

Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests

Gregory P Asner* and Roberta E Martin

Tree canopies play an enormous role in the maintenance of tropical forest diversity and ecosystem function, and are therefore central to conservation, management, and resource policy development in tropical regions. However, high-resolution mapping of tropical forest canopies is very difficult, because traditional field, airborne, and satellite measurements cannot resolve the number of canopy species, or particular species of interest, over the large regional scales commensurate with conservation goals and strategies. Newer technologies, such as imaging spectroscopy and light detection and ranging (lidar), are just now reaching performance levels that will allow monitoring of tropical forest diversity from the air, but the methods for applying these technologies are not yet ready. Here, we present concepts that combine chemical and spectral remote sensing perspectives to facilitate canopy diversity mapping. Using examples from our ongoing work in the Hawaiian Islands, we demonstrate how a new “airborne spectranomics” approach could revolutionize tropical forest monitoring in the future.

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The high biological diversity in tropical forests challenges our ability to make ecological observations, understand ecosystem function, develop conservation strategies, and manage these systems (Myers *et al.* 2000). We know relatively little about the local and regional diversity of many forests in the tropics, or about how tree diversity is responding to climate change and human activities (Curran *et al.* 1999; Clark 2004). Recently, we have also come to realize that nutrient variation in tropical forest canopies is tightly linked to species diversity, and that understanding this chemical diversity is crucial to understanding ecosystem function (John *et al.* 2007; Townsend *et al.* 2007). However, our ability to accommodate both chemical and taxonomic diversity in our general understanding of tropical forest function is hindered by too few measurements at regional scales.

The potential ties between the taxonomic and chemical diversity of tropical forest canopies also bear on conservation, management, and resource policy development. The

success and sustainability of conservation lands depend on our ability to maintain a portfolio of taxonomically diverse and/or unique assets, which may translate to chemically diverse assets, thereby benefiting ecosystem function. However, these taxonomic portfolios are difficult to inventory and assess in tropical forest regions. Ground-based studies of canopy diversity are limited in geographic coverage, and current satellite measurements do not contain the information needed to dissect a landscape of forest canopies into taxonomic maps.

Airborne remote sensing has been used for many years to assess the extent and even the composition of forest ecosystems (Wulder and Franklin 2003). Certain types of species are likely to stand out in basic color-infrared images, such as when broadleaf trees are observed among needleleaf species on a landscape, or when a particular species is in flower. However, spectral differences among tropical forest canopy species, which are usually broadleaf evergreen trees, are far more subtle, and thus often invisible in traditional aerial photographs.

Imaging spectroscopy, also known as hyperspectral imaging, measures the reflectance of the Earth in hundreds of narrow spectral bands, thereby resolving the subtle spectral features associated with the chemical composition of materials (Goetz *et al.* 1985). Only recently have high-fidelity imaging spectrometers, or HiFIS, been developed to performance specifications that allow for reliable remote chemical determinations of plants and ecosystems from aircraft (Ustin *et al.* 2004). Airborne HiFIS observations provide the familiar two-dimensional image, but with a third dimension containing a detailed spectroscopic signature of plant canopies.

In a nutshell:

- Canopy diversity in tropical forests is important from ecological, conservation, and management perspectives
- Tropical forest diversity is poorly understood at regional scales, and remote sensing has not yet provided the needed information
- A new spectranomics approach, based on the chemistry, physics, and taxonomy of canopies, could change how tropical forests are measured, monitored, and managed

Department of Global Ecology, Carnegie Institution, Stanford, CA

* (gpa@stanford.edu)

Although HiFIS has come of age technologically, the theories and algorithms required to extract taxonomic information from the spectra remain in the early stages of development. Whereas many studies with imaging spectrometers demonstrate that a range of plant chemicals, including multiple photosynthetic and photoprotective pigments, water, nitrogen, and carbon constituents, can be remotely measured from the airborne vantage point (reviewed in Ustin *et al.* 2004), rarely has the chemical information derived from HiFIS measurements been used to estimate the taxonomic composition of plant canopies. Instead, most studies have sought the direct spectral–taxonomic relationships that might allow for mapping plant species or functional types (Roberts *et al.* 1998; Townsend and Foster 2002; Clark *et al.* 2005). These approaches have proven successful locally, yet their scalability and portability remain unclear, since few conceptual models have been put forward to systematically link what HiFIS is supposedly most sensitive to – canopy chemistry – with species diversity.

