



Remote sensing of terrestrial plant biodiversity

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ABSTRACT

Biodiversity is essential to healthy ecosystem function, influencing productivity and resilience to disturbance. Biodiversity loss endangers essential ecosystem services and risks unacceptable environmental consequences. Global biodiversity observations are needed to provide a better understanding of the distribution of biodiversity, to better identify high priority areas for conservation and to help maintain essential ecosystem goods and services. Traditional in situ biodiversity monitoring is limited in time and space and is usually a costly and time-consuming enterprise. Remote sensing can provide data over a large area in a consistent, objective manner and has been used to detect plant biodiversity in a range of ecosystems, typically based on relating spectral properties to the distribution of habitat, species or functional groups. Recent years have witnessed the emergence of methods using imaging spectroscopy to assess biodiversity via plant traits or spectral information content. However, questions regarding the complex drivers of plant optical properties and the scale dependence of spectral diversity – biodiversity relationship confound diversity monitoring using remote sensing and must first be better understood before these methods can be operationally applied. To address some of these topics, we (1) review the history of remote sensing approaches in biodiversity estimation, summarizing the pros and cons of different methods, (2) illustrate successes and major gaps of remote sensing of biodiversity, and (3) identify promising future directions. We focus on emerging methods using spectral diversity (optical diversity) as a proxy for terrestrial plant diversity that offer to revolutionize the study of diversity in its different dimensions (phylogenetic, taxonomic, and functional diversity) from remote sensing. We also discuss remaining knowledge gaps and ways spectral diversity might be effectively integrated into a global biodiversity monitoring system, bridging a gap between ecology and remote sensing.

1. Introduction

Many biodiversity studies have addressed biodiversity losses due to human action, with many studies concluding we are now facing the beginning of a mass extinction (the Sixth Extinction) (Barnosky et al., 2011) and by the middle of the current century, up to half of the Earth's species may disappear (Thomas et al., 2004; Wake and Vredenburg, 2008). Phylogenetic and functional diversity loss, range collapse, habitat loss, population declines, species invasions, altered community composition, and rapid environmental changes are relevant indicators of imminent species loss (Pereira et al., 2010a). Many of these changes can lead to unexpected and often negative effects on ecosystem function (Pereira et al., 2010a). Human wellbeing depends upon the ecosystem goods and services provided by diverse and stable ecosystems.

Starting in the late 1990s, experimental studies began to explore the effects of biodiversity on ecosystem function, and biodiversity loss

emerged as an important global change issue in its own right (Pimm et al., 1995; Sala et al., 2000; Pereira et al., 2010a). Biodiversity affects productivity (Tilman et al., 1996; Isbell et al., 2009; Isbell et al., 2015), community and ecosystem stability (Tilman and Downing, 1994; Tilman et al., 2006), invasibility (Naeem and Li, 1997; Naeem et al., 2000), and nutrient use and retention (Hector and Bagchi, 2007; Maestre et al., 2012; Midgley, 2012), illustrating its critical role in maintaining healthy ecosystem function. Variation in the relationship between biodiversity and ecosystem function has been reported and is known to depend on resource availability (Reich and Hobbie, 2013), environmental drivers (Tilman and Haddi, 1992; Isbell et al., 2015) and scale (Whittaker, 2010; Fraser et al., 2014). For example, a variety of biodiversity-productivity relationships, including positive, negative, hump-shaped and U-shaped have been reported at local scales (Adler et al., 2011; Fraser et al., 2015), while a positive relationship has been found at broad spatial scales (Oehri et al., 2017).

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An explicit field survey of all species can provide detailed information on biodiversity for a particular location, but it is infeasible to apply this kind of census for every case and species in a region through time (Robinson et al., 1994; McCollin et al., 2000). Sampling method, with attention to factors like sampling objectives, where, when and how to sample, size and number of sampling units, and randomly or systematically selected sampling units, must be considered to estimate biodiversity (Bonar et al., 2010). Traditional field sampling generally requires a lot of time, and human resources, and can be remarkably expensive when sampling over a large area (Levrel et al., 2010; Pereira et al., 2010b). Furthermore, sampling results are known to be context-dependent, varying with environmental conditions and spatial scale (Gaston, 2000; Palmer et al., 2002) and can be confounded by human bias, even when conducted by experts (Asko et al., 2018).

The well-discussed gap between our knowledge of species, and the estimated total number of species (sometimes called the “Linnaean Shortfall” (Lomolino, 2004; Whittaker et al., 2005)), has led to calls for monitoring biodiversity using remote sensing (Turner et al., 2003), since consistent and repeatable remote sensing measurement can provide efficient and cost-effective means to determine plant and ecosystem diversity over large areas (Nagendra, 2001) and can be critical to long term global biodiversity assessment (Turner, 2014). Early studies were typically based on habitat assessment (Stoms & Estes 1993; Nagendra 2001; Turner et al., 2003). More recent remote sensing approaches have often involved the provision of remotely detectable variables, like biomass or productivity and canopy structure (height, LAI) that can be used as proxies to estimate species richness or distribution patterns (Turner et al., 2003). The proposed “Essential biodiversity variables” (EBVs) provide a means to relate remote sensing measurements to ecosystem function or community composition variables (such as biomass or productivity, phylogenetic and taxonomic diversity, phenology, and habitat structure) in ways that can help predict responses of EBVs to environmental drivers at large scales (Pereira et al., 2013). While there is a clearly identified need for a global biodiversity monitoring system, it is less clear how such a system should be designed, and the exact role remote sensing can play. In addition, field biodiversity sampling criteria do not always match those of remote sensing metrics, so it remains a challenge to relate metrics derived from remote sensing to independently derived field metrics. Recently, new methods of assessing biodiversity via spectral diversity (optical diversity) have emerged, offering new ways to explore the relationships between remote sensing and traditional metrics of biodiversity.

In this review, we briefly examine the history of remote sensing of biodiversity and outline major and emerging applications involving biodiversity assessment using remote sensing. We include a particular focus on recent advances in detection of plant diversity through spectral diversity (aka “optical diversity”) because the rapid advances in this field offer a level of direct detection not previously possible, and because these new methods may offer significant contributions to a proposed global biodiversity monitoring system (Jetz et al., 2016; Proença et al., 2017; National Academies of Sciences, 2018). Ecological theory and empirical evidence suggests that spectral diversity may work as an indicator of biodiversity at several dimensions, a term we refer to as the “surrogacy hypothesis,” building on a history of observations that diversity at one taxonomic level often relates to diversity at another level (Magurran, 2004). We also consider the issue of sampling scale in remote sensing of biodiversity, because this represents a major knowledge gap and emerges as an area needing further research (Gamon et al., in press).

