Chapter 5

Lessons Learned from Spectranomics: Wet Tropical Forests

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5.1 Introduction

One of the major challenges for biodiversity science is how to measure biodiversity at spatial scales relevant for conservation and management (Turner 2014). Supported by technological, computational, and modeling advances, along with increased data availability, remote sensing (RS) has become an essential tool for ecologists and land managers because it provides data on the optical properties of the Earth's surface at landscape to global scales (Jetz et al. 2016). At the same time, increasing awareness of how little we know about the species inhabiting our planet has led to a surge in ground-based activities to catalog what's out there and establish baselines such as Conservation International's Rapid Assessment Program and/or community aggregated information needed for biodiversity assessment (Myers et al. 2000). In addition, advances in genetic analysis, physiological experiments, and trait-based studies have advanced our understanding of functional biodiversity (Cavender-Bares et al. 2006; Kress et al. 2009; Baraloto et al. 2012). Despite these knowledge gains, linking the information from these disparate sources in a useful manner presented a new hurdle. In 2007 the Spectranomics approach was launched to address this challenge using canopy functional traits and their resultant spectral properties.

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Plants play a foundational role in establishing and maintaining ecosystem function, biogeochemical cycling, hydrological cycling, and biodiversity (Mooney et al. 1996; Schimel et al. 2013). More specifically, canopy plants (those that occupy the sun-facing portion of a landscape) serve as dominant primary producers through the capture and utilization of light. Their structures also provide habitat for vast numbers of species living in the shadows. To maintain this premier position in a forest ecosystem, plants have evolved a vast array of strategies for growth, defense, and longevity, largely manifested as chemical and/or structural adjustments in their leaves (Reich et al. 2003; Wright et al. 2004; Diaz et al. 2016). The molecular arrangement of these foliar properties generates an optical reflectance spectrum that can be measured at a variety of scales with spectroscopy (Curran 1989; Jacquemoud and Ustin 2001; Ustin et al. 2009; Ustin and Jacquemoud, Chap. 14). The ultimate result is a massive number of tree species coalescing into forest communities of varying complexity, with unique taxonomic compositions and functional roles that can potentially be mapped across a forested landscape (Reichstein et al. 2014 and others).

Despite understanding the important role different canopy species and communities of species play in creating and maintaining biodiversity, the measurement, mapping, and monitoring of forest canopy composition and functional diversity has remained a challenge. Current Earth-observing satellite technology is limited to detecting changes in vegetation cover as well as major differences in vegetation type and photosynthesis (Running et al. 1994; Tucker and Townshend 2000) and does not easily reveal compositional differences or changes over time (Turner et al. 2003). Tropical forest canopy diversity is especially underexplored because spatial and temporal variation often exceeds our ability to adequately utilize field-based approaches (Marvin et al. 2014). Airborne imaging spectroscopy can provide an intermediate solution; however, a fundamental prerequisite for determining whether species diversity or a particular species might be successfully mapped is an assessment of chemical uniqueness and diversity among plant taxa. This is important because the spectroscopy of canopies is driven primarily by the chemical composition of the foliage (Curran 1989; Asner et al. 2015).

5.2 Spectranomics Approach

The Spectranomics approach was developed to link plant canopy functional traits to their spectral properties with the objective of providing time-varying, scalable methods for remote sensing (RS) of forest biodiversity (Asner and Martin 2009). In the pool of potentially important plant functional traits, foliar chemicals stand out as core physiologically based predictors of plant adaptation to environmental conditions (Díaz et al. 1998; Wright et al. 2010). We selected a suite of 23 canopy chemical traits based on their strong ecological and evolutionary relevance, spatial variation in species and communities, and measurable spectral properties. These traits consist of those that (i) mediate or are indicative of photosynthesis and carbon uptake (chlorophyll *a* and *b*, carotenoids, nitrogen, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$; non-soluble car-

