Spectral biology across scales in changing environments

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Abstract

Understanding ecosystem processes on our rapidly changing planet requires integration across spatial, temporal and biological scales. We propose that spectral biology, using tools that enable near- to far-range sensing by capturing the interaction of energy with matter across domains of the electromagnetic spectrum, will increasingly enable ecological insights across scales from cells to continents. Here, we focus on advances using spectroscopy in the visible to short-wave infrared, chlorophyll fluorescence-detecting systems, and optical laser scanning (light detection and ranging, LiDAR) to introduce the topic and special feature. Remote sensing using these tools, in conjunction with *in situ* measurements, can powerfully capture ecological and evolutionary processes in changing environments. These tools are amenable to capturing variation in life processes across biological scales that span physiological, evolutionary and macroecological hierarchies. We point out key areas of spectral biology with high potential to advance understanding and monitoring of ecological processes across scales—particularly at large spatial extents—in the face of rapid global change. These include: the detection of plant and ecosystem composition, diversity, structure and function as well as their relationships; detection of the causes and consequences of environmental stress, including disease and drought, for ecosystems; and detection of change through time in ecosystems over large spatial extents to discern variation in and mechanisms underlying their resistance, recovery and resilience in the face of disturbance. We discuss opportunities for spectral biology to discover previously unseen variation and novel processes and to prepare the field of ecology for novel computational tools on the horizon with vast new capabilities for monitoring the ecology of our changing planet.

Why spectral biology has high potential to advance knowledge of ecological processes across scales

In this era of rapid global change, understanding how biological variation at one scale influences emergent properties at other scales—including the functioning of organisms, ecosystems, and the biosphere—is important to developing an integrative understanding that will allow us to actively support a sustainable future for humanity. The approach we term 'spectral biology' encompasses integrative measures of biological systems that harness the interaction of electromagnetic radiation in ways that are scalable and support standardized, repeated measurements (Fig. 1). These spatio-temporally scalable tools provide a means to measure biological variation and related emergent properties across levels of organization. For example, the reflection of electromagnetic radiation by plants is influenced by their phenotypic, chemical, structural, and functional properties, thereby providing a means to measure biological variation and related emergent properties across levels of organization. Spectral information thus provides a consistent data type to integrate aspects of the evolutionary and physiological variation within and among plant species, the interactions of species within communities, and their consequences for ecosystems responses to global change. The rapidly expanding use of the tools of spectral biology in ecology (Fig. 2) provides the impetus to synthesize the capabilities and opportunities within the field and consider the path forward.

The goal of this special feature is to explore how spectral biology enables integration across spatial, temporal and biological scales to reveal novel insights in plant ecology, ecosystem dynamics and global change biology. Focal areas represented in articles that are part of this special feature range from quantitative genetics, phylogenetic ecology, ecophysiology, forest dynamics, global change biology, and phenological variation in ecological systems, to biodiversity-ecosystem function relationships.

What is spectral biology?

We define spectral biology as the spectrally resolved observation of the interaction of electromagnetic radiation with biological systems. We emphasize these interactions in the solar domain, specifically in the visible-to-shortwave infrared (VSWIR, 400-2500 nm) but also include ultra-violet (UV, 100-400 nm) as well as thermal emissions (3-14 μm) and active and passive microwave (0.1-1m) domains that enable the discernment of biological properties. We focus on advances made in this new discipline through studying plant life using reflectance, transmittance, and absorbance spectroscopy, as well as chlorophyll fluorescence emission, including solar-induced fluorescence (SIF), which is coupled to photosynthetic function (Fig. 3). We also include thermal emission, which provides observations of temperature and water content/flux; microwave emission, which can be used to determine soil moisture; and LiDAR (light detection and ranging)—an active sensing system, which provides detailed three-dimensional structural information through the measurement of distance by pulsed lasers. These tools of spectral biology can help decipher the causes and consequences of biological variation across scales. Spectral variation in reflected, absorbed, transmitted or re-emitted electromagnetic radiation results from the variation of chemical, anatomical, morphological, and architectural plant traits, as well as variations in viewing geometry due to sun position, topography or sensor position. The biological variation may originate due to selection, evolutionary history, community composition, diversity, plasticity and their varied responses to environmental drivers.

Spectral biology encompasses a continuum of close- to far-range measurements, which are often described as contact (e.g., using a leaf contact probe attached to a spectrometer), proximal (such as a handheld measurement above a canopy, from a tower or low-flying drones [< 100 m]), or remote (higher altitude aerial to space-based or orbital). Remote and proximal sensing of spectral variation most often involve measuring reflectance. Full-range surface reflectance in the solar domain is calculated as a fraction of incoming (atmosphere-penetrating) solar radiation across the electromagnetic spectrum, which is highest in the visible to short wave infrared (400 - 2500 nm); or as a fraction of artificial, standardized light sources providing a similar source spectrum for irradiating targets at close range. Surface reflectance in this range—e.g., the surface of whole ecosystems or a plant leaf, depending on the scale of measurement—is detected at each wavelength (or band of multiple wavelengths) by a sensor that can be placed on a range of platforms (Fig. 1). Spectral signatures can distinguish among different kinds of molecules in plants (Jacquemoud and Ustin 2019), are sensitive to differences in plant traits (Fig. 3c), and reveal variation across a range of scales from leaves of individual plants, within and among species across the tree of life, and within and among plant communities, ecosystems, and landscapes across the global biosphere (Gamon et al. 2020). Beyond full-range, spectrally highly resolved (often termed 'hyperspectral') reflectance data, we include in the set of tools multispectral sensors which capture reflectance in many fewer bands that may each span a range of wavelengths of interest; fluorescence sensors; associated technologies such as LiDAR; and new applications that emerge from the interpretation of these signals in biological realms.

Chlorophyll fluorescence has long been used at the leaf level to assess photosynthetic light use efficiency (Genty et al. 1989, Schreiber et al. 1994) and to scale from leaves to ecosystems (Gamon and Qiu 1999, Cavender-Bares and Bazzaz 2004). Chlorophyll fluorescence associated with photosynthesis can be captured proximally from UAVs, or remotely from aircraft and from space through measurements of solar-induced fluorescence emission in specific wavelengths that overlap with "dark features" of the Earth's incoming or reflected light spectrum (Joiner et al. 2013) (Fig. 3b). Within these wavelengths, sunlight is partially absorbed by oxygen (O_2-A or O_2-B bands, centered at 760 and 687 nm, respectively). Dark features can also include wavelengths where gases in the Sun's atmosphere absorb outgoing radiation (Fraunhofer lines). Such absorption features where solar radiation is diminished are critical because they allow distinction between the relatively weak signal emitted by plants as fluorescence and the much stronger signal of solar radiation and reflectance (e.g., Köhler et al. 2018, Moya and Cerovic 2004, Sun et al. 2018, Mohammed et al. 2019). Like spectral data, solar-induced chlorophyll fluorescence detection can involve a range of platforms from satellites (Köhler et al. 2018), aircraft (Frankenberg et al. 2018, Porcar-Castell et al. 2021), towers or movable carts (Kebabian et al. 1999, Flexas et al. 2000) to leaf-level measurements (Magney et al. 2017) that vary in the specific detection approach and sensor used.

LiDAR (Light Detection And Ranging) instruments uses pulsed laser light and detect the return time of pulses. This provides distance information and is used to generate three-dimensional point clouds with the level of detail depending on point density. The resulting three-dimensional models reveal information that can be interpreted ecologically in terms of form and structure (e.g., Davies and Asner 2014). Long used in archeology and in the automotive industry, sensors can be hand-held, placed on uncrewed aerial vehicles (UAVs) or on aircraft as well as on platforms orbiting the Earth (GEDI, Dubayah et al. 2020). Many LiDAR instruments are also able to measure echo intensity, providing additional information that can be used to classify targets (Wagner et al. 2006).

By harnessing these tools, spectral biology provides powerful and integrated means to capture biological variation—or biodiversity—from leaves to landscapes and to determine the causal factors that give rise to that variation. It is particularly powerful when spectral and remotely sensed information and tools are coupled with deep biological knowledge across subdisciplines that span scales. The spectral biology toolkit complements other tools, such as gas exchange systems, flux towers, and isotopic measurements that can provide more precise, or different types, of information at specific biological scales. The toolkit may enable biologists across disciplines to consider a greater breadth of relevant scales when designing research to study focal processes, loosening constraints to focus on a specific scale imposed by familiar tools and expertise.

What is the potential of spectral biology to advance ecological research?