2. History of remote sensing of biodiversity

Although the early terrestrial observation satellites were launched in the 1970s, the potential of using remote sensing to measure, map, monitor, and model spatial patterns and trends in biodiversity was

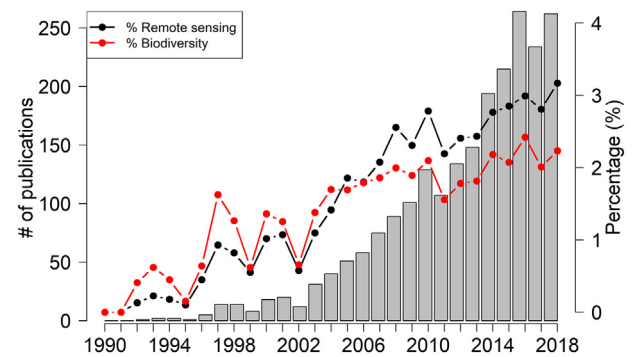


Fig. 1. The yearly number of publications on ‘remote sensing of biodiversity’ (combining the search terms “biodiversity” and “remote sensing,” bar graph, left Y-axis) and percentages of the total number of publications found using search terms ‘remote sensing’ or ‘biodiversity,’ respectively (lines, right Y-axis) from 1990 to 2018 in Web of Science core collection (updated in Jan, 2019).

largely ignored until the 1990s (Stoms and Estes, 1993). A simple survey of the number of published articles using “Remote Sensing” and “Biodiversity” as Topic in Web of Science reveals the increasing interest in using remote sensing for assessing biodiversity (Fig. 1). By 1990, only one publication was found that used satellite remote sensing to assess biodiversity and this tracked the effects of tropical forest loss on the changes in species abundance (Westman et al., 1989). A larger number of studies on this topic started to emerge in the 1990s (65 publications from 1990 to 2000, defined as the number of publications in the Web of Science core collection) and the numbers increased steadily in the first 15 years of this century (Fig. 1). Clearly, the remote sensing of diversity topic is receiving ever-increasing attention in both ecological and remote sensing communities and is generating new efforts to better integrate these two seemingly disparate fields.

The early applications of remote sensing in biodiversity estimation mostly focused on mapping landscape or habitat through land cover classification mainly using optical remote sensing products without providing detailed verification of the habitat diversity – biodiversity relationship (Stoms and Estes, 1993). Progress in this topic was constrained by a limited ecological understanding of the effects of biodiversity on ecosystem function, limited information provided by the early remote sensing sensors, insufficient imaging processing techniques (e.g., simple classification methods with no indices specifically designed for biodiversity assessment), and lack of understanding of how to interpret ecological information contained in the remote sensing products (Stoms and Estes, 1993). Imaging spectroscopy and Light Detection and Ranging (LiDAR) systems have greatly enriched the dimensionality of remotely sensed data (Asner et al., 2012; Thompson et al., 2017) and have expanded the range of detectable plant biochemical, physiological and structural properties that can contribute to an assessment of diversity (Ustin and Gamon, 2010; Asner et al., 2012). Furthermore, the price and availability of these technologies have been improving, making it easier for more people to use remote sensing for diversity monitoring.

3. Remote sensing of plant diversity

Studies exploring diversity using remote sensing can be generally categorized into four types (Fig. 2): studies that estimate biodiversity indirectly through habitat mapping; those that map distributions of individuals as a basis for assessing community composition and diversity; studies that estimate functional diversity through plant functional traits; and studies that assess species composition from patterns of spectral variation (spectral diversity aka optical diversity) to yield plant diversity. Here we treat these separately, but recognize that these methods can also be used in combination.

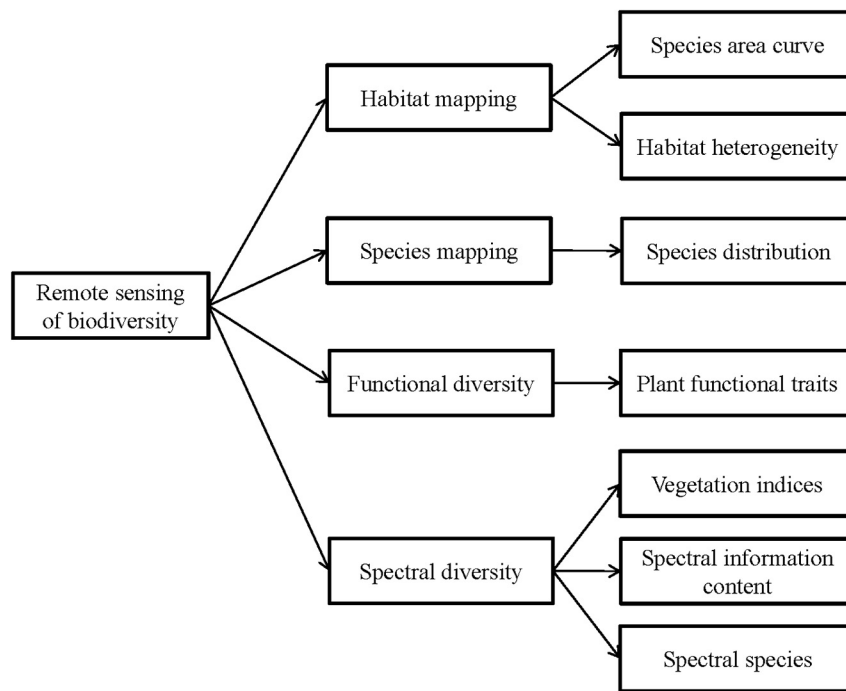


Fig. 2. “Taxonomy” of remote sensing of biodiversity, illustrating four broad methodological categories, along with examples of specific sub-methods. Examples of each category of biodiversity assessment are further discussed below.

3.1. Estimating biodiversity indirectly with habitat mapping

Historically, habitat-based approaches have utilized indirect methods of assessing biodiversity, e.g. via species-area curves (Stoms & Estes 1993, Turner et al 2003) or via habitat heterogeneity, often using textural metrics (Tuanmu & Jetz 2015). Habitat heterogeneity has been regarded as one of the most important factors governing species richness and has been predicted to have a positive relationship with biodiversity (Stein et al., 2014), since habitats with higher heterogeneity may be able to provide more niche space for species coexistence, persistence and diversification (Hutchinson, 1957; Tews et al., 2004; Stein et al., 2014; Tuanmu and Jetz, 2015). Even heterogeneity of the physical environment at small scales (< 1 km²) can be important to biodiversity because it defines the resource environment at scales relative to many organisms (Hjort et al., 2015). Estimating biodiversity through habitat mapping often applies remotely sensed indices to assess environmental parameters related to “geodiversity” (e.g., climate and habitat structure (Gaston, 2000; Nagendra, 2001; Turner et al., 2003), also geology and topography (Gray, 2008; Hjort and Luoto, 2012; Beier et al., 2015)) and either relates the heterogeneity of the habitats to biodiversity (Kerr et al., 2001; Bailey et al., 2004) or integrates this information with regional models (e.g., National Gap Analysis Program (GAP) (Jennings, 2000) or local models (Parviainen et al., 2009)) to estimate biodiversity. Land cover mapping is one of the earliest and most widely used applications of optical remote sensing and can serve as the basis of habitat maps for biodiversity indicator extraction (Stoms and Estes, 1993; Tomaselli et al., 2013). At the beginning of this century, land cover data had been found to be helpful for predicting the distributions of both individual species (Jennings, 2000; Saveraid et al., 2001) and species assemblages (Kerr et al., 2001), establishing habitat mapping as a useful way of applying remote sensing to infer spatial patterns of biodiversity. This method is particularly useful for identifying potential habitat of key species and has been an important tool for conservation purposes (Corbane et al., 2015; Lucas et al., 2015; Tuanmu and Jetz, 2015).

The accuracy of biodiversity estimation using habitat mapping is highly scale dependent (Tews et al., 2004) and is affected by

characteristics of the species involved (Kerr and Ostrovsky, 2003). Typically, land cover mapping estimates potential rather than real species distributions for species that do not occupy all suitable habitats (Kerr and Ostrovsky, 2003), analogous to the concept of the fundamental niche (Hutchinson, 1957; Tews et al., 2004). For example, the estimation of the distributions of particular butterfly, plant or bird species in Yellowstone National Park is possible when their distributions fit a specific habitat requirement, the number of their individuals are abundant, or both (Saveraid et al., 2001). It is less practical to assess distribution of rare species or species that are not specific to particular habitats even from remarkably accurate and detailed land cover data (Kerr and Ostrovsky, 2003).

