

CHAPTER TWELVE

A chemical-evolutionary basis for remote sensing of tropical forest diversity

GREGORY P. ASNER

Carnegie Institution for Science

12.1 Introduction

One of ecology's fundamental pursuits centres on explaining controls over the distribution of species. Interest in species distributions is also increasing in the context of global change. There is a growing emphasis on providing information to decision-makers on where to protect and restore ecosystems and the species they harbour. Nowhere does this seem more obvious, or more pressing, than in tropical forests. Land-use change continues to strike deep into tropical forest regions, and climate change has come to the forefront in tropical forest conservation and planning. Temperature, precipitation and other climatic factors are shifting in some regions, or they are becoming highly variable (Cox *et al.* 2004; Williams, Jackson & Kutzbach 2007), and these changes are placing species in novel conditions that will force them to adapt, move or die (Asner, Loarie & Heyder 2010; Loarie *et al.* 2009).

We currently have few tools for mapping species distributions in tropical forests under these changing conditions, and our ability to monitor distributional changes remains limited despite their critical importance to ecology and conservation. Today, our understanding of species distributions comes from contrasting, and geographically limited, information sources. On the one hand, we have incredibly dense information at small scales of up to 50 hectares or so (Condit *et al.* 2005; Hubbell & Foster 1986). This information is key to understanding local-scale community patterns (Harms *et al.* 2001), but sparsely distributed plots cannot resolve ecological and biogeographic processes operating at the scales of long-range dispersal, migration or landscape evolution. On the other hand, we have longer-range, transect-based information on species occurrence, which does not provide the comprehensive inventories required for ecological modelling, although it is critical to basic conservation planning (<http://fieldmuseum.org/explore/department/ecco>). Emerging satellite-based methods, especially when combined with field observations, are beginning to fill in the geographic void with predictions of community patch-matrix patterns (Higgins *et al.* 2011; Turner *et al.*



Figure 12.1 As in much of Amazonia, lowland forests of Madre de Dios, Peru appear as vast expanses of green canopy, incised by water bodies and deforestation (gold mining at A). Even a careful eye will pick out only the most basic variation in forest composition, such as swamp areas dominated by *Mauritia flexuosa* palm trees (B). See plate section for colour version.

2003), but current approaches do not constitute direct measurements of species distributions or diversity levels. With mainstream technologies, it is not possible to monitor spatially explicit change in species distributions and biological diversity, which is likely to be non-random over landscape, regional and global scales.

From above, tropical forests look like monotonous green carpets, at least until a river or forest clearing is encountered to expose water, soils and man-made materials (Figure 12.1). A few species are conspicuous and identifiable, like some palm (e.g. *Mauritia*) or flowering trees (e.g. *Tabebuia*), but things generally seem green and hard to differentiate. Being able to identify species, or to map gradients in species richness, in the canopy of tropical forests would represent a substantial scientific advance, facilitating unprecedented forms of conservation and resource planning. Aerial photographs have been used for years to estimate the cover and abundance of conspicuous temperate or plantation species (e.g. Swetnam, Allen & Betancourt 1999), and some of that capability has been transferred to high-resolution spaceborne cameras (Thenkabail *et al.* 2004). Yet standard imaging cameras have yielded little information on species distributions or richness in tropical canopies.

Here I explore new possibilities for mapping canopy species diversity in humid tropical forests based on both the traits expressed among canopy taxa and the technologies needed to access information on those traits. I refer specifically to the Carnegie Airborne Observatory (CAO; <http://cao.ciw.edu>) because I developed it to focus mapping measurements on the plant traits that might best express the diversity of canopies in tropical forests. I also consider the ecological and evolutionary basis for trait-based remote sensing, with emphasis on the chemical attributes of canopy species. The ultimate purpose of the CAO and its biodiversity monitoring capabilities is to track compositional and/or functional changes in ecosystems, particularly under conditions of rapid global change.