We write “supposedly most sensitive” in recognition of a long-standing problem in efforts to account for spectroscopic variation, caused by issues having little to do with, or that are only indirectly related to, canopy chemistry. Changes in sun and viewing angle, topography, and canopy three-dimensional structure are also major determinants of the spectral variation measured by HiFIS or any other optical sensor (Kennedy *et al.* 1997; Sandmeier *et al.* 1998; Diner *et al.* 1999). In response to these limitations, new systems and methods that integrate HiFIS with light detection and ranging (lidar) technology are now changing the way that canopy spectroscopic measurements are made from the air (Asner *et al.* 2007). This evolution will be central to the taxonomic mapping concepts we develop here.

The challenge of mapping species richness, or a particular species, in tropical forests is particularly daunting, given the high taxonomic diversity within plant functional groups, such as among broadleaf evergreen trees. We suggest that there is a sufficient theoretical basis to link the spectral, chemical, and taxonomic diversity of tropical tree species in a way that is generic and scalable, but only when the measurements are of high quality, and are collected under a set of well-controlled observing conditions. Making these measurements, and developing the know-how to convert them to species diversity, could revolutionize how aircraft are used to measure and map natural and human-caused changes in tropical forest composition and function.

The approach requires new instrumentation, taxonomic databases, and methods for airborne spectro-chemical analysis. We call this combination of science and technology “spectranomics”, which is emerging from aspects of established remote sensing research, but with new ideas to causally link the chemistry, spectroscopy, taxonomy, and community ecology of tropical canopies. Here, we present the basic concepts behind the approach,

while highlighting current shortcomings in our knowledge, needed to make a method operational. After presenting the core scientific concepts, we then reveal prototype airborne instrumentation to highlight how new airborne measurements are ready to support and test the spectranomic concepts discussed here.

■ Do plant species have unique chemical fingerprints?

A fundamental prerequisite for determining whether species richness or a particular species might be mapped with airborne imaging spectrometers 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; Jacquemoud *et al.* 1995). To develop this concept, we consider trees found in lowland Hawaiian rainforests, where taxonomic variation is enormous, given the introduction of thousands of species from all over the world (Wagner *et al.* 1999). Using one community found in a single lowland rainforest on the island of Kaua'i, we assess the chemical diversity of species based on two of the most common metrics of canopy chemistry – leaf nitrogen (N) and phosphorus (P) concentrations (Figure 1a). We then repeat the analysis with seven leaf properties that have proven measurable remotely, in field and airborne studies (Figure 1b). Here, we use standardized chemical properties to develop chemical “fingerprints” of species. The length of each segment in the fingerprint quantitatively represents differences in each leaf property among species, as well as the relative contribution of that leaf property to the total fingerprint.

The fingerprints demonstrate a moderate degree of differentiation among species, based solely on N and P chemistry (Figure 1a). No two species are exactly alike, but many are close in N and P composition, and they therefore share similar color bars. However, the chemical fingerprints of the species rapidly diversify when we include additional constituents, such as photosynthetic and photoprotective pigments and water, as well as measures of leaf structure (eg specific leaf area, or SLA; Figure 1b). Many of these leaf properties are poorly inter-correlated, and are therefore not redundant measures (WebFigure 1). Using this combination, Figure 1b shows that there are no common chemical fingerprints among the trees found in our Kaua'i site. Adding other chemicals would further diversify these fingerprints among species, but doing so might create a chemical combination that does not determine the spectroscopic signatures of the plants, and would therefore not be distinguishable remotely.

We note here the importance of within-species variation in leaf chemistry (Kobe *et al.* 2005), which is not included in the example of chemical fingerprints shown in Figure 1. However, we have found that the *relative*