Habitat mapping using remote sensing is often applied at coarse scales (Wulder et al., 2004; Corbane et al., 2015; Tuanmu and Jetz, 2015) (Table 1). Global land cover data can be provided by using MODIS sensors at 500 m pixel size (Friedl et al., 2010), while regional land cover data have been retrieved using moderate resolution satellite products such as Landsat that has a 30 m spatial resolution (Tiede et al., 2010). Detailed information on landscape complexity is lost when using such relatively coarse resolution satellite products. As a consequence, this approach, although useful and easy to apply, usually ignores within-habitat variability by using a single mean value to predict diversity within each land cover class (Hernández-Stefanoni et al., 2012). At a finer spatial scale, aerial photography has been used for forests assessment since the 1990s (Wulder, 1998) and is still widely applied today (e.g., Alberta Biodiversity Monitoring Institute, 2015)). However, the limited spectral information contained in those products limits the accuracy of habitat mapping and precludes widespread usage or direct linkage to functional vegetation biophysical and biochemical properties (e.g., pigment levels, nitrogen content, leaf or canopy structure, etc.) that are often related to patterns of biodiversity.

3.2. Mapping distributions of species or functional types

Unlike habitat mapping, species mapping requires fine spectral and spatial details, and most satellite data are too coarse spectrally and spatially for direct species mapping. Species mapping using remote

Table 1

Examples of diversity estimation through habitat mapping, showing target ecosystems, sensors and platforms, specific methods used, and references.

Ecosystem & location	Sensor or Platform	Methods	Reference
Grassland and deciduous woodland (Scotland)	Landsat	Unsupervised classification	(Austin et al., 1996)
Grassland and deciduous woodland (Great Britain)	Landsat	Classification	(Griffiths and Lee, 2000)
Greater Yellowstone Ecosystem (USA)	SPOT	Classification	(Saveraid et al., 2001)
Pan Canada	AVHRR, SPOT	Classification by Canada Centre for Remote Sensing and Canadian Forest Service	(Kerr et al., 2001)
Boreal agricultural landscape (Finland)	Landsat	Supervised classification	(Luoto et al., 2002)
Great Basin (USA)	Landsat	Maximum and heterogeneity of productivity	(Bailey et al., 2004)
Great Britain	AVHRR	NDVI, temperature	(Foody, 2005)
Pine/aspen forest (South Dakota, USA)	LiDAR, IKONOS	Vegetation index	(Clawges et al., 2008)
Evergreen forest, transitional between lowland rain forest and montane forest (Uganda)	Landsat, Quickbird	NDVI, PCA	(Stickler and Southworth, 2008)
Northern boreal forest (Finland)	Landsat	NDVI and local greenness models	(Parviainen et al., 2009)
Coastal plain (Carolina, USA)	Landsat, MODIS	Mean NDVI - productivity	(Costanza et al., 2011)

Table 2

Examples of species or functional types mapping with remote sensing.

Ecosystem & location	Sensor or platform	Methods	Reference
California Chaparral (California, USA)	AVIRIS	Endmember spectral mixture analysis (classification)	(Roberts et al., 1998)
Forest tree species in urban area	AVIRIS	Spectral mixture analysis (Classification)	(Xiao et al., 2004)
Invasive forest species (Hawaii, USA)	AVIRIS	PLSR	(Asner et al., 2008b)
Wetland (California, USA)	PROBE	Classification	(Zomer et al., 2009)
Tundra (Alaska, USA)	Hyperion	Discriminant analysis	(Huemmerich et al., 2013)
Mediterranean type ecosystem (California, USA)	CAO-AToMS	PLSR	(Dahlin et al., 2013)
Invasive species urban area (British Columbia, Canada)	CASI	Spectral angle mapper classification	(Chance et al., 2016)

sensing has long been of interest to forest management and conservation sectors (Fassnacht et al., 2016). This approach has benefited greatly from the availability of airborne hyperspectral and LiDAR data that can provide high spatial resolution products with detailed spectral and structural information at local or regional scales (Roberts et al., 1998; Ustin et al., 2004; Xiao et al., 2004; Asner et al., 2008b; Somers and Asner, 2013; Liu et al., 2017) and has most widely been used for vegetation with large crown sizes (e.g. trees), which can be resolved with the typical grain size (pixel size) of airborne remote sensing instruments (Table 2). Airborne spectra have also been successfully related to leaf traits (further discussed in section 3.3, below), providing an approach to map functional types particularly when the pixel size can be matched to the crown size, and when pixels can be stratified according to their crown position and illumination (Asner and Martin, 2009; Dahlin et al., 2013; Féret and Asner, 2014; Singh et al., 2015). Although it is typically impossible to distinguish every species using remote sensing (Price, 1994), it is often feasible to differentiate dominant species or community types using spectral differences (Ustin and Gamon, 2010). For example, invasive species may have distinct reflectance and 3D structural properties from that of native species (Asner et al., 2006; Asner et al., 2008a), and plants of different functional types, e.g., nitrogen-fixing and non-fixing species, can often be separated due to their biochemical composition (Asner et al., 2008a; Asner et al., 2008b). Moreover, canopy structure, which can accentuate certain leaf spectral properties through multiple scattering and contrasting illumination, can influence the overall canopy optical signal, which may help distinguish different species or functional groups (Roberts et al., 2004; Ollinger, 2011). By integrating imaging spectroscopy and LiDAR, both leaf traits and canopy structure can be captured together. As a consequence, mapping individual species can succeed when there is sufficient biochemical and/or structural variation between species (Ustin and Gamon, 2010) and adequate a priori knowledge about the optical properties of all the possible present species (Price, 1994). A recent literature review on tree species classification using remote sensing (Fassnacht et al., 2016) illustrates the power of this approach.

An alternative approach for mapping dominant species or vegetation types is based on spectral mixture analysis (SMA) (Gamon et al.,

1993; Roberts et al., 1998; Roth et al., 2012; Thorp et al., 2013; Dudley et al., 2015). SMA assumes that the spectral signal collected by a spectrometer is either a linear or nonlinear combination of endmembers (Somers et al., 2011). Constituent species and relative amount within a mixed pixel can be identified by applying endmembers that have been obtained from field or laboratory measurements or simulated using radiative transfer models (Somers et al., 2016). As a consequence, the accuracy of this approach depends heavily on the quality of the end-member library that accounts for a priori knowledge of species' spectra and the endmember variability. It also requires the species to be spectrally distinct, and this can be confounded when there is a high degree of within species variability. Furthermore, it is difficult to distinguish every species when the number of species within a single pixel is large (Price, 1994). Nevertheless, this approach can be used to map "indicator species" that might have conservation importance.

3.3. Estimating functional diversity through plant functional traits

Plants traits reflect both evolutionary history (Wright et al., 2005) and environmental and resource limitations through leaf life span, allocation to defense, rates of photosynthesis and respiration (Wright et al., 2004; Niinemets et al., 2015), and investment in photoprotection (Gamon et al., 2005, 1997). As a result, an individual organism's traits represent the interaction between its genome, the changing environment, and random events (Fusco and Minelli, 2010; Cavender-Bares et al., 2016a). Many plant traits affect plant light absorption and scattering and consequently, cause variation in plant optical properties that can be detected with remote sensing (Ustin et al., 2009; Ustin and Gamon, 2010; Asner and Martin, 2016; Cavender-Bares et al., 2017).