bohydrates); (ii) are related to structure (leaf mass per area and water content, lignin, cellulose, and hemicellulose) and chemical defense (phenols and tannins); and (iii) are defining general metabolic processes (macro- and micronutrients; here calcium, magnesium, phosphorus, potassium and boron, iron, manganese, zinc) (Table 5.1). The distribution and variation of these traits in plant canopy leaves evolve as a function of stoichiometric relationships among constituents in response to biotic and abiotic pressures and are often formulated differently at the species level (Díaz et al. 1998). This evolved chemical makeup of plant canopies and its similarity and uniqueness among species, which we call *chemical phylogeny*, is an essential component of Spectranomics (Fig. 5.1a).

Table 5.1 Summary statistics for 22 foliar chemical traits and leaf mass per area (LMA) from top-of-canopy leaves collected from 12,012 individual trees at sites across the wet tropics as part of the Spectranomics Program

	Mean	Standard deviation	Minimum	Maximum	Median	Skew	Kurtosis
<i>Light capture and growth</i>							
Chlorophyll <i>a</i> (mg g ⁻¹)	4.67	1.96	0.01	26.71	4.40	2.47	1.76
Chlorophyll <i>b</i> (mg g ⁻¹)	1.73	0.78	0.01	11.32	1.62	0.86	0.58
Carotenoids (mg g ⁻¹)	1.38	0.53	0.01	7.87	1.31	0.80	0.59
Nitrogen (%)	2.01	0.70	0.35	6.15	1.91	1.21	0.91
NSC (%)	46.20	11.56	12.73	86.33	45.72	31.40	25.61
δ ¹³ C (‰)	-30.59	1.89	-36.40	-19.90	-30.70	-32.90	-34.00
δ ¹⁵ N (‰)	1.38	2.70	-10.30	10.50	1.40	-2.00	-4.00
<i>Structure and defense</i>							
LMA (g m ⁻²)	113.63	44.44	15.65	622.36	105.33	66.92	51.68
Water (%)	58.40	8.28	9.17	90.79	57.57	48.92	44.87
Carbon (%)	49.30	3.31	31.60	65.00	49.70	45.00	41.80
Lignin (%)	24.15	9.94	0.25	81.08	23.47	11.67	7.65
Cellulose (%)	17.82	5.75	1.08	56.60	17.30	10.89	8.41
Hemicellulose (%)	11.63	5.03	0.00	49.31	11.25	5.72	2.84
Phenols (mg g ⁻¹)	101.11	53.63	0.00	358.19	101.71	27.02	10.54
Tannins (mg g ⁻¹)	46.45	26.82	-0.64	238.79	43.14	15.27	5.66
<i>Macronutrients</i>							
Calcium (%)	0.96	0.81	0.00	8.36	0.74	0.18	0.08
Magnesium (%)	0.26	0.15	0.02	2.71	0.23	0.11	0.08
Phosphorus (%)	0.12	0.07	0.02	0.86	0.10	0.05	0.04
Potassium (%)	0.76	0.45	0.13	5.64	0.65	0.35	0.25
<i>Micronutrients</i>							
Boron (μg g ⁻¹)	27.19	23.48	1.16	321.89	20.03	8.35	5.31
Iron (μg g ⁻¹)	80.58	206.63	7.13	9470.68	47.78	26.55	19.47
Manganese (μg g ⁻¹)	304.32	512.14	3.03	7331.67	103.80	19.75	11.55
Zinc (μg g ⁻¹)	17.08	44.47	1.65	2535.98	11.77	6.49	4.62

NSC nonstructural carbohydrates

Fig. 5.1 The essential interactive elements of the Spectranomics Database include phylogenetic, chemical, and spectral information on canopy species. **(a)** Assays of 23 foliar chemical traits combined are collected, organized, and analyzed phylogenetically, producing a new tree of life based on the relatedness of functional trait signatures. This generic phylogeny shows the chemical relatedness of thousands of species in the Spectranomics Database. **(b)** An example of a remotely sensed canopy reflectance spectrum of one species is shown along with indicators of key chemical contributions to the spectrum (Curran 1989; Ustin et al. 2009; Kokaly et al. 2009). **(c)** Chemometric