Advancing our understanding of Earth's biodiversity and its response to global environmental change at scales from molecules to ecosystems, revealing mechanisms that can be targeted for management, is critical for societal capacity to adapt to, and mitigate, changes in biodiversity (Cavender-Bares et al. 2022a). Here we define the term 'biodiversity' not simply in its most common usage as species diversity at a community scale but to encompass the diversity of life on Earth including variation in functional and evolutionary components within and among biological scales, ranging from cells to organs, to individuals to ecosystems and regions. Decades of research on species diversity at the community scale and its relationship to ecosystem functions have revealed its importance for how ecosystems cycle elements (Weisser et al. 2017, Schuldt et al. 2023), produce biomass (Isbell et al. 2018, Huang et al. 2018), and respond to environmental change (Reich et al. 2001, Loreau and de Mazancourt

2013). These functions are critical to providing ecosystem services that contribute to human well-being (Mori et al. 2021, O'Connor et al. 2021). Integration across biological subdisciplines is required to address fundamental questions that remain poorly understood, including how biodiversity varies across scales—from genes and molecules within cells and tissues, to ecosystem variation. Our capacity to understand and monitor changes in these biological processes at different scales is critical to sustainably managing Earth's life support systems (Gonzalez et al. 2023). However, the scientific advances required to tackle this set of problems have been hindered by the fragmentation of biology into specialized sub-disciplines that are conceptually and methodologically divergent and do not meaningfully connect these vastly different scales. The lack of a common data type to discern processes across scales has contributed to these constraints.

Critical scales in biology

We focus on three kinds of biological hierarchies that form the basis of biological integration and scaling: physiological, evolutionary, and macroecological (Fig. 4). The physiological hierarchy considers the functional or metabolic units within a plant from genes and metabolites (molecular products of metabolism) to organelles, cells, leaves, and other organs, to the whole plant. The evolutionary hierarchy encompasses the nested and fractal organization of the tree of life from individuals nested within populations, species and clades, or lineages of increasing size. Finally, the macroecological hierarchy refers to the ecological processes at nested spatial and temporal scales that drive the distribution and diversity of life—from density- and frequency-dependent neighborhood interactions, to sorting of species across environmental gradients, and the dispersal, migration, and long-term biogeographic processes that form the variation in ecosystems within and across biomes, and drive their function as well.

How spectra help integrate across scales to address complex ecological problems

As biological and ecological subdisciplines have become increasingly specialized, addressing complex questions that span biological scales requires bridging subdisciplines. For example, resting within a single subdiscipline, it is difficult to understand how climate change and landscape fragmentation influence the genetic variation within species; or the complex ecological processes by which community composition of ecosystems across biomes at broad geographic scales impacts changes in ecosystem function and stability. Successful integration requires both conceptual and technical advances. Conceptually, we seek to understand biological processes using a common data type across scales, including across evolutionary hierarchies that capture the nature of phenotypic and functional variation within and among populations, species and major lineages (Fig. 5a) and across temporal and spatial scales (Fig. 5b) to help elucidate how processes at one scale affect processes at other scales and their combined influences on observed patterns, properties, and dynamics.

The technological dimensions involved in generating common data types create a path forward for the practical aspects of integrating across scales to address complex problems. An important point is that monitoring methods should align with biological scales. For example, contact probes are appropriate at the leaf scale, UAVs and low-flying piloted aircraft are often most appropriate at the community scale, and satellites capture phenomena at landscape to global scales (Fig. 5b). Analysis and interpretation of spectral measurements differ significantly based on measurement scale, due to the range of confounding factors expressed at different scales. These factors may include atmospheric interference for high-altitude and orbital imaging, or the influence of detector distance from the object of measurement (e.g., leaves or canopies), or variation unrelated to biological factors due to source-sensor-object geometry. These issues can be addressed through various data processing approaches (e.g., Queally et al. 2022). On the conceptual side, advances emerge when we bridge subdisciplines across scales, fusing expertise from different realms. For example, knowledge of genetic variation within species and how different genotypes respond physiologically to environmental change emerges from the realms of quantitative genetics and ecophysiology. These differences can be connected with typical functional differences among co-occurring species that influence their interactions, and community dynamics that influence ecosystem processes spanning community and ecosystem ecology. This integration may include linkages between above- and belowground processes that drive long-term responses of nutrient cycling to community change, integrating soil and microbial science (Cline et al. 2018, Cavender-Bares et al. 2022b). In another important example, detecting changes in biodiversity in plants at the leaf level is advanced by our understanding that spectra are coupled to genetic and phylogenetic information (Cavender-Bares et al. 2016, Meireles et al. 2020, Stasinski et al. 2021, Griffith et al. 2023, Li et al. 2023). Recent evidence finds similar relationships at canopy scales (Czyż et al. 2020, 2023, Seeley et al. 2023, Griffith et al. 2023). The physiological processes and stress responses that spectra reveal also appear to scale from leaf to canopy levels (Sapes et al. 2024). These findings are important for understanding physiological processes that underlie disease symptoms and can help monitor and map diseases to aid management (Sapes et al. 2022, Guzmán et al. 2023). Spectral biology thus facilitates scaling from individual leaves to their aggregated properties at the scale of landscapes and global observations, because it provides a common measure for investigating how foliar tissue and photosynthetic processes interact with the environment, biological phenomena that can be examined from microscopic to ecosystem scales. Spectral information can also be combined with other measures, such as gas flux rates across scales, to gain insight into how processes at one scale result in emergent properties at others. All of these advances in integration emerge from conceptual and technological efforts.

Avenues for major advances in spectral biology

We address five dimensions of ecology in which spectral information will help to bridge scales and subdisciplines to address complex ecological problems that affect humanity: 1) detecting the composition, structure, function, and diversity of biological components, 2) measuring the consequences of composition, structure, function and diversity for functions of plants and ecosystems, and 3) measuring how those consequences will vary with global environmental change, enabling us 4) to characterize and quantify how those consequences play out at differing temporal and spatial scales, including detecting the resistance and recovery of vegetation in response to disturbance given the ecosystem composition and diversity; and 5) discovery of novel biological phenomena through detection of emergent processes and patterns enabled by cross-scale observation. These dimensions build on each other (Fig. 6). The characterization of composition and diversity is key to understanding how they influence ecosystem function. Deciphering linkages between biodiversity and ecosystem function at large spatial extents provides a baseline for understanding how ecosystems and the components within them respond to stress and global change. Determining the resilience of ecosystems depends on our ability to measure and understand their response to perturbations over time. The fifth dimension highlights the importance of detecting phenomena we are not yet aware of and preparing for new advances in other realms. We chose these dimensions to highlight the potential of spectral biology to advance understanding and monitoring of ecological processes across scales—particularly at large spatial extents—in the face of rapid global change. All are relevant to managing our biosphere for sustainability. We recognize that properties and processes in each dimension interact with those in all others, but we view this organization as enabling us to discuss and investigate key elements in an unfolding or expanding fashion (Fig. 6).

1. Composition and Diversity

Spectral biology has made considerable advances in characterizing the identity and composition of organisms, particularly plants, and in quantifying the diversity and composition of vegetation in ecosystems. These developments also have potential to support evaluating the many organisms that depend on plants for their life cycles and livelihoods. We first consider these capabilities and future potential before discussing how they may be impacted by environmental change.

Composition

One of the most powerful attributes of spectral data is its ability to discern identity and composition by coupling reflectance information across many wavelengths with pattern detection, including machine learning approaches. While spectroscopy has been widely used to identify stars and the presence of specific gases and elements in space, its application to differentiating genotypes, species and lineages of plants on Earth has more recently expanded (Asner and Martin 2016). Species and functional group identification from airborne spectra are well-established for temperate forest trees (Roberts et al. 1998, Plourde et al. 2007, Williams et al. 2020, Sapes et al. 2022) and remain challenging in hyperdiverse tropical systems (Baldeck et al. 2015), particularly from satellites, due to restrictions on spatial resolution and signal-to-noise ratio for instruments in orbit (Papeş et al. 2010). The ability to classify plant species depends crucially on spatial resolution and scale (Wang and Gamon 2019). Across biological scales from genotypes within species (Stasinski et al. 2021, Li et al. 2023), species within lineages and lineages within larger clades, classification appears to have high accuracy at the leaf level (Meireles et al. 2020) and even across canopies (Torabzadeh et al. 2019, Seeley et al. 2023, Griffith et al. 2023). Classification approaches may have greater accuracy or consistency at phylogenetic scales above the level of the species (Cavender-Bares et al. 2016), in other words at the scale of lineages that roughly correspond to genera or subgenera. Detecting lineages rather than species may be critical in highly diverse tropical regions where species-level information is often impossible to obtain on the ground.