One benefit of mapping plant functional traits is that it focuses on capturing the range and variation in traits that can be related to diversity of species' niches or functions (Cadotte et al., 2011) without necessarily having to identify every single species (Singh et al., 2015; Anderson, 2018). Statistical methods like partial least squares regression (PLSR) yield coefficient spectra that can serve as proxies, combining biochemical and structural traits to indicate plant functional diversity (Kokaly et al., 2009; Schweiger et al., 2017). Remote sensing

Table 3
Examples of estimating functional diversity through plant functional traits.

Ecosystem & location	Sensor & Platform	Methods	Reference
Tropical forest (Australia)	Leaf reflectance (ASD)	PLSR	(Asner and Martin, 2008)
Raised bog and minerotrophic fen complex (Germany)	HyMap	PLSR	(Schmidtlein et al., 2012)
Mediterranean type ecosystem (California, USA)	CAO-AToMS	PLSR	(Dahlin et al., 2013)
Natural forest (north central and north eastern USA)	Leaf reflectance (ASD)	PLSR	(Serbin et al., 2014)
Natural forest (Northeast USA)	AVIRIS	PLSR	(Singh et al., 2015)
Andes-to-Amazon	CAO-AToMS	PLSR	(Asner et al., 2015)
Grassland (Swiss)	APEX	PLSR	(Schweiger et al., 2017)
Grassland (Minnesota, USA)	Leaf reflectance and ground (Headwall)	PLSR	(Schweiger et al., 2018)

has been applied to map plant functional diversity through plant functional traits at both leaf scale (Asner and Martin, 2008; Serbin et al., 2014; Schweiger et al., 2018) and canopy scale (Asner et al., 2015; Singh et al., 2015; Schweiger et al., 2017) (Table 3).

High variability in plant traits within functional groups (Violle et al., 2012), which might be due to difference in soil conditions, microclimate, hydrology, topography, can introduce uncertainties in plant functional diversity estimation using remote sensing (Dahlin et al., 2013; Schweiger et al., 2017). Similarly, seasonal change in plant traits due to leaf age and ontogeny can further confound trait detection (Chavana-Bryant et al., 2017). Mapping plant functional traits (PFTs) using remote sensing can also be sensitive to vegetation percentage cover, since optical signals can be confounded by soil reflectance in gaps between canopies and this can become a major problem for ecosystems with low vegetation cover (Homolová et al., 2013) and for sensors lacking sufficient spatial resolution (Anderson, 2018). Despite these challenges, a recent review on imaging spectroscopy of forest chemical traits revealed the potential of applying remote sensing to monitor vegetation functional diversity (Hill et al., 2019).

3.4. Assessing diversity directly through spectral diversity

The spectral variation hypothesis (SVH) (Palmer et al., 2000, 2002), relates the spectral heterogeneity or variability (the spatial variability of remote sensed signal) to environmental heterogeneity, providing a proxy of species diversity. This hypothesis has been reviewed by (Rocchini et al., 2010) who concluded that the performance of this approach depends on instrument characteristics, target vegetation types, and metrics derived from remote sensing data (Schmidtlein and Fassnacht, 2017; Rocchini et al., 2018).

“Spectral diversity”, sometimes called “optical diversity” (Ustin and Gamon, 2010), indicates variation in spectral patterns detected by optical remote sensing, which can in itself be related to species diversity, functional diversity, and genetic diversity. The spectral (optical) diversity hypothesis links ecological resource theory to fundamental physical principles to provide a rapid and accurate approach to measure biodiversity via optical patterns (Ustin and Gamon, 2010). Optical type is regarded not only as an indicator of plant physiological and biochemical properties but also as a fundamental vegetation property, resulting from “ecological rules” driven by strategies of resource allocation. Instead of mapping species per se, spectral diversity typically detects spectral patterns related to functional and structural properties, which vary among species or functional groups (“optical types”) (Gamon et al., 1997; Ustin and Gamon, 2010). The underlying reason is that phylogenetic differences and resource limitations (e.g., light, water, and nutrients) affect plant growth and leaf traits (e.g. carbon and nitrogen composition, pigment or water content, dry mass and structural parameters such as lignin), canopy structure (e.g. leaf area and leaf angle distribution) and phenology.

Many remote sensing indices based on spectral patterns have been proposed to assess biodiversity (Table 4). In this context, an “index” represents an abstract, statistical metric derived from spectral patterns, representing either the information content of a set of spectra or the

number of kinds of spectra, as opposed to the more traditional concept of a “vegetation index,” although such traditional indices also carry considerable information content and can be used to infer biodiversity (Gould, 2000; Fairbanks and McGwire, 2004; Gillespie, 2005; Levin et al., 2007). We suggest that spectral diversity indices can be grouped into three major categories: 1) metrics based on variation in vegetation indices, 2) metrics based on information theory (e.g. spectral entropy); and 3) metrics based on spectral species (Fig. 2).

The mean and variance of specific wavebands or traditional vegetation reflectance indices have been used to estimate biodiversity (Gould, 2000; Gillespie, 2005; Carlson et al., 2007). A classic example is the Normalized Difference Vegetation Index (NDVI), which often scales with species richness (e.g. (Gillespie, 2005; Wang et al., 2016b)), in part due to the well-known link between productivity and biodiversity (Tilman et al., 2001; Zhang et al., 2012; Oehri et al., 2017).

Spectral diversity can also be related to plant diversity by condensing spectral information into a number of statistical metrics of variability or information content. This category of full-spectral metrics includes the coefficient of variation (CV) of spectral reflectance across space (Wang et al., 2016a), spectral angle mapper (SAM) (Zhang et al., 2006), convex hull area or volume (Gholizadeh et al., 2018), or the distance from the spectral centroid (Palmer et al., 2002). Alternatively, these indices can be calculated based on patterns in principal component space that compact spectral information and remove noise and band collinearity. Examples include the distance from the centroid in principal component space (Rocchini, 2007; Möckel et al., 2016) and convex hull volume in principal component space (Dahlin, 2016). All of these metrics provide information on the “dimensionality” of a dataset for a given area, which can then be related to the number of species present in that area. It is worth noting that several of these spectral diversity metrics can be confounded by illumination conditions and optical properties of background materials, since optical properties of different backgrounds, such as soil and litter, can increase the image heterogeneity that captured by the information based spectral diversity metrics (Gholizadeh et al., 2018; Hakkenberg et al., 2018; Wang et al., 2018b) (Table 4).

An alternative approach categorizes spectra according to a distinct set of types or “spectral species.” Here, we expand the term ‘spectral species’ (Féret and Asner, 2014) to a broader scope that includes a classification, either unsupervised classification (Féret and Asner, 2014) or supervised classification (Schäfer et al., 2016; Wang et al., 2018b), to remotely sensed images and estimated biodiversity using spectral types rather than actual species. In this case, spectral species are considered proxies or analogues for biological species, and spatial variation in spectral species can be used to infer species richness or other metrics of α diversity (diversity at local scales), and over larger areas, β diversity (variability in species composition among sites) (Whittaker, 1960; 1972). Species-based spectral diversity metrics may be less sensitive to soil background than the information content-based metrics (Wang et al., 2018b) because different backgrounds, which are often spectrally unique, can be accurately classified given high spatial resolution (Roth et al., 2015; Gholizadeh et al., 2018). However, species-based metrics are of limited value for characterizing canopy with mixtures of several

Table 4
Examples of diversity assessment through spectral (optical) diversity.

