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REVIEW

Grime Review: What can remote sensing do for plant ecology?

Plant spectra as integrative measures of plant phenotypes

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Abstract

1. Spectroscopy at the leaf and canopy scales has attracted considerable interest in plant ecology over the past decades. Using reflectance spectra, ecologists can infer plant traits and strategies—and the community- or ecosystem-level processes they correlate with—at individual or community levels, covering more individuals and larger areas than traditional field surveys.
2. Because of the complex entanglement of structural and chemical factors that generate spectra, it can be tricky to understand exactly what phenotypic information they contain. We discuss common approaches to estimating plant traits from spectra—radiative transfer and empirical models—and elaborate on their strengths and limitations in terms of the causal influences of various traits on the spectrum. Many chemical traits have broad, shallow and overlapping absorption features, and we suggest that covariance among traits may have an important role in giving empirical models the flexibility to estimate such traits.
3. While trait estimates from reflectance spectra have been used to test ecological hypotheses over the past decades, there is also a growing body of research that uses spectra directly, without estimating specific traits. By treating positions of species in multidimensional spectral space as analogous to trait space, researchers can infer processes that structure plant communities using the information content of the full spectrum, which may be greater than any standard set of traits. We illustrate this power by showing that co-occurring grassland species are more separable in spectral space than in trait space and that the intrinsic dimensionality of spectral data is comparable to fairly comprehensive trait datasets. Nevertheless, using spectra this way may make it harder to interpret patterns in terms of specific biological processes.
4. *Synthesis*. Plant spectra integrate many aspects of plant form and function. The information in the spectrum can be distilled into estimates of specific traits, or the spectrum can be used in its own right. These two approaches may be complementary—the former being most useful when specific traits of interest are known in advance and reliable models exist to estimate them, and the latter being most useful under uncertainty about which aspects of function matter most.

Shan Kothari and Anna K. Schweiger contributed equally to this article.

KEYWORDS
dimensionality, functional ecology, leaf-level, plant traits, remote sensing, spectroscopy

1 | INTRODUCTION

The way plants interact with light is one of the key determinants of their success in particular environments and one of most important processes structuring plant communities (Canham et al., 1994; Pacala & Tilman, 1994; Williams et al., 2020). The balance between striving for and avoiding excess light (Kothari et al., 2018; Kothari et al., 2021) influences plant growth and architecture (Jucker et al., 2015; Williams et al., 2017), water and resource use (Ellsworth & Reich, 1993), creating complex environments that shape plant communities. The processes surrounding plant light use are tightly bound with a variety of chemical, morphological and anatomical adaptations, ranging from trade-offs between fast and slow return on investment traits (Wright et al., 2004), to cuticular structures reducing water loss through evaporation, and leaf thickness altering heat dissipation. Because these adaptations alter how plants reflect and absorb light, such optical properties provide a window into plant-environment relationships.

When light interacts with plants, or any substance for that matter, three things can happen: light can get (1) absorbed by plant tissues; (2) scattered in the forward direction, which is called transmittance; or (3) scattered in the backward direction, which is called reflectance. The partitioning among these three processes depends on the chemical and structural characteristics of plants, including leaf chemistry, anatomy and morphology (Ustin & Jacquemoud, 2020)—and, when measured from a distance, canopy architecture (Serbin & Townsend, 2020). Spectroscopic methods measure absorptance, transmittance, or (most often) reflectance of light in many narrow, spectrally contiguous bands. While the first spectrometers were laboratory instruments predominantly used for leaf-level studies, today spectroscopy is used across multiple scales, from the leaf level, to proximal remote sensing using spectrometers in a fixed (e.g. in growth chambers, as scanners in a conveyor belt setting) or moving fashion [e.g. fixed on bicycles, on unoccupied aerial vehicles (UAVs)], to airborne and spaceborne remote sensing. Most remote sensing instruments do not just measure one spectrum in their field of view, but are 'imaging spectrometers' that capture reflectance pixel per pixel in spatially co-registered images (Schaepman, 2007). Measurements typically include the visible (wavelengths between 400–700 nm, VIS), near-infrared (700–1000 nm, NIR) and often also the shortwave infrared (1000–3000 nm, SWIR) ranges of the electromagnetic spectrum. Together, these ranges account for >94% of solar radiation reaching the Earth's surface (American Society for Testing and Materials, 2020), which makes plants' interactions with light in these ranges particularly revealing about their adaptations to the environment.

Reflectance spectroscopy is increasingly becoming an important tool in plant ecology. However, the spectral properties of plants have been studied for several decades (Billings & Morris, 1951; Gates et al., 1965; Knipling, 1970; Shull, 1929). For instance, Shull (1929) described how variation in chlorophyll content throughout leaf ontogeny changes spectral reflectance and examined spectral differences among plant species, between healthy and diseased plants, green and albino plants, and upper and lower surfaces of leaves. Gates et al. (1965) likewise describe changes in spectra with leaf development and the use of spectra to differentiate plant and lichen species. Starting around the 1970s, more and more studies began using plants' spectra to predict their chemical and structural traits, and the development of first airborne imaging spectrometers set in motion plant trait mapping at the canopy level (Knipling, 1970). Wessman et al. (1988) achieved a major milestone by creating maps of canopy nitrogen (N) and lignin content based on spectral images captured by NASA's AIS (Airborne Imaging Spectrometer).

Today's applications of spectroscopy range from modelling and predicting leaf (Asner et al., 2014; Serbin et al., 2014) and canopy traits (Asner et al., 2017; Singh et al., 2015), to detecting plant stress (Asner et al., 2016) and natural enemies (Pontius et al., 2005; Sapes et al., 2022), to differentiating species and broader taxonomic clades (Féret & Asner, 2013; Meireles et al., 2020; Sapes et al., 2022). Indeed, maps of species (Roth et al., 2015), functional group composition (Schmidtlein et al., 2012; Schweiger et al., 2017), and traits of individual plants (Asner & Martin, 2009) or plant communities (Cavender-Bares et al., 2022) are highly valuable for investigating a plethora of ecological questions beyond the scale of individual research plots. In addition to trait and species mapping, plant spectroscopy over the past decade has also seen the growing use of spectra as integrated measures of plant phenotypes (Cavender-Bares et al., 2017; Ustin & Gamon, 2010), including in biodiversity-ecosystem function research (Schweiger et al., 2018, 2021; Williams et al., 2021) and as measures of plant diversity (Draper et al., 2019; Féret & Asner, 2014; Frye et al., 2021; Rocchini et al., 2010; Schweiger et al., 2018; Schweiger & Laliberté, 2022; Wang & Gamon, 2019). Instead of mapping traits, these studies use spectra of plants directly as a means to understand how plants interact with their environment.

This wide range of ecological uses of spectra carries the promise of alleviating the geographic, taxonomic and temporal biases in global plant data (Jetz et al., 2016), which arise because most traditional field-based research in plant ecology occurs in mid-latitudinal ecosystems of the global North (Meyer et al., 2016) around the peak of the growing season. Imaging spectroscopy allows consistent and repeated measurements of plant traits and plant community characteristics across large spatial extents (Schimel et al., 2013; Turner, 2014). Although it is unlikely that airborne imaging spectroscopy can overcome geographic bias due to its cost, current and upcoming satellite platforms, including EnMap

(Chabrillat et al., 2021), CHIME (Rast et al., 2021), PRISMA (Cogliati et al., 2021), and SBG (Cawse-Nicholson et al., 2021), promise more equitable access through their open data policies. Simultaneous data collections across spatial scales, including field data (Schweiger & Laliberté, 2022), and the development of robust models for scaling between different levels of observations (Gamon et al., 2020) will allow global spectral biology to improve predictions of how vegetation composition and biogeochemistry will respond global environmental change (Cavender-Bares et al., 2021).