Detection of ecosystem composition and identity of component lineages, species, or genotypes is made challenging by shifts in spectral signatures through time (Chlus and Townsend 2022), by the expression of both genetically and environmentally driven variation within taxa (Madritch et al. 2014, Czyż et al. 2020), and by the many complications of different sensors and conditions across observations (Li et al. 2023). The nature of these technical challenges shifts from handheld instruments to uncrewed aerial vehicle (UAV) sensors to airborne sensors and the myriad satellite sensors (Schneider et al. 2017, Helfenstein et al. 2022). Of the space agency-funded satellites, all have resolutions of 30 m or coarser, requiring statistical approaches to discern identity at the scale of individual organisms that will be smaller than the pixel size.

Using 30 m pixel satellite data (Landsat Thematic Mapper (L1TP) and Hyperion imaging spectroscopy from NASA's EO-1 satellite, Visser et al. (2025, this feature) were able to differentiate lianas, as a functional group, from trees. They used radiative transfer models that detect differences in leaf angles and revealed larger apparent leaf areas and increased light scattering in the NIR and SWIR regions in lianas, which they attributed to their less costly leaf construction compared to tree leaves.

Diversity

Various approaches have emerged for linking remotely sensed spectral diversity and *in situ* measures of ecosystem diversity (Rocchini et al. 2010). Ecosystem diversity has sometimes been predicted by taking advantage of identity detection using spectral libraries. For example, Williams et al. (2020) used airborne spectroscopic imagery from AVIRIS NG at 1 m resolution to classify forest canopies in a young experimental forest. By detecting species co-occurring within communities, they predicted forest diversity with high accuracy (up to 12 species). They subsequently used remotely sensed predictions of forest biomass to accurately predict tree diversity - ecosystem function relationships. Plant diversity has also been directly predicted from spectra and from spectral diversity using methods that do not rely on identity detection and range from simple measures of the coefficient of variation (CV) among spectra retrieved from a vegetation plot to detection of spectral species (e.g., Frye et al. 2021). Wang et al. (2018) used the coefficient of variation of spectra from experimental prairie systems at pixel sizes that ranged from 1 mm to 1 m. Here the scale and resolution were critical, and spectral diversity was only predictive of plant diversity at resolutions similar to that of whole plants, leaves, or stems. Gholizadeh et al. (2019, 2020) used a similar approach in more diverse prairie systems and found that the CV of spectra predicted plant diversity even at coarser resolutions up to ~ 4 m. Further studies (Schneider et al. 2017, Kamoske et al. 2022, Rossi et al. 2022) using additional spectral diversity metrics (e.g., convex hull volume [CHV], spectral species [SS], total variance [TV]) found that accurate predictions will also depend on the metric used to assess plant diversity from above. For example, some metrics are more susceptible to outliers than others and thus did not capture the variability of local plant communities (Rossi et al. 2022). Despite challenges, the variability of even a small number of spectral bands has enabled successful detection of boreal forest diversity variation in time and space (Xi et al 2024).

The spectral species concept—pixels with similar signatures in the spectral space (sensu, Féret and Asner 2014)—has gained traction as a conceptual and analytical means to predict plant species and communities (Féret and de Boissieu 2020, Rocchini et al. 2022). Using spectral species, Pinto-Ledezma et al. (in press) found consistent predictions across multiple dimensions of plant diversity across multiple

NEON sites and biomes in the United States. Guzman et al. (2025, this feature) used structural diversity based on UAV LiDAR measurements across the season to predict forest diversity and consequences for ecosystem function in an experimental forest. Forest communities that changed more in their structural diversity across the season also had greater ecosystem productivity.

Connecting spectra to the tree of life

Species and lineages represent points along a continuum from genetic variation among cells and individuals, to quantitatively increasing genetic differentiation defining clades across the tree of life (Fig. 5a). In this way, genetic diversity is not distinct from species or clade diversity, but a finer point to put on our understanding of biological diversity. Genetic diversity concerns differences that are passed on through generations, and therefore subject to evolutionary processes, such as gene flow, selection, mutation, and genetic drift. These processes can result in genotypic diversity and differentiation between populations that have phenotypic consequences. Spectra are information-rich measures of the phenotypes that result from the interaction between genotypes and the environment and, consequently, can be used to address genetic and evolutionary questions (Babar et al. 2006, Cavender-Bares et al. 2017, Kothari and Schweiger 2022). The same kinds of features that allow the separation of species and clades by their spectra (Meireles et al. 2020) can also help assess within-species genetic variation, including differentiation among genotypes and populations (Cavender-Bares et al. 2016). Recent work has indicated that, within specific environments, genetically more diverse populations of plants are also spectrally more diverse (Hernandez-Leal, in review; Li *et al*. 2023) and that spectra can differentiate some genotypes and their F1 crosses as intermediate between signatures of the parent genotypes (Seeley et al. 2023). Similarly, in naturally occurring stands of hybrid poplars, Deacon et al. (2017) showed that spectral phenotypes were intermediate between the parental species.

Studies in this area can draw on the rich toolkit of quantitative genetics, a discipline that has dissected the quantitative relationship between phenotypic and genotypic variation since before the nature of genetic material was known (Falconer and Mackay 1996). More recently, as whole-genome sequencing techniques became increasingly affordable and available, genome-wide association studies (GWAS) became a staple of quantitative genetics (Bazakos et al. 2017). In this issue, Li and co-authors test approaches to apply GWAS to spectra, as well as to spectral features related to specific traits (aspects of phenotypes). They quantify narrow-sense heritability that different parts of a spectrum represent, i.e., the extent to which additive genetic variation contributes to additive variation in spectra; and associate specific genetic and spectral variants. Spectra have also been shown to capture genomic variation in the face of biological processes that blur the lines between populations, such as gene flow, and species, such as hybridization. Stasinski et al. (2021) used leaf spectra to differentiate two species of Dryas that co-occur and hybridize and to furthermore distinguish populations within each of those species and showed that the degree of genetic ancestry of an individual plant can be predicted from spectra.

2. Linking composition and diversity to ecosystem function

Spectral biology further enables us to predict plant and ecosystem function—including structural, chemical, photosynthetic and productivity dimensions—making possible large-scale assessments of the relationships between ecosystem diversity, composition and function. Consistent, large-scale applications of this potential remain untapped.

Plant and ecosystem function

The capacity of spectral information to predict a wide array of plant functional traits opens new doors for mapping plant function across ecosystems (Wang et al. 2019, 2020b) and scaling up to the biosphere (Jetz et al. 2016, Dechant et al. 2024). Spectral data and derived traits relate directly to photosynthesis, carbon dynamics and resource allocation (Serbin et al. 2015, DuBois et al. 2018). These advances will ultimately enable the inclusion of satellite-detected changes in plant function in Earth system models that predict biosphere dynamics on our rapidly changing planet.

Pierrat et al. (2025, this feature) demonstrate the use of proximal remote sensing of solar induced chlorophyll fluorescence (SIF) to discern seasonal changes in photosynthetic yields in *Pinus palustris* and other evergreen needleleaf species at needle and canopy scales. This builds on long-standing efforts to use SIF to measure ecosystem photosynthesis and productivity (Morales et al. 1999, Flexas and Medrano 2002, Freedman et al. 2002, Moya and Cerovic 2004, Sun et al. 2018) and to scale up from leaves to ecosystems (Gamon and Qiu 1999, Cavender-Bares and Bazzaz 2004, Asner and Martin 2008). Detection of ecosystem function has been a major global effort, with robust indices (NDVI) to detect GPP and the development of Earth surface models e.g., (Sellers et al. 1996) and is at a highly advanced stage in terms of predicting productivity and its change through time (Mohammed et al. 2019) in a range of diverse ecosystems (Zhang et al. 2022, Dąbrowska-Zielińska et al. 2022). The coupling of space-borne LiDAR and satellite data is rapidly enhancing global accuracy in monitoring of global ecosystem structure and function (Saarela et al. 2018, Schneider et al. 2020, Di Tommaso et al. 2021, Liu et al. 2022).

Biodiversity-Ecosystem Function relationships

More recent developments have involved using detection of diversity and ecosystem function to decipher how dimensions of biodiversity, including spectral diversity are associated with ecosystem function (Madritch et al. 2014, Schweiger et al. 2018, Williams et al. 2020). While a large body of evidence has shown relationships between species diversity and ecosystem function in experimental systems for a quarter of a century (e.g., Tilman 1999, Reich et al. 2001, Isbell et al. 2015, Grossman et al. 2017, Huang et al. 2018), similar relationships in natural systems have been demonstrated more recently (Liang et al. 2016, Oehri et al. 2017, Chen et al. 2023, Liu et al. 2024) albeit with some inconsistency across scales, biomes and climates (Chisholm et al. 2013, Cheng et al. 2023). Spectral biology approaches are only beginning to be applied at large spatial extents to detect these relationships (Oehri et al. 2020, Schuldt et al. 2023, Liu et al. 2024). Williams et al. (2025, this feature) detect the influence of forest canopy composition on the transmittance of light, showing how experimental forest communities of different phylogenetic lineages change the light quality and quantity that reaches the understory. Guzmán et al (2025, this feature) use remotely sensed lidar across the growing season to decipher changes in forest structure that are associated with critical dimensions of forest diversity and predict ecosystem biomass.