Type of methods	Ecosystem & location	Sensor or Platform	Methods	Reference
Index based	Low-shrub tundra (NWT, Canada)	Landsat	Variation in NDVI	(Gould, 2000)
	Subtropical vegetation communities (California, USA)	AVHRR	Variation in NDVI	(Fairbanks and McGwire, 2004)
	Tropical forest (Florida, USA)	Landsat	Mean and standard deviation of NDVI	(Gillespie, 2005)
	Evergreen Mediterranean plants (Mount Hermon, Israel)	Landsat, Aster, Quickbird	Mean and standard deviation of NDVI	(Levin et al., 2007)
	Grassland (Minnesota, USA)	Ground (Unispec)	Mean NDVI	(Wang et al., 2016b)
	Dry, moist, and wet forest (Panama)	Landsat, AIRSAR	Mean and standard deviation of NDVI, radar backscatter	(Gillespie et al., 2009)
	Grassland (Inner Mongolia, China)	MODIS	MODIS-derived GPP and NDSVI	(John et al., 2008)
	Lowland rain forest (Hawaii, USA)	AVIRIS	Range of spectral values	(Carlson et al., 2007)
	Meadows and woodland (Mississippi, USA)	HyMap	CV of reflectance indices	(Lucas and Carter, 2008)
	Tropical forest (Panama)	CAO-2 ATOMS	CV of reflectance	(Somers et al., 2015)
Information content	Grassland (Minnesota, USA)	Ground (Headwall)	First- and second- order image texture measurements	(Wang et al., 2016a)
	Tropical forest and savanna (Mexico)	Landsat	Distance from the spectral centroid	(Palmer et al., 2002)
	Tallgrass prairie (Oklahoma, USA)	Aerial photograph	Distance from the spectral centroid	(Rocchini, 2007)
	Wetland (Tuscany, Italy)	Quickbird, Landsat	Convex hull area in spectral space	(Gholizadeh et al., 2018)
	Grassland (Minnesota, USA)	Ground, AISA Eagle	Distance from the spectral centroid in principal component space	(Oldeland et al., 2010)
	Savannah (Central Namibia)	HyMap	PLSR regression	(Fava et al., 2010)
	Meadow (Central Alps, Valtellina, Italy)	Ground (ASD)	First principal component values	(Rocchini et al., 2011)
	Vascular plants (Switzerland)	Landsat	Distance from the spectral centroid in principal component space	(Möckel et al., 2016)
	Wildland forest – agriculture (Michigan, USA)	HySpex	Convex hull volume in principal component space	(Dahlin, 2016)
	Forest (Australia)	AVIRIS	Supervised classification (multiple discriminant analysis)	(Lucas et al., 2008)
Spectral species	Peruvian Amazon	CASI	Unsupervised classification	(Féret and Asner, 2014)
	Ngangao Forest (Kenya)	CAO-2 ATOMS	Object-based classification	(Schäfer et al., 2016)
	Managed and unmanaged groves (Israel)	AisaFenix	Supervised classification (support vector machine)	(Paz-Kagan et al., 2017)
	Grassland (Minnesota, USA)	Headwall E-Series (tram)	Supervised classification (PLSR)	(Wang et al., 2018b)

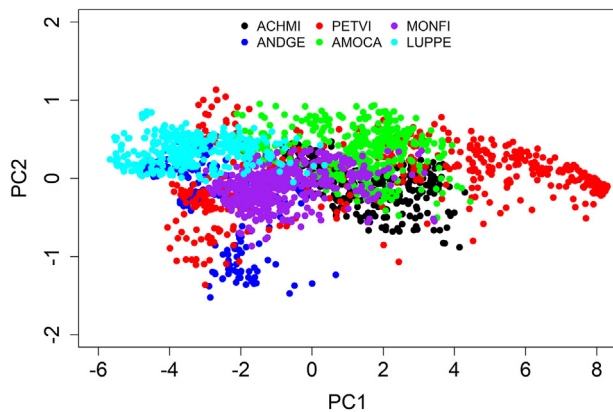


Fig. 3. Within- and between-species spectral variation for six prairie grassland species: *Achillea millefolium* L. (ACHMI), *Andropogon gerardii* Vitman (ANDGE), *Petalostemum villosus* Nutt. (PETVI), *Amorpha canescens* Pursh (AMOCA), *Monarda fistulosa* L. (MONFI), and *Lupinus perennis* L. (LUPPE). The large intra-specific variation in *Petalostemum villosus* Nutt. confounded the spectral diversity-biodiversity relationship in this particular case. Reflectance data were collected using an imaging spectrometer (E Series, Headwall Photonics Inc., Fitchburg, MA, USA) mounted on a tram system (Wang et al., 2018a). Axes are the first and second principal components. Figure modified from (Wang et al., 2018b).

species when the pixel size of the data cannot support the identification of individual plant (Somers and Asner, 2014; Fassnacht et al., 2016). For this reason, data involving coarse pixels (e.g. typical global satellite data) are generally not suitable for this method (Schmidtlin and Sassini, 2004; Fassnacht et al., 2016).

The spectral diversity - biodiversity relationship can be sensitive to vegetation community composition (e.g., species richness, evenness, and composition), particular sampling methods, and spectral diversity metrics (Gholizadeh et al., 2018; Wang et al., 2018b). Several studies demonstrate that species richness and evenness together can influence spectral diversity (Rocchini et al., 2010; Wang et al., 2018a, 2018b). Adding species evenness incorporates additional information on stand composition that affects spectral variation and, as a result, combining species richness and evenness typically yields a stronger relationship between spectral diversity and biodiversity relative to either diversity measure alone. Species identity substantially affects both categories of spectral diversity metrics (information content-based and spectral species-based), as species with large intra-specific variation in spectral reflectance can also influence spectral diversity-biodiversity relationships (Fig. 3), sometimes complicating the estimation of true diversity (Dahlin et al., 2013; Peña et al., 2013; Roth et al., 2015; Wang et al., 2018b).

Despite the challenges mentioned above, spectral diversity metrics are emerging as a powerful set of tools for assessing plant biodiversity, particularly with the advent of field spectrometers and imaging spectrometers from proximal and airborne platforms. New developments in this area, including the advent of UAVs, promise further advances, particularly as the spectral dimensionality expands. These emerging methods provide rich alternatives to satellites for local and regional biodiversity assessment and allow explicit studies of the biodiversity-spectral diversity relationships at multiple scales, as further discussed below.

4. Scale in remote sensing of biodiversity

4.1. Spatial scale

The spatial scale dependence of patterns are central topics in both ecology (Levin, 1992; Costanza and Maxwell, 1994) and remote sensing (Woodcock and Strahler, 1987). In ecology, the concept of spatial scale

defines the grain size and spatial extent at which a variety of ecological processes occur in a landscape (Turner et al., 1989), and can also apply to our sampling terminology. In remote sensing, spatial scale refers to the resolution (pixel size, determined by sensor technology, sampling platform, and flight characteristics) and extent (the total area measured). Increasing the grain size changes the level of observation, and includes more objects e.g., leaves, branches, multiple crowns and multiple species, decreasing the accuracy of vegetation discrimination when pixel size is larger than the target size (Roberts et al., 2004), and leading to information loss by applying spatial smoothing to the data (O'Neill and King, 1998). Explicit scaling studies in remote sensing of biodiversity are challenging and relatively rare because most campaigns collect data at a single resolution and extent pre-determined by the engineering requirements of the instrument and sampling platform.