This review addresses both the use of spectroscopy to derive plant traits and its potential to go beyond commonly measured traits by using spectra as integrated measures of plant phenotypes (Figure 1), as well as the challenges of each approach. Our central question is: What can spectroscopy contribute to plant ecology beyond providing more estimates of things (plant traits and taxonomic groups) that we can already measure in other ways? Indeed, only a handful of plant traits have distinct enough absorption features that they can be predicted from spectra with physical models, and these traits are not always the most important ones for understanding how plants respond to or alter their environment (Section 2). However, we argue that the phenotypic variation that spectra capture is likely to also include a wide range of ecologically important factors that are harder to characterize and are still not well understood (Section 3). Lastly, many traits that are widely important—particularly those pertaining to organs not visible through remote sensing—have no direct influence on the spectrum and can be estimated (if at all) only via their covariance with other traits. Using spectroscopy effectively in plant ecology requires understanding, or at least acknowledging, how spectra are generated by the complex entanglement of many structural and chemical factors with varied ecological relevance (Ustin & Jacquemoud, 2020). We will discuss the challenges to using the phenotypic information in spectral data, as well as potential paths forward, by tackling the following questions:

1. What is the role of trait covariance in the detection of plant traits that do not cause clearly identifiable absorption features (Section 2)?
2. What can we learn by working directly with spectra compared to spectrally derived plant traits (Section 3)?
3. How can we leverage the full information content of spectra and how should the major dimensions of spectral variation be interpreted? What is the intrinsic dimensionality of spectra? (Section 4: Case studies)

We focus on leaf- and canopy-level 'hyperspectral' instruments that measure reflectance in tens to hundreds of wavelength channels (or spectral bands) with overlapping sensitivities in their spectral response curves, allowing them to characterize spectra in a

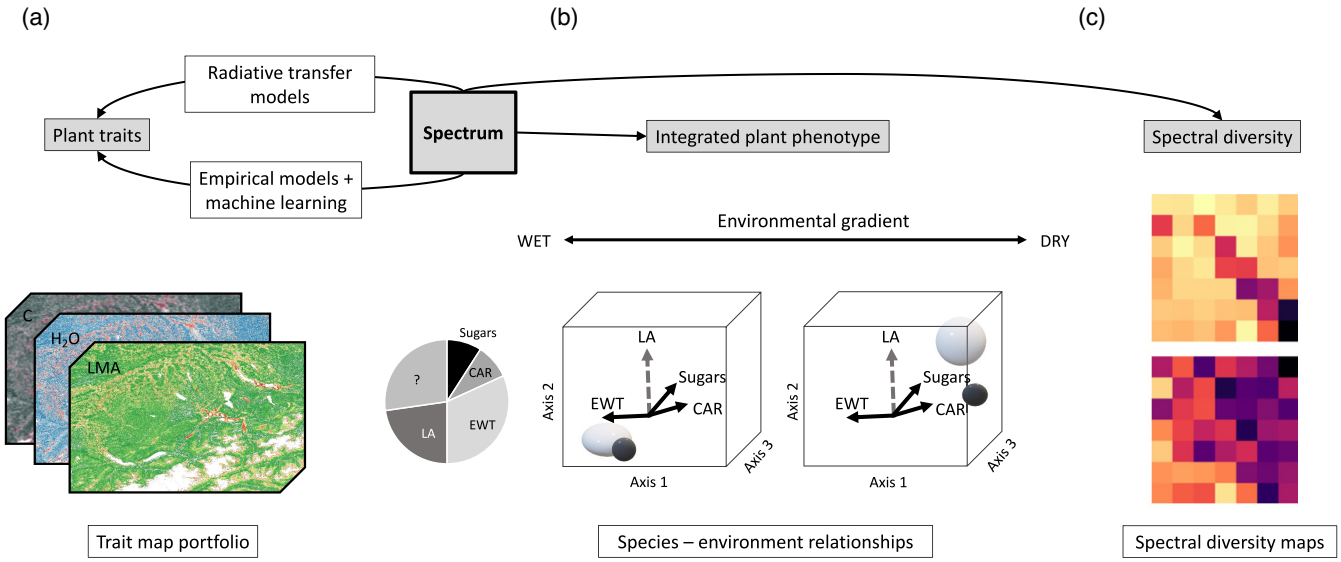

FIGURE 1 A conceptual figure illustrating what spectroscopy can do for plant functional ecology. (a) Plant traits (C = carbon content, H_2O = water content, LMA = leaf mass per area) can be mapped from spectra using radiative transfer models or empirical machine learning approaches. (b) Spectra can also be used as integrated measures of plant phenotypes, as for example when assessing species hypervolume size and position in spectral space along environmental gradients. Here, we depict a hypothetical gradient from wet to dry ecosystems. We show the position of species in three-dimensional space of canopy reflectance spectra, e.g. along the three main axes of spectral variation. Four traits are designated by arrows pointing in their direction of maximum correlation with the spectral axes: Soluble sugars, carotenoid content (CAR), equivalent water thickness (EWT), and leaf angle distribution (LA). The arrow for LA is dashed to denote that it is a trait that is seldom measured directly, but can strongly influence canopy spectra. In our hypothetical example, drought causes the species to shift along the three spectral axes. Under drought, the species separate along Axis 2 (correlated positively with LA), a difference in drought responses that may be hard to describe using directly measured traits alone. The pie chart depicts the percentage of spectral variation that might be statistically explained by these four traits, with some variation left unexplained. (c) Spectral data can also be used directly to map spectral diversity, for instance to estimate plant functional diversity

continuous way. We will not cover multispectral sensors, such as the Landsat and Sentinel satellites or multiband cameras, because they lack the spectral resolution needed to infer many traits (Shiklomanov et al., 2016) or to think about spectra in the continuous, integrative way that we seek to highlight in this review.

2 | ESTIMATING PLANT TRAITS FROM SPECTRA

2.1 | Physical and empirical approaches to estimating plant traits from spectra

Estimating traits from spectra can save considerable amounts of time and resources in the lab and field. For example, a hand-held spectrometer with a leaf clip allows users to derive traits from dozens of leaves within a few hours without destructive sampling, material transportation to the lab or chemical analyses. However, estimating traits from spectra requires a model, typically either: (1) a physics-based radiative transfer model (Féret et al., 2017; Féret et al., 2021; Jacquemoud & Baret, 1990), or (2) an empirical model built using multivariate techniques, among which the most commonly used for spectral data is partial least-squares regression (PLSR; Burnett et al., 2021; Martens et al., 2001; Wold et al.,1983).

Radiative transfer models (RTMs) like PROSPECT (Jacquemoud & Baret, 1990) are based on physical principles which makes them generally valid for the broad class of leaves that come close to meeting their assumptions, and the approach can be extended to the canopy scale (e.g. using PROSAIL; Jacquemoud et al., 2009). In PROSPECT, leaves are represented as one or several absorbing plates with rough surfaces, giving rise to isotropic scattering. The model uses two classes of input variables: a leaf structure parameter representing the average number of air–cell wall interfaces within the mesophyll, and the contents of leaf chemicals. However, only a handful of leaf traits have well-defined absorption features that influence spectral reflectance in a strong, direct, and easily characterized way. Prominent examples are various pigments, dry matter content and water content (Figure 2), which can be estimated by inverting PROSPECT. In addition, the newest generation of PROSPECT splits dry matter into protein and carbon-based constituents (Féret et al., 2021).

It is highly unlikely, though, that the number of leaf traits that can be estimated from physical models will increase dramatically in the future. This is because for most chemical traits, absorption features in the 400–2500 nm range measured by classic spectrometers are actually harmonics or overtones of fundamental features in the UV (10–400 nm) and middle-infrared (2500–6000 nm) ranges (Ustin & Jacquemoud, 2020). In addition, as countless chemical and structural leaf traits have subtle and often overlapping effects on spectral reflectance, it is tricky to tease apart the specific effects of individual traits. While the traits that can be estimated using RTMs have important functional roles, they are not necessarily those that are most important for understanding plants' ecological strategies and their effects in any particular environment; focusing only on this set of traits can thus limit our ability to understand ecological processes.

This limitation of RTMs is a major motivation behind the use of empirical machine learning techniques like partial least-squares regression (PLSR). PLSR was specifically designed to reduce the severity of assumptions of multivariate linear regression (Martens, 2001; Wold et al., 1983). Since its main purpose is prediction, PLSR does not depend on a clear, mechanistic understanding of the relationships among the dependent variables and the independent variables, and it allows the use of many, highly collinear predictors. These qualities make it well suited for spectral data, which are inherently multicollinear. Using the sample × wavelength matrix (X) and the sample × trait matrix (Y), PLSR calculates component vectors oriented to maximize the total variance explained in X and Y and the covariance between X and Y. Models created using PLSR or similar algorithms have long been used in chemometrics to quantify chemical components in the pharmaceutical and agricultural sectors, and have in many cases become routine algorithms readily implemented in proprietary instrument software (Marten et al., 1985). In vegetation spectroscopy, PLSR has been successfully applied to predict leaf mass per area (LMA) and a series of chemical traits, including the contents of N, carbon (C), carbon fractions (lignin, cellulose, hemicellulose, soluble cell components), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and pigment composition (chlorophylls and carotenoids), at the leaf level (Schweiger et al., 2018; Serbin et al., 2014) and scaled up to the canopy level (Asner et al., 2014; Singh et al., 2015; Wang et al., 2019; Wang et al., 2020).

