

ON THE NATURE OF THINGS: ESSAYS

New Ideas and Directions in Botany

Harnessing plant spectra to integrate the biodiversity sciences across biological and spatial scales¹

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Plants provide the productive basis for all other life, and their diversity is critical for the Earth's life support systems. Many plant species are at risk for extinction due to global change factors, including drought stress, exotic species invasions, pathogens, land-use change combined with altered disturbance regimes (e.g., fire), application of chemicals, and overexploitation. One in five species within the Plant Kingdom is thought to be threatened with extinction (Kew Royal Botanic Gardens, 2016). Given the multifaceted consequences of plant biodiversity for providing the ecosystem services on which humans depend, including the food we grow, the regulating services that maintain our fresh water supply and provision the multitude of organisms we care about, plant biodiversity is important to understand and to monitor across scales from genetic variation at local scales to the entire plant tree of life. Here we argue that deeper understanding and wider application of plant electromagnetic spectra—the patterns of light absorbed, transmitted, and reflected at different wavelengths from plants—can integrate previously disparate sectors of biodiversity science and the remote sensing community at multiple biological and spatial scales.

WHAT ARE SPECTRA?

Plants synthesize a wide variety of chemical and structural compounds to support physiological functions for survival and growth. Leaf reflectance spectra are aggregate indicators of plant chemistry,

physiology, water content, and both internal and external structure (Fig. 1A). Since foliar properties influence how leaves interact with light, many attributes of plants can be detected using spectral reflectance from leaves, plant canopies, and ecosystems. In the visible range (VIS, 400–700 nm), light is strongly absorbed by pigments, including chlorophyll, carotenoids, and anthocyanins. In the near-infrared range (NIR, 700–1100 nm), energy is scattered by leaf surface characteristics, tissue components, and anatomical structures including intercellular spaces inside the leaf. The short-wave infrared (SWIR, 1100–2500 nm) spectral region also shows relatively high reflectance, but shows distinct absorption features for water and specific plant biochemicals, such as lignin, cellulose, phenolics, and is influenced by anatomical and morphological attributes of plants (Ustin et al., 2009). These SWIR regions of plant spectra tend to be most phylogenetically conserved (McManus et al., 2016). Thermal infrared (TIR) spectra (5–10 μm) are influenced by leaf surface temperature and also include features associated with physiological processes.

As the spatial scale of spectral observations shifts from the leaf to canopies, landscapes, and larger scales (Fig. 1B) using imaging spectroscopy via airborne or satellite platforms, influences of the atmosphere, sun angle, and terrain must be addressed. Leaf and canopy spectra are generally responsive to similar fundamental properties, given that a large proportion of what is captured in remotely sensed vegetation data are foliar features. However, atmospheric effects, solar illumination, and the three-dimensional structure of the vegetation introduce additional variation, as do reproductive and other nonfoliar structures, as well as canopy gaps and soils. These all add “features” to spectral measurements that confound properties of interest that are measured at the leaf level, although in some cases they may actually help in the assessment of biodiversity. These issues highlight the importance of in-situ field measurements to independently validate image corrections and properly interpret remote spectra.

NEW PARADIGM

Plant spectra can be sampled at different spatial scales providing a means to link an array of biological disciplines at different scales.

