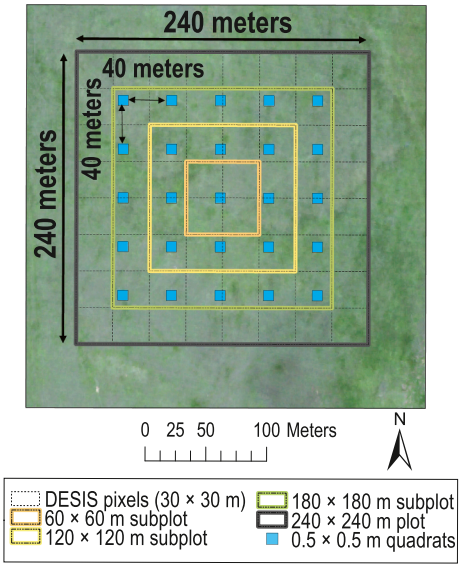

Fig. 2. The orange square shows a 60 m × 60 m plot consisting of 4 DESIS pixels; the yellow square shows a 120 m × 120 m plot consisting of 16 DESIS pixels; the green square shows a 180 m × 180 m plot consisting of 36 DESIS pixels; the large black square shows a 240 m × 240 m plot consisting of 64 DESIS pixels. Quadrats are not drawn to scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recently-burned plots. To illustrate this contrast, we selected two plots with short distance from each other (approximately 1 km) but with different time since fire: a recently-burned plot (Fig. 5a) and a plot at the pre-prescribed fire stage (Fig. 5b). Results obtained from both airborne (Fig. 5c) and DESIS data sets (Fig. 5d) highlighted the clear contrast between these two plots. Specifically, the recently-burned plot had higher spectral diversity across all regions of the spectrum. Of specific note are two regions of the electromagnetic spectrum with high spectral variability: one region in the 670–680 nm range (Fig. 5c-d) and another region in the ~2000–2350 nm range within the SWIR portion of the spectrum (Fig. 5c).

3.1.1. Assessing the impact of time since fire on measured and remotely-sensed plant diversity across scales using species- and spectral diversity-area curves

Species-area curves: As expected, species-area curves for plots with different time since fire were not the same (Fig. 6a). The curve for the recently-burned plots had the highest final species richness value whereas the plots at the pre-prescribed fire stage had the lowest final species richness. In terms of initial values of the curves, recently-burned plots and those at the transitional and pre-prescribed fire stages had comparable species richness values, confirming the lack of significant difference in species richness observed in Fig. 3a. The curve generated by pooling data from all plots, regardless of time since fire, fell between the recently-burned and transitional-stage curves. Contrary to our expectation, the slope of four curves (in the natural log-log space), which is an indicator of β-diversity across scales, was not significantly different (Fig. 6d; see Table S1 in Supplementary material for statistical analysis results).

Spectral diversity-area curves: Similar to species-area curves, the shape of the spectral diversity-area curves obtained from airborne and DESIS data varied with time since fire (Fig. 6b-c). In addition, spectral diversity-area curves for the recently-burned plots had the highest overall spectral diversity and largest initial values. Plots at the pre-prescribed fire and transitional stages had overlapping curves for smaller sampling areas (i.e., smaller values on x-axes). Comparing the

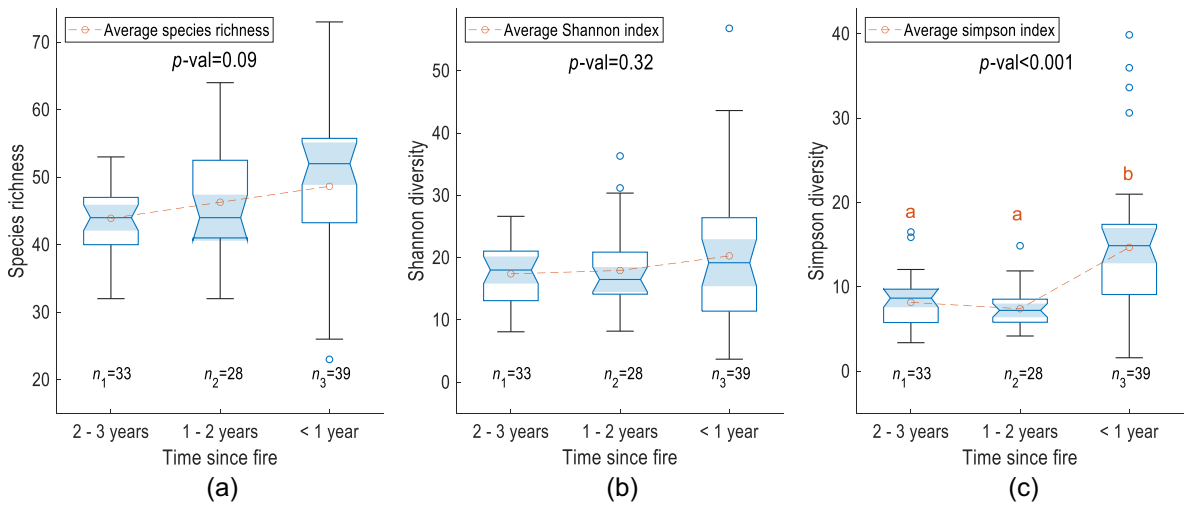

Fig. 3. (a) Species richness, (b) Shannon diversity, and (c) Simpson diversity of our 240 m × 240 m plots with different time since fire. We used ANOVA test to assess differences between groups at significance level of 0.05. Numbers below each boxplot show the number of plots in each treatment. In these boxplots, each box shows the middle 50% of the data points, whiskers represent the rest of the data points excluding outliers, the blue horizontal line in each box indicates the data median, the shaded regions can be used to assess whether medians are significantly different from each other, and hollow blue circles show outliers. Outliers are defined as values that are larger than 1.5 × interquartile range away from the top or bottom edges of each box. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