12.2 Canopy chemistry: a window into biodiversity?

Canopy chemistry may represent a window into mapping biological diversity in tropical forests. Plants synthesise a wide variety of leaf compounds utilising numerous chemical elements and, for purposes here, it is convenient to group them into three functional categories: (i) light capture and growth, (ii) longevity and defence, and (iii) maintenance and metabolism (Table 12.1). While not independent, these groups are easily recognised by plant physiologists and ecologists, and thus can be traced throughout the scientific literature. Light capture–growth compounds include photosynthetic pigments such as chlorophylls and carotenoids, nitrogen and phosphorus, as well as the immediate products of photosynthesis such as soluble carbon compounds (Chapin III 1991; Evans 1989; Niinemets *et al.* 1999). Longevity compounds include lignin and cellulose that are structurally tough, lasting much of a leaf's lifetime (Melillo, Aber & Muratore 1982), while the defence category extends this list to more dynamic polyphenols (Coley, Kursar & Machado 1993). Maintenance–metabolism elements are those required in small quantities to support and mediate myriad functions within the leaf, but

Table 12.1 *A portfolio of chemical compounds and elements provides a multi-dimensional signature of foliar investment in light capture and growth, longevity and defence, and maintenance and metabolism.*

Light capture and growth	Longevity and defence	Maintenance and metabolism
Anthocyanins	Carbon (C)	Potassium (K)
Chlorophylls	Hemi-cellulose	Calcium (Ca)
Carotenoids	Cellulose	Magnesium (Mg)
Nitrogen (N)	Lignin	Zinc (Zn)
Phosphorus (P)	Phenols	Manganese (Mn)
Water	Tannins	Boron (B)
Soluble carbon		Iron (Fe)

few are considered to be highly specialised. An overarching or synthetic structural trait is leaf mass per area (LMA); while not a chemical *per se*, LMA is linked to growth traits (Wright *et al.* 2004; Poorter *et al.* 2009).

Much work has focused on the ecological significance of these foliar compounds and elements. Biogeochemists tend to look at nitrogen, phosphorus and base cations (Ca, Mg, K), as well as lignin, in mediating productivity and decomposition (Aber & Melillo 1991; Schlesinger 1991). Physiologists often consider photosynthetic compounds and nutrients affecting trade-offs among growth-related processes (Peterson *et al.* 1999; Wright, Reich & Westoby 2001). Here I take a broad view, thinking of the leaf chemical portfolio as expressing strategic trade-offs among investments in light capture–growth, longevity–defence and maintenance–metabolic needs. By doing so, we can treat the chemical portfolios as ‘signatures’. If chemical signatures are organised phylogenetically, then this might reflect variation in biological diversity at some taxonomic level. However, if the chemical phylogenetic signal is highly conserved, then closely related species may have similar chemical signatures, described broadly by Ackerly (2009) and for defence compounds by Agrawal (2007). Or if chemical phylogenies are highly dispersed, then species may prove to be chemically distinct from one another within a community (Kursar *et al.* 2009). Independent of phylogeny, ensembles of chemical signatures – compared among taxa at the community level – will probably describe functional diversity among tropical forest canopies. Without such chemical information, one might mistake many tropical forests as functionally similar or floristically monotonous when using chemical remote-sensing methods to map them.

12.3 Factors suggesting evolution in canopy chemical traits

There are a number of issues to consider when assessing whether or not canopy chemical traits, and particularly chemical signatures, exist among taxa. These include intraspecific variation, inter-trait correlation and chemical phylogenetic organisation. Depending upon the patterns that exist, chemically based windows to biodiversity mapping may or may not emerge.

12.3.1 Intraspecific variation

Temperate forest ecologists sometimes observe such high intraspecific variation that it would surprise them to find substantial chemical signature differentiation among taxa. However, in the temperate zone, such as in boreal or mixed deciduous forests with relatively few tree taxa (Latham & Ricklefs 1993), species are often adapted to span a wide range of climate conditions. They span these variable conditions while negotiating nitrogen-limited substrates spread over huge geographic areas (Vitousek & Howarth 1991). Variable climate and low nitrogen availability are associated with higher intraspecific plasticity in leaf traits (Karlsson & Nordell 1998; Niinemets,

Valladares & Ceulemans 2003; Reich, Walters & Ellsworth 1997). As a result, variation in the chemistry of a temperate species might be heavily driven by environmental factors, with adaptations centred more on increasing intra-specific variation among relatively fewer species to negotiate environmental gradients in space and time, thereby trumping phylogenetic expression of chemical variation.