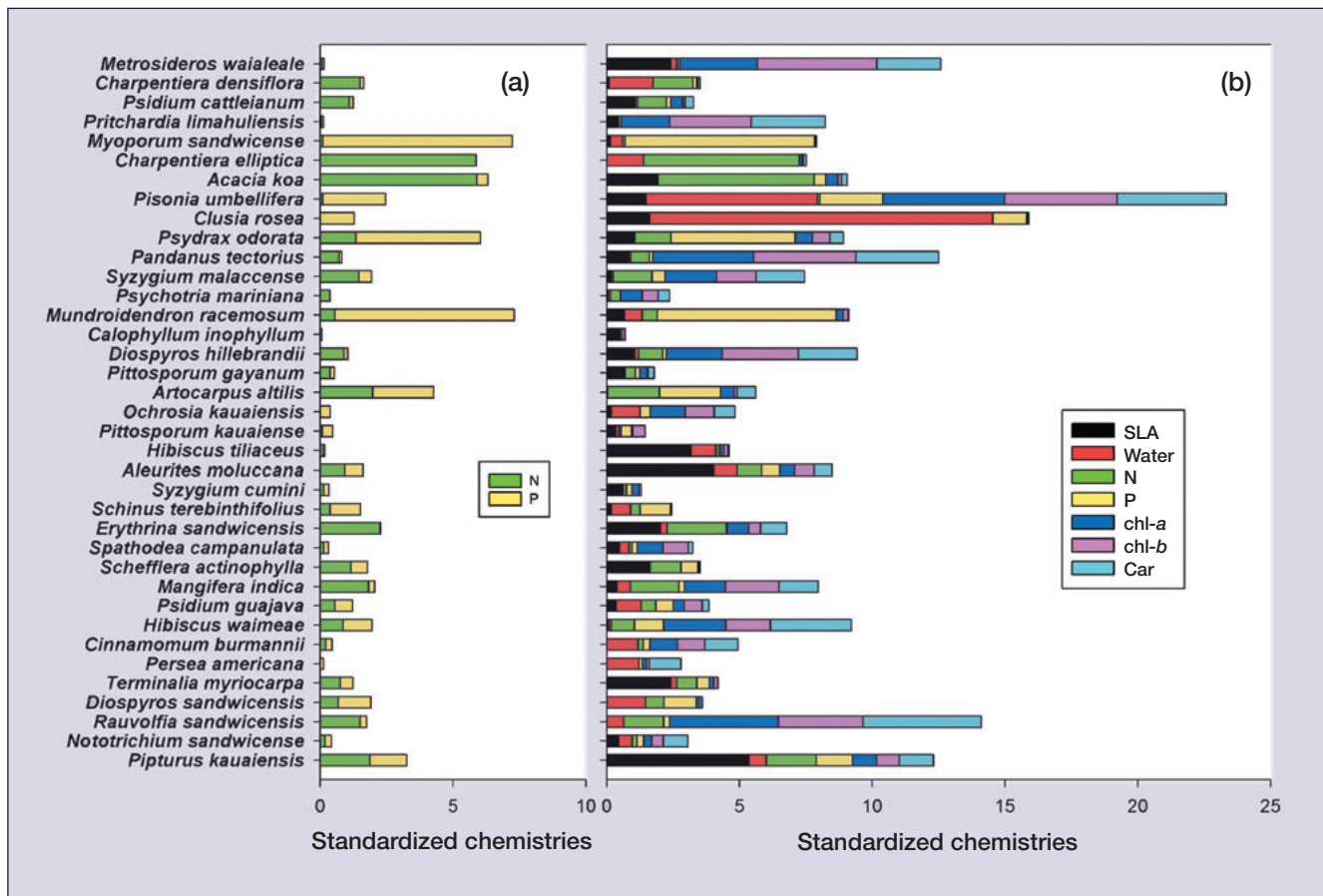


Figure 1. Chemical fingerprints of canopy species found in a rainforest site on Kaua'i, based on (a) only leaf nitrogen and phosphorus concentrations and (b) seven leaf properties. SLA denotes specific leaf area, chl-a denotes chlorophyll a, chl-b denotes chlorophyll b, and Car denotes total carotenoid pigments. Note that the absolute differences in each leaf constituent contribute to the uniqueness of each species' chemical portfolio. Shown are standardized data values that allow for visualization and analysis of both the absolute differences in chemistries among species and the relative importance of each constituent as it defines the chemical fingerprint of each species. The standardization is calculated using the common method: $(x - \bar{X})/SD$, where x is the chemical value, \bar{X} is the mean value for all species, and SD is the standard deviation of the chemical data among all species.

contribution of each chemical comprising the fingerprint of a species is far more constant than the absolute value of any single chemical (eg nitrogen), at least in live, green foliage. Nonetheless, we allow variation in leaf chemicals among species in Figure 1 to play a role in the canopy diversity modeling in a subsequent section of this paper. In addition, there are known substrate effects on leaf chemical properties, such as those from a roughly 4 million-year-old chronosequence in Hawai'i, where one particularly plastic tree species, *Metrosideros polymorpha*, displays variation in leaf N and P concentration with substrate age (Vitousek 2004). However, our studies with that species and others along substrate gradients strongly suggest that environmental effects are small when considering the relative contribution of each leaf constituent to the integrated chemical fingerprint of species (Martin *et al.* 2007; Martin and Asner 2009) and to differences in these fingerprints among species (Figure 1b). Moreover, using a global tropical leaf dataset, Townsend *et al.* (2007) show that substrate effects were small in comparison to taxonomic variation in leaf chemistry.

■ Do spectral signatures correspond to chemical fingerprints in plants?