Marcilio-Silva et al. (2025, this feature) use GEDI LiDAR data from space in urban forest patches coupled with ground-based measurements of forest diversity and structure to map urban forests. In doing so, they uncover the importance of management legacies in urban forest structure. Understanding the linkages between plant canopies that can be spectrally observed from above and the soils processes that both influence and are influenced by them are critical spectral detection of belowground ecosystem processes (Madritch et al. 2014, 2020, Cavender-Bares et al. 2022b).

3. Environmental factors, stress, and global change

In a world exposed to increasing threats from climate change, expansion of pests and pathogens, disturbance and land-use change, and increasing pollution loads in the environment, spectral biology has the potential to help detect and differentiate stressors of plants at large spatial extents. Doing so across scales from leaves of individual plants to tree canopies and whole landscapes will require a range of methodologies that may be combined for deeper understanding of mechanisms and interactions of multiple stressors. We emphasize the importance of framing spectral biology in terms of careful integration of spectroscopic and remote sensing methods with stress physiology and pathology, including in-depth understanding of the life-cycle and natural history of biotic stress agents and disease progression, as well as the physiological responses of plants to drought, pollution and their synergies with biotically-induced disease. Stress leaves markers in spectral signatures of leaves, canopies and landscapes, some of which can be generalized and scaled up using spectral regions that show changes in photosynthetic biology, carotenoid and photoprotective pigments and changes in foliar water content across spatial resolution and extent. Other stress markers are more idiosyncratic of specific stress factors and may involve spatial or temporal patterns at the canopy or landscape scale that are diagnostic of a specific pathogen. The degree to which more general stress signatures or system-specific responses are useful in addressing questions regarding ecological processes depends on prior knowledge of organismal function and species interactions as well as the scale of inquiry.

Using a unique open-air field experiment in Minnesota, USA, Stefanski et al (2025, this issue) examined the spectral signature of experimental warming by collecting leaf spectral reflectance (400-2400 nm) at the peak of the growing season for three years on juveniles (two to six years old) of five tree species. They found that the imprint of environmental conditions, including those associated with experimental warming, experienced by plants hours to weeks prior to spectral measurements was linked to spectral regions associated with stress, in particular the water absorption regions of the near-infrared and shortwave infrared. In contrast, the conditions plants experienced during leaf development, again including those associated with climate manipulations, left lasting imprints on the spectral profiles of leaves measured much later in the growing season; those imprints were related to structural and chemical leaf attributes (e.g., pigment content and associated ratios). Moreover, after accounting for species differences, spectral responses to warming did not differ among species, suggesting that developing a general framework for quantifying forest responses to climate change through spectral biology may be feasible.

Signatures of stress across scales

Spectral and point cloud data are increasingly being used to detect trees that are dead or dying as a consequence of drought, disease, and other global change-related stressors (Pontius et al. 2008, Hanavan et al. 2015, Asner et al. 2016, 2018). Detecting mortality and discerning its causes is essential to managing ecosystems in the face of multiple simultaneous stressors. Rapid detection of disease is critical to management in stopping the spread of a pathogen. Less expensive containment measures can be used when disease invasion is detected early, reducing cost.

Plants respond to environmental stress with a limited set of physiological symptoms that can often be detected spectrally. At the level of physiological function in leaves, for example, reduced photosynthetic function and water content are common responses to drought and wilting diseases as a consequence of damage to the photosynthetic apparatus or reduced vascular function, which limits water supply for gas exchange. Changes in chlorophyll concentration and in water content in leaves are readily detectable signatures of stress from leaves to canopies to landscapes (Sapes et al. 2022, 2024, Guzmán et al. 2023). Increases in expression of pigments used for photoprotection may be another general stress response (Savage et al. 2009, Ramirez-Valiente et al. 2015, Encinas-Valero et al. 2021, Kothari et al. 2021). When photosynthetic rates are slowed due to stress (e.g., drought, cold, low nutrients, disease, pollution), less absorbed light can be used for photochemistry. Consequently, plants often upregulate photoprotective pigments (xanthophyll-cycle carotenoid pigments) that dissipate light energy as heat to prevent oxidative damage to the protein components involved in photosynthesis (Demmig-Adams and Adams 2000). Increased expression of carotenoids, detected by spectral regions in the visible—including indices such as the photochemical reflectance index (PRI, (Gamon et al. 1997)) and the chlorophyll carotenoid index (CCI, Gamon et al. 2016)—may be fairly generalizable responses to stress that can be detected across spatial resolutions and extents. At the same time, each disease or disease syndrome may have a distinct temporal and spatial progression pattern, enabling early and/or rapid detection of specific pathogens and differentiating them from drought.

Across plant taxa, environmental stress alters not only the phytochemical composition of leaves, but also the structure–and ultimately function–of canopies, impacting remote sensing signals. For example, drought stress causes notable physiological and chemical shifts aimed at facilitating plant survival through regulating key biological processes through hormonal signaling (McDowell et al. 2022, Rai et al. 2024, Sato et al. 2024). Similarly, drought has also been shown to affect leaf chemical and structural attributes–including changes in amino acids and pigment composition (Demmig-Adams and Adams 2006, Yang et al. 2021), leaf size and density (i.e., leaf area index), orientation, and water content. The extent of these changes are highly dependent on the severity and duration of stress, resulting in high temporal and spatial variation. It can be challenging to disentangle the contribution of canopy structural changes and leaf-level physiological changes, particularly when the spatial resolution of the sensor is course relative to the size of leaves or canopies, making this a fertile area for investigation.

Understanding the biology of the disease can be critical to detecting it remotely. Pests and pathogens tend to be lineage-specific, often requiring biological knowledge of the host, the pathogen and the biotic vector. Within the oaks, the oak wilt fungal pathogen (*Bretziella fagacearum*) is considered the most deadly threat to the genus, particularly the red oak lineage (*Quercus* section Lobatae). Its spores are spread overland long distances by nitidulid sap beetles that can infect vulnerable trees if the cambium is exposed from cracks or cuts (Juzwik et al. 2011). The spread to neighboring oak trees can be quite rapid when roots from an infected tree graft with a neighbor, allowing the fungus to move from one tree to the next (Koch et al. 2010). As trees succumb to the disease, there is a temporal progression of symptoms that aid detection using time series data, as well as a characteristic spatial pattern.

Spectral signatures are capable of differentiating disease symptoms of the pathogen from drought stress at leaf and canopy scales in both indoor (Fallon et al. 2020) and outdoor experiments (Sapes et al. 2024) due to differences in the spectral features that are affected and the rate of change. Heterogeneity in pigment concentrations in foliage across the canopy, as a consequence of tylose formation in the xylem that causes some branches to wilt, is characteristic of the disease and can be used to differentiate it from drought using even inexpensive multispectral UAV sensors. At landscape scales, both spectral features that can be characterized at the whole-plant level as well as temporal and spatial patterns can be detected spectrally. Features in spectroscopic airborne imagery take advantage of host specificity in the disease to help detect vulnerable hosts. Sapes et al. (2022) developed models to differentiate oaks from other tree species, oak lineages vulnerable to oak wilt from less susceptible oaks and ultimately healthy from diseased oaks, for accurate detection of the disease. At regional scales, land surface phenological metrics used understanding of the temporal progression of disease to detect healthy, symptomatic and dead oak trees of specific lineages using currently available satellite data (Sentinel2 and Landsat 8) in near-real time with accuracies sufficient to aid management (Guzmán et al. 2023). Rapid and accurate detection increases management options, from early options that may only involve girdling a single tree and injecting herbicide, to more expensive options that involve the use of a vibratory plow and removal of surrounding trees. If the disease is not treated early, it can spread to such extents that the cost of effective treatment becomes prohibitive.

Spectral detection of stress responses are often not diagnostic of specific diseases (Pontius and Hallett 2014, Pontius et al. 2020). The extent to which particular host-disease systems are discernable and whether those diagnostic responses are idiosyncratic or themselves generalizable is an open question, but one where rapid progress is being made. Drought predisposes many trees to infection by pests and pathogens. Most tree lineages are threatened by multiple pests and pathogens, with similarities in symptoms. Deciphering the cause of decline and mortality is likely to remain complicated. Spectral biology has the potential to detect ecosystem-scale stress and connect it to whole-organism understanding of biotic and abiotic stress responses as a means of understanding underlying mechanisms of forest decline to aid management.