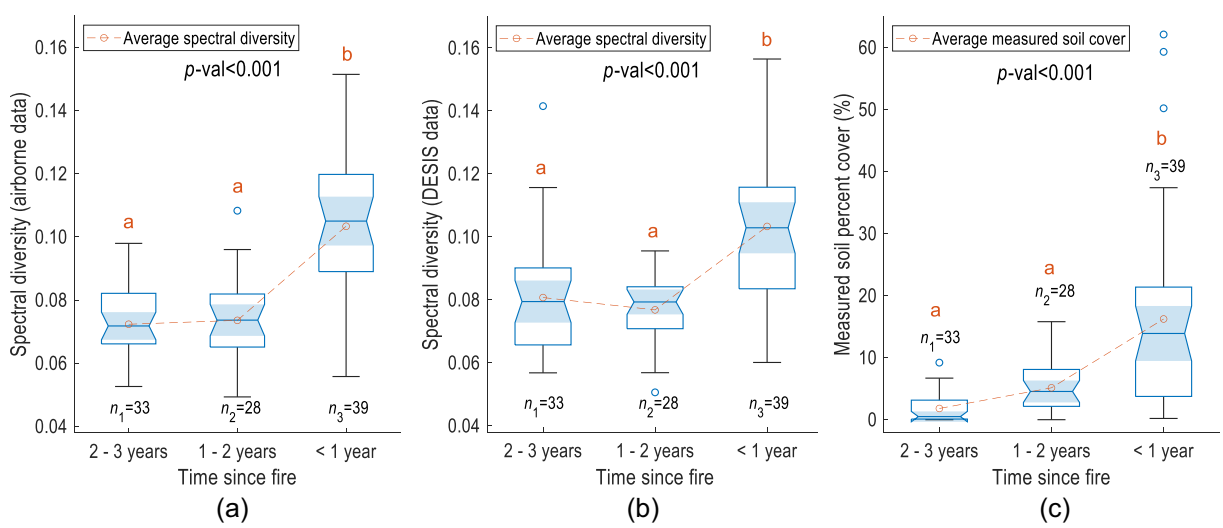

Fig. 4. (a) Spectral diversity calculated using the 1-m airborne data, (b) spectral diversity calculated using the 30-m DESIS data, and (c) field-measured soil percent cover in plots with different time since fire. We used ANOVA test to assess differences between groups at significance level of 0.05. Numbers below each boxplot show the number of plots in each treatment. Note: In (c), "soil" refers to percent cover of soil and exposed rocks together. In these boxplots, each box shows the middle 50% of the data points, whiskers represent the rest of the data points excluding outliers, the blue horizontal line in each box indicates the data median, the shaded regions can be used to assess whether medians are significantly different from each other, and hollow blue circles show outliers. Outliers are defined as values that are larger than 1.5 × interquartile range away from the top or bottom edges of each box. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

results obtained from airborne and DESIS data revealed that there was a larger overlap between the spectral diversity-area curves over smaller sampling areas when we used DESIS data (Fig. 6c). These results indicate that mapping heterogeneity over smaller areas using the coarse-resolution DESIS VNIR data may be challenging. Similar to the species-area curve (Fig. 6d), the slope of the spectral diversity-area curves for airborne and DESIS data were not significantly different (Fig. 6e-f; see Tables S2–3 in Supplementary material for statistical analysis results).

3.2. *Capability of remotely-sensed data as proxies for grassland plant α-diversity*

3.2.1. *Results obtained from airborne data*

We first assessed the association between grassland plant α-diversity and spectral diversity using airborne data with spatial resolution of 1 m. Specifically, we compared species richness, Shannon diversity, and Simpson diversity with spectral diversity. When stratifying our plots based on time since fire, there was no significant relationship between

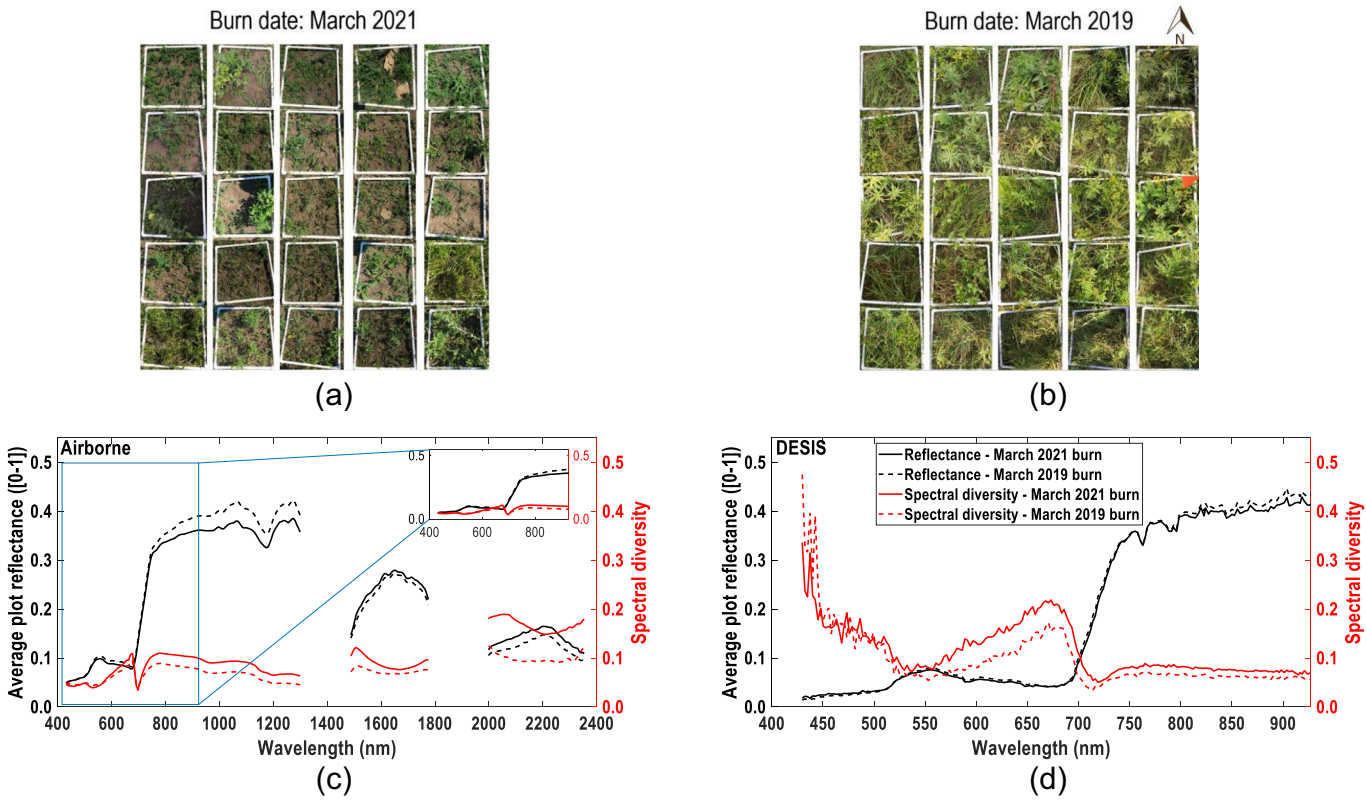

Fig. 5. Our 25 sampling quadrats from two plots with the highest and lowest measured soil percent cover: (a) A plot burned on March 2021 (recently-burned stage with measured soil percent cover of 61%), and (b) a plot burned on March 2019 (pre-prescribed fire stage with average soil percent cover of 0%). The order of quadrats is the same as Fig. 1b (e.g., the top left panels in a-b represent the northwestern quadrat in Fig. 1b). The white frame in each panel is our 0.5 m × 0.5 m sampling quadrat. The corresponding reflectance and spectral diversity spectra of these two plots from (c) airborne data and (d) DESIS data. The inset in (c) shows the same wavelength range as DESIS data in (d).

species richness and spectral diversity (Fig. 7a). When we combined all plots together regardless of time since fire, we observed a very weak species richness-spectral diversity relationship (Fig. 7a; $R^2 = 0.08$; p-val $= 0.001$).