Another step in determining whether airborne biodiversity mapping could work involves connecting the chemical fingerprints and spectral signatures of rainforest species. There are at least two ingredients required to make this connection: (1) determine if spectral signatures of species are unique, and (2) determine if the spectra quantitatively represent the chemical fingerprints of species. For the Kaua'i site, leaf spectroscopic properties are highly variable (WebFigure 2), as depicted in a hierarchical cluster analysis of the species based on their spectra (Figure 2). This clustering approach statistically organizes the species into a dendrogram, similar to that used in phylogenetic research (WebPanel 1). The colors in the graph show absolute differences in reflectance by wavelength, and the dendrogram to the far right maps the similarity of the spectral signatures. The most prominent feature of this cluster diagram is the unique spectroscopic nature of most species – a result we find in much larger datasets collected from tropical forests in Australia and

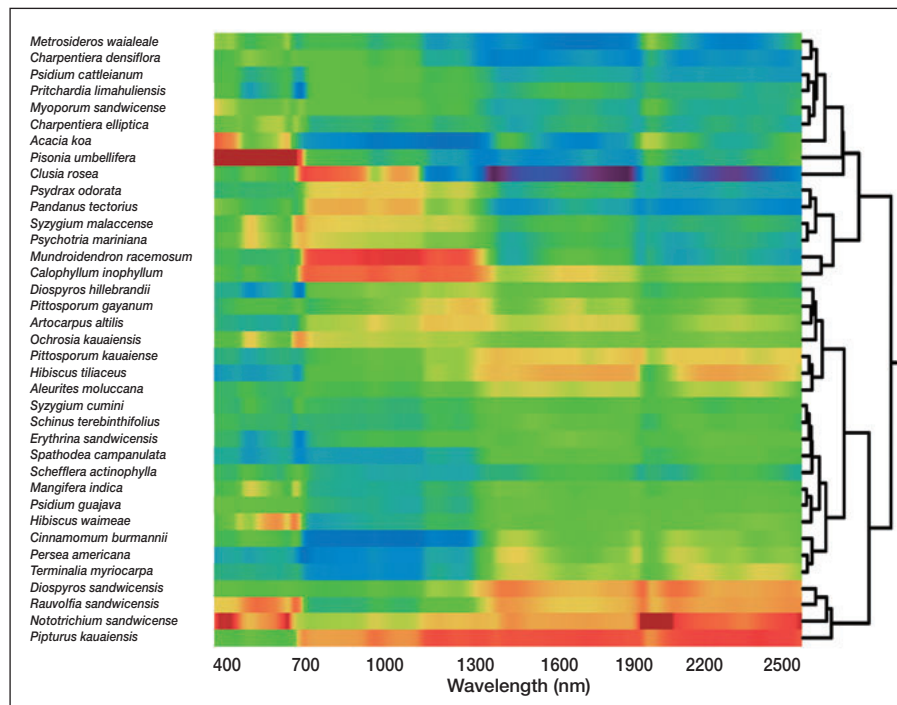


Figure 2. A spectroscopic cluster analysis of Kaua'i rainforest species based on their reflected light from 400 to 2500 nm. The color codes show the spectral signatures of each species, with yellows–reds and greens–blues showing high and low reflectance, respectively. The dendrogram to the right shows the spectranomic clustering of the species. The method for calculating the cluster dendrogram is provided in WebPanel 1.

Amazonia, as well (<http://spectranomics.stanford.edu>). Here, even small variations in color indicate quantitative differences among spectral features, so there are subgroups of only 2–3 species with similar signatures. The uniqueness of each signature, in turn, results in a generally weak overall clustering solution in the dendrogram. In short, the spectral signatures of species are often unique.

It is critical, then, to demonstrate that the spectra of Figure 2 do, in fact, represent the chemical fingerprints of the species as shown in Figure 1. Using constrained partial least squares (PLS–PRESS) regression analysis (WebPanel 1), Figure 3 establishes the link between the spectral signatures and each chemical (and SLA) of the species from our spectranomics database. The strength of the prediction of each leaf constituent varies (r^2 ranging from 0.47 to 0.81; $P < 0.01$), but, overall, the ensemble of leaf properties can be estimated with very high-fidelity spectroscopy. It is important to note that these are leaf-level relationships, but research has consistently shown that many leaf properties are amplified at canopy scales (Baret *et al.* 1994; Fourty *et al.* 1996; Sims and Gamon 2002; Smith *et al.* 2003; Gamon *et al.* 2005; Ollinger and Smith 2005). Moreover, new remote sensing methods that retrieve leaf-level spectroscopic data from canopy spectral observations are providing a means to directly estimate multiple leaf chemical properties and even SLA from airborne HiFIS systems (Asner and Vitousek 2005; Asner 2008), but these methods are still in their infancy.

We also note that, although the spectra predict the portfolio of leaf properties contributing to their chemical signatures (Figure 3), a cluster analysis of species based on the chemicals we measured is not identical to a cluster analysis using spectroscopic measurements. This is due to plant spectroscopic signatures containing more information than is currently accounted for by our chemical fingerprints or by the state-of-the-art models used to simulate spectral properties of plant leaves and canopies (Curran 1989; Jacquemoud *et al.* 1996). New approaches for integrating spectral and chemical measurements in cluster analyses are needed.