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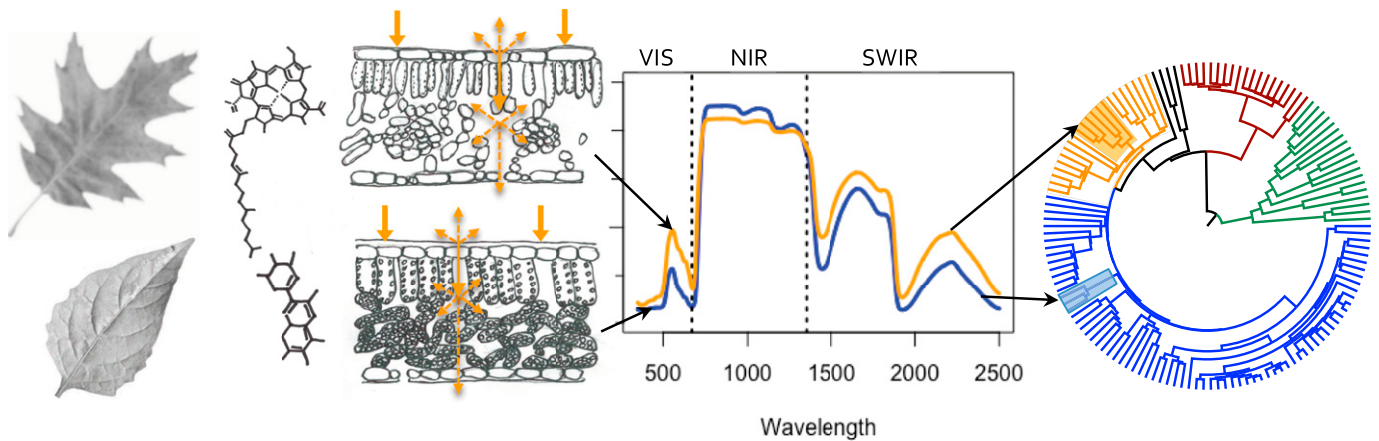
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A Linking spectra to functional and phylogenetic diversity