2.2 | Trait covariance and trait estimation

Trait mapping using empirical models on spectral data is an increasingly common approach to inferring community or ecosystem processes over large scales (Chadwick & Asner, 2018; Jucker et al., 2018)—so it is important to know when trait models return accurate enough estimates, and when they instead break down. At times, PLSR and other empirical approaches to predicting traits from spectra may seem unreasonably effective. It seems apt enough that we can accurately predict chemical or structural traits that have strong absorption features, like LMA or water content, at the leaf and canopy scales (Asner et al., 2011; Serbin et al., 2019; Wang et al., 2020). But leaf-level PLSR models can also let us predict (with varying accuracy) nutrients or isotopes (e.g. K, Ca, Mg; $\delta^{15}N$) that have little direct, measurable impact on leaf absorption within the VIS to SWIR range (Asner et al., 2011; Kothari, Beauchamp-Rioux, Laliberté, et al., 2022; Nunes et al., 2017; Wang et al., 2020). Similarly, PLSR models applied to remotely sensed imagery can yield estimates of non-leaf traits like wood density (Jucker et al., 2018), or even make reasonably accurate predictions of forest plots' dominant mycorrhizal associations (Fisher et al., 2016; Sousa et al., 2021). The apparent success of these models, however modest, creates a puzzle: How could a plant trait be predicted when it has no direct effect on the spectrum?

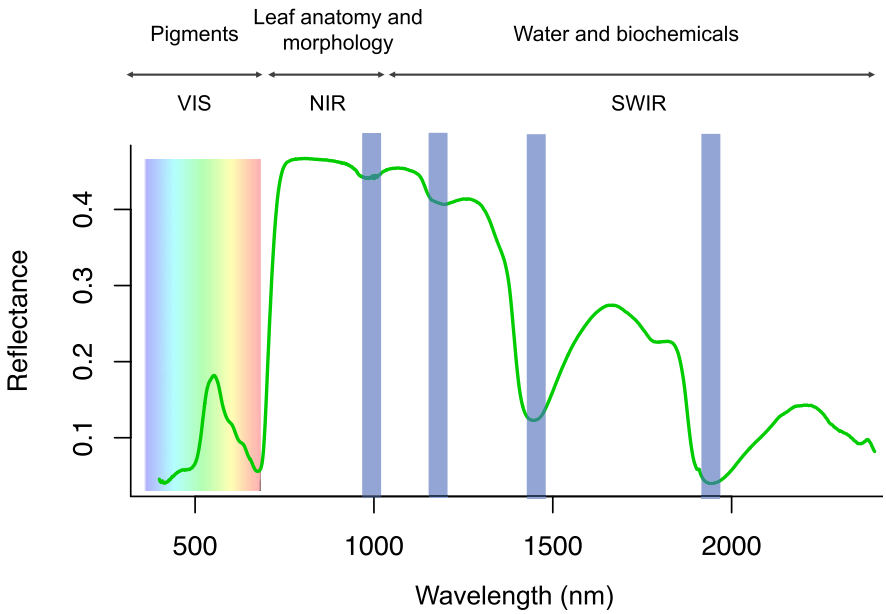

FIGURE 2 Example of a foliar reflectance spectrum. Indicated are the three main regions of the spectrum (visible [VIS], near-infrared [NIR] and shortwave infrared [SWIR]), as well as the main groups of chemical and structural leaf traits influencing reflectance. The absorption features of water are indicated by the four blue bars. Mapping additional leaf traits onto spectra is challenging, because the primary absorption features of most chemical leaf components occur outside of the spectral range spectrometers typically measure (400–2500 nm). Because of this, what we actually detect are harmonics and overtones of these absorption features which are subtle and overlapping, and cannot be illustrated in an easy way

A likely solution to this puzzle is that model-building algorithms leverage the covariance of these unobservable traits with traits that do directly influence spectral properties. For example, wood density tends to correlate with leaf or whole-canopy traits like LMA or total leaf area (Chave et al., 2009; Mencuccini et al., 2019), which influence reflectance spectra more directly. Drawing on Chadwick and Asner (2016), Nunes et al. (2017) coined the term 'constellation effect' to describe how empirical models may predict a target trait by leveraging its covariance with a constellation of other traits, a phenomenon that can be confirmed using synthetic data (Figure 3). This sort of effect may be most conspicuous among traits that have no direct influence on the spectrum. However, it may also affect models for traits that do have absorption features of their own if they also covary with other traits that have strong absorption features.

Ecologists often expect traits to covary with each other in ways that emerge from physical principles and evolutionary constraints (Cavender-Bares et al., 2020). Particular suites of correlated traits are given names like the leaf economics spectrum (Díaz et al., 2016; Wright et al., 2004), the wood economics spectrum (Chave et al., 2009) and Corner's rules (Corner, 1949). Reich (2014) provides a broad overview of trait covariance within and across plant organs. Many of the foundational papers on trait coordination are based on analyses of global trait databases and have validated the reliability of these correlations at global scales (Chave et al., 2009; Díaz et al., 2016; Joswig et al., 2022; Wright et al., 2004). However, these patterns need not be consistent under all circumstances. Indeed, trait correlations often become more variable or even reverse signs at finer phylogenetic or spatial scales (Anderegg et al., 2018; Osnas et al., 2018; Zhou et al., 2022). Biogeographic origins can also alter the relationships between traits (Heberling & Fridley, 2012). In addition, although the leaf economics spectrum (Díaz et al., 2016; Wright et al., 2004) and other low-dimensional trait spaces (Joswig et al., 2022) have received great attention, real networks of trait covariance can be more complex and diffuse and may include traits beyond those most commonly measured (Valverde-Barrantes, & Blackwood, 2016; Wei et al., 2017).

The potential ubiquity and scale-dependence of constellation effects raises the question of what attitude ecologists should take towards models that may rely on them. This problem has analogues in other domains: for example, statistical models of disease risk from genomic data that work well within a population often transfer poorly among populations. Mathieson (2021) argues that this phenomenon emerges because the models leverage not just 'core' genes with a direct causal effect, but also 'peripheral' genes whose influence is contingently mediated by the core genes. We might likewise think of traits as lying along a continuum from core to peripheral, where core traits are those that have a strong, direct influence on the spectrum—which often allows them to be included in RTMs—as well as strong correlations with other traits. Associations between the spectrum and peripheral traits are mediated (at least in part) by correlations between core and peripheral traits (Figure 3).

Even when the relationship between peripheral and core traits seems empirically reliable, it may be hard to quell some lingering doubt about using trait estimates from spectral models that rely on constellation effects. The range of possible attitudes may be illustrated by a case study: Ollinger et al. (2008) reported strong,