Despite current methodological limitations, our work reveals two important concepts supporting the spectranomics approach: (1) species possess chemical fingerprints that become increasingly unique when additional constituents are incorporated, and (2) spectroscopic signatures determine a portfolio of chemicals found in plants. We believe that additional steps to create inter-relationships among species, chemicals, and spectral signatures will open new doors for canopy diversity mapping in tropical forests and elsewhere. However, advancing this concept also requires an understanding of chemical, spectral, and taxonomic variation across forest landscapes.

■ Does chemical and spectral variation correspond to species diversity?

Given the often unique chemical fingerprints and spectral signatures of tropical forest tree species, we can predict that chemical and spectral diversity should increase with taxonomic diversity. However, it is unclear when the variation among canopy species saturates on a given landscape. Does it stop increasing at 5, 10, 50, or more species locally? This question is important, because it affects how we would map species richness using an airborne spectranomics approach.

To address this question, we developed a model to simulate the chemical diversity of tropical forests (Asner 2008). The model randomly populates a virtual forest with tree species and their measured chemical fingerprints. First, a single species is randomly selected from the total community of species observed in the forest. The average chemical fingerprint of this species is taken from the database, along with the variance of the fingerprint, to accommodate natural within-species variability. Other

species are then randomly selected and added to the landscape in the same way, until the local-scale (alpha) diversity of the forest canopy is achieved. As the species richness of the virtual forest increases, the model tracks the change in the variance among the chemical fingerprints until the entire community is populated. The model uses a statistical Monte Carlo approach to calculate an average change in the chemical diversity of thousands of virtual forests as species diversity is increased. The model can be run for a single standardized chemical constituent (eg N), multiple chemicals (eg N and P), or for a chemical fingerprint index (α) that incorporates any number (n) of leaf properties (C) per species (i) as:

$$\alpha_i = [\sum [(C(n)_i / C(n)_{\min})^2]]^{1/2}.$$

Here, we use our example Kaua'i trees first to calculate local-scale diversity of plant N as well as N combined with P. As species richness increases, the variability of N and N + P increases non-linearly, quickly reaching an asymptote, after which adding new species has a small effect on chemical diversity (Figure 4). However, combining all of the chemicals in the single metric α serves to greatly diversify the chemical portfolio of each species. As a result, the α metric has a far wider dynamic range and very weak asymptote in comparison to the simulations based on one or a few chemical properties. The increased information content of α is therefore key to developing the most flexible and applicable chemical fingerprint for tracking species diversity. We then repeated the analysis using the spectral data to provide an optical equivalent (λ) for analyzing taxonomic variation; the same equation was applied, but with 10-nm-wide wavelength bands spanning the 400–2500 nm range. It is clear that the spectral diversity of the virtual forests closely tracks their chemical diversity (Figure 4).

■ Can airborne diversity mapping work?

We contend that the spectral diversity of tropical species can track local taxonomic diversity, and that this occurs in step with changing chemical diversity. This finding recently prompted a study to map canopy richness in lowland Hawaiian rainforests using actual airborne imaging spectroscopy (Carlson *et al.* 2007). Canopy richness mapping works in lowland Hawai'i because the spectral signatures of the plants differ more among species than within species (Asner *et al.* 2008), as has been determined in other tropical forest settings (Cochrane 2000; Clark *et al.* 2005). Despite this