Rapid detection of stress physiology is now possible at scales and frequencies that would be infeasible from the ground. Even if the mechanism of stress is not discernable, detecting the location of stress in ecosystems aids management. Forests are expressing novel phenotypes due to rapid rates of change and the emergence of novel environments (Housset et al. 2018). An important question is whether ecosystem-level responses to stress are generalizable or whether each specific system is distinct, requiring specific local knowledge to decipher stress responses. Is there convergence in system-level responses across ecosystem types and host-disease systems, from lodgepole mountain pine beetle attack to oak wilt, in terms of stress physiology? Or do we need more detailed information about life histories of pests and pathogens to understand how each disease is expressed? Integration among subdisciplines is critical, with remote sensing of spectral information providing one tool, but only partial answers. Unique combinations of stress that do not have historical analogs may produce unique signatures of stress. Given the rate of global change, it is more important than ever to detect these kinds of stress responses, and it is now possible to examine interacting stress factors in ways we could not before. Rapid detection of stress is critical to replanting and reforesting and will advance restoration and rehabilitation efforts mandated in the Global Biodiversity Framework of the Convention on Biological Diversity.

Genetic variation in stress response detectable from spectral phenotypes

Stress detection has received enormous attention in crops and with the goal of connecting spectrally derived functional information to genomic mechanisms (Mohd Asaari et al. 2018, Wang et al. 2020a, Calzone et al. 2021). Regulation of suites of genes in response to stress changes spectrally observable phenotypes (Tirado et al. 2020). In ecology and evolution, we often need to assess the performance of individual organisms or groups as indicators of their acclimation or fitness in the face of stress, but we do not have complete ways to measure performance. Traditionally, we measure one or a few traits as a proxy. In the worst case, one trait such as biomass accumulation is set as "equivalent" to performance, which is misleading and inhibits deeper thinking about organisms as agents, and mechanisms and facets of resilience. Having a more integrative measurement that lends itself to spatial and temporal scaling may help us to better consider how, when, and in what ways to assess different aspects of performance, and remind us that we are evaluating a multifaceted phenomenon.

4. Resistance, recovery, and resilience

Resistance, recovery, stability and resilience are concepts receiving increased attention in ecosystem and global change ecology, in relation to both strong event-type disturbances and chronic pressures. Despite inconsistent definitions (which harms progress), conceptual coherence and a variety of useful approaches make this an area of current and future focus and importance (Yi and Jackson 2021, Tai et al. 2023). Investigating these concepts over relevant time scales (decades to centuries) requires repeated observations that are challenging to acquire with direct observations. In contrast, remotely sensed data, which often is possible to acquire repeatedly over time, plays a special role in the development of both resilience theory and its testing (Pontius et al. 2020, Liu et al. 2021, Yi and Jackson 2021, Tai et al. 2023). Spectral biology enables us to observe ecosystems through time to test how diversity and composition influence resistance, recovery, and stability (Isbell et al. 2015): processes receiving increasing attention as important in a changing world (Wilcox et al. 2020, Avolio et al. 2021).

Frequent (e.g. every 1-2 weeks) or infrequent (e.g. seasonal to annual) satellite measurements provide spectral information on ecosystems and how they change, which encompasses ecosystem resistance and resilience (Fig. 6). Capturing transition states and predicting shifts in ecological function under global change (Tai et al. 2023) will increasingly be critical to understanding how the Earth is changing and provide important input for the sustainable management of ecosystems.

Diversity likely plays a key role in resilience. Linkages between diversity (e.g. species richness, phylogenetic diversity, functional diversity) and stability are well established; for example, evidence is increasing that forest diversity increases drought resistance in experimental systems (Blondeel et al. 2024). Such evidence has required long-term experiments, constraining analyses to small spatial extents, a handful of biomes, and relatively few species. Time series data collected across the Earth's surface can be used to feed or test models predicting relationships between diversity and function, and help decipher how trends in ecosystem function are related to processes of resistance, compositional turnover, and recovery after disturbance that influence resilience (Xu et al. 2022). Studies of tipping points and their signatures indicate that increased variability can precede a regime shift to an alternative degraded state of an ecosystem (Scheffer et al. 2001, Scheffer and Carpenter 2003, Steffen et al. 2015).

A mechanistic understanding of change will increase predictive capacity, even in non-linear ecosystem dynamics – where detecting thresholds is critical. Changes in biome extent over time have long been detected using NDVI (Simms and Ward 2013). Shifts in alpine ecotones in response to warming climates have been detected in the Western US (Wei et al. 2020). Remotely sensed resilience data enabled prediction of subsequent drought mortality across the continental US (Tai et al. 2023). An important element is understanding the mechanisms underlying ecosystem transitions, which includes deciphering causes of mortality, stress, and disturbance. High spectral resolution is important to understand compositional changes and pinpoint changing physiological functions. Historically, scientists have considered different stress factors in isolation. Complexities of interacting stress result in emergent properties that can be detected using a holistic measurement approach such as that of spectral biology, and untangled through a mechanistic approach by extracting specific information from spectral time series in combination with other data types.

For example, Sturm et al. (2022) used changes in the canopy Normalized Differential Water Index (NDWI) from a time series of multispectral satellite imagery from Sentinel-2 to calculate the resistance, resilience, and recovery of forests across Switzerland to an unusually severe drought event in 2018. They explained differences among forests based on landscape characteristics and forest mixing ratios (e.g. proportion of needle versus broadleaf trees). Helfenstein et al. (2024) used the same approach to study the relationships of resistance, resilience, and recovery with functional diversity as calculated from pigments and water content in the same forests (using different images for diversity metrics versus the time series calculations) and found positive relationships of functional richness with both resistance and resilience to drought. These kinds of patterns can also be detected in managed, urban, or naturally assembled ecosystems through spectral and LiDAR information over time that is well-connected to measured biological processes on the ground (Marcilio-Silva et al. 2025, this feature). Ultimately, these approaches will enable mechanistically informed monitoring of forest stress responses and resilience.

5. Discovery

Finally, spectral biology will advance the realm of discovery by opening our capacity to observe Earth and the living world around us. What new patterns can we quantify as a consequence of the ability to "see" deep patterns and mechanisms across spatial and temporal scales? The new frontiers that will emerge will encompass measurements of the linkages among the full range of biological organization, and evolutionary and environmental drivers of plant distributions and functions, as well as their genetic structure, competitive interactions and relationships to components of ecosystems such as microbes or pathogens, detected by other methods. The capability of spectral biology to detect diversity, composition and function of ecosystems, and how they change in response to stress through space and time, enables new pathways for discovery at vastly divergent scales.

The high dimensionality of spectra provides insurance against our ignorance

Through the linkage of spectroscopy with biology, the potential of spectral biology goes beyond what our frameworks and methods currently allow for (Townsend et al. 2013). For example, VSWIR spectroscopy (400 – 2500 nm) captures coherent (i.e., non-noise) information beyond the variables we currently estimate from the imagery (Schimel et al. 2020, Cawse-Nicholson et al. 2022) or use to model leaf reflectance via physical models (e.g., Féret and De Boissieu 2024). The high dimensionality of spectral data can enable future discoveries unlocked by advances in machine learning models, computational power, technological advances in associated areas, and conceptual breakthroughs (Hong et al. 2024).

Stronger links between genetic diversity and spectra can be forged as the cost of genomics and transcriptomics come down and spectral biology becomes more democratized. Spectral biology can help guide genomic and transcriptomic analyses for scientists and ecosystem managers alike by identifying promising relationships for deeper investigation: it may help to more efficiently search for the proverbial needle in a haystack. Specifically, advances in scalable monitoring of biological diversity enable measurement prioritization. In particular, the emerging Earth observation platforms that we envision will lower barriers to entry to spectral biologists and provide the foundation for more effective monitoring of biological diversity with tighter links of monitoring to mechanism and response.

Ultimately, the ability to detect patterns at broad spatial extents through time will facilitate the discovery of phenomena relevant to understanding biological processes across scales. The broad spatial perspective will allow us to test whether relationships we observe at fine scales or from experimental studies are generalizable at regional-to-planetary scales, and, if not, why. Thus, we expect that advances in technology will be followed by increases in the spatial extent of composition, functional, and stress measurements that will facilitate either verification or falsification of hypothesized mechanisms, or, alternatively, reveal patterns of variation not previously characterized. Already it is clear that more functional variation emerges when functional traits are spatially mapped from above than is predicted from functional trait measurements on the ground, largely due to the vastly increased sample size that results from using image data (Wang et al. 2020b). In order to produce comparable measurements at the pace of fieldwork, most functional ecologists adhere to specific protocols for how and when traits are measured on plants, and focus on specific seasonal and ontogenetic life stages, prioritizing certain organs over others. Remotely sensed and spectrally derived functional variation is agnostic to these protocols and can pick up otherwise hidden functional variation. The "insurance against ignorance" is that we have only scratched the surface of our understanding of the drivers of spectral variation, meaning that our archived records provide a repository of data that can be re-mined into the future as we build out our knowledge in spectral biology.