Another component of Spectranomics is the spectral properties of plant canopies (Fig. 5.1b). Canopy spectra are derived from the way plant foliage interacts with solar radiation, and this interaction is strongly determined by foliar chemicals. Across the full solar spectrum, from the ultraviolet to the visible to the near-infrared and the shortwave-infrared regions of the electromagnetic spectrum (350–3500 nm), plants have many common and yet also unique patterns of interaction with solar energy. Chemometric studies determine how these chemicals relate to reflectance spectra, and the methods today range from traditional spectroscopic assays and newer machine learning approaches (Wold et al. 2001; Serbin et al. 2014; Feilhauer et al. 2015). Spectral properties also provide a tantalizing pathway forward to scale up from leaves to landscapes (Ustin et al. 2004) to the planetary level (Jetz et al. 2016), but only if we can accurately and repeatedly measure and interpret the spectra of plants over increasingly larger portions of Earth (Fig. 5.1c–e).

The realization of Spectranomics rests in a number of choices made early on to attempt to reduce unwanted sources of variation combined with extensive sampling. We focused on humid tropical forests for their high diversity and relative freedom from extreme phenological changes brought about by seasonal cycles such as those experienced in temperate regions but may not completely eliminate smaller phenological variation that might arise in reaction to drought or solar variations. We targeted only mature, fully sunlit, top-of-canopy leaves (trees and lianas) to limit variation attributable to intra-canopy shade and ontogeny and to best relate leaf properties to airborne and satellite-based spectral measurements. Prior to Spectranomics, our work and that of many others did not follow a strategically consistent, integrated method for global spectral-functional trait database building needed to reveal canopy plant functional spectral-chemical patterns at the biospheric scale.

We have collected, cataloged, and stored more than 13,000 canopy tree and liana specimens, in over 3 million tissue samples, representing about 10,000 species biased to humid tropical ecosystems (Fig. 5.2a). For perspective, this number approaches the total number of tree species in the Amazon basin (roughly 11,000; Hubbell et al. 2008), a value that would put the global tropical tree inventory at 30,000 species if we liberally extrapolate to the entire Neotropics plus the African and Asian-Oceanic tropics. The Spectranomics database focuses only on species found in the canopy, meaning they are in full sunlight and are observable from above. Since roughly 30–60% of tree species in a tropical forest plot makes it to the canopy (e.g., Bohlman 2015), the current Spectranomics database contains at least

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Fig. 5.1 (continued) equations are derived to quantitatively relate canopy functional traits (chemicals) to spectral data. Example relationships are shown for foliar lignin, nitrogen (N), and polyphenols. The x-axis indicates spectral wavelengths of 400–2500 nm; the y-axes indicate relative importance of the spectrum to each example chemical constituent shown. **(d)** An example of spectra from individual crowns clustered based on their spectral variation. **(e)** A 3-D view of a portion of lowland Amazonian forest canopy. Different colors indicate different species detected based on 15 chemical traits using airborne imaging spectroscopy

Fig. 5.2 An illustration of functional biodiversity mapping from foliar traits. (a) The 2018 global distribution of 128 forest landscapes contributing to the Spectranomics database. (b) Example maps of four foliar traits generated for the Andes-to-Amazon region of Peru using airborne imaging spectroscopy and modeling (Asner et al. 2017). (c) Map of 36 forest functional communities derived from a classification based on seven forest canopy traits derived from airborne imaging spectroscopy

half of the known tropical forest canopy species worldwide with measured foliar traits (Table 5.1). From investigations of these data and the fundamental patterns they uncover, Spectranomics has evolved into a new pathway to biological and ecological discovery, as well as a new tool for conservation-relevant mapping, particularly in high-diversity tropical forests.