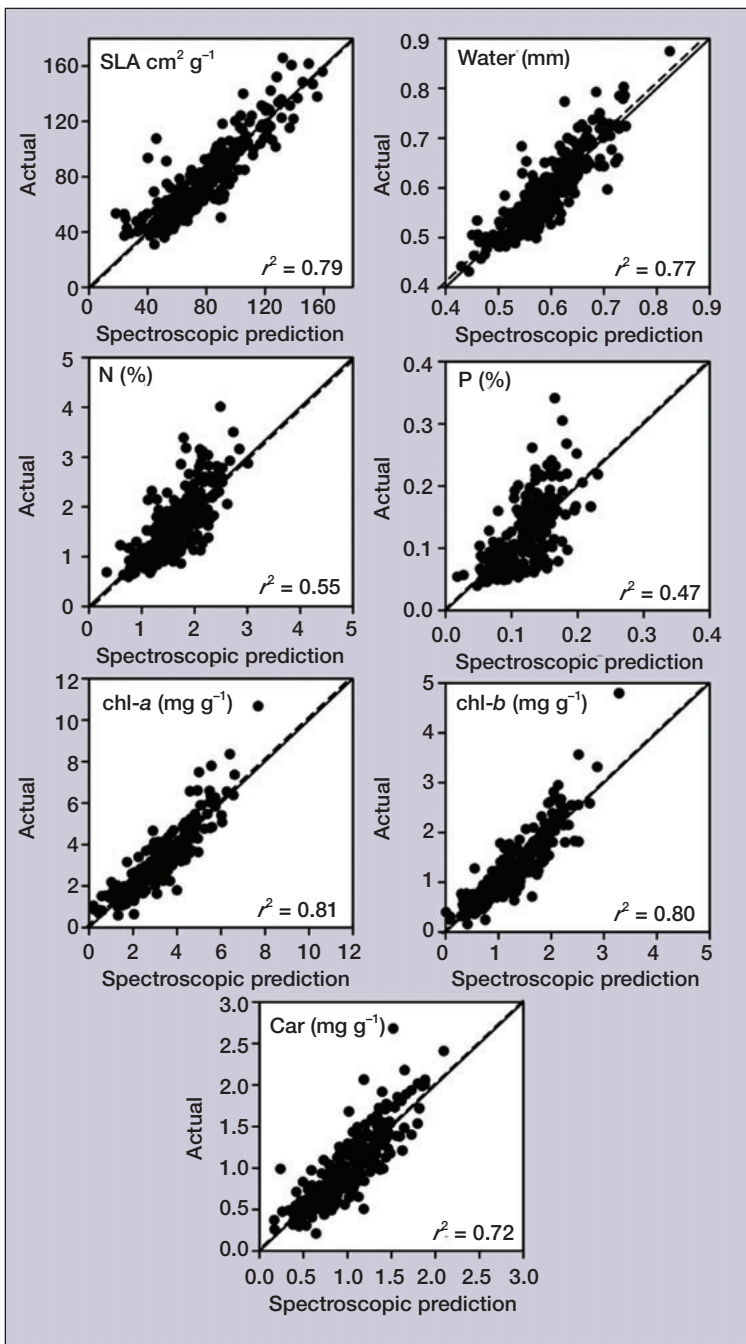


Figure 3. Relationship between chemical fingerprints of species measured in the field (Figure 1) and those retrieved by spectral analysis (Figure 2). The strength of the relationships (r^2) indicates the absolute importance of each chemical in determining the spectral properties of the species. Leaf pigments, water, and SLA are most critical ($r^2 = 0.72$ – 0.81), with secondary contributions from N and P ($r^2 = 0.47$ – 0.55). The method for calculating these relationships is provided in WebPanel 1.

step forward, we recognize that richness only corresponds to the number of species per area, and not necessarily the presence or abundance of particular species. Although an operational approach to species richness mapping from aircraft would be an enormous step forward, including additional information on species composition would further support ecological studies and conservation efforts.

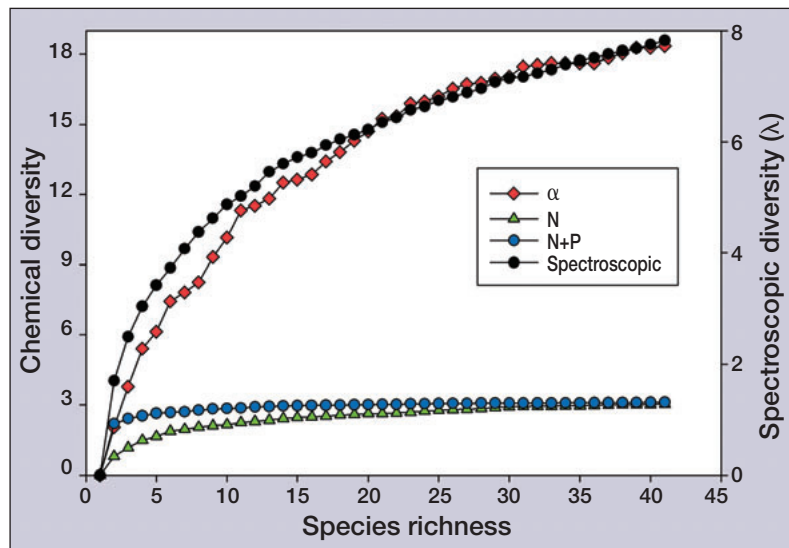


Figure 4. Changes in three chemical and spectral diversity indices with increasing richness of rainforest trees on Kaua'i: the usual N and N + P measurements of canopy chemistry, as well as a plant fingerprint α comprised of six constituents, including N, P, chlorophylls, carotenoids, water, and SLA. The equivalent spectral diversity index (λ), derived from the spectroscopic signatures of species in Figure 2, shows a similar pattern of unsaturated growth with species richness. Notice how α increases without a clear asymptote, whereas N and N + P diversity level off at local richness values of just 5–15 species.