We will no doubt detect patterns that we could not see in other ways, and there is room for pattern discovery in remote sensing across spatial and temporal scales, similar to the development of genomics. Much of the focus of spectral biology to date has been on readily detected patterns, such as quantification of traits that drive photosynthesis, like chlorophyll and nitrogen concentrations or leaf mass per area. What is truly exciting is the potential to detect unanticipated anomalies or exceptions to expected relationships—e.g., where predicted trait-trait or trait-environment relationships break down—or where new relationships are observed that had not previously been identified as important. Advances in modeling and computational tools may allow us to learn from the signals obtained across scales and study planet Earth as a system, finally deciphering how processes at one scale influence and are influenced by those at all other scales.

At the same time, it is important to acknowledge that many gaps remain in accurate interpretation of signals, and excitement about advancing technology can result in overselling its potential. Signals can only be interpreted to the extent that we can connect them to meaningful biological processes and patterns that are carefully measured, understood, and verified in appropriate ways. There are technical issues with signal detection from a distance based on geometry and atmospheric interference, as discussed earlier. Near-surface remote sensing data are hard to acquire over time and require considerable training and infrastructure investment; multiple interacting biological and environmental factors can be difficult to disentangle. There is no shortcut to conducting the careful *in situ* work to decipher mechanisms underlying biological phenomena that enables extension of our understanding across spatial and temporal scales.

Conclusions

We close by emphasizing that spectral biology has enormous potential to expand the spatial extents and timeframes at which we can decipher ecological processes relevant to managing our planet. Importantly, ecologists have a critical role to play in conducting the research to enable accurate biological interpretation of signals, whether from spectral measurements made at fine scales, or from the sky. The theoretical frameworks and extensive field, experimental, and laboratory observations and analyses that underpin the inferences made from spectral data are critical to the effective use of these measurements. The tools of spectral biology, which still present challenges to accurate interpretation, also provide keys to understanding and monitoring vegetation on Earth from the finest scale to our entire planet in ways that have not been possible before. Moreover, by linking across components of the ecosystem, such as soil biota, animals and microbes, we can further disentangle trophic and other complex or non-linear dynamics operating across spatial and temporal scales. Spectral biology is one framework that will help us to harness the information necessary for local to global efforts to manage ecosystems and sustain a habitable planet. The framework and tools will increasingly play an important role in knowing how we are doing in meeting the goals and targets of the Global Biodiversity Framework (Kissling et al. 2018, Skidmore et al. 2021, Cavender-Bares et al. 2022a, Gonzalez et al. 2023).

Acknowledgements

This work was supported by the NSF Biology Integration Institute ASCEND (Advancing Spectral Biology in Changing Environments to understand Diversity; NSF-DBI-2021898). The figures were partially designed by seanquinn.studio.

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Figure Legends

Fig. 1. Capturing biological variation across spatial and temporal scales to understand ecological and evolutionary processes in changing environments. Shown are biological scales of measurement (circles) from genes and leaves to the biosphere and some of the tools of spectral biology that capture optical information across these scales. Spectroscopy, SIF and LiDAR from satellite, aircraft, UAVs, towers and hand-held instruments showing remote, proximal and in-situ sensors that capture plant foliar chemistry, structure and function, photosynthesis and productivity, and vegetation height and structure. The figure emphasizes the visual to the short-wave infrared (VSWIR) solar domain (400-2500 nm), but the UV (100 - 400 nm), thermal emission (3 – 14 μm) as well as active and passive microwave (0.1-1m) domains provide critical information, for example about light quality, ozone and SO_2; land surface temperature, water content and flux; and soil water content or atmospheric water and ozone content, respectively. Towers in a fixed location close to focal observation sites can support Phenocams, continuous spectroscopic measurements, terrestrial laser scanning, and other sensor types. Combined with ground-based measures and understanding of biological processes, spectral biology can contribute to measuring and understanding life's variation (biodiversity components at any scale), ecological and evolutionary processes and their emergent properties, and how they are changing with global environmental forces.

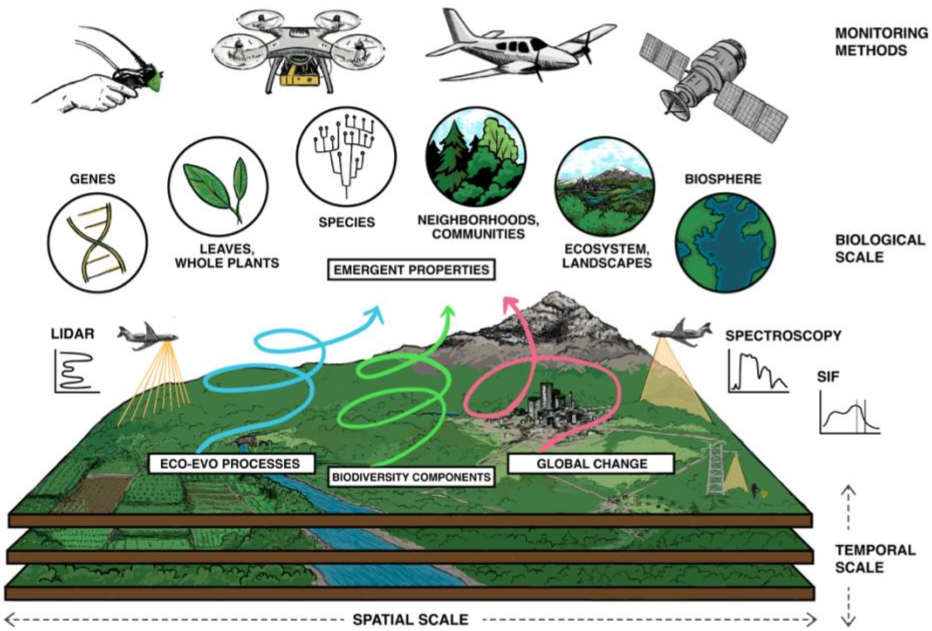

MONITORING METHODS
GENES
LEAVES, WHOLE PLANTS
SPECIES
NEIGHBORHOODS, COMMUNITIES
ECOSYSTEM, LANDSCAPES
BIOSPHERE
BIOLOGICAL SCALE
EMERGENT PROPERTIES
LIDAR
SPECTROSCOPY
SIF
ECO-EVO PROCESSES
BIODIVERSITY COMPONENTS
GLOBAL CHANGE
TEMPORAL SCALE
SPATIAL SCALE

Fig. 2. Number of publications listed within Web of Science over time from 1978 to 2024 with the queries ‘ecology and spectroscopy or hyperpsectral’ (black), ‘ecology and remote sensing’ (orange), ‘ecology and SIF’ (green), and ‘ecology and LiDAR’ (brown).