Similar to species richness data, spectral diversity did not have a significant relationship with Shannon diversity for any of the time since fire categories we measured (Fig. 7b). When we considered all plots together regardless of time since fire, the Shannon diversity-species richness relationship remained non-significant.

In contrast to species richness and Shannon diversity, Simpson diversity was highly associated with spectral diversity for plots at the transitional stage (i.e., burned 1–2 years before airborne data collection; Fig. 7c; $R^2 = 0.47$; p-val < 0.001). We also observed four outliers in our Simpson diversity-spectral diversity relationship (see the inset in Fig. 7c) in the recently-burned plots with high soil percent cover (average soil percent cover of 61%, 59%, 50%, and 21%); three of these had the highest soil percent cover among our 100 plots. When we removed these four outliers, the Simpson diversity-spectral diversity relationship for the recently-burned plots and all plots combined was significant (Fig. 7c; $R^2 = 0.37$ and p-val < 0.001 for recently-burned plots and $R^2 = 0.45$ and p-val < 0.001 when considering all plots).

3.2.2. Results obtained from DESIS data

Results obtained from DESIS data (spatial resolution of 30 m) agreed with those from airborne data, although the R^2 of in-situ plant diversity-spectral diversity relationships were consistently weaker for DESIS data. We did not observe significant species richness-spectral diversity relationship for any of our time since fire categories; however, we observed a very weak species richness-spectral diversity relationship when all plots were combined regardless of time since fire (Fig. 7d; $R^2 = 0.07$; p-val $= 0.01$). Similar to airborne data, no significant Shannon diversity-spectral diversity relationship was observed for any of our time since fire categories and all plots combined (Fig. 7e). Spectral diversity calculated using DESIS data had a significant relationship with Simpson diversity for plots at the transitional stage (Fig. 7f; $R^2 = 0.28$; p-val $= 0.00$) and recently-burned stage (Fig. 7f; $R^2 = 0.35$; p-val < 0.001), and all plots combined (Fig. 7f; $R^2 = 0.33$; p-val < 0.001) after excluding four outliers in our recently-burned plots.

3.2.3. Association between spectral diversity and plant diversity before and after controlling for the effect of soil

Partial correlation results indicated that, for airborne data with spatial resolution of 1 m, after controlling for the effect of soil cover, associations between species richness and spectral diversity in recently-burned plots and Shannon diversity and spectral diversity for all data points combined became significant (Table 2). For DESIS data with spatial resolution of 30 m, after controlling for the effect of soil cover, partial correlations between Simpson diversity and spectral diversity in recently-burned plots became non-significant (Table 3).

Since the Simpson diversity-spectral diversity association was, in general, the only consistently significant relationship among the three metrics of plant diversity for both airborne and DESIS data, we limited our subsequent analyses to Simpson diversity.

3.2.4. Synthesizing results obtained from airborne and DESIS data

Three main findings emerged from analyzing the relationship between field- and remote sensing-based plant α-diversity (Fig. 8). First, the association between plant diversity (Simpson diversity) and spectral diversity was strongly affected by time since fire. Specifically, although remotely-sensed spectral diversity was not capable of capturing plant