To make the leap to a comprehensive canopy diversity sensing approach, it is important to establish particular spectranomic signatures for specific taxa. At what taxonomic level would this work: species, genus, or family? Our experience is that most plant families do not display unique spectranomic signatures, due to extremely variable chemical and spectral properties at this broad level of taxonomic aggregation. In the tropical forests of Australia, Amazonia, and elsewhere, we have found that plant genera, and often species, play out as unique contributors to the chemical and spectral diversity of any given rainforest, just as we saw in the Kaua'i example. However, this ultimately depends on the particular landscape of canopies and their associated chemistries. At this point, we do not know enough to predict the level of taxonomic detail to which a tropical forest might be remotely explored.

An equally challenging task involves the design of airborne taxonomic mapping systems, and today there are very few technologies up to the task. Very high-performance airborne HiFIS are needed at spatial resolutions that can resolve individual tree crowns, which is necessary for species-level determinations. In addition, canopy observational control – the ability to select specific portions of tree crowns to analyze spectrally – is almost always lacking in airborne spectroscopic measurements. The shape and orientation of tree crowns, solar illumination, and sensor geometry exert enormous influence over airborne spectroscopic signatures (Zarco-Tejada *et al.* 2000). A new technological approach is required.

The major steps in the new approach are outlined with

the real-life example shown in Figure 5, derived from a prototype system called the Carnegie Airborne Observatory (Asner *et al.* 2007). This new airborne instrumentation provides simultaneous, precision-aligned HiFIS and lidar measurements. The lidar determines the shape of each tree crown, along with precisely measured aircraft orientation, and thus sun and sensor viewing orientation, which guides the HiFIS to extract the spectral signatures of the most comparable portion of each tree crown (Figure 5, steps 1–2). Without this control, the HiFIS measurements often vary as much within a tree crown or species as they do among multiple species, yielding false identifications of individual species or providing confusing indications of their functional properties. The HiFIS–lidar data are collected in three-dimensional image form, such that a spectral diversity algorithm can then be applied to test for variation in plant canopy signatures that express spatial variations in richness (Figure 5, steps 3–4). Once relative richness levels are known, areas of low richness can often be analyzed to the species level using

spectral detection algorithms that already exist today (Roberts *et al.* 1998; Chang 2003), but only if the probability is high that the species exists in the spectranomic database (Figure 5, steps 5–6). This approach has already proven viable for detecting specific invasive tree species in Hawaiian forests (Asner and Vitousek 2005; Asner *et al.* 2008): Figure 5 shows specific detections of an invasive *Ficus* species in the Hawai'i Experimental Tropical Forest in Laupahoehoe, Hawai'i (Figure 5, step 6). In general, Figure 5 represents the spectranomics approach, both conceptually and operationally, showing linkages from the technology required to isolate and to extract particular spectral signatures, to the spectral diversity mapping step that is now operational, and to the database that is still needed to translate chemical and spectral signatures to species richness and composition.

Conclusions

Tropical tree species often have unique chemical fingerprints that increase in complexity and uniqueness when additional chemical constituents are measured. We also know that the spectroscopic signatures of species are often equally or more diverse than their chemical fingerprints.

It is difficult to overstate the potential payoff in developing an airborne spectranomics approach for biodiversity studies. Such an effort is daunting in many ways, but no other technologies have proven as suitable, and now the science needs to catch up with the hardware. We are just now populating a spectranomics database with tropical forest species (<http://spectranomics.stanford.edu>).