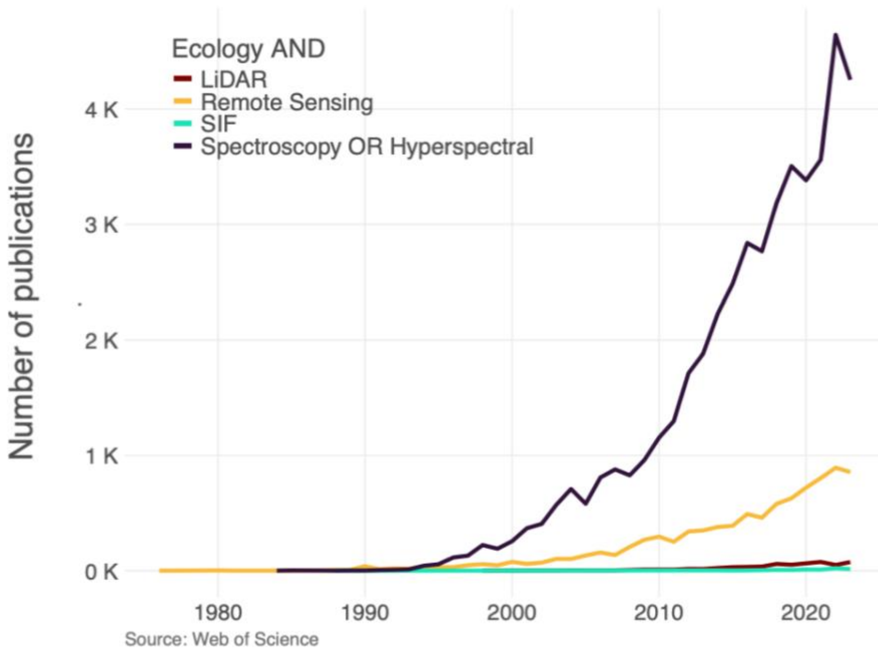
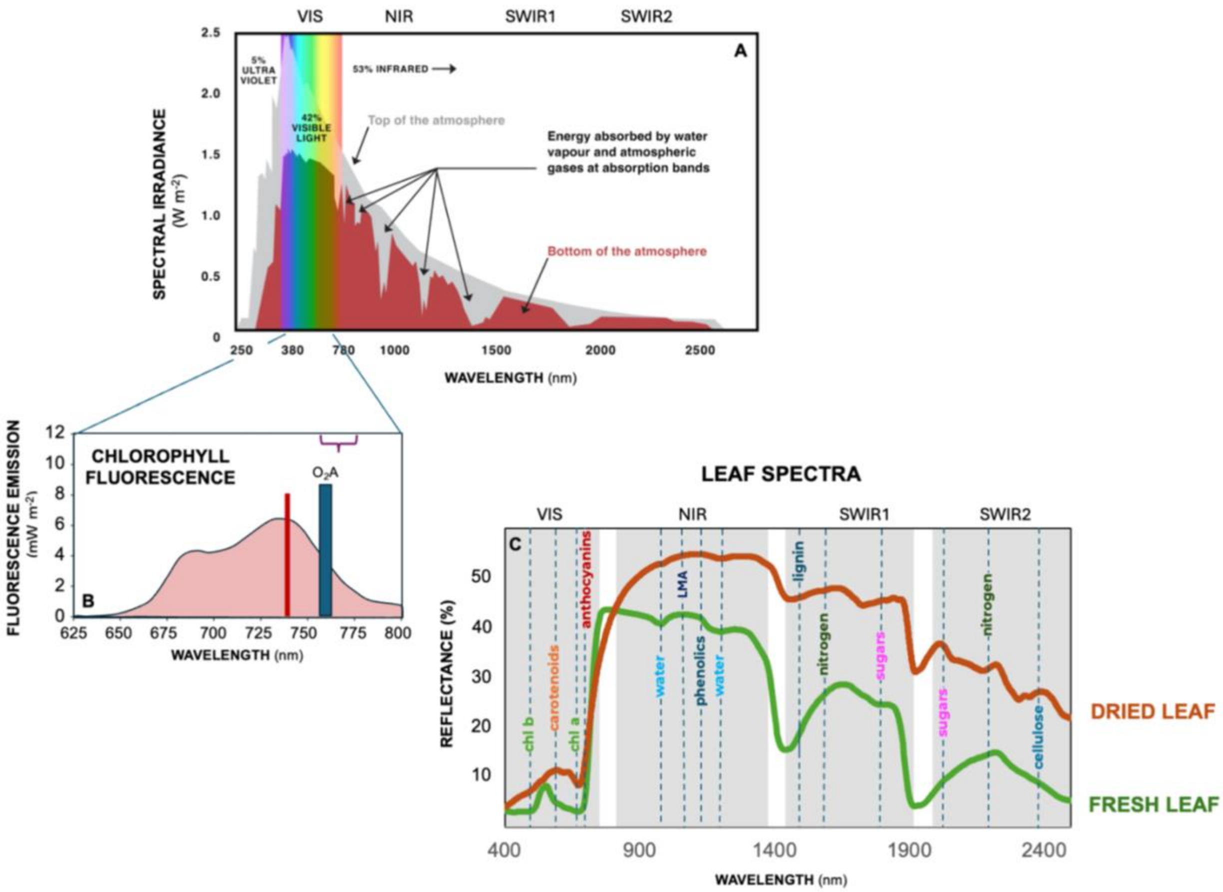


Fig. 3. Spectral biology is defined as the interaction of electromagnetic energy, shown for (A), with biological systems to reveal patterns and processes, such as (B) chlorophyll fluorescence emission (middle) and (C) reflectance from plant tissues (bottom). A) Solar irradiance at the top of the atmosphere (gray) and the sun's energy that penetrates the atmosphere to reach the Earth's surface (red) falls mostly within the range of 250-2500 nm, spanning the ultraviolet (UV), visible range (VIS), near-infrared (NIR), and two short-wave infrared regions (SWIR1, SWIR2). Plants absorb energy primarily in the red and blue wavelengths for photosynthesis and re-emit a small fraction of the energy as chlorophyll fluorescence (B) within the range of 625 to 800 nm, with peak emission shown at 737 (red vertical line). Solar-induced fluorescence (SIF) can be differentiated from solar irradiance within features such as the O_2A band, where oxygen absorbs (vertical blue band), providing a means to detect photosynthesis. Satellite sensors designed to retrieve SIF capture emission within the range of 758–771 nm, indicated by the curly bracket, taking advantage of the O_2A band. Different parts of the chlorophyll emission spectrum are used by different sensors, depending on distance from the vegetation and depth of the atmosphere. C) Spectral reflectance of fresh (green) and dried (brown) leaf tissue include features from the visible to the short-wave infrared that are informative for predicting plant functional traits (e.g., leaf mass per area, LMA), indicated as dotted lines. Reflectance spectra (solid curves) show the percent of incoming light reflected at each wavelength within the VIS, NIR and SWIR1 and SWIR2.



VIS
NIR
SWIR1
SWIR2
A
5% ULTRA VIOLET
53% INFRARED
42% VISIBLE LIGHT
Top of the atmosphere
Energy absorbed by water vapour and atmospheric gases at absorption bands
Bottom of the atmosphere
SPECTRAL IRRADIANCE (W m-2)
2.5
2.0
1.5
1.0
0.5
0
250
380
780
1000
1500
2000
2500
WAVELENGTH (nm)
CHLOROPHYLL FLUORESCENCE
O2A
B
FLUORESCENCE EMISSION (mW m-2)
12
10
8
6
4
2
0
625
650
675
700
725
750
775
800
WAVELENGTH (nm)
LEAF SPECTRA
C
chl b
carotenoids
chl a
anthocyanins
water
LMA
phenolics
water
lignin
nitrogen
sugars
sugars
nitrogen
cellulose
REFLECTANCE (%)
50
40
30
20
10
400
900
1400
1900
2400
WAVELENGTH (nm)
DRIED LEAF
FRESH LEAF

Fig. 4. Three critical scaling hierarchies in spectral biology. Left: the physiological hierarchy encompasses how functions are expressed within nested levels of organization from genes, to molecules, organelles, cells, tissues (leaves) and the whole organism. Middle: the evolutionary hierarchy captures the fractal nature of the tree of life based on shared ancestry, where variation among individuals is nested within populations, which are in turn nested within species, and within clades of larger and larger size. Right: the macroecological hierarchy traverses the ecological processes that shift with spatial and temporal scales, shown here spanning the density-dependent interactions of individual trees, environmental filtering that sorts species based on niche preferences operating at the scale of critical environmental gradients, dispersal processes driven by migration and propagule movement, and the biogeographic and macroevolutionary processes that operate at deeper temporal and larger spatial scales.
Three critical hierarchies in biology: 1) the physiological hierarchy with nested biological components from DNA to the whole organism, 2) the evolutionary hierarchy where variation among individuals is nested within populations, which are in turn nested within species and increasingly larger clades across the tree of life, and 3) a macroecological hierarchy in which ecological processes shift with spatial and temporal scale from density-dependent processes that involve organismal and species interactions in local environments, to environmental sorting and dispersal and migration processes at landscape scales, to long-term biogeographic and evolutionary processes at continental scales that extend deep in time. A typical spatial resolution (grain size) is shown below each spectral image associated with the different spatial scales. This figure is adapted with permission from Cavender-Bares et al. (2021).