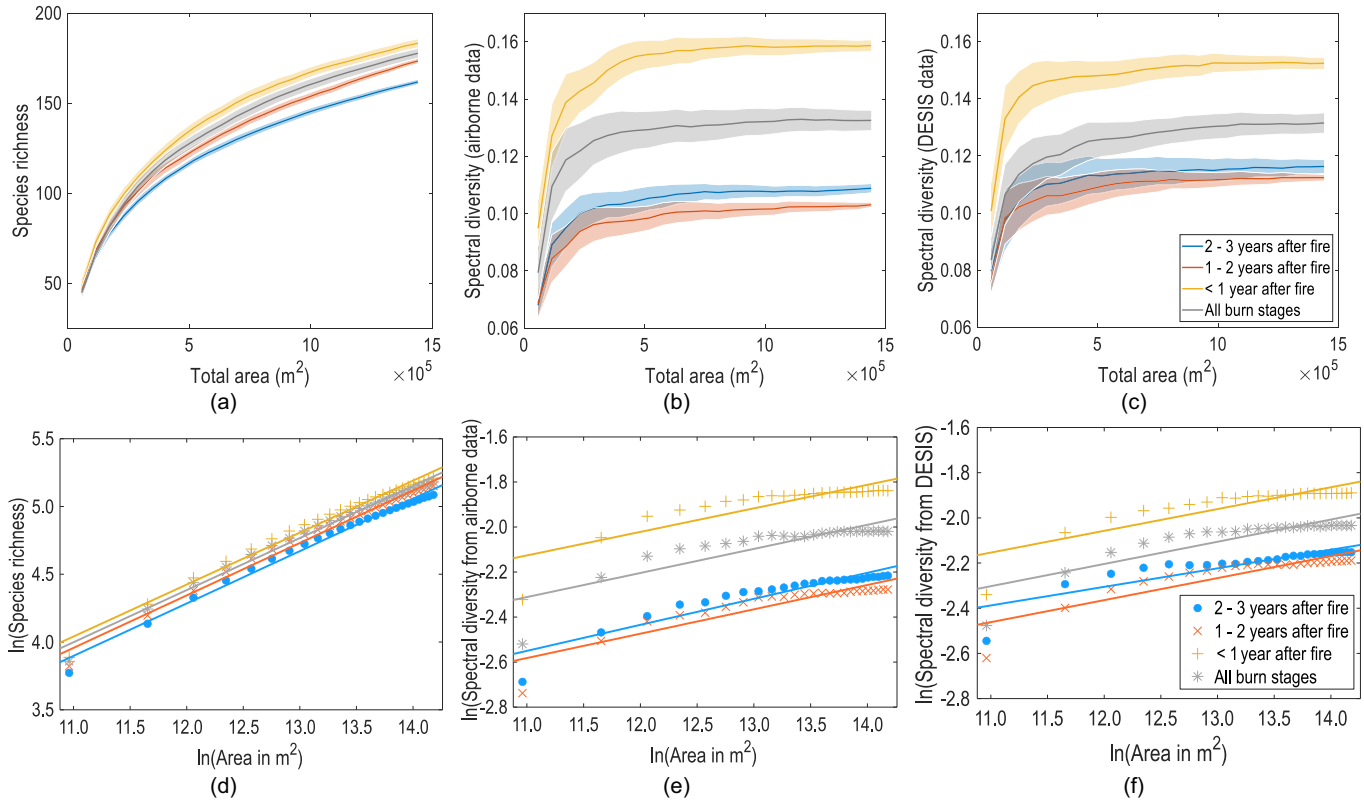

Fig. 6. (a) Species-area curves, (b) spectral diversity-area curves calculated from 1 m-resolution airborne data, (c) spectral diversity-area curves calculated from 30 m-resolution DESIS data, (d) species-area curves in ln-ln (natural logarithm) space, (e) airborne spectral diversity-area curves in ln-ln space, and (f) DESIS spectral diversity-area curves in ln-ln space. In these graphs, blue lines and symbols represent plots at the pre-prescribed fire stage, orange lines and symbols represent plots at the transitional stage, yellow lines and symbols represent recently-burned plots, and grey lines and symbols represent all burn stages combined. The shaded regions in (a-c) show 95% confidence intervals from 100 runs. Note: The species-area curves in (a) are generated using a subset of plots as discussed in Section 2.4.3. In addition, most of the species in our site are rare with low probability of being sampled. The low probability of detecting rare species means that a reasonable and representative sampling effort will not capture all species in the system. Therefore, the curves or whether they reach an asymptote need to be interpreted accordingly and cautiously. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diversity in plots at the pre-prescribed fire stage (blue line in Fig. 8a), the association between plant diversity and spectral diversity was significant at the transitional and recently-burned stages across different spatial resolutions ranging from 1 m to 30 m (dark orange and yellow lines in Fig. 8a).

Second, results suggested that spectral diversity calculated using coarse-resolution DESIS data can be used as a proxy for plant diversity at transitional-stage and recently-burned plots with R^2 ranging from 0.28 to 0.35 (dark orange and yellow pentagram symbols in Fig. 8a). When we combined all plots together regardless of time since fire, the association between plant diversity and spectral diversity was significant across different spatial resolutions and for both airborne and DESIS data (grey line and pentagram in Fig. 8a).

Third, the results obtained from full-range (Fig. 8a) and VNIR airborne data (Fig. 8b) showed the added value of SWIR region of the spectrum for enhancing our ability to map plant diversity remotely. For instance, including SWIR bands increased the percent of explained variance (% R^2) in plant diversity by approximately 10% across different spatial resolutions–including 30-m pixel size–when we combined all plots together (see Fig. S2 in Supplementary material).

3.2.5. Capability of remotely-sensed data for mapping grassland plant diversity: Impact of plot size

Sampling plot size had a considerable impact on our observed plant diversity-spectral diversity association (Fig. 9). While we did not observe any significant relationship between plant diversity and spectral diversity for smaller 60 m × 60 m and 120 m × 120 m plots, the relationship significantly improved for our larger 180 m × 180 m and 240 m × 240 m plots at transitional and recently-burned categories, and for all plots combined (Fig. 9b-d). Another notable finding was the comparable performance of coarse-resolution DESIS data with fine-resolution airborne data, particularly in recently-burned plots (Fig. 9c) and all plots together (Fig. 9d). Collectively, these findings indicate that, in our experiment, the plant diversity-spectral diversity relationship was stronger at larger plot sizes for both airborne and spaceborne data.

4. Discussion

4.1. Remote sensing of plant diversity in naturally-assembled grasslands

The challenges associated with mapping grassland plant diversity remotely have largely been attributed to the small size of grassland plant species compared to the spatial resolution of spectroscopic imagery (commonly referred to as "scale mismatch"; see Section 4.2 below or Gamon et al., 2020). Management practices in naturally-assembled grasslands also strongly influence heterogeneity–here, defined as variability of vegetation and soil cover, vegetation composition, or stature–adding to the challenges of remote sensing of grassland plant diversity. Despite its importance for prairie biodiversity conservation (Fuhlendorf et al., 2009), the impact of management-induced heterogeneity on remote sensing of plant diversity remains a critical knowledge gap that limits our ability to monitor plant diversity at large spatial extents.