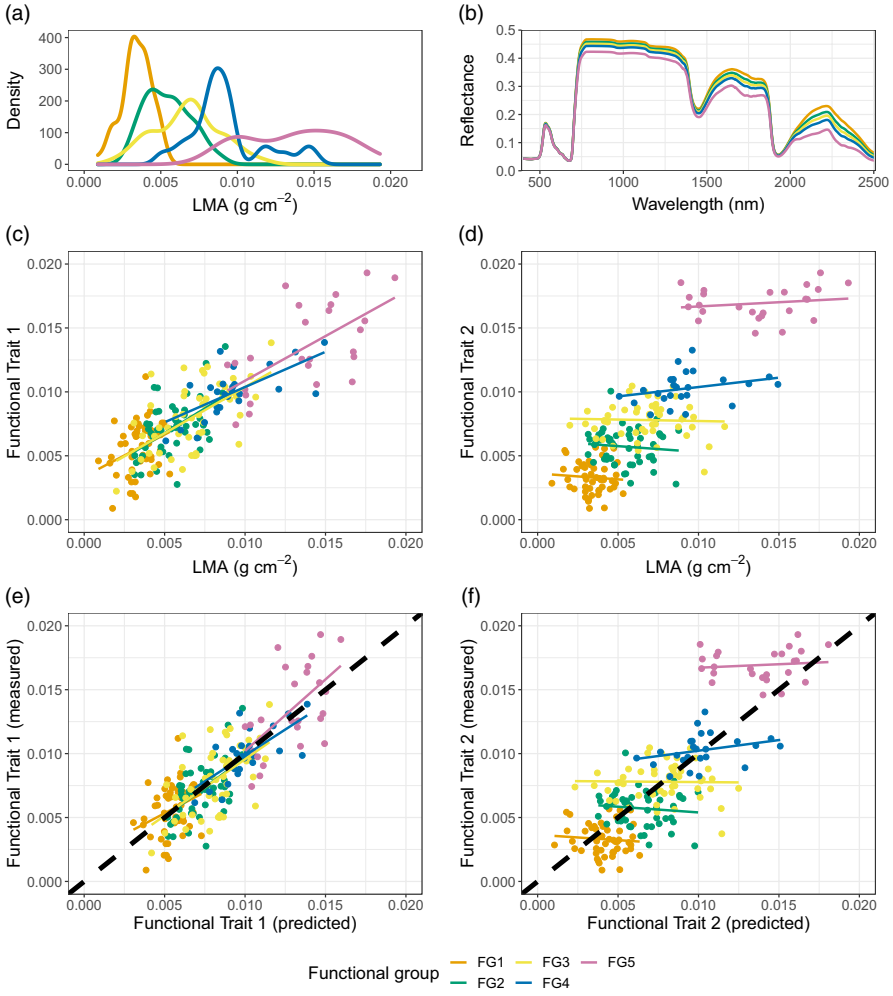

FIGURE 3 We can illustrate the role of covariance in trait estimation using a simple synthetic dataset. (a) We designated five functional groups (FG1-5) with different but overlapping distributions of leaf mass per area (LMA). (b) We simulated 200 spectra using PROSPECT-D (Féret et al., 2017), holding all parameters constant except LMA (equivalent to PROSPECT parameter C_m). We then simulated two other functional traits: (c) Functional Trait 1 (FT1) was generated by adding random noise to LMA; (d) Functional Trait 2 (FT2) was generated such that it correlates with LMA across but not within functional groups. While both traits are positively correlated with LMA (FT1 $R^2 = 0.657$; FT2 $R^2 = 0.666$), neither has any direct influence on the spectrum. (e and f) Training a PLSR model on the simulated spectra with 10-fold cross-validation, we can estimate LMA ($R^2 = 1$; not shown), FT1 ($R^2 = 0.640$), and FT2 ($R^2 = 0.646$) across all functional groups. But while estimates of FT1 are correlated with their true values *within* functional groups, estimates of FT2 are not. The thick black dashed line is the 1:1 line

positive correlations among stand-level foliar N concentration, C assimilation, and remotely sensed canopy NIR reflectance across a range of temperate and boreal forests. Re-examining the relationship, Knyazikhin et al. (2013) argued that a positive correlation between foliar N and NIR reflectance made little sense in terms of the physics of leaf-level radiative transfer. Instead, it arose as an artefact of the disparate canopy structures and leaf surface characteristics of N-poor conifer and N-rich broadleaf trees, which varied in relative abundance across the stands. The question arises: If the strong correlation between foliar N and NIR reflectance is induced by canopy structure, should the models still be used to predict foliar N or C assimilation? Knyazikhin et al. (2013) proposed that attempts to retrieve leaf chemistry using remote sensing might generally be confounded by canopy structure and leaf-level albedo, and expressed scepticism at empirical approaches that are not heavily reinforced by radiative transfer modelling. In a comment, Townsend et al. (2013) argued two points. First, increased spectral range and resolution could improve direct empirical estimation of biochemical traits that, for many of the reasons we discussed earlier, are not amenable to radiative transfer modelling. Second, even when a relationship is indirect and mediated by trait covariance, it need not be considered spurious. In this case, they argued that correlations between leaf chemistry, leaf structure and canopy structure arise from well-described and ostensibly reliable physical and evolutionary constraints that researchers can exploit for trait mapping. One might argue that trying to avoid taking advantage of these correlations can in fact result in worse predictions.

2.3 | When are empirical models good enough?

Regardless of the merits of different modelling approaches, we can ask *when* empirical models that leverage trait covariance are sound enough to use, given that relationships may shift across regions or taxonomic scales. One might suspect that the relationship between foliar N and NIR reflectance that holds across North America's temperate deciduous and boreal forests might do a poor job of predicting N within deciduous forests alone, or in non-forested biomes—but in this case, the relationship tends to be quite robust (Hollinger et al., 2010; Wicklein et al., 2012). However, traits may vary in the consistency of their correlations with other traits across settings, which can be assessed by looking at empirical patterns of trait covariance (Anderegg et al., 2018; Shiklomanov et al., 2020). It may also be useful to examine model performance across a range of ecosystems and species. For instance, if an empirical model shows good performance across a

wide range of species but poor performance within subgroups (e.g. specific ecosystems, functional groups or species), it may suggest that the model relies on global trait covariance patterns that weaken at finer scales (Figure 3f). One interesting case study is Meacham-Hensold et al. (2019), who used transgenic lines to show that PLSR could predict photosynthetic parameters even when their usual positive correlation with leaf N was broken. In addition, simulations coupling radiative transfer models with synthetic trait datasets may elucidate when or how well trait covariance networks propagate trait-spectral relationships to more peripheral traits (Figure 3).

More generally, dramatic differences between the conditions for which a model has been built and the conditions to which a model is being applied carry a risk of inaccurate or biased estimation (Schweiger, 2020). Best practices for predictive model building include covering the range of values of the plant trait(s) of interest, as well as the species, phenological stages, growth forms and environments for which predictions shall be made (Burnett et al., 2021; Schweiger, 2020). Notably, although the transferability of empirical models has generally been considered limited, recent success in calibrating accurate continental-scale PLSR models for a range of traits (Serbin et al., 2019; Wang et al., 2020) suggests that these models can be applied across wide geographic ranges given that the training data covers these ranges adequately. At the same time, it seems reasonable to expect that models that are specifically calibrated for local sites and phenological stages might outperform global models, but this still needs to be assessed. In any event, collecting external validation data to assess on-site performance of empirical models calibrated for a particular environment and time is good practice (Burnett et al., 2021; Schweiger, 2020).

Besides asking when empirical models are valid, we can also ask if there really are a few core traits whose clear influence on optical properties and coordination with other peripheral traits aids the estimation of those other traits—and if so, what are these core traits? Determining what directly drives a multivariate empirical model, such as in PLSR, requires careful interpretation, and hints can come from multiple sources. Interpretive tools like plots of model coefficients, loadings plots or the variable influence on projection (VIP) metric for PLSR (Wold et al., 2001) offer heuristics for gauging which bands help predict a given trait. Bands of high importance can be checked against known absorption features of specific constituents (e.g. Curran, 1989) for interpretation. For example, across studies, many traits show high VIP across the green hump and the red edge (Ely et al., 2019; Kothari, Beauchamp-Rioux, Laliberté, et al., 2022; Yan et al., 2021), which suggests that their estimation may be aided by their covariance with pigment contents or leaf structure. Nevertheless, assigning unambiguous interpretations to these patterns is often challenging because many components' features are shallow and overlapping.

These considerations about constellation effects illustrate that empirical models may often take advantage of trait covariance, especially for estimating traits that only have subtle influences on the spectrum. More generally, they also underscore the complexity of the relationships between the spectrum and traits that have varying degrees of influence on it. Traits each influence reflectance at many spectral bands, and each band is also influenced by the complex physical interactions among many traits. These phenomena give rise to the covariance among bands (which is likely further strengthened by covariance among traits) that produces the distinctive shape of spectra from green leaves (Figures 2 and 3b). The very complexity of these interactions can make it challenging to disentangle all the information in the spectrum into a discrete set of traits. At the same time, the integrative nature of reflectance spectra motivates uses that are not dependent on estimating standard traits, but use spectra in their own right.

3 | BEYOND TRAITS: TREATING SPECTRA AS THEIR OWN ENTITY TO CAPTURE PLANT PHENOTYPES

3.1 | Optical types: More than the sums of plant traits?

In most cases, the spectrum of a plant is treated as an epiphenomenon of some set of underlying traits, which are the true determinants of plant fitness. However, there are some circumstances under which the spectrum itself may be treated as a trait subject to ecological or evolutionary selection. Naturally, absorptance in the VIS range corresponds to light capture by photosynthetic and photoprotective pigments. Absorptance is also part of the leaf energy balance—a consideration that motivated some of the first studies of leaf optical properties (Billings & Morris, 1951; Shull, 1929). This line of research was continued by later researchers, often with a focus on avoidance of high leaf temperature (Blonder et al., 2020; Ehleringer et al., 1981; Mooney et al., 1977)—and even extended to flowers (Roddy, 2019). Another context in which spectral properties themselves may or may not be adaptive is among plant–animal interactions, where both the reflectance of plant tissues and the spectral sensitivity of the animals' eyes matter. For example, the appearance of a plant to potential herbivores may influence susceptibility to herbivory (Kemp & Ellis, 2019; Strauss & Cacho, 2013). Competition or mutualism related to pollinator attraction may also influence the co-occurrence of flowers with different optical properties (van der Kooi et al., 2016). In such cases, the change in average spectral properties or spectral diversity through time or space might indicate which environmental pressures shape those properties.