At coarse scales (several meters to hundreds of meters), airborne (Oldeland et al., 2010; Hakkenberg et al., 2018) and satellite images (Rocchini, 2007) have sometimes been used to evaluate the effects of spatial scale on spectral diversity-biodiversity relationship. Results generally indicate that the power of detecting biodiversity through spectral variability varies with spatial scales (Hakkenberg et al., 2018) and pixel size (Rocchini, 2007). Not surprisingly, it has also been reported that the spectral variability hypothesis failed at the landscape scale when MODIS data (pixel size: 0.5 km by 0.5 km) was related to vascular plant species richness in Germany (Schmidtlin and Fassnacht, 2017). Therefore, it appears that most conventional satellite pixels are too coarse to directly assess α diversity, and care should be taken when using remote sensing product to assess biodiversity at these relatively large pixel sizes, although such large scales may be effective when used with other approaches (e.g. broad-scale habitat mapping, described above).

Recently, imaging spectroscopy has been applied to test the spatial scale dependence of spectral diversity-biodiversity relationship in experimental grassland plots at a range of fine scales (1 mm² to several square meters) (Lopatin et al., 2017; Wang et al., 2018a; Gholizadeh et al., 2018, 2019). In these studies, the optical detectability of local (α) biodiversity greatly declined with decreasing spatial resolution (Fig. 4) and the optimal pixel size for distinguishing α diversity approximates a spatial scale similar to the size of an individual plant leaf or crown (pixel size < 1 cm²). In some studies, most information on α diversity was lost by a 1 m² grain sizes, the pixel size of many airborne imaging spectrometers (Wang et al., 2018a). In contrast to these small experimental plots, other studies showed that spectral diversity metrics calculated using airborne data at approximately 1 m² scale correlated well with biodiversity metrics in another restored prairie experiment (Gholizadeh et al., 2019) and a natural prairie ecosystem (Wang et al., 2016a). In these latter cases, the large extent captured in airborne sampling in these landscapes may have introduced higher-level diversity effects (e.g., β diversity), which might be missed in the smaller experimental plots (Wang et al., 2018a; Gholizadeh et al., 2019). The underlying reasons for such variation between sites, even within the same biome, remain unclear, but point to the challenges of developing operational approaches to remote sensing of local biodiversity that are universally applicable.

Estimates of β diversity using remote sensing derive from (1) the principle that landscapes with a larger variability in species composition have a larger difference in spectral properties, measured as vegetation indices (He et al., 2009) or the spectral similarity index (Somers et al., 2015), or (2) the concept of spectral types by applying classification methods to remote sensing data and calculating the Bray-Curtis dissimilarity index (Bray and Curtis, 1957) based on species classified at different sites (Baldeck and Asner, 2013; Féret and Asner, 2014). An alternative approach (Hernández-Stefanoni et al., 2012) incorporated the spatial dependence by applying a regression kriging procedure in mapping β diversity in a tropical landscape in Yucatan Peninsula. Remote sensing, especially airborne remote sensing, shows great potential in β diversity estimation given the ability of providing spatially

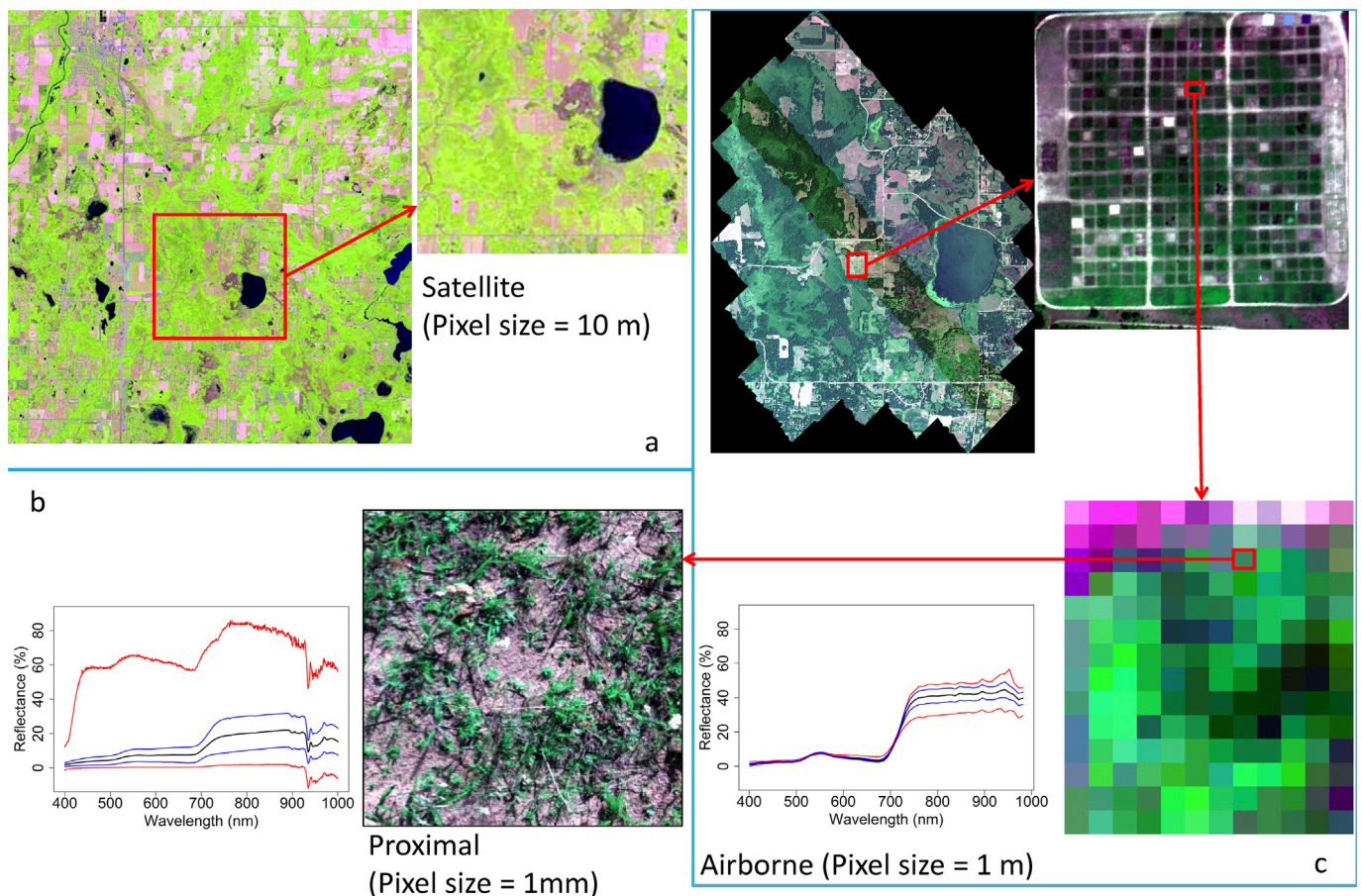


Fig. 4. Different datasets for the same location (Cedar Creek Ecosystem Science Reserve, Minnesota, USA, including the BioDIV experiment at 45.4086° N, 93.2008° W) illustrating scale dependence of remote sensing of biodiversity. Sampling at coarser scales leads to information loss seen as decreased spectral variation and, as a consequence, decreases the accuracy of biodiversity estimation through spectral diversity. Data include satellite (a), proximal (b) and airborne (c) imagery and spectra. The three-band satellite image (a) was taken by Sentinel 2-A, on June 21, 2016, and had the largest pixel size, the fewest bands, and the weakest ability to detect diversity of all data shown here. By contrast, the proximal imagery (b) had the smallest pixel size, the most bands, and the greatest ability to distinguish diversity levels. The dimension of the proximal remote sensed image (b) was 1000 × 1000 mm pixels (approx. 1 × 1 m), obtained by the Headwall E Series imaging spectrometer on a tram system in summer 2016 (data are available from from NASA LPDAAC, doi: <https://doi.org/10.5067/Community/Headwall/HWHYPCCMN1MM.001>). Airborne data (c) were intermediate in spatial scale (approx. 1 m pixels), and collected with an imaging spectrometer (Aisa Eagle, Specim, Oulu, Finland) operated by CALMIT, University of Nebraska-Lincoln, on July 22, 2016. Colored lines in the spectral plots show mean (black), standard deviation (blue) and min/max (red) reflectance values for proximal (b) and airborne (c) imagery, with the spectral variation providing an indicator of spectral diversity (Wang et al., 2018a, 2018b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

continuous information over large areas (Rocchini et al., 2018).