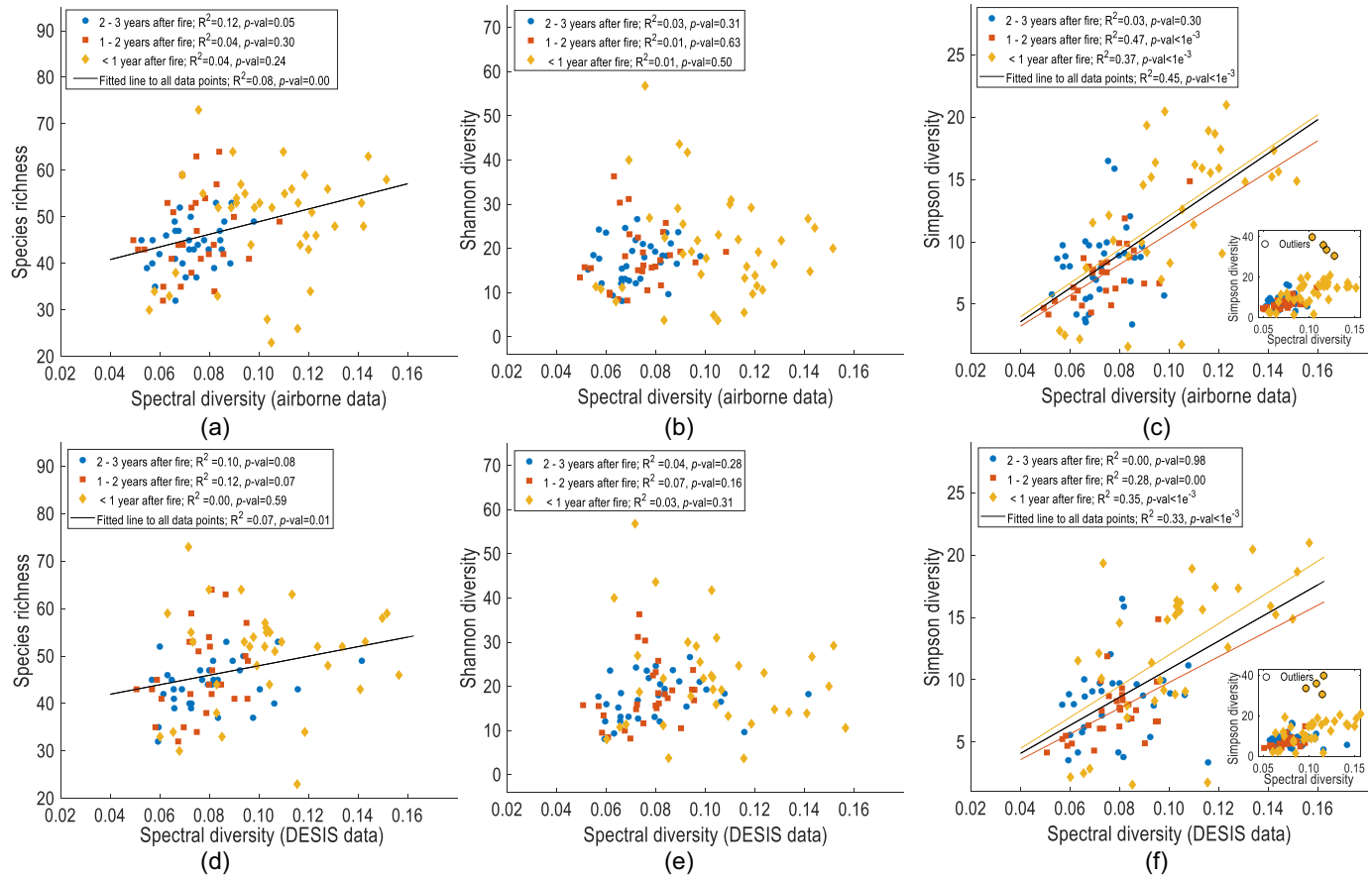

Fig. 7. Association of (a) species richness, (b) Shannon diversity, and (c) Simpson diversity with spectral diversity calculated using airborne data (spatial resolution of 1 m). Relationship of (d) species richness, (e) Shannon diversity, and (f) Simpson diversity with spectral diversity calculated using DESIS data (spatial resolution of 30 m). Blue circles represent plots at the pre-prescribed fire stage, dark orange squares show plots at the transitional stage, and yellow diamond symbols represent recently-burned plots. The small insets in (c) and (f) show all plots, including four outliers which are identified with dark circles around them. In the graphs, fitted lines only for significant relationships at significance level of 0.05 are shown. Equations for Shannon and Simpson diversity indices can be found in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Association between spectral diversity obtained from full-range airborne hyperspectral data with spatial resolution of 1 m and plant diversity before and after controlling for soil cover. In this table, "NS" indicates non-significant relationship at significance level of 0.05. Please see Table S4 for partial correlations between spectral diversity and plant diversity whilst controlling for the effect of soil cover.

Time since fire	Species richness-spectral diversity relationship		Shannon diversity-spectral diversity relationship		Simpson diversity-spectral diversity relationship	
	Before controlling for the effect of soil	After controlling for the effect of soil	Before controlling for the effect of soil	After controlling for the effect of soil	Before controlling for the effect of soil	After controlling for the effect of soil
2–3 years after fire	NS	NS	NS	NS	NS	NS
1–2 years after fire	NS	NS	NS	NS	Significant	Significant
< 1 year after fire	NS	Significant	NS	NS	Significant	Significant
All years combined	Significant	Significant	NS	Significant	Significant	Significant

4.1.1. Spectral diversity calculated from airborne and spaceborne data was associated with some but not all components of plant diversity in our site

Our findings showed that spectral diversity calculated from both airborne and DESIS data was, in general, strongly associated with Simpson diversity (Fig. 7-8). However, when we measured plant diversity using species richness or Shannon diversity, the plant diversity-spectral diversity relationship was either very weak or non-significant. The superior performance of spectral diversity at estimating Simpson diversity compared to Shannon diversity and species richness has been reported in previous studies in grasslands (Wang et al., 2018a) and tropical forests (Schäfer et al., 2016), and is likely a consequence of dominant species markedly influencing electromagnetic radiation reflected from plant communities.

Specifically, Simpson diversity places more weight on dominant species in the plant community (see Table 1 and Chao et al., 2014), and we presume this bias towards dominant species might explain why Simpson diversity was strongly associated with spectral diversity calculated from both airborne and spaceborne data. Although we documented 253 species during our in-situ data collection campaign, most of them were rare species. For instance, the 10 most dominant species in our site altogether covered >65% of TGPP and the 20 most dominant species covered approximately 80% of our research site (Fig. S3 in Supplementary material). Each of the remaining species had average percent cover of around or <1% indicating that these rare

Table 3
Association between spectral diversity obtained from VNIR DESIS hyperspectral data with spatial resolution of 30 m and plant diversity before and after controlling for soil cover. In this table, "NS" indicates non-significant relationship at significance level of 0.05. Please see Table S5 for partial correlations between spectral diversity and plant diversity whilst controlling for the effect of soil cover.

Time since fire	Species richness-spectral diversity relationship		Shannon diversity-spectral diversity relationship		Simpson diversity-spectral diversity relationship	
	Before controlling for the effect of soil	After controlling for the effect of soil	Before controlling for the effect of soil	After controlling for the effect of soil	Before controlling for the effect of soil	After controlling for the effect of soil
2–3 years after fire	NS	NS	NS	NS	NS	NS
1–2 years after fire	NS	NS	NS	NS	Significant	Significant
< 1 year after fire	NS	NS	NS	NS	Significant	NS
All years combined	Significant	Significant	NS	NS	Significant	Significant

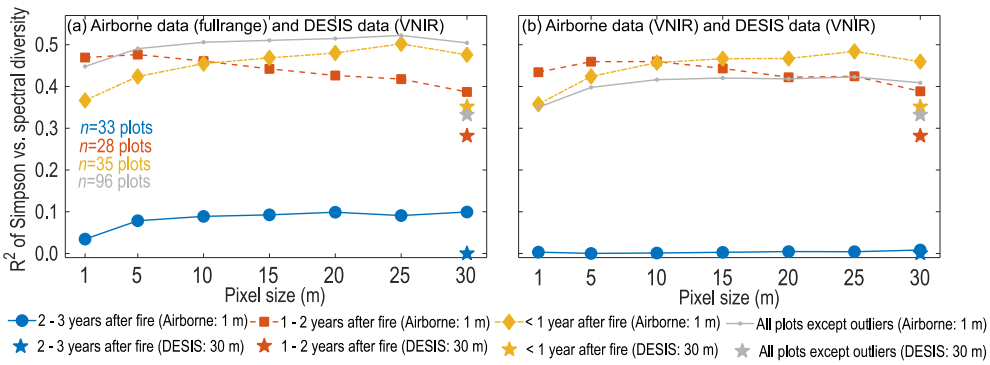

Fig. 8. Association between measured plant diversity expressed as Simpson diversity vs. spectral diversity using airborne hyperspectral data with pixel size of 1 m, DESIS hyperspectral data with pixel size of 30 m, and resampled airborne data at 5 m, 10 m, 15 m, 20 m, 25 m, and 30 m resolutions. Airborne data used in (a) are full-range data (but without water vapor absorption bands) while airborne data used in (b) include VNIR bands (here, defined as wavelengths shorter than 927 nm to match the spectral coverage of DESIS). Four outliers identified in Section 3.2 were not included in these graphs. Since species richness and Shannon diversity did not show any significant relationship with spectral diversity (see Section 3.2), we only show Simpson diversity-spectral diversity results here.