In humid tropical forests, growth conditions are generally good, and although rock-derived nutrient availability may be low, especially for phosphorus and calcium (Vitousek & Sanford Jr. 1986; Vitousek, Turner & Kitayama 1995), production often remains high (Clark *et al.* 2001). High net primary production is maintained because nitrogen flows in relative abundance in many humid forests (Martinelli *et al.* 1999), and canopy species have evolved to recapture other nutrients even before discarded foliage reaches the soil surface (Vitousek 1982, 1984). However, good growth conditions are also associated with herbivory and parasitism in humid tropical forests, and it is in these environments where some of the strongest expressions of taxonomic order in canopy chemistry can be found, beginning with observations of relatively low intraspecific variation. For LMA, the within-species variation for thousands of taxa averages just 16% (Asner *et al.* 2011b), albeit only if samples are taken from upper, sunlit positions in the canopies.¹ Observations of low intraspecific variation of LMA at the top of tropical forest canopies are mirrored in many leaf chemical traits (Figure 12.2). Light capture–growth traits vary within species by an average of about 20%, depending upon the trait, in the upper canopy (Asner *et al.* 2009). Longevity–defence compounds also display low intraspecific variation, although often higher for phenols. Elements supporting maintenance and multiple metabolic functions (i.e. Mn, B, Zn) often display the highest levels of within-species variation (Figure 12.2).

12.3.2 Inter-trait correlation

Determining whether consistent combinations of leaf chemicals – or signatures – exist also requires an understanding of potential relationships between the contributing compounds and elements. Strong correlation between traits reduces the complexity and diversity of chemical signatures, whereas orthogonality among traits increases them. Growth factors such as chlorophylls, nitrogen and phosphorus are, on average, about 50–60% inter-correlated (Wright *et al.* 2004), and these correlations may be more strongly expressed when nitrogen is limiting growth, thereby down-regulating all growth-related chemicals

¹ Without this control, variability in LMA and nearly all other growth compounds and nutrients is dominated by variation in lighting and shading conditions. Sticking with the upper canopy provides critically important control for comparative and phylogenetic analysis, and it is also extremely important in the effort to measure leaf traits with remote-sensing technology that is most sensitive to upper canopy foliage.

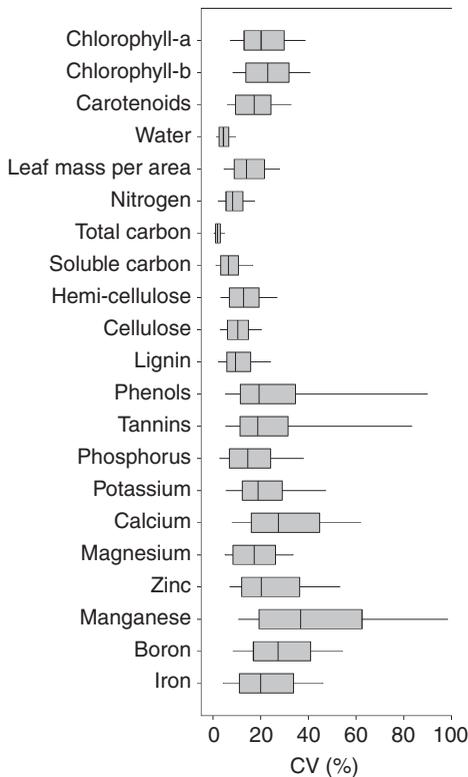


Figure 12.2 Intraspecific variation of foliar chemistry (expressed as a percentage coefficient of variation, CV, within species) is generally low in the upper canopy of humid tropical forests. This example shows mean and standard deviation (box plot), as well as minimum and maximum (whisker lines), for 21 leaf traits collected from sunlight positions in more than 200 species in the Peruvian Amazon. Adapted from Asner and Martin (2011).