Depending upon the sampling scale and metrics used (Tuomisto, 2010a, 2010b), β diversity can be confounded by α diversity and vice-versa (Jost, 2007; Anderson et al., 2011). Consequently, a remaining challenge in the remote sensing of biodiversity is clarifying the combined and separate effects of α and β diversity on the sensor, since both influence the optical signals detected and both can be scale dependent (Gamon et al. in press). Since remote sensing cannot always perfectly match the scale of individual organisms in field sampling and is characterized instead by the operational scale of the sensor and platform, it is often not clear that to what extent we are detecting α or β diversity, or some combination of the two. It should be noted that effects of spatial scale summarized here would most likely differ between vegetation types and biomes due to the different canopy sizes, but this topic has not yet received much attention, with most studies of scale to date focusing on a single vegetation type or biome. While direct detection of α diversity via spectral diversity is clearly possible, the effects of sampling scale must be carefully considered, and it is likely that high-resolution remote sensing methods (e.g. drones and aircraft) will be instrumental in developing these applications in the near future. Further discussion of the scale dependence of the spectral diversity –

biodiversity relationship can be found in recent reviews (e.g. Anderson, 2018; Gamon et al., in press).

4.2. Spectral scale

Spectral resolution and range also affect the spectral diversity-biodiversity relationship (Rocchini, 2007; Wang et al., 2018a). Many satellite applications to date have focused on the NDVI related bands (red and near infrared) (He and Zhang, 2009; Hernández-Stefanoni et al., 2012). Besides NDVI bands, the Landsat short wave infrared band has been reported to have strong association with species richness in a tropical forest ecosystem (Hernandez-Stefanoni et al., 2009). In most remote sensing of biodiversity studies, the spectral information has been condensed into simple metrics (e.g., NDVI, CV or indices in the principal component space). It is arguable that using full range spectra including the shortwave infrared (400–2500 nm) adds information on plant biochemical properties, e.g. leaf water content, pigment, nitrogen content, and lignin (Asner and Martin, 2009). The effects of different wavelengths on biodiversity detection warrant further investigation, but most existing studies showed that more spectral bands are better than fewer bands (Asner and Martin, 2009; Wang et al., 2018a).

4.3. Temporal scale

Temporal effects on remote sensing of biodiversity have not received as much attention as the spatial distribution of biodiversity due to 1) limited knowledge of temporal changes in ecological communities and 2) biodiversity data collection are time consuming and expensive so that sampling campaigns are usually short-term (Magurran, 2008; Magurran et al., 2010). Additional information about vegetation phenology might be able to improve the performance of spectral diversity metrics (Clark & Roberts, 2012). On the other hand, changing phenological state, e.g., due to leaf age (Chavana-Bryant et al., 2017), seasonal adaptation (Wong and Gamon, 2015) and drought stress (Cavender-Bares et al., 2016b) can also lead to spectral variability within individual canopies as large as intra- and interspecific variations in leaf morphological, biochemical and spectral traits and possibly confound the spectral diversity - biodiversity relationship. Studies have also shown that the biodiversity-productivity relationship can vary across the growing season (Wang et al., 2016b) and proper timing can to some extent compensate for the lower spectral resolution in terms of mapping invasive species that have different phenological properties, e.g., flowering phase (Müllerová et al., 2017b). Consequently, understanding the temporal changes of spectral diversity is also critical to remote sensing of biodiversity and is an area needing further research.

5. Surrogacy hypothesis

Despite the limitations of spatial scale described above, remotely sensed indices of spectral diversity often display significant correlations with independent metrics of α and β diversity, even when the pixel sizes appear to be too coarse for direct assessment of individual plant crowns. One reason why these methods work may be due to the fact that spectral diversity ties to various types of biodiversity through physical and ecological rules, leading to the concept of “surrogacy.”

Many studies of biodiversity depend upon assumptions of surrogacy, where biodiversity of one kind or dimension relates to biodiversity of another kind or dimension. The classical surrogacy hypothesis has three main aspects: 1) high species richness in one taxon is related to high richness in others (cross-taxon surrogacy), 2) high genetic or family richness is related to high species richness (within-taxon surrogacy), and 3) high environmental e.g., temperature or topographical, diversity is related to high species richness (environmental surrogacy) (Magurran, 2004). For example, macrolichens serve as a good indicator of species richness of mosses, liverworts, and woody plants in the Indian Garwhal Himalaya (Negi and Gadgil, 2002), family and genus-level diversity metrics are reported to be very good indicators of species diversities (Lee, 1997) and vegetation canopy diversity is highly correlated with total plant diversity in a forest landscape (Hakkenberg et al., 2018).

Here we expand the original surrogacy hypothesis (Magurran, 2004) to explain how variations in spectral information can encompass several ‘dimensions’ of diversity (phylogenetic, taxonomic and functional diversity), even when they are not all equally visible (Gamon, 2008). Presumably, species richness is often related to functional biodiversity, which can be captured by species and organismal traits that affect one or more aspects of ecosystem functioning (Tilman, 2001; Petchey and Gaston, 2002; Cadotte et al., 2011). Therefore, a more diverse ecosystem should have a greater variety of functional behaviours as shown by plant traits that reflect different biochemical content, leaf structure, and physiological function. This variation of plant traits can affect the optical properties of plants and lead to spectral detectable features. Spectral (optical) diversity, which has been related to plant functional traits (PFTs), might be able to provide more information than field PFT measurements (Schweiger et al., 2018).

As further examples of surrogacy, spectral diversity can provide an indirect indicator of phylogenetic diversity (Cavender-Bares et al., 2016b; Schweiger et al., 2018). Leaf spectra are associated with

phylogenetic similarity among species and genetically-based phenotypic differences among populations, species and clades can be differentiated even when environmental heterogeneity is present (Cavender-Bares et al., 2016b). Plant canopy traits can indicate hidden below-ground diversity or composition through biogeochemical cycles, and canopy spectra can sometimes discriminate aspen genets more accurately than canopy chemistry or below-ground traits (Madritch et al., 2014). These examples suggest a hierarchical organization of biodiversity that facilitates the remote detection of different levels and aspects of diversity, often in surprising ways, even when we lack direct methods of detection, and this may explain some of the power of remote sensing to detect different “dimensions” of biodiversity. Further work on this concept would likely clarify the basic principles behind the plant phylogenetic - functional- spectral relationship that could provide further insights into the remote sensing of biodiversity.