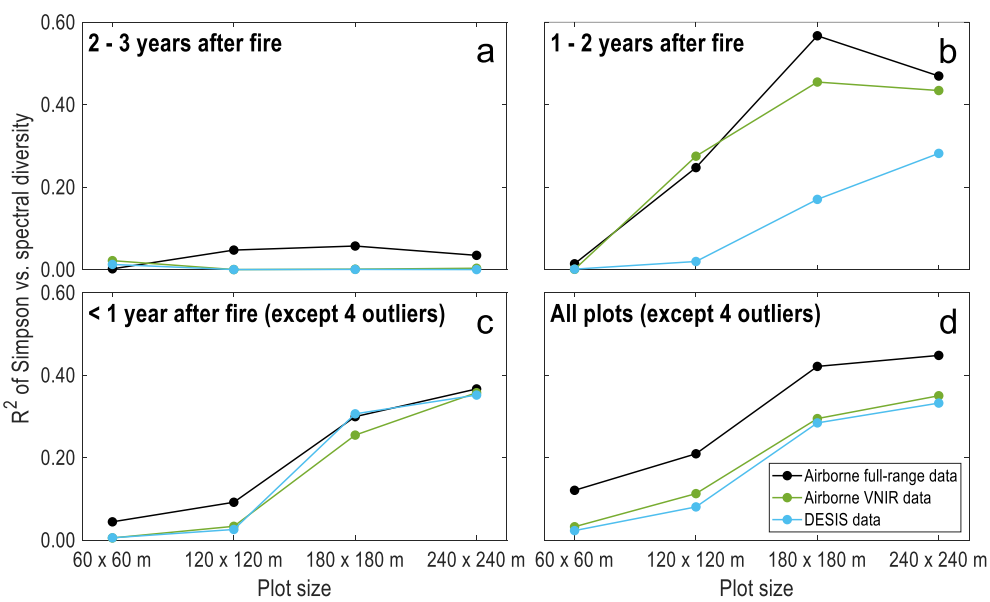

Fig. 9. In addition to our 240 m × 240 m plots, we defined smaller plot sizes, including 60 m × 60 m, 120 m × 120 m, and 180 m × 180 m plots and recalculated the plant diversity-spectral diversity association for our 1-m full-range airborne data (black lines) and VNIR airborne data (green lines) as well as 30-m DESIS data (blue lines) for three different time since fire categories (panels a-c) and all plots combined (except the four outliers; panel d). Our sampling design is shown in Fig. 1b and Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species would likely occupy a very small portion of a pixel surface; this small percent cover is far less than the required abundance fraction for a phenomenon to be remotely-detectable even using subpixel methods (see Matteoli et al., 2010 for example). Further, as spatial resolution of remotely-sensed data becomes coarser (Fig. 8), the spectral signal of dominant species would be presumably still present. Simply put, although spatial resolution is coarser, remote sensing data may still see the spectrum of dominant species. This might explain why spectral diversity calculated using the 30-m DESIS data was still strongly associated with Simpson diversity despite the smoothing and adjacency effects in coarse-resolution images (i.e., when neighboring pixels have similar spectral signals).

4.1.2. *Remote sensing of plant diversity is affected by grassland management practices*

Time since fire significantly impacted remote estimation of plant diversity presumably by impacting heterogeneity, specifically vegetation and soil percent cover and vegetation height (Fig. 5). We observed a strong relationship between Simpson diversity and spectral diversity for plots at the transitional stage and those that were burned recently; but

found no Simpson diversity-spectral diversity relationship in plots at the pre-prescribed fire stage (Fig. 7-8). A multi-temporal study across a small experimental restored grassland in Central Nebraska, USA (Gholizadeh et al., 2020) also reported a strong response of spectral diversity to time since fire, where spectral diversity was capable of estimating observed species richness two months after fire but did not effectively estimate species richness four months after fire. Results from our experiment (see Fig. 3a) and Gholizadeh et al. (2020) indicate that time since fire may not necessarily affect species richness but it does affect spectral diversity (Fig. 4a-b), with the recently-burned plots having the highest spectral variability. We speculate that grassland management practices can influence spectral diversity through modifying both horizontal and vertical heterogeneity (Fig. 5a-b) and soil exposure (Fig. 4c); such management-driven impacts on spectral diversity were evident in our spectral diversity-area curves (Fig. 6b-c).

We also note that disentangling the impact of soil cover on remote sensing of plant diversity in naturally-assembled grasslands can be complex, partly due to associations between heterogeneity–which also entails soil cover–and biodiversity at different levels of ecological organization. There might be situations where soil cover can be an indicator of heterogeneity and biodiversity. In these cases, soil is not only an indicator of biodiversity but it increases spectral diversity at the same time, and thereby aids remote sensing of biodiversity. There also exist situations–similar to Fig. 5a–where soil exposure significantly influences remote sensing signals apart from any changes in biodiversity, hampering our ability to capture plant diversity remotely (Gholizadeh et al., 2018). As a result, the degree to which soil exposure matters for remote sensing of plant diversity appears to vary along a continuum.

The impact of management practices on plant and community characteristics goes beyond just affecting structural characteristics (e.g., vegetation and soil percent cover or vegetation height). Prescribed fire can also cause variability in other remotely-observable vegetation functional traits that can influence spectral signals and eventually the detectability of diversity (Serbin and Townsend, 2020; Wang et al., 2020). For example, fire can affect plant nutrients (Allred et al., 2011) as well as soil nutrients (see Section 1.3), which are also strongly linked to aboveground vegetation chemistry and other functional attributes (Cavender-Bares et al., 2021). Although we did not evaluate the impact of management practices on vegetation functional traits in this study, assessing the linkages between spectral diversity and remotely-observable functional traits in grasslands under different management practices remains an exciting research topic that is worth exploring, especially as full-range imaging spectroscopic data are becoming more accessible.