Even when the spectrum itself does not directly influence fitness, another reason to use spectra directly to make ecological inferences rather than estimating traits is that they integrate many aspects of plant form and function into one single measurement (Cavender-Bares et al., 2017). But what does this mean? If plants are more than the sum of their traits, how can we get a handle on the contributions to plant function of traits that are commonly measured vs more 'fuzzy' traits that might not even yet have a name? This brings us to questions frequently asked in plant functional ecology:

What are the 'correct' traits for investigating specific ecological phenomena? What is the importance of traits that are not associated with major, well-described axes of trait variation? And, are we even able to define and measure all traits that matter for plant life? While spectroscopy will not be able to answer these questions directly, it can reduce barriers to investigating them further. For example, a large share of effort in plant functional ecology goes towards measuring a few traits (Kattge et al., 2020), which are relatively cheap and straightforward to measure, and appear to be of general importance across plant communities worldwide (Westoby, 1998). However, recent work suggests that the effect of functional traits on fitness is often multidimensional (Kraft, Godoy, & Levine, 2015) and dependent on local context (Blonder et al., 2018); in many cases, aspects of function that are less well-studied or more challenging to measure may be important for understanding the role of plants in their environment. Spectra can help us incorporate a broader set of plant functions than we might otherwise be able to, including ones that are seldom studied or that manifest in such diverse ways across the plant tree of life that they are hard to measure in standardized ways (Pérez-Harguindeguy et al., 2013). These may include defence compounds and other secondary metabolites (Couture et al., 2016; Kokaly & Skidmore, 2015), cuticular waxes, leaf hairs (Ehleringer et al., 1981), anatomical traits like mesophyll structure (Karabourniotis et al., 2021) and canopy traits such as leaf inclination angles and branching structure. In addition, the speed of leaf-level or proximal spectral measurements lowers the barrier to incorporating intraspecific variation—an important yet oft-neglected aspect in community ecology (Violle et al., 2012)—and even intra-individual variation within canopies (Schweiger, Lussier Desbiens, et al., 2020).

The optical type concept (Ustin & Gamon, 2010) is central to using spectra of plants as their own entities. It posits that, since plants vie for resources, including light, nutrients and water which all influence the spectral response, optical types can be delineated along resource use axes that can be measured spectrally and capture plant functional identity along a continuum. This concept gave rise to a series of studies using spectral diversity, or the dissimilarity among leaf or canopy spectra, as means to capture plant diversity (Draper et al., 2019; Féret & Asner, 2014; Gholizadeh et al., 2018; Rocchini et al., 2010; Schweiger & Laliberté, 2022; Wang & Gamon, 2019). While the main axes of spectral variation have not yet been fully described (Section 4.2), it has been shown that spectral dissimilarity among plant species is associated with their functional dissimilarity and evolutionary divergence time (Frye et al., 2021; Schweiger et al., 2018). The association between plant spectral, functional and phylogenetic distance is currently best understood at the leaf level (Frye et al., 2021; Meireles et al., 2020; Schweiger et al., 2018). Although leaf spectra do not capture all traits that shape how plants interact with their environment, they do integrate many plant traits that are important for resource capture and stress tolerance, including the contents of pigments, water, cellulose and defence compounds. Through trait covariance, they may also indirectly capture other leaf traits like macro- and micronutrients, as well as traits of other organs like flowers, stems, roots and seeds.

At the remote sensing level, variation in spectra captures differences in plant growth form, leaf orientation and plant architecture as well as leaf traits. However, these structural canopy characteristics are difficult to quantify spectrally and active remote sensing techniques, including SAR (synthetic-aperture radar) and LiDAR (light detection and ranging) are much better suited to derive indicators of vegetation structure (Antonarakis et al., 2011; Bergen et al., 2009; Lenoir et al., 2022). Nevertheless, plant growth form, leaf orientation and canopy architecture create illumination patterns that are influenced by the spatial distribution of light and shade, and proportions of leaf tissue and bark (Gower et al., 1999; Kuusinen et al., 2021). These illumination patterns may influence the spectral signal in a way that contributes to spectral dissimilarities among species, broader taxonomic or functional groups. Studies partitioning the contributions of leaf and canopy traits to spectral diversity or species differentiation are needed to clarify the degree to which effects of canopy structure on spectra benefit or hamper plant diversity assessments using remotely sensed spectra.

3.2 | The spatial organization of plant spectral diversity

Spectrometers can be operated from platforms, including UAVs, airplanes and satellites, that cover a range of spatial scales. The size of image pixels, or spatial resolution, depends mostly on the distance between the sensor and the ground. While imaging spectrometers operated from UAVs can achieve a spatial resolution of a few centimetres, spectral images captured from airplanes typically have spatial resolutions at the m-level and from satellites at the 30-m level. The plant to pixel-size ratio is an important aspect of imaging spectroscopy: when pixels exceed the size of individual plants, a focal plant's surroundings—which can include neighbouring plants and non-vegetated areas—add to the spectral signal. In other words, while airborne data with 1 m pixels might capture individual trees in a mature forest, the same pixel size would capture entire plant communities in grassland ecosystems. This makes it necessary to consider the spatial organization of plant diversity.

The partition between alpha-, beta- and gamma-diversity proposed in Whittaker's (1960) classic work is particularly well suited for working with continuous spatial information as provided by imaging spectrometers. Plant alpha-diversity—the diversity within communities—can best be estimated from spectral data when individual plants are at least as large as image pixels (Fassnacht et al., 2016; Schweiger & Laliberté, 2022; Wang et al., 2018). Therefore, while it might make sense to estimate plant alpha-diversity by calculating spectral alpha-diversity from 2 m image pixels in forests, the same approach might not make sense in grasslands. When individual plants are substantially smaller than image pixels, it seems more useful to work at the beta-diversity scale, using the spectral dissimilarity among image pixels to capture differences in plant community composition (Schweiger & Laliberté, 2022). There are different approaches to calculating spectral diversity, including metrics based

on spectral species (Féret & Asner, 2014) and spectral information content (Wang & Gamon, 2019). One of these approaches—spectral variance partitioning (Laliberté et al., 2020)—has the interesting yet under-explored property that it can be used to calculate the local contributions of individual image pixels and the contributions of individual spectral bands to the spectral diversity of a particular area. This property may help illuminate the spatial and spectral sources of diversity patterns (Laliberté et al., 2020). However, it is not clear whether the spectral contributions of non-vegetated areas should be viewed as adding to the distinctiveness of plant communities or as noise (Gholizadeh et al., 2018).

The spatial arrangement of spectral variation can be useful for investigating community assembly or ecosystem function. Ecologists are often keen to test hypotheses about processes from patterns of functional diversity or functional identity through time or space; such hypotheses could likewise be examined through the lens of spectral diversity or identity (i.e. position in spectral space). For example, Smith et al. (2013) argued that functional diversity-area (FAR) relationships could be used to make inferences about trait-based assembly mechanisms; this method was later extended continuously over landscapes using trait estimates derived from imaging spectroscopy (Durán et al., 2019; Schneider et al., 2017). Inspired by the FAR approach, Dahlin (2016) constructed spectral diversity-area relationships using imaging spectroscopy to consider the roles of environmental filtering and stochastic drift in a mixed agricultural-forest landscape. Draper et al. (2019) and Bongalov et al. (2019) have since addressed similar questions by comparing the roles of the environment and geographic distance in explaining spectral beta-diversity within highly diverse tropical rainforests. These studies reveal the potential for spectral data to shed light on core issues in community assembly over large scales—and they are only possible because spectral dissimilarity or diversity can act as a surrogate for functional dissimilarity or diversity (Schweiger et al., 2018; Ustin & Gamon, 2010). However, the inference of ecological processes from patterns of spectral diversity may face many of the same challenges and ambiguities as inference from patterns of trait diversity (Kraft, Adler, et al., 2015).

3.3 | Spectra as integrated measures of plant phenotypes

Studies that have used spectra as their own entity also include investigations into resource partitioning. Schweiger et al. (2018, 2021) have found that individual plant growth as well as community productivity can be predicted from the spectral space an individual plant or a plant community occupies. This means that individuals and communities that grow more show greater spectral variation and occupy larger spectral hypervolumes than individuals and communities that grow less. The authors propose that differences in resource use strategies, in particular in light use, might be responsible for the large hypervolumes occupied by productive individuals, species and communities.