6. A global biodiversity monitoring system (GBMS)

Recently, there have been several calls for a global biodiversity monitoring system incorporating satellite data (Jetz et al., 2016; Proença et al., 2017; National Academies of Sciences, 2018). Here we examine the potential of such a system and provide a few caveats based on our current state of knowledge. The ideal global biodiversity monitoring system would include observations at different scales and address different “dimensions” of biodiversity by assessing morphological and structural features of the target ecosystem including remote sensing measurements (satellites and aircrafts, drones and other proximal sensors), field diversity sampling, and lab work (e.g., genomics) (Turner, 2014). We would expect that the global coverage that comes from continuous satellite measurements could provide wide context and measures of environmental drivers at coarse scales, while the specific but critical details could be provided by “drilling into” particular areas of interest with a combination of fine scale remote sensing observations and fieldwork (Gamon et al. in press). By connecting local and regional biodiversity measurements, biodiversity monitoring system can fill gaps in the current biodiversity observation and enhance efforts to conserve the Earth's biodiversity.

6.1. Tools for proximal remote sensing

Novel ground-level remote sensing platforms have been introduced to ecological studies and have transformed ecological research (Anderson and Gaston, 2013). For example, newly automated and low-cost sensors allow great flexibility to accomplish continuously sampling that can be used to monitor plant phenology (Gamon et al., 2015; Yang et al., 2017), which can provide phenological information related to biodiversity estimation. Remote sensors, such as cameras or hyperspectral and LiDAR sensors (Sankey et al., 2017), carried by unmanned aerial vehicles (UAVs) have been successfully used in mapping invasive species (Wan et al., 2014; Michez et al., 2016; Müllerová et al., 2017a) and distinguishing vegetation types (Ahmed et al., 2017; Komárek et al., 2018). Other methods (e.g. sound recording and radar) can also be integrated with optical remote sensing as part of a monitoring system, and these modern technologies are beginning to provide quantitative and detailed information about our Earth and expanding our abilities to detect the changes in Earth properties and processes (Turner, 2014).

6.2. Advancing Earth observation technologies

Most biodiversity studies using satellite remote sensing have been limited to data with a few bands and often at coarse spatial scales, although some early work has shown that hyperspectral satellite data can be used to distinguish functionally distinct vegetation types (Huemmrich et al., 2013). Incorporating hyperspectral satellite data in the future might enable us to better utilize the temporal and spectral

information in biodiversity estimation than by using broad band vegetation indices available from current platforms. Proposed hyperspectral satellite missions, such as HISUI (Iwasaki et al., 2011), HYPXIM (Michel et al., 2011), PRISMA (Stefano et al., 2013), EnMAP (Guanter et al., 2015), and HypsIRI (Lee et al., 2015), currently renamed Surface Biology and Geology (SBG) (The National Academies of Sciences, Engineering, and Medicine, 2018) would provide repeat coverage spanning a wide range of the solar spectrum (300–2500 nm) at fine spatial resolution. For maximal effectiveness a “biodiversity monitoring system” would also include regional and local monitoring (e.g. ground and airborne sensing) nested within global monitoring (e.g. global satellites with repeat coverage), and suitable data systems for storing, analyzing and sharing the vast amounts of data collected.

6.3. Sharing data and tools between remote sensing and ecology communities

The potential for collaboration between remote sensing and ecological communities has been discussed for a long time (Stoms and Estes, 1993; Kerr and Ostrovsky, 2003; Turner et al., 2003; de Araujo Barbosa et al., 2015). Yet, these two communities do not always coordinate and much work remains to be done to integrate remote sensing tools into ecological studies (Pettorelli et al., 2014). Data dispersion and accessibility rapidly becomes compounded by the large volumes of spectral and image data associated with remote sensing and data affordability and access limited the usage of remote sensing products (Turner et al., 2015). Although agencies and archives like United States Geological Survey (USGS), National Aeronautics and Space Administration (NASA), Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC), Land Processes Distributed Active Archive Center (LP DAAC), and European Space Agency (ESA) provide open access to some public satellite products e.g., Landsat, MODIS and Sentinel, commercial satellite products are still very expensive, and accessible archival solutions for large datasets collected by individual research programs remain largely unresolved. Furthermore, some remote sensing products are too big or complicated for easy usage, in part due to the shortage of software tools (Pettorelli et al., 2014; Cavender-Bares et al., 2017). There is a need for better sharing tools e.g., open-source software and algorithms, along with public databases, allowing ecologists to obtain and process remote sensing images for biodiversity information.

6.4. Citizen science

Citizen science (aka community science) has grown immensely and been regarded as a tool for studies in ecology, conservation biology, and environmental science over the last 10 years (Dickinson et al., 2010; McKinley et al., 2017). Citizen science can provide data spanning large spatial or temporal extents that can usually be laborious and costly (Theobald et al., 2015; Turrini et al., 2018). For example, a study estimated that species monitoring currently done by volunteers in France would cost 0.6 million to 4 million Euros per year if professionals were to be hired (Levrel et al., 2010). These data can either complement remote sensing measurements (Mihalik et al., 2012) or serve as calibration and validation data for remote sensing data (Chandler et al., 2017). With the advent of low price drone and other sensors (LiDAR), and advanced computational capacities providing machine learning algorithms for imaging processing and pattern recognition (Krizhevsky et al., 2012), citizen science holds a great potential for future diversity monitoring.

6.5. Integration of remote sensing and environmental DNA (eDNA)

Environmental DNA indicates ‘obtaining information of species, populations, and communities by retrieving DNA from environmental samples’ (Thomsen and Willerslev, 2015). It holds the potential to

provide a unique way to monitor biodiversity at different taxonomy scales and has been applied in sediments and contemporary terrestrial surface soil and aquatic ecosystems (Thomsen and Willerslev, 2015). Combining eDNA and remote sensing can provide complementary information about the ecosystem: eDNA can assess diversity of organisms that cannot be directly estimated with remote sensing, such as microbes or animals, while remote sensing can deliver information on ecosystem variables such as productivity and phenology that are not achievable from eDNA (Yamasaki et al., 2017). The use of eDNA in diversity studies is greatly expanding (e.g. Madritch et al., 2014; Bush et al., 2017), and combining eDNA and remote sensing holds great potential in global biodiversity monitoring at vastly different scales (Turner, 2014).

7. Conclusions

Biodiversity loss is a form of “global change” with consequences that may exceed those of climate change in generating unpredictable perturbations to the Earth system (Rockström et al., 2009) with potentially unacceptable consequences for human wellbeing. Given the shortfall in biodiversity information (e.g. Jetz et al., 2016), the projected decline in biodiversity in the Anthropocene (Crutzen, 2002; Pereira et al., 2010a) and the socioeconomic importance of biodiversity (Mace et al., 2012), better methods of assessing biodiversity over large areas are urgently needed.

In this review, we summarized the pros and cons of different remote sensing methods in terrestrial plant diversity detection over the last three decades and proposed that spectral (optical) diversity can be related to diversity in different dimensions (phylogenetic, taxonomic, and functional diversity) in part by expanding the concept of surrogacy. We also point out two major gaps in our current understanding of remote sensing of plant diversity studies that deserve further work in the future: the underlying drivers of phylogenetic – functional – spectral relationships and the scale dependence of the spectral (optical) diversity – biodiversity relationship.

It might be still too early to say that remote sensing has started a new paradigm of biodiversity research, but there is little doubt that remote sensing does offer novel perspectives on global diversity monitoring and can contribute to future biodiversity conservation. To make full use of this potential, we need to develop effective collaborations between experts in remote sensing and experts in biodiversity monitoring and conservation (Pettorelli et al., 2014). To be truly effective at a policy level, emerging remote sensing methods will also need to be better integrated with ecological, sociological, political and economic aspects of biodiversity (e.g. Mace et al., 2012). By enhancing co-operation from multidisciplinary scientists, policy makers, natural resource managers, economists and others, we can improve global biodiversity estimation and conservation.

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