4.2. Spatial scale is more than just spatial resolution: Plot size also needs to be considered in remote sensing of plant diversity

Spatial scale has different components, such as quadrat size (or grain size), extent, number, shape and even distribution of grains (Palmer and White, 1994). Our interpretation of ecosystems, to a large degree, depends on how we define spatial scale, and this makes spatial scale a complex topic. Understanding how spatial scale impacts our estimation of biodiversity has been a major endeavor in ecology, and there is a large body of literature on the issue of scale and scaling rules (Levin, 1992; O'Neill et al., 1996; Wiens, 1989).

4.2.1. Impact of spatial resolution on remote sensing of plant diversity

In remote sensing of biodiversity, spatial resolution (i.e., pixel size) has often been considered as a primary determinant of spatial scale, but it is only one aspect of spatial scale. The influence of spatial resolution on grassland plant diversity-spectral diversity relationship has been studied extensively, partly because the exercise of simulating coarse-resolution data from fine-resolution imagery and re-evaluating the plant diversity-spectral diversity relationship–similar to what we did in Fig. 8–is straightforward. Such scale-dependence experiments test the ecological rule that the grain size of observation should match the size of phenomena in question (Levin, 1992). Expressly, this means that the pixel size of remote sensing data should be comparable to the size of the plant canopy being observed. Obviously, this criterion is rarely met in remote sensing studies of plant diversity, especially when using coarse-resolution remotely-sensed data.

Using proximal VNIR hyperspectral data at Cedar Creek Ecosystem Science Reserve in Minnesota, USA (Tilman et al., 2001), a significant correlation between species richness and spectral diversity was reported only for very fine spatial resolutions (1 mm to 10 cm; R^2 ranging from approximately 0.5 to 0.2; Wang et al., 2018a). In another experiment in a restored prairie at Wood River, Nebraska, USA, significant species richness-spectral diversity relationships existed for VNIR airborne imaging spectroscopic data with larger pixel sizes (0.5 m to 4 m; R^2 between 0.7 and 0.4; Gholizadeh et al., 2019). In our experiment, we observed much weaker or non-significant relationships between species richness and spectral diversity for airborne and DESIS data (R^2 ranging between approximately 0.07 and 0.08 at best; Fig. 7a and d), showing that mapping species richness across naturally-assembled heterogeneous grasslands (as opposed to manipulated experimental plots) might be challenging (see Section 4.1). These results, altogether, suggest that appropriate pixel size for estimating grassland plant diversity is site-specific and varies from one site to another; therefore, identifying a universally optimal spatial resolution for capturing grassland plant diversity remains complicated.

4.2.2. Impact of plot size on remote sensing of plant diversity

One of the aspects of spatial scale that has been largely overlooked in remote sensing studies of plant diversity is plot size, which is used to estimate plant diversity across a fixed extent within a plant community. In our study, by defining and sampling large 240 m × 240 m plot sizes in the field, we had the opportunity to study the impact of plot size operationally through looking at the plant diversity-spectral diversity relationship at different plot sizes, including 60 m × 60 m, 120 m × 120 m, 180 m × 180 m, and 240 m × 240 m plots. In recently-burned and transitional stage plots, the plant diversity-spectral diversity relationship was significant for 180 m × 180 m and 240 m × 240 m plot sizes (Fig. 9); for smaller 60 m × 60 m and 120 m × 120 m plot sizes, the plant diversity-spectral diversity relationship was not significant. This was an important finding indicating that our remote sensing data were not capable of mapping grassland α-diversity for small plot sizes, even when we used fine-resolution airborne data. For instance, in case of 120 m × 120 m plots, we had 14,400 pixels in our airborne data to calculate spectral diversity for each plot, yet spectral diversity was not capable of capturing observed plant diversity estimated from 10 quadrats (Fig. 9; see Fig. 2 for sampling design). Our results were in agreement with Oldeland et al. (2010) where a stronger plant α-diversity-spectral diversity relationship was reported for larger sampling plots, presumably due to higher species and spectral diversity value ranges over larger areas. These results indicate that, in our site, remotely-sensed data might be capable of capturing regional diversity (i.e., γ-diversity, composed of both α- and β-diversity) rather than local diversity (i.e., α-diversity) alone. These findings, together, revealed that in addition to spatial resolution (i.e., pixel size), dimensions of a sampling plot is an equally important aspect of spatial scale that we need to consider in remote sensing of plant diversity.

The importance of plot size is usually overlooked in remote sensing studies despite the fact that prior ecological studies have suggested that plot size influences our estimates of plant diversity (Kettenring and Adams, 2011; Meier and Hofer, 2016). Plot size–or field sampling design as a more comprehensive term–in remote sensing studies of plant diversity is often decided and finalized prior to planning remote sensing data collection or independent from it to address other goals that might not overlap with the remote sensing study goals. We consider this mismatch between remote sensing and field sampling design a missed opportunity. Remote sensing is probably the only feasible means of

providing spatially continuous estimates of plant diversity globally, beyond small plots. Consequently, it is important to examine what remote sensing can measure from above and what the limits are. A central question is whether we can measure plant diversity for small geographical extents at fine resolution (i.e., α-diversity) or whether it would be more accurate to focus on mapping species turnover (i.e., β-diversity) or plant diversity across large geographical extents at coarser resolution (i.e., γ-diversity). This effort may not be fully realized without considering field sampling design in remote sensing studies. In the next several years, a number of spaceborne imagers, such as SBG and CHIME will be launched; if we are to develop remote sensing metrics to map plant diversity and eventually design a global biodiversity monitoring network, assessing different components of spatial scale, including plot size and sampling strategy is warranted.

4.3. SWIR region of the spectrum enhances remote sensing of plant diversity

A few studies have explored the contribution of different regions of the spectrum to the plant diversity-spectral diversity relationship (Wang et al., 2018b). Gholizadeh et al., 2018, for example, reported that the 670–680 nm range can facilitate distinguishing plant communities with different levels of species richness. However, to our knowledge, the impact of remotely-sensed SWIR bands versus VNIR bands on the plant diversity-spectral diversity relationship has not been extensively studied, with most studies using one or the other depending upon the instrument available. Comparing results obtained from our airborne data with and without SWIR bands showed that including this region of the electromagnetic spectrum enhanced our ability to map plant diversity (Fig. 8 and Fig. S2 in Supplementary material). Contribution of SWIR bands can point to the significant impact of specific plant traits, especially water–which dominates reflectance in the SWIR region (Carter, 1991)–along with traits such as cellulose, lignin, proteins, and several nutrients (Curran, 1989; Fourty et al., 1996; Kokaly et al., 2009). Collectively, these findings indicate the promise and utility of full-range airborne–and even SBG-like spaceborne data–for mapping plant diversity in grasslands.