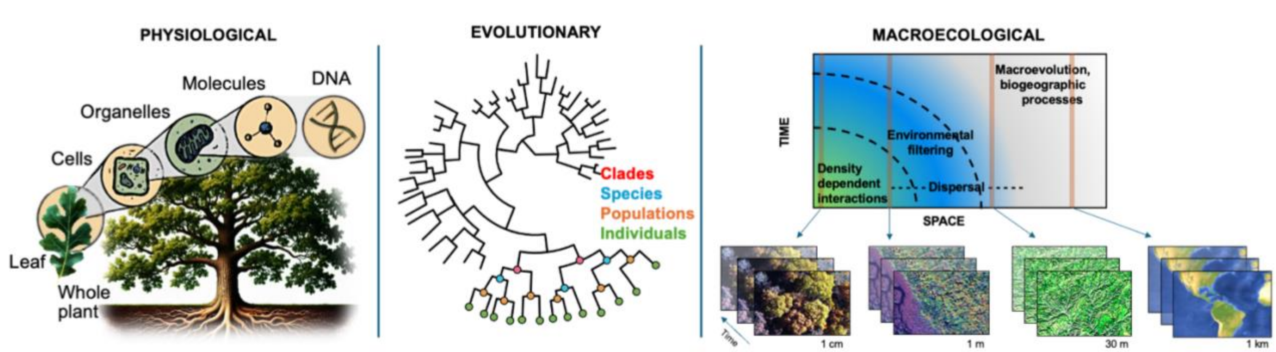
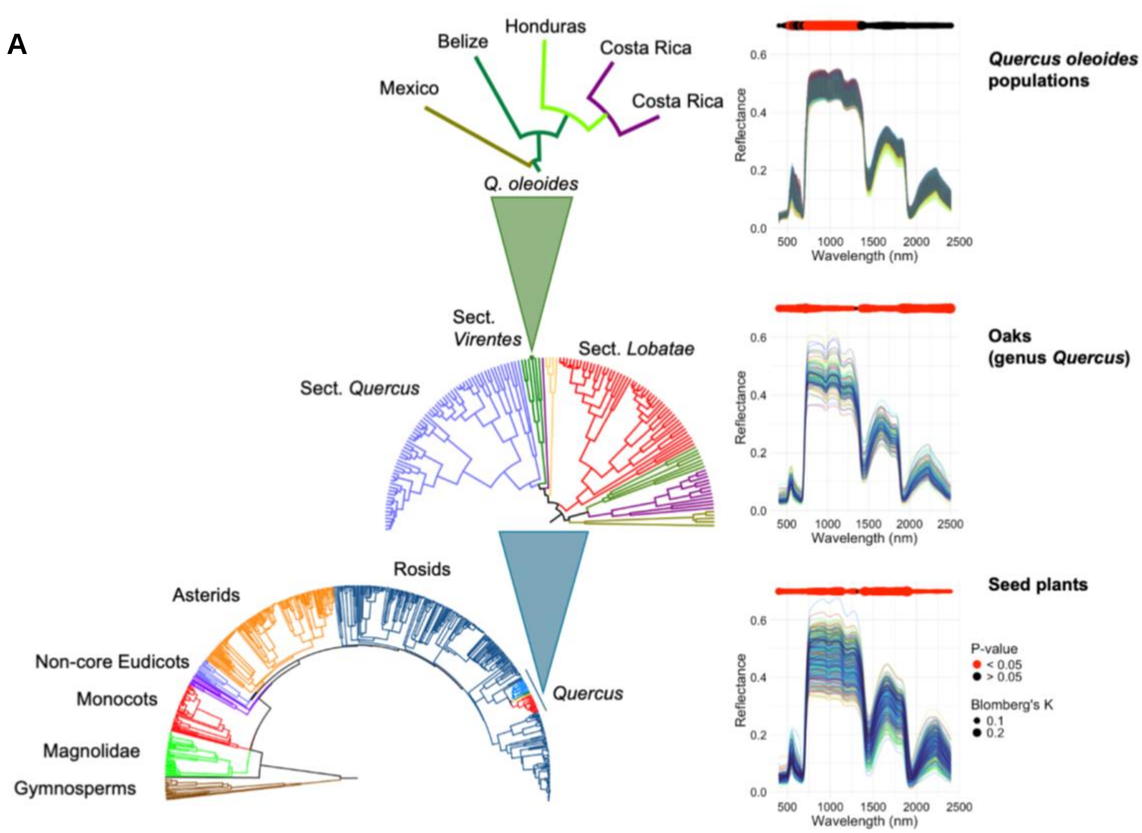


Fig. 5. Using a common data type (spectral reflectance) across evolutionary (A) and macroecological scaling hierarchies (B). A) Phylogenetic signal across wavelengths and phylogenetic scales from seed plants to an adaptive radiation within a single genus (*Quercus*, the oaks) to populations within a single species. Phylogenetic relationships and spectra from fresh leaves are shown for species across the seed plants (bottom), for species of the oak genus *Quercus* (middle), and for the variation among individuals within populations of a single species (top). A filled red circle for a given wavelength indicates that close relatives have a more similar normalized spectral reflectance value than expected at random. Data are redrawn from Meireles et al. 2020 and Cavender-Bares et al. 2016. B) A range of instruments from handheld devices, uncrewed aerial vehicles (UAV), aircraft and satellites capture reflectance spectra and image cubes of vegetation reflectance at every biological scale. Spectral reflectance from different platforms has the potential to advance ecological integration across spatial and temporal scales.



B

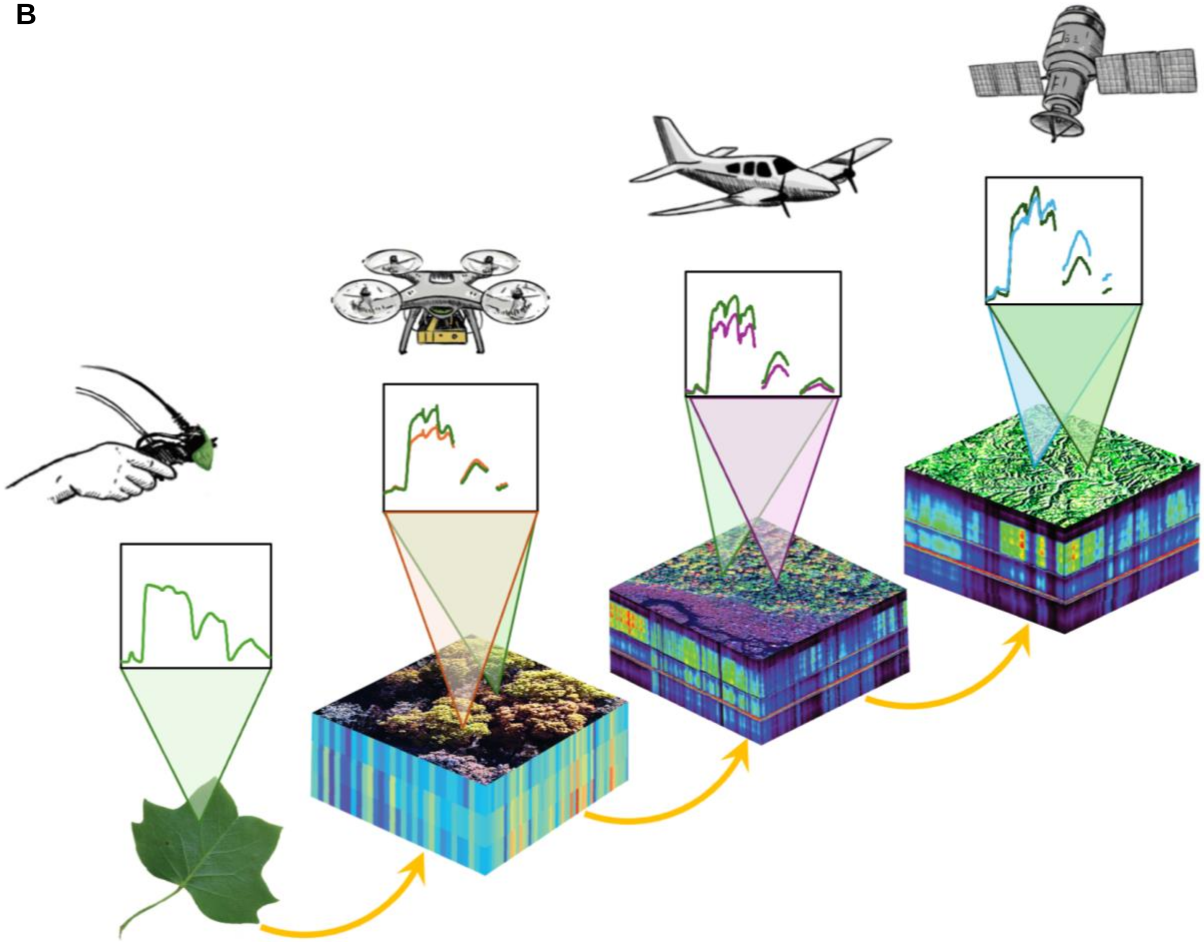


Fig. 6. Key realms for advancement in spectral biology. The realms are conceptual and nested. A) Plant identity, diversity, and composition as well as plant and ecosystem structure and function can be spectrally detected in ambient steady state conditions using vegetation spectra, SIF and/or LiDAR. B) The average responses of ecosystems to global change and environmental stress can also be detected spectrally, across space, time or experimental treatments. C) Differences over time can further be used to understand the dynamics of ecosystem responses to change, including their resistance and capacity to recover from disturbance, both of which help capture the nature and underlying mechanisms of resilience of ecosystems.