Using plant spectra in community ecology can provide an opportunity to differentiate plant characteristics that matter under particular circumstances into those that are captured by specific sets of traits and those that remain unmeasured but are captured spectrally. One strategy could be partitioning the total variance of the ecological phenomenon of interest into two fractions, one that is explained by measured traits and one that is explained by spectra alone (Figure 1b). Examining the wavelengths that contribute most to the explanatory power of the spectral component could allow drawing inferences about unmeasured, yet important traits that help explain the ecological phenomenon of interest. Another strategy could be to investigate the main axes of spectral variation together with the traits that are associated with them. Through the successive inclusion of additional sets of traits, it might become possible to decipher which characteristics of plants are captured spectrally. In any case, it is likely that spectra capture characteristics of plants yet to be named.

While this approach of treating spectra as a standalone entity can be powerful, it does come with challenges. Changes in spectral identity or diversity are not as immediately interpretable in biological terms as changes in functional identity or diversity. Using spectra on their own also makes it harder to control the weights assigned to various aspects of plant function, as one might aim to do when calculating functional diversity (Laliberté & Legendre, 2010). At the leaf level, the greatest share of spectral variation is usually due to overall NIR reflectance and the depth of water absorption bands in the SWIR range, which are controlled mainly by factors like leaf surface characteristics, mesophyll structure, LMA and water content. At the canopy level and after accounting for illumination differences, leaf area and leaf angle distribution might be the dominant factors explaining spectral variation, followed by the foliar traits mentioned above. But these traits may not always be commensurately important for fitness or ecosystem function, and traits that account for a smaller share of total spectral variation may be more ecologically important. In other words, although using spectra on their own may allow ecologists to take advantage of more phenotypic information than what most plant trait assessments typically capture, it may also not allow them as much control over what information exactly their analyses include. Methods to bring out the most salient information about plant-environment interactions from spectra could be a useful topic for future research.

4 | DIMENSIONALITY OF SPECTRA

As we have emphasized, plant reflectance spectra are powerful tools because they integrate many aspects of plant form and function into a single measurement. Much of this review is concerned with the question: '*What* and *how much* information about plant function is contained in the reflectance spectrum?' This question is important because the power of a trait dataset to explain or predict patterns in community ecology depends on its *intrinsic dimensionality*—the number of parameters needed to account for the dataset's properties (Laughlin, 2014). The logic of this claim is that each axis of phenotypic variation (or cluster of correlated traits) can be the subject

of selection by different environmental filters, so including more independent axes means that predictions can take into account the effects of more filtering variables. For efficiency's sake, a researcher might want to design a trait measurement campaign to include as many independent dimensions with as few measurements as possible (Laughlin, 2014). Spectra might serve this goal—but only if the phenotypic information they contain is relevant to the environmental filters that may be acting in a given community, which may not be known in advance.

Spectral datasets are made up of a much larger number of variables (spectral bands) than the vast majority of trait datasets, but spectral bands are often highly correlated—both because any given trait influences multiple bands and because traits covary. Radiative transfer models like PROSPECT can generate much of the variation found in real spectra with just a few variables (eight in PROSPECT-PRO; Féret et al., 2021), but are by necessity simplifications; the intrinsic dimensionality of spectral data has seldom if ever been explored empirically. Here, we use two example analyses to take a look at the information spectra contain, with the hope that they will inspire more comprehensive investigations in the future.

4.1 | Species differentiation in spectral versus trait space

In this case study, we used fresh-leaf spectra and trait data of 902 individuals from 14 grassland–savanna perennials sampled in 35 plots of the Cedar Creek Biodiversity (BioDIV) experiment (see Supplementary Methods). The traits included are foliar C, N, soluble cell compounds, hemicellulose, cellulose and lignin concentration (%), the content of chlorophyll a + b (μmol m^{-2}), and ratios relative to chlorophyll content of beta-carotene, lutein and xanthophyll (violaxanthin + antheraxanthin + zeaxanthin) pigments. We z-standardized each trait to mean 0 and standard deviation 1 across the dataset. We used linear discriminant analysis (LDA) to illustrate species dissimilarity in spectral and trait space, and we tested the degree to which plant species can be correctly identified based on spectra and traits using partial least squares discriminant analysis (PLSDA; Brereton & Lloyd, 2014).

Visual inspection of LDA results revealed that species were more distinct in spectral than in trait space (Figure 4). In spectral space, all non-graminoid species clearly separated along the first four LDs (Figure 4a,b), and LDs 11 and 12 separated the graminoids (Figure 4c). In trait space, however, only a few species formed distinct clusters, and we found no combination of LDs that separated the four graminoids species from each other (Figure 4d–f). As a result, species identification models based on spectra (accuracy = 93%, Kappa = 0.81) consistently outperformed species identification models based on traits (overall accuracy = 66%, Kappa = 0.63; Figure 5).

To some extent, better separability of species based on foliar spectra could be due to redundancy in the traits we measured. In our case, light gradients are probably the dominant source of environmental variation, and all leaf traits measured in our study are to some degree influenced by variation in light. For instance, the ratio of chlorophyll and carotenoid pigment levels reflects biochemical acclimation to stress under different light environments (Gamon &

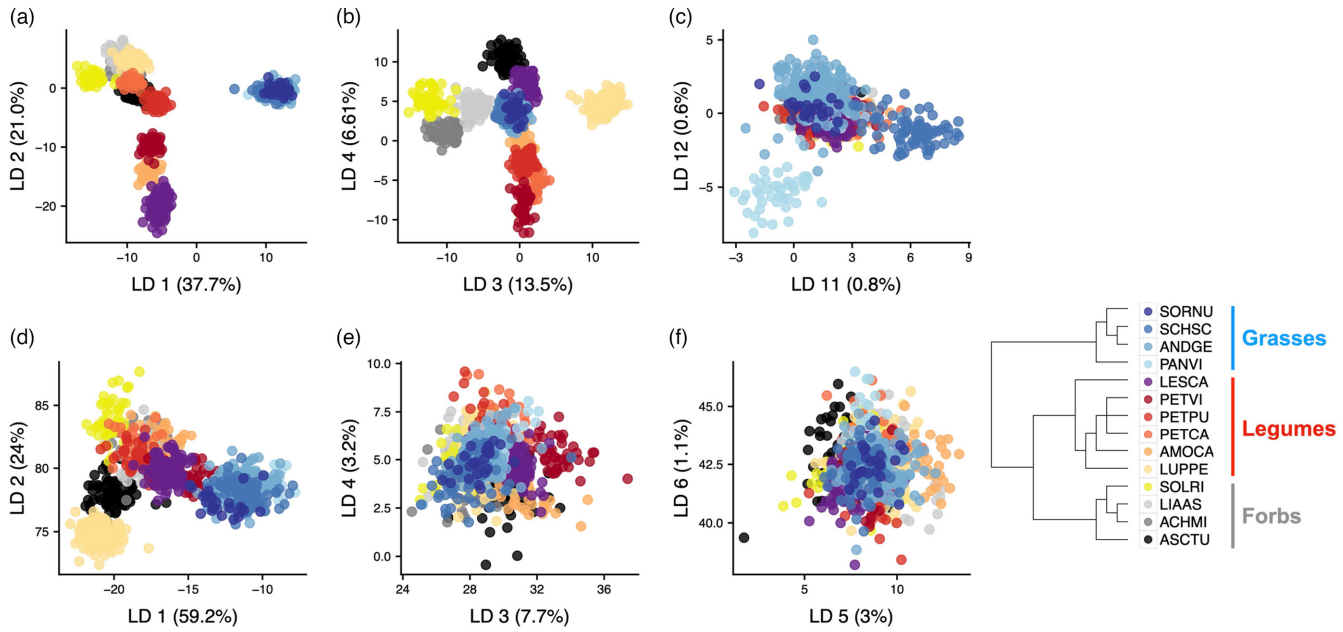

FIGURE 4 Species clustering along linear discriminant axes (LDs) maximizes the differences among species based on (a–c) spectra and (d–f) traits. Overall, species are more distinct in spectral space compared to trait space. In spectral space, it was even possible to distinguish closely related and functionally similar graminoid species, which was not possible in trait space (d–f), along LD axes 11 and 12 that only explain a small portion of the total variance in the data (c). The amount of total variance explained by each LD is shown in parentheses; for species abbreviations and number of individuals per species see Supplementary Methods. Species' phylogenetic relationships and major functional groups are shown on the right.