4.4. Limitations and future work

4.4.1. In-situ data collection efforts need to be intensive

While collecting, pre-processing, and analyzing airborne and spaceborne hyperspectral data with fine and coarse spatial resolution from relatively large geographical regions is feasible thanks to recent technological and methodological advances, these remotely-sensed data need to be accompanied with in-situ data to make more reliable inferences. Although we sampled species composition and percent cover extensively across a total of 2500 locations within 100 plots in a naturally-assembled grassland under different management practices, this sampling still had its own limitations. Of note is the total surveyed area per plot. We sampled 25 equally-spaced 0.5 m × 0.5 m quadrats within each 240 m × 240 m plot. This total surveyed area per plot cannot fully capture species diversity, particularly for locations in diverse and heterogeneous communities, where the probability of sampling all rare species is low (Reichert et al., 2010). While our in-situ sampling effort was one to two orders of magnitude larger than previous published efforts in terms of the number of sampled locations, the extent of the study area, total surveyed area, and person-hours spent on in-situ data collection, we still encourage future efforts to be more intensive when possible. Such intensive in-situ data collection efforts can further reduce the uncertainty associated with validating remote sensing of biodiversity results.

4.4.2. There are many metrics to express in-situ and remotely-sensed plant diversity

In this study, we used three metrics to express in-situ plant diversity (Table 1). However, there are a plethora of approaches to express in-situ species diversity that we did not test (Maurer and McGill, 2011). Similarly, while we used three different spectral diversity metrics and reported the results of one of these metrics (CV), there are many more approaches that we did not use. These metrics can be continuous collapsed approaches (similar to CV), discrete spectral species approaches (Féret and Asner, 2014), or even those based on vegetation indices that assume a positive biodiversity-productivity relationship, although we did not observe strong association between measured plant diversity and proxies of productivity in our site (Fig. S4 in Supplementary material). Different in-situ or remote sensing metrics of biodiversity are used in the literature not necessarily because they are perfect but rather because they have been commonly applied in the past or they are easy to derive. Therefore, assessing different metrics of biodiversity to identify under what circumstances each of these metrics work is still an open question in remote sensing studies of biodiversity.

4.4.3. Impact of seasonal variation on remote sensing of plant diversity

The majority of remote sensing studies of plant diversity select an optimal time for data collection which is determined based on the ecosystem under study (e.g., peak growing season for temperate grasslands). In our experiment, we collected data at one point in time and therefore we did not assess the impact of plant phenology–in and of itself–on spectral diversity. In other words, focusing on one remote sensing data collection campaign limited our ability to study the impact of temporal variation on vegetation and remote sensing of plant diversity. Although there was only one cloud-free DESIS image over the growing season in our site, promising results obtained from DESIS data indicate that forthcoming spaceborne hyperspectral imagers, which will have much finer temporal resolution than DESIS, can assist with multi-temporal assessment of plant diversity.

4.4.4. Remote sensing of grassland plant diversity needs to be tested under a variety of management practices

Management across our site is conducted to promote heterogeneity (i.e., variability in vegetation and soil cover, vegetation composition, or stature in space and time) with the goal of maintaining and enhancing grassland biodiversity. We note that not all grassland management regimes are similar in their approach regarding biodiversity maintenance or their ability to promote heterogeneity (Fuhlendorf et al., 2012). There is a distinct dichotomy between some traditional grassland management practices and those at our site. Briefly, traditional practices have historically promoted homogenization of grassland landscapes in line with utilitarian objectives such as livestock production. For example, some traditional management practices have historically included annual prescribed fires applied to the whole landscape (instead of different patches as in our experiment) and used infrastructure to promote uniform distribution of grazing animals across the landscape. Such traditional management practices, which have been referred to as "managing for the middle" (Fuhlendorf and Engle, 2004) are based upon ecological theories, including the intermediate disturbance hypothesis, predicting that intermediate levels of disturbance lead to maximum biodiversity (Connell, 1978). As a result of such striking differences in grassland management approaches and how they influence the landscape (e.g., promoting heterogeneity vs. uniformity), we suggest that conducting similar experiments in other grasslands with different management practices can be a promising future research avenue which benefits both the remote sensing and conservation communities.

5. Conclusions

In this study, we assessed the capability of remotely-sensed hyperspectral data for mapping plant α-diversity in a naturally-assembled heterogeneous tallgrass prairie of high conservation importance. We tested for associations between spectral diversity and plant diversity by comparing fine-resolution airborne (spatial resolution of 1 m) and

coarse-resolution DESIS spaceborne imagery (spatial resolution of 30 m) to robust in-situ species diversity data. Our results showed that when we expressed plant diversity as species richness or Shannon diversity, the plant diversity-spectral diversity relationship was non-significant or very weak across spatial resolutions (i.e., pixel sizes) ranging from 1 m to 30 m. Simpson diversity, on the other hand, was strongly associated with spectral diversity calculated using both airborne and spaceborne data for grassland plots at the transitional stage or those that were burned recently. We found no significant relationship between Simpson diversity and spectral diversity in plots at the pre-prescribed fire stage. We also found that regardless of spatial resolution and time since fire, there was no significant relationship between plant diversity and spectral diversity for small plots (i.e., 60 m × 60 m and 120 m × 120 m). These results show that (1) management-induced heterogeneity affects remote sensing of plant diversity; therefore, considering the history of management practices is necessary for proper interpretation of remote sensing results, (2) fine- and coarse-resolution remotely-sensed data can be used to estimate grassland plant diversity metrics that are biased towards dominant species (e.g., Simpson diversity), and (3) attention to sampling design and plot size in remote sensing studies of plant diversity is warranted.

By using DESIS data, our study also provided a first-cut look at the potential of forthcoming spaceborne imagers for mapping plant diversity in grasslands. Although DESIS collects data only in the VNIR portion of the spectrum and does not include SWIR bands, it was still capable of estimating grassland plant diversity, when expressed as Simpson diversity. These results indicate the promise of forthcoming hyperspectral missions–such as NASA's SBG mission or ESA's CHIME with comparable spatial resolution to DESIS but superior spectral coverage with data collection capabilities at both VNIR and SWIR regions–for capturing plant diversity in naturally-assembled grasslands. Our study contributes to the development of an operational global biodiversity monitoring system which can eventually facilitate a deeper understanding of the effectiveness of different grassland management practices to maintain biodiversity in the face of rapid environmental change.

Data availability

Processed full-range 1-m airborne hyperspectral data are available to download free of charge from the NASA EOSDIS Land Processes Distributed Active Archive Center at https://lpdaac.usgs.gov/products/aehyp1tppokv001/.

Author contributions

H.G., J.G., J.C.B., R.H., and S.F. designed and conceived the study. A. D., K.P., H.G., and N.M. contributed to collecting species inventories. H. G. analyzed the data. All authors contributed to writing the manuscript.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rse.2022.113254.

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