5.3 Lessons Learned from Spectranomics

As the Spectranomics database has grown through the years, new relationships among plant phylogeny, canopy chemical traits, and spectral properties have emerged that reveal patterns at nested biogeographic scales. The extent of sampling across continents, along regional environmental gradients, and within local tree communities, coupled with consistent methods and analysis, has provided for quantitative testing of these relationships at multiple scales such that they can now be used to forecast the functional traits and biodiversity components that can be remotely mapped and monitored with spectral RS instrumentation.

5.3.1 *Nested Geography of Canopy Chemical Traits in Humid Tropical Forest*

Humid tropical forests cover over 20 million km of land area, span an enormous range of environmental conditions from hot lowland forests to cool montane rainforests along equatorial tree line at almost 3500 m on a variety of geological substrates, and support thousands of tree species. The high degree of complexity of this region provided an ideal setting to develop and use Spectranomics to test how environment and phylogeny interact to sort the spectral-chemical diversity of forest canopies. Based on results from multiple field studies throughout this region (Martin et al. 2007; Asner and Martin 2011; Asner et al. 2014b; McManus Chauvin et al. 2018) as well as their collective analysis (Asner and Martin 2016), we discovered that canopy chemical trait diversity of humid tropical forests occurs in a nested pattern driven by long-term adjustment of tree communities to large-scale environmental factors, particularly geologic substrate and climate. More specifically, geographic variation at the soil order level, expressing broad changes in fertility, underpins major shifts in foliar phosphorus (P) and calcium (Ca) (Fig. 5.2). Additionally, elevation-dependent shifts in average community leaf dry mass per area (LMA), chlorophyll, and carbon allocation (including nonstructural carbohydrates) are most strongly correlated with changes in foliar Ca. We also found that chemical diversity within communities is driven by differences between species rather than by plasticity within species. Finally, elevation- and soil-dependent changes in nitrogen (N), LMA, and leaf carbon allocation are mediated by canopy compositional turnover,

whereas foliar P and Ca are driven more by changes in site conditions than by phylogeny. In short, Spectranomics led us to understand that canopy functional traits can be nested regionally by environmental setting but expressed locally within any given environment by their evolutionary origin.

5.3.2 *Spectral Properties of Humid Tropical Forest Canopies*

In concert with chemical trait collections, we measured the spectral properties of canopy foliage from thousands of humid tropical tree canopies and determined that all 23 chemical traits can be remotely sensed to varying degrees (Asner et al. 2011; Chadwick and Asner 2016; Martin et al. 2018). Utilizing leaf-level spectral-chemical relationships, we discovered that the spectral properties of canopy foliage closely tracked canopy functional trait responses to macro-environmental changes such as broad differences in soil fertility (Asner and Martin 2011; Asner et al. 2012b). Similar to the functional trait findings, we discovered that the spectral properties of foliage within communities along elevation gradients were largely determined by phylogenetic identity (Asner et al. 2014a). Consequently, canopy functional traits and spectral properties tracked one another at nested ecological scales, a result that suggests what we might find if we collected map-based spectral data over a much larger geographic area using RS instrumentation.

When coupled with DNA analyses, Spectranomics data indicate that forest canopies show strong phylogenetic organization of their foliar spectral properties, particularly in the shortwave-infrared (1500–2500 nm) wavelength region (McManus et al. 2016). This finding suggests that mapping of forest canopies with airborne imaging spectroscopy may provide spatial insight to the genetic distribution and genealogy of forest canopy taxa. Growth-form-specific studies using the Spectranomics approach revealed that lianas (woody vines) maintain functional traits and spectral properties unique from their host tree canopies (Asner and Martin 2012). Lianas are important drivers and limiters of biodiversity and carbon cycling in tropical forests (Schnitzer and Bongers 2011), and these measured differences predicted and underpinned the subsequent mapping of lianas in tropical forests using airborne imaging spectroscopy (Marvin et al. 2016).