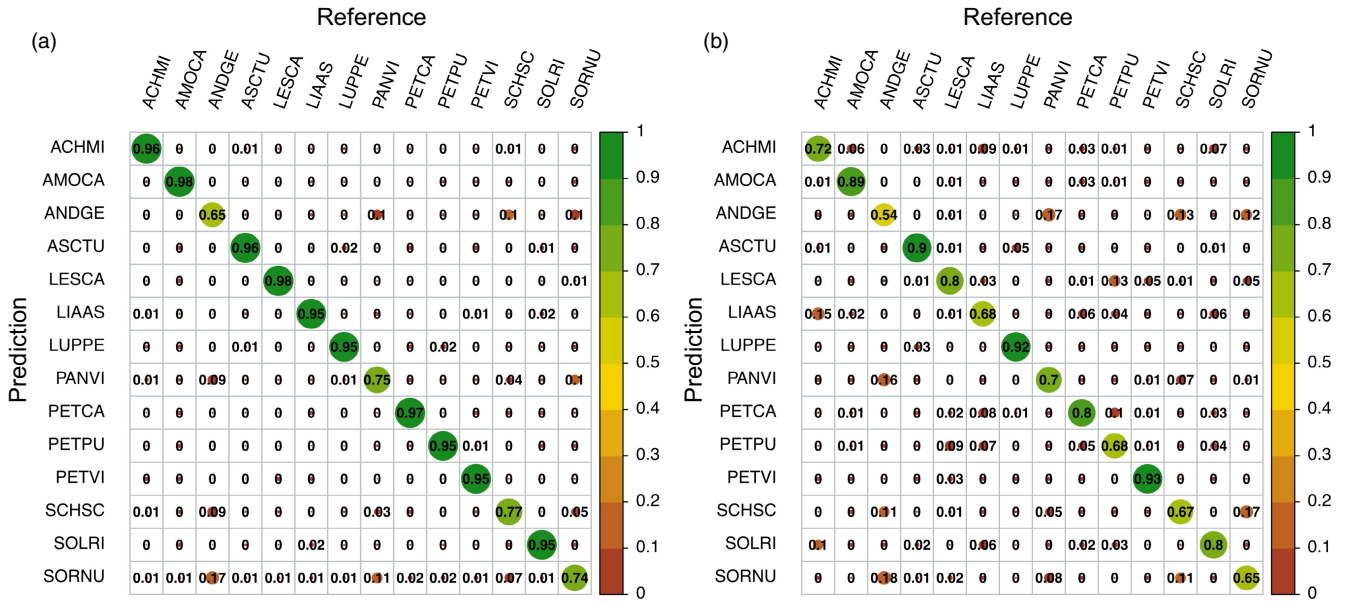

FIGURE 5 Results from species identification models. Confusion tables for PLSDA (partial least squares discriminant analysis) models showing the proportion of correctly identified (diagonal) and misidentified (off-diagonal) species based on (a) leaf spectra and (b) traits. For species abbreviations and number of individuals per species see Supplementary Methods

Berry, 2012; Kothari et al., 2018). Likewise, the contents of different carbon fractions are tied to morphological adaptations to light gradients (Niinemets, 2007), such as leaf thickness and LMA. In this way, what we think of as multiple traits can also be thought of as different proxies for the same or overlapping traits (Gamon et al., 2019). Overall, leaf spectra seemed to capture differences in leaf chemistry, structure and morphology among species more completely than the traits we measured. Interestingly, LDs 11 and 12, which separated the graminoid species, each contributed <1% to the total variation in leaf spectra, while LDs 1–4, which separated the other species, accounted for more than 78%. This highlights that minor axes of spectral variation can bring out important but subtle differences in species' foliar characteristics. Hypotheses regarding which foliar traits might contribute most to LDs 11 and 12, and thus to leaf-level differences among the four graminoid species in our study, would be interesting to test. However, this would require additional trait measurements. The spectral bands contributing most to species' separability along the first LD axes aligned with regions in the foliar spectrum indicative of leaf chlorophyll, carotenoid, lignin and protein content (Figure S1). These foliar traits also contributed most to species separability in functional trait space (Figure S1), and all except chlorophyll content showed evidence of phylogenetic signal (Table S1), indicating that these traits might contribute to species identification across ecosystems.

4.2 | The dimensions of leaf spectra

Next, we sought to quantify the dimensionality of spectra. We used fresh-leaf spectral and trait data from the Canadian Airborne Biodiversity Observatory (CABO) comprising samples of woody and herbaceous plants in Canada and Australia (see Supplementary Methods). We included at most 10 samples per species (leaving $n = 905$; species = 106). We z-standardized the reflectance at each wavelength to avoid placing particular emphasis on bands that have more absolute variation in reflectance and picked a subset of 73 spectral bands to reduce representation of highly correlated wavelengths. We considered the following nine foliar traits: equivalent water thickness (EWT), LMA, C, N, hemicellulose, cellulose, lignin, total chlorophyll and total carotenoids. We converted all traits besides EWT and LMA to a normalization-independent basis (sensu Osnas et al., 2018) to remove their statistical dependence on LMA.

Researchers have often found that leaf chemical traits are estimated better from ground-leaf spectra than from fresh-leaf spectra (Couture et al., 2016; Kothari, Beauchamp-Rioux, Laliberté, et al., 2022; Wang et al., 2020). On some CABO samples, we had also measured spectra after the samples were pressed like herbarium specimens, and again after they were dried and ground (Kothari, Beauchamp-Rioux, Laliberté, et al., 2022). Among these samples, we again chose no more than ten samples per species ($n = 228$; species = 66), and z-standardized and subsampled bands. Lastly, as a benchmark, we used PROSPECT-D (Féret et al., 2017) to generate a synthetic dataset of 1000 spectra with a known dimensionality of 4 by independently varying leaf structure, chlorophyll, water and dry matter content. We z-standardized and subsampled bands as in the real data.

We sought to describe and compare the intrinsic dimensionality of the spectral and trait datasets. Inspired by Laughlin (2014), we used a number of techniques for estimating dimensionality (Table 1) and aimed to see what patterns emerged rather than attempt to reach a single, precise estimate of the true dimensionality. Most of these techniques are non-linear, meaning that they can account for non-linear relationships among input variables like bands or traits.

TABLE 1 Estimated intrinsic dimensionality using a variety of techniques on data from the Canadian Airborne Biodiversity Observatory (CABO)

	n = 905		*n* = 228				
	Spectra	Traits	Fresh	Pressed	Ground	PROSPECT	Citation
Correlation integral	4.7	4.2	4.1	4.4	5.9	3.5	Grassberger and Procaccia (1983)
Maximum likelihood	4.4	4.5	3.8	4	4.9	3.6	Levina and Bickel (2004)
Manifold-adaptive nearest neighbour	4.3	5.0	4.5	4.4	5.8	3.4	Farahmand et al. (2007)
Non-iterative nearest neighbour	3.9	4.3	3.3	2.6	4.1	3.3	Pettis et al. (1979)
Minimum neighbour distance–maximum likelihood	4.7	4.7	4.2	4.4	5.2	3.7	Rozza et al. (2012)
PCA scree test	5	5	5	4	6	4	Cattell (1966)
Isomap scree test	3	3	3	4	3	3	Tenenbaum et al. (2000)

The PROSPECT-generated dataset with a known dimensionality of 4 had estimated dimensionality between 3 and 4. This result suggests that these methods can capture the dimensionality of spectral data, perhaps with a tendency towards underestimation. For both the measured spectral and trait datasets, most methods returned a dimensionality of about 4–5. Using many of the same methods, Laughlin (2014) had shown that large whole-plant trait databases tended to return a dimensionality of 4–6. The fact that leaf-level spectra come close to (and sometimes exceed) the dimensionality of large trait databases suggests that they may have great promise for explaining and predicting community assembly. This potential could be tested, for example, by using species' positions in spectral space as inputs into predictive models of trait-based community assembly (Laughlin & Laughlin, 2013).

On the samples with spectra from fresh, pressed and ground tissue, fresh- and pressed-leaf spectra often had similar dimensionality (mainly 3.5–4.5), but ground-leaf spectra were considerably higher on average (mainly 4–6). We suspect that water and leaf structure may reduce dimensionality by obscuring or overwhelming the small absorption features of specific dry matter constituents in the SWIR range (Elvidge, 1990; Peterson et al., 1988). But since water and leaf or canopy structure are unavoidable in remote sensing—and important for plant function—this finding may have limited relevance for inferring ecological processes over large scales.

Given an estimate of spectral dimensionality, one may wonder what aspects of plant function the dimensions correspond to. We used the manifold learning technique Isomap (Tenenbaum et al., 2000) on the full fresh-leaf spectral data (n = 905) to visualize the major dimensions of leaf spectral variation and their relationship with traits. Isomap approximates the geodesic distances among points on a curved manifold and applies classical multidimensional scaling (MDS) on the distance matrix. Because the relationship between spectral bands is often non-linear, Isomap may be better suited than linear methods to discovering the underlying structure of spectral data.