B Spectral diversity at different spatial scales

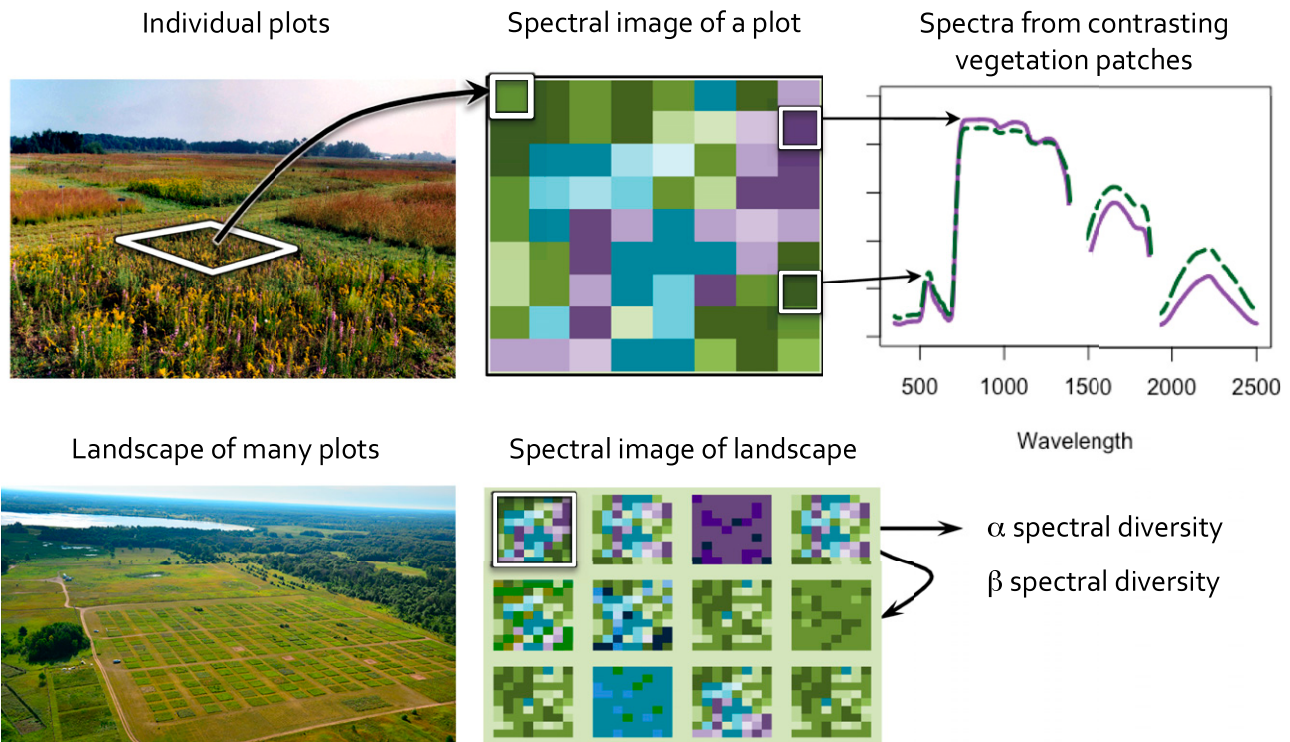


FIGURE 1 (A) Leaves have evolved different chemical properties and structures, which influence how leaves interact with light and result in different spectral signatures. These spectra can be used to estimate chemical and structural traits of a leaf as well as locate a species or lineage in the tree of life to estimate biodiversity. (B) Detecting spectral diversity in plant assemblages. Images of individual and landscape level experimental plots are from the BioDIV experiment at Cedar Creek Ecosystem Science Reserve (top left and bottom left, respectively). Heterogeneity in vegetation within assemblages can be detected with imaging spectroscopy shown schematically for the pixels of a single plot (top middle) and for a landscape of plots (bottom middle). Differences in spectra among pixels within an assemblage can be used to calculate alpha (α) spectral diversity, and among assemblages for beta (β) spectral diversity, similar to metrics of α and β diversity for species or for phylogenetic distances between species.

Leaf reflectance itself integrates within- and between-species differences in morphology, foliar chemistry, life history strategies, and responses to environmental variation. As a consequence, spectra can be used to address basic questions in physiology, ecology, and evolution as well as applied questions in agriculture and forestry.

For instance, scientists focusing on the origins and consequences of plant biodiversity, as well as both the regulating and provisioning services they render, can use spectral patterns to understand physiology, community assembly, and nonvisual phenotypic variation linked to genetic and phylogenetic variation. The multiscale nature

of spectral data reveals a growing suite of information about leaves, whole plants, communities, and ecosystems offering new insights into plant function and potential for integration across disciplines. Spectral diversity is thus emerging as an important component of biodiversity, alongside functional and genetic or phylogenetic diversity.

PHYSIOLOGICAL AND FUNCTIONAL INSIGHTS FROM LEAF LEVEL AND CANOPY SPECTRA

Spectral measurements have allowed rapid and nondestructive detection of foliar traits for research in areas such as physiology, crop breeding, and plant health. A broad suite of functional traits, including many leaf economic spectrum (LES) traits associated with plant life history strategies, can be detected and accurately predicted using spectral data (Serbin et al., 2014). Spectral variation is thus becoming increasingly used in quantitative genetics for high-throughput plant phenotyping and in functional ecology to gain information on the life history strategies and stress tolerance of plants (Fig. 1A). At the whole plant or canopy scale, the chemical and structural composition of plants influences reflectance spectra (Fig. 1B). Spectra can be obtained by high-fidelity imaging spectrometers at various distances from the ground, which alters the size of the measurement unit (pixel). Vegetation traits can be estimated for each pixel in an image by scaling leaf level trait data by species to the pixel level using allometric approaches (Singh et al., 2015) or through direct estimation of canopy traits (Dahlin et al., 2013; Chadwick and Asner, 2016). While many of the basic features of plant spectra are well understood, considerable challenges remain in analyzing and interpreting the subtle dynamics of these features in time and space, as well as in processing and storing large data volumes.

GENETIC AND PHYLOGENETIC DIVERSITY FROM SPECTRA

Plant genotypes, species, and phylogenetic lineages differ in their morphology, anatomy, and how they acquire and allocate resources. These differences result from their evolutionary histories and genetic backgrounds and are further influenced by environmental conditions. Spectra are increasingly used to detect different levels of diversity, from intraspecific phenotypic and genetic variation to phylogenetic lineages, despite environmentally caused variation. For instance, genotypes of *Populus tremuloides* have been distinguished using imaging spectroscopy (Madritch et al., 2014), and populations of tropical live oaks (*Quercus oleoides*) have been distinguished based on leaf-level spectra (Cavender-Bares et al., 2016). Tools that leverage spectral data can facilitate rapid selection in plant breeding based on suites of important traits, including anatomical or chemical attributes that influence reflectance at wavelengths outside the range of visible light (400–700 nm), and hence are not visually observable; these nonvisible spectral traits can be statistically associated with yield (or other remotely sensed fitness proxies, such as biomass) (Babar et al., 2006).