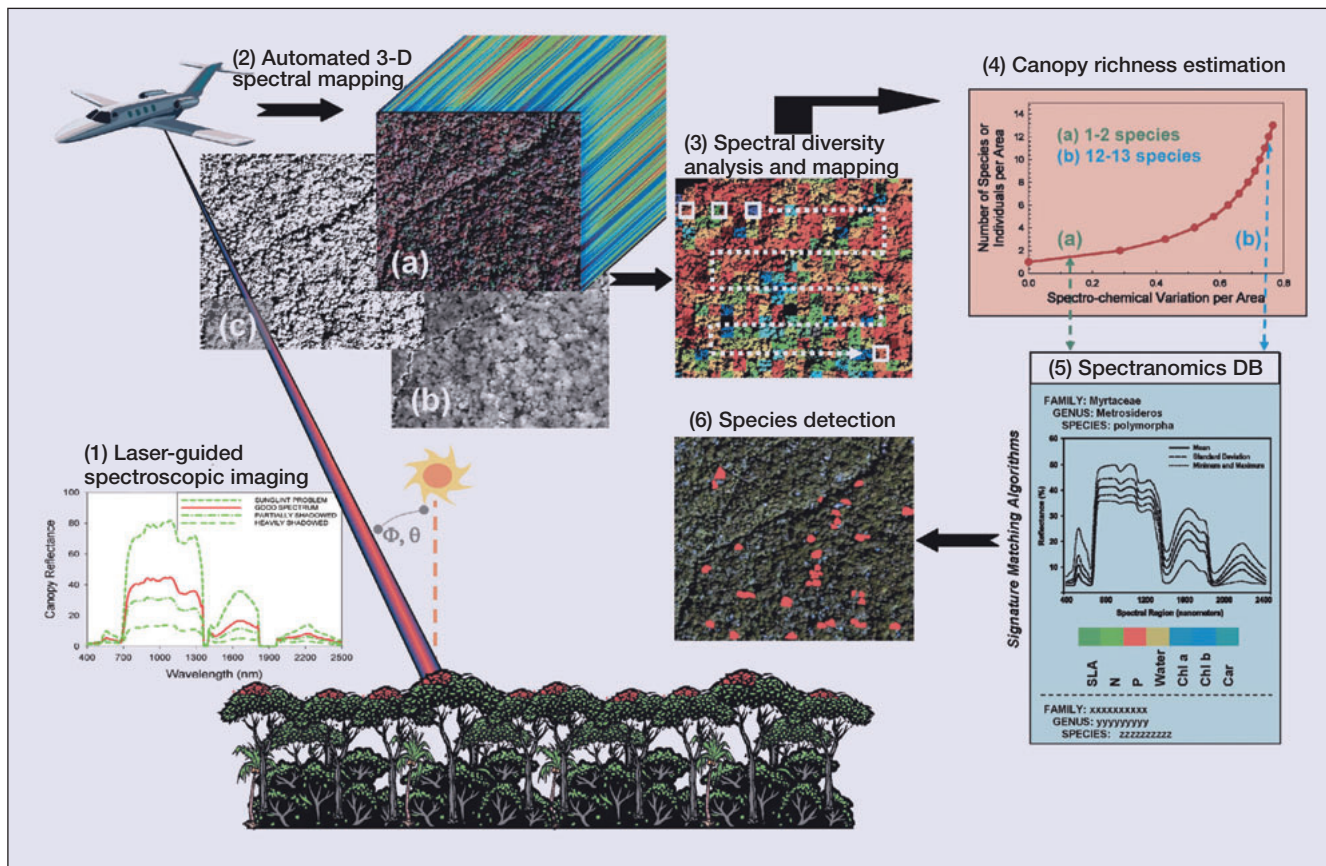


Figure 5. A conceptual representation of the airborne spectranomics approach, with actual data provided by the Carnegie Airborne Observatory (Asner et al. 2007). A hybrid, high-fidelity imaging spectrometer (HiFIS) and light detection and ranging (lidar) system are flown over a rainforest site. (1) The lidar provides laser guidance for the spectroscopic sampling of rainforest canopies, while controlling for variation in three-dimensional architecture and solar and sensor viewing angles. This step selects and extracts the best spectra (shown in red), which can be statistically compared to spectra collected from neighboring canopies. (2) The selected spectral signatures are compiled at high spatial resolution in (a) an image format, along with the canopy structural data from (b) the lidar that allows for automated, high-precision masking of (c) intra- and inter-crown shadows and other non-canopy surfaces. (3) The selected canopy spectra are reduced to equivalent leaf spectra using radiative transfer model inversion methods (Asner and Vitousek 2005), followed by an algorithm that calculates spectral diversity at a prescribed spatial resolution (eg 1 ha). Here, red shows high spectral diversity, and green shows low spectral diversity. (4) Spectral diversity is converted to plant species richness (eg number of species per ha) using a method detailed by Carlson et al. (2007). (5) The spectral signatures are also converted to chemical fingerprints using PLS-PRESS methods, and together the spectra and chemicals are used to search a database for potential matches at functional group, family, genus, and, potentially, species levels, depending upon environmental setting and geographic area. (6) Additional detections are carried out at different taxonomic scales, to identify particular species of interest (eg Roberts et al. 1998; Clark et al. 2005).

Other ecosystems and biomes should be considered, and may actually display fundamentally different linkages between chemical and spectral diversity.

Additional aircraft sensors that can resolve individual canopies, their spectral signatures, and three-dimensional structure are going to be critical to any future spectranomics approach. The Carnegie Airborne Observatory is the first of its kind designed specifically to address this problem, but other systems are planned. For example, the National Ecological Observatory Network (www.neon.org) is engaged in the development of a hybrid airborne HiFIS-lidar system.

Still, the technology will only be a part of the story; canopy spectranomics requires the fusion of biogeochemistry, taxonomy, community ecology, and physically based

remote sensing. Investment in the conceptual and analytical approaches, along with global databases of key taxa, will be a way forward to a truly futuristic capability in airborne research and mapping. Tropical forests, with their vast diversity, represent an ideal proving ground for the developments needed to make diversity mapping a reality.

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