Much like MDS, the orientation of Isomap output is arbitrary. Here, we rotated the Isomap coordinates using Procrustes analysis to maximize its similarity to the trait dataset. We caution that, while Procrustes analysis helps us interpret spectral variation in terms of the traits in our dataset, it may obscure dimensions of spectral variation that correspond to unmeasured traits. We focus on the first four dimensions after rotation, following the estimates in Table 1, but further dimensions may still have functional importance.

The Isomap analysis helps to visualize the spectral differences among functional groups (Figure 6). Conifers occupy much of the quadrant high on both Axes 1 and 2, while many of the samples high on Axis 1 but not 2 are forbs or wetland graminoids. Shrubs and broadleaf trees tend to be low on both axes. EWT correlates strongly with Axis 1 and LMA with Axis 2; the conifers with high values on both axes have high EWT and LMA, while many forbs and wetland graminoids have high EWT but not LMA. Functional groups separate less along Axes 3 and 4, which correlate with a greater variety of traits but less strongly. Axis 3 is associated with high C and lignin and low EWT, while Axis 4 correlates primarily with N and pigments. Low values along Axis 3 are dominated by graminoids and forbs. These plots can give us a basic sense of the way spectral variation is distributed among functional groups and the traits that underpin it.

We hope these preliminary analyses provide the inspiration for future exploration with larger spectral and trait datasets that represent a larger share of the world's floral diversity. It may be possible to carry out similar analyses using remotely sensed imagery and map plant traits or ecosystem functions onto the space of canopy spectral variation (Feilhauer et al., 2011). New algorithms (e.g. UMAP; McInnes et al., 2020) could allow researchers to interpret their spectral data within a well-understood low-dimensional embedding, much as they can for traits (Segrestin et al., 2021). Given the right data and computational tools, ecologists could eventually describe the major axes of spectral variation and their implications for plant strategies. This advance would make it easier to discern the meaning of changes in spectral identity or diversity across environmental gradients.

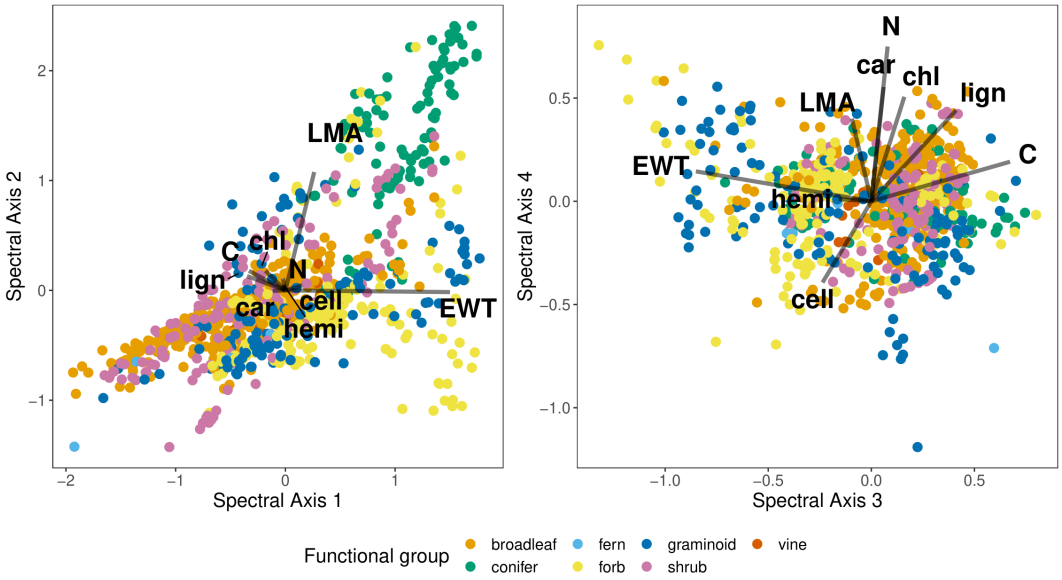

FIGURE 6 A visualization of spectral data from the Canadian Airborne Biodiversity Observatory (CABO) along four Isomap axes. The line segment for each trait is oriented in the direction along which it shows the greatest change within the two-dimensional spectral space, and its relative length within the panel is proportional to the Pearson's correlation coefficient (*r*) between the trait and that direction. All traits besides LMA and EWT were made normalization-independent (sensu Osnas et al., 2018). hemi, hemicellulose; cell, cellulose; lign, lignin; chl, total chlorophylls; car, total carotenoids

5 | CONCLUSIONS

At the leaf and canopy scales, vegetation reflectance spectra contain an extraordinary wealth of information about the ways that plants function. For much of the early history of vegetation spectroscopy, the main way to distill this information into an interpretable form was to calculate indices or estimate traits related to specific aspects of plant function. Mainly within the last decade, researchers have begun to use the full, multidimensional spectrum itself as a tool to investigate ecological processes at the community or ecosystem scales.

In this review, we have sought to describe both the use of spectroscopy to derive plant traits as well as the potential to use spectra directly as integrated measures of plant phenotypes, and also how these two approaches are complementary. The motivations for choosing to use spectra directly can be multifaceted. In some cases, it may be motivated by a lack of models or in situ data for a wide range of traits (Dahlin, 2016). It may also be motivated by the aspects of plants' function governing their impacts on or response to the environment in a given case being highly complex or uncertain. And just as there are aspects of trait variation that are not readily captured by reflectance spectra due to weak or absent optical features, there are aspects of spectral variation that have not yet been interpreted or modelled in terms of commonly measured traits. Because these aspects of spectral variation stand a good chance of being ecologically meaningful, spectra can complement standard traits in assessing the ways plants impact and respond to their environment.

With further methodological and conceptual improvements, both approaches could continue to develop and complement each other. Progress in the area of trait modelling and mapping may lead to ensembles of machine learning methods that allow the mapping of global trait distributions and associated uncertainties, combined perhaps with local scale models adjusted to specific site conditions. Global model repositories combined with cloud computing might allow dynamic trait maps to be produced by selecting appropriate models based on the scale of observation. Progress in the area of using spectra as their own entity may lead to better understanding regarding the separate contributions of suites of traits to spectral variation and their role in ecosystem functions and processes. A wider usage of spectral variance partitioning may also help us understand the ecological roles of rarely measured traits that affect spectra, including leaf anatomy, surface hairs and waxes, defence compounds, and—at the canopy level—leaf angle distribution.

As our examples illustrate, plant reflectance spectra serve as integrative measures of plant phenotypes that can be used to address long-standing ecological questions at the community or ecosystem scales. At the leaf scale, reflectance spectra can be measured quickly and at low marginal cost from many samples. At the canopy scale, imaging spectroscopy allows aspects of plant phenotypes to be mapped continuously over entire landscapes. Among other objectives, these advantages could help to lower the barriers to incorporating intraspecific variation and a broader range of plant functions in our research.

In summary, spectroscopy of plants and vegetation is fundamentally connected to functional ecology. Using spectra to draw ecological inferences can benefit from a combination of spectral and trait analyses. We hope that the growing incorporation of spectroscopy into the standard toolkit of plant ecology will spur the advancement of ecological remote sensing—in other words, remote sensing grounded in ecological theory and praxis. Ultimately, this will allow targeted and explicit assessment and monitoring of plant biodiversity and ecosystem functions and processes, providing the basis for

meaningful action to counteract negative effects of environmental change from local to global scales.

AUTHOR CONTRIBUTIONS

Shan Kothari and Anna K. Schweiger contributed equally to writing the review paper. Anna K. Schweiger conceptualized the review paper, analysed BioDIV data and led the writing for Section 4.1. Shan Kothari analysed CABO data and led the writing for Section 4.2.

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CONFLICT OF INTEREST

No conflict of interest to declare. Anna Schweiger is an Associate Editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13972.

DATA AVAILABILITY STATEMENT

The BioDIV data used in Section 4.1 are available from the EcoSIS Spectral Library (Schweiger, 2016) and from the Digital Repository for University of Minnesota (DRUM; Schweiger, Lapadat, et al., 2020; Schweiger, Fredericksen, et al., 2020; Schweiger, Lapadat, & Cavender-Bares, 2020). The R code for PLSDA can be found on GitHub at https://github.com/annakat/speciesID (Schweiger, 2022). The CABO data used in Section 4.2 is available on EcoSIS (Kothari, Beauchamp-Rioux, Blanchard, et al., 2022). The R scripts for Section 4.2 can be found on GitHub at https://github.com/ShanKothari/CABO-trait-models (Kothari, 2022).

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