Spectranomics data have been collected and archived under stringent field and analytical standards, which has facilitated the development new quantitative linkages between canopy foliar spectroscopy and canopy functional traits (Feilhauer et al. 2010, 2015; Féret et al. 2011, 2017). Spectral modeling studies showed that full-spectrum (350–3500 nm) data provided retrieval capability for three times the number of chemicals as 350–1300 nm data from less expensive, more common visible to near-infrared spectrometers. These studies also pointed to the need for sampling fully sunlit foliage in higher-density portions of tree crowns to minimize the effect of canopy structure on chemical trait retrievals. These findings were key guiding components in the development of laser-guided imaging spectroscopy that links Spectranomics field surveys to remotely sensed spectra to generate consistent canopy chemical trait retrieval at multiple geographic scales.

5.3.3 *Spectranomics for Biodiversity Mapping*

The Spectranomics fieldwork pointed toward two particular forecasts. First, Spectranomics suggested that spectral mapping from current aircraft and future satellites will reveal where whole forest communities are functionally similar and where they are unique. Second, Spectranomics suggested that spectral RS will reveal the presence and patterning of specific canopy species, within communities and across environmental gradients, based on their functional trait “signatures.”

Both forecasts were subsequently proven correct during mapping studies. Numerous landscape-scale studies now show that location of particular forest canopy species and their evolved canopy functional traits mirror soil nutrient resources mediated by topography, parent material, and climate (Higgins et al. 2014; Chadwick and Asner 2016; Balzotti et al. 2016). These findings demonstrate that Spectranomics directly connects plants to ecosystem processes such as biogeochemical cycles, which form an essential link to the rest of the Earth system. At a larger scale, a 2016 report on Andean and Amazonian forests mapped with airborne imaging spectroscopy confirmed the forecasted ecological shifts in forest canopy functional composition, sorted geographically by large-scale environmental factors including elevation, geology, soils, and climate (Fig. 5.2b, c; Asner et al. 2017). While the Spectranomics database provided a field-based preview of how communities of species would differ from one another, the mapping step provided a first synoptic view of the geographic distribution. Importantly, the mapping phase also revealed numerous new combinations of functional traits that had not been detected in the field program. The new canopy functional trait maps are a key stepping-stone to biogeographic assembly, not only of the functional diversity of the Andes-to-Amazon but also of the biological diversity of the region. The approach from Peru is currently being applied in Ecuador as well as Malaysian Borneo.

The second forecast from Spectranomics—which coexisting species within communities can maintain relatively unique canopy functional traits and spectral properties—has been explored and confirmed in a series of studies using airborne and space-based imaging spectroscopy. From Hawaii to Panama, and from Africa to the Amazon, hundreds of target species have been mapped based on their spectral signatures, underpinned by a knowledge of their functional traits (Fig. 5.3; Carlson et al. 2007; Papeş et al. 2010; Colgan et al. 2012; Baldeck and Asner 2014; Baldeck et al. 2015; Graves et al. 2016). Further, the new concept of “spectral species” was developed to map species richness (alpha diversity) and compositional turnover (beta diversity) in forest landscapes without the need to detect individual species (Féret and Asner 2014). The separability of the spectral species is determined by their canopy functional traits.

More broadly, Spectranomics has enabled a different kind of interaction between field or laboratory studies of plants and RS of functional and biological diversity of ecosystems. The forecasting capability made possible with the Spectranomics database has been central to planning whether and how to undertake spectral mapping activities in different regions and under what environmental conditions the RS technology will yield new insight. In turn, this has transformed the interaction