Estimating the placement of an unknown spectral sample in the tree of life (Fig. 1A) may now be within reach, given that spectra appear to follow evolutionary models (Cavender-Bares et al., 2016), and large regions of spectra are highly phylogenetically conserved (McManus et al., 2016). Combined with species distribution models

that provide information on which species are or are not likely to occur in a geographic region, spectral approaches that locate plants within the tree of life have potential to estimate levels of plant diversity, including phylogenetic diversity, at a range of spatial scales (Jetz et al., 2016).

INSIGHTS FROM SPECTRA FOR COMMUNITIES, ECOSYSTEMS, AND LANDSCAPES

Quantifying community responses to global changes and biotic invasions across landscapes is an emerging ecological application of spectral measurements. Turnover in plant species composition across landscapes has been detected and related to productivity in prairie landscapes (Wang et al., 2016) and to biochemical composition in tropical forests (Feret and Asner, 2014). A major decline in healthy hemlock (*Tsuga canadensis*) stands in the northeastern United States due to invasion of the exotic woolly adelgid (*Adelges tsugae*) was documented from NASA AVIRIS imagery (Hanavan et al., 2015). Forest canopy water loss across California ecosystems in response to prolonged drought has allowed identification of regions most at risk for widespread tree mortality (Asner et al., 2016). Each of these studies illustrates the effective use of plant spectral patterns to assess changing ecosystem function, with implications for biodiversity.

While there is high potential to leverage spectra for community ecology, very little has been done to include linkages of plants to other trophic levels and to analyze co-occurrence patterns that might reveal insights into coexistence mechanisms and community assembly processes. Carbon-based defense traits (Couture et al., 2016) are well retrieved from spectral information, facilitating integration of information on host-specific herbivores and pathogens with leaf chemical composition and abundance.

We can expect spectral variation to represent variation in biomass and leaf chemistry that is linked to the chemistry of belowground root exudation. Aboveground plant functional diversity may influence the diversity of substrates available as food for soil organisms and have concomitant effects on the activity of enzymes secreted by soil microorganisms, decomposition, and nutrient cycling. Live and dead plant parts may include a diversity of organic molecules such as cellulose, hemicellulose, lignin, and tannins, among others. For example, foliar spectral variation in aspen correlates well with variation in canopy chemistry, including condensed tannin, lignin, and nitrogen concentrations, which is in turn linked to variation in belowground processes (Madritch et al., 2014).

GLOBAL BIODIVERSITY MONITORING FOR MANAGING PLANET EARTH

Given its high potential for monitoring global biodiversity, there is growing emphasis on satellite missions that support imaging spectroscopy capabilities (Turner, 2014; Schimel et al., 2015; Jetz et al., 2016). To the extent that the botanical community advances understanding and application of plant spectra from a multitude of perspectives on the ground, in the field, in the laboratory, from aerial and airborne platforms, and from space, such missions stand to revolutionize biodiversity science. The transformation will come both from the technological capability to detect changes in plant functional composition and diversity (Asner et al., 2017) through

time across the globe (Jetz et al., 2016) and from our ability to identify hotspots of change that may inform management decisions. However, major advances will require intentional integration across biological and spatial scales and a deeper understanding and wider application of spectra. We will also need to establish a common language and body of knowledge across the biodiversity sciences and develop mechanisms for reconciling and sharing data across instruments and users. Currently, we lack a clear understanding of the scale-dependence of the spectral–biodiversity relationship, and this is likely to vary for different ecosystems (Wang et al., in press). The temporal dynamics of spectra also deserve further study. Going forward, we will need to integrate field studies, airborne studies, and satellite monitoring and develop new informatics approaches. The reward will be a new understanding of plant ecology and a highly powerful set of tools for monitoring and understanding changes in biodiversity across the globe, a requirement for sustainable management of planet Earth.

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