Fig. 5.3 Three scale-dependent views of the Peruvian Andes-Amazon region derived from airborne imaging spectroscopy using data and information from Spectranomics. (a) Peru-wide map shows the distribution of functionally distinct forests. Different colors indicate varying combinations of remotely sensed canopy foliar nitrogen (N), phosphorus (P), and leaf mass per area (LMA) (Asner et al. 2016). (b) Zoom image from the Peru-wide map indicates major changes in canopy N, P, and LMA with a lowland Amazonian forest (Asner et al. 2015a). Red indicates higher N + P and lower LMA relative to yellow and blue. (c) Individual species detections within the zoom box of panel b, derived using species-specific canopy spectra (Féret and Asner 2013; Baldeck et al. 2015)

between field and RS work from the traditional approach of mapping and ground truthing to one based on botanical, ecological, and biophysical knowledge in the interpretation of remotely sensed data.

This interaction between Spectranomics and RS also provided the scientific guidance, and initial funding, for a new class of mapping instruments, starting with a next-generation, high-fidelity visible-to-shortwave infrared (VSWIR) imaging spectrometer, built by the California Institute of Technology's Jet Propulsion Laboratory (JPL) for the Global Airborne Observatory, formerly the Carnegie Airborne Observatory (Asner et al. 2012a). JPL then built an identical instrument for NASA's Airborne Visible/Infrared Imaging Spectrometer (AVIRIS; <http://aviris.jpl.nasa.gov>) program, as well as several copies for the US National Ecological Observatory Network (NEON, <https://www.neonscience.org>; Kampe et al. 2011).

5.3.4 *Scientific and Conservation Opportunities*

An important outgrowth of Spectranomics is an emerging opportunity to partner discovery-based science with applied environmental conservation at large geographic scales. Conservation and management actions are usually limited in scope and effectiveness by numerous interacting financial, logistical, cultural, and political factors. An increasing ability to map canopy diversity may provide an avenue to identify the location and essential components of high-value conservation targets. Moreover, near-real-time scientific discovery from spectral RS can lead to more tactical conservation decision-making. Our specific experience is that, as land use pressures expand, intensify, and change over time, a mapping capability built upon the details of forest canopy function and composition, rather than just forest cover, supports improved conservation discussions and planning. This type of approach is needed to identify current and potential threats to, as well as current protections and opportunities for new protection of, species, communities, and ecosystems. The evolving biodiversity mapping capabilities made possible through Spectranomics are providing a tool set to support the current portfolio of Global Airborne Observatory activities (e.g., <http://www.theborneopost.com/2016/04/06/3d-mapping-to-decide-on-land-use/>).

The Spectranomics approach is starting to catch on in the scientific community, as highlighted in chapters throughout this book as well as new programs such as NEON and Canada's recently announced Spectranomics program for boreal forests (the Canadian Airborne Biodiversity Observatory; <http://www.caboscience.org/>), but there is much more to do to bring our approach to the global level. First, more scientists could get involved through building plant canopy trait laboratories and databases, paired with a specific style of leaf-level spectral measurements in the field. Currently, many functional trait and spectral measurement protocols are incompatible with the Spectranomics approach. For example, many foliar trait studies have involved the collection of samples in understory or shaded settings,

in part because this foliage is easier to reach, yet spectral RS is most sensitive to canopy-level foliar chemical and structural traits (Jacquemoud et al. 2009). Additionally, most field-based trait studies do not include the use of a high-fidelity field spectrometer, which must be applied on fresh foliage to ensure connectivity to biotic and environmental conditions. Moreover, high-fidelity imaging spectrometers needed for mapping, such as the Global Airborne Observatory or AVIRIS, demand stringent and consistent field and laboratory trait measurement practices. Most of these issues can be remedied by incorporating one or more of the protocols provided on the Spectranomics website (<https://gdc.asu.edu/labs/martinlab/spectranomics>). More could be done to boost capacity throughout the science community to generate data suitable for Spectranomics-type applications. Community-wide efforts to develop a global biodiversity monitoring system (Geller, Chap. 20) will greatly enhance humanity's ability to monitor and manage biodiversity for sustainability in the Anthropocene.

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