(Cordell *et al.* 2001). However, outside the circle of the most growth-related traits, it can take 15 or more statistical degrees of freedom to explain the covariation among 21 light-growth, longevity-defence and maintenance-metabolism traits (Asner & Martin 2011; Asner, Martin & Suhaili 2012). It is not clear whether this occurs primarily in tropical forests, or if it is common among plants or canopy species. Nonetheless, for humid tropical forests, the measurements demonstrate the multidimensionality of leaf chemical signatures, and these patterns are highly suggestive of multivariate trait evolution.

12.3.3 Taxonomic organisation

A taxonomically nested pattern for a chemical trait would suggest some evolutionary basis to that trait, and such patterns have been uncovered in recent studies in Hawaiian (Asner & Martin 2009), Amazonian (Asner & Martin 2011; Fyllas *et al.* 2009), Australian (Asner *et al.* 2009) and Malaysian (Asner, Martin & Suhaili 2012) tropical forest canopies. There is often strong taxonomic organisation among leaf traits in humid tropical forest canopies, starting with LMA: Asner *et al.* (2011b) found that 70% of the LMA variation among 2873 canopy individuals, collected from a wide range of humid tropical forests, could be explained to the species level. This finding for LMA extends to foliar

chemicals: Fyllas *et al.* (2009) found that up to 50% of variation in about eight canopy foliar chemicals collected throughout Amazonia could be attributed to phylogeny, independent of site conditions. In a detailed site-level study in the Peruvian Amazon, Asner and Martin (2011) extended that finding to 21 traits among 600 coexisting canopies, finding that nearly 90% of the chemical variation among canopies could be attributed to taxonomic affiliation. This pattern has repeated itself at many sites throughout the global humid tropics (Carnegie Spectranomics Database; <http://Spectranomics.ciw.edu>).

12.4 Expressions of functional and biological diversity in hyperspectral imagery

As described, tropical forest canopies contain foliage with emergent, predictable chemical properties, including relatively low intraspecific variation, low inter-trait correlation when considering chemicals beyond the core growth-related compounds, and demonstrable taxonomic organisation. This combination may facilitate biodiversity assessment using remotely sensed data because these emergent chemical patterns mediate canopy spectral properties as measured with certain types of remote-sensing instruments. Many research groups have reported taxonomic variation associated with leaf and canopy spectral properties (e.g. Castro-Esau, Sanchez-Azofeifa & Caelli 2004; Féret & Asner 2011; Sanchez-Azofeifa *et al.* 2009; Williams 1991). In particular, a rich history of study in imaging spectroscopy (also known as hyperspectral remote sensing) has demonstrated that many of the chemicals can be measured remotely (reviews by Kokaly *et al.* 2009; Ustin *et al.* 2009). Further, Asner *et al.* (2011a) recently quantified the relationship between spectral and chemical data for thousands of tropical forest canopies. Another synthesis is not my goal here. Instead, with the aid of CAO imagery, I present evidence for canopy chemical diversity among tropical forest individuals, and discuss how chemical diversity is linked to biological diversity.

The CAO includes two high-fidelity imaging spectrometers that measure light reflected from canopies in up to 480 narrow spectral bands. By computing a principal components analysis of the CAO spectrometer data, and then classifying the results by spectral features, I have uncovered evidence for taxon-specific spectral signatures, such as for the well-known 50-hectare Center for Tropical Forest Science (CTFS; <http://www.ctfs.si.edu>) plot on Barro Colorado Island, Panama (Figure 12.3). The image reveals the possibility that spectral – and thus chemical – diversity exists in the canopy on very short distance scales of individual crowns. If this were not the case, then colours in the image would appear speckled and randomly distributed. Instead, spectral diversity is expressed crown by crown, and where variation does exist within a crown, close inspection of the original imagery indicates the presence of partial crown mortality, lianas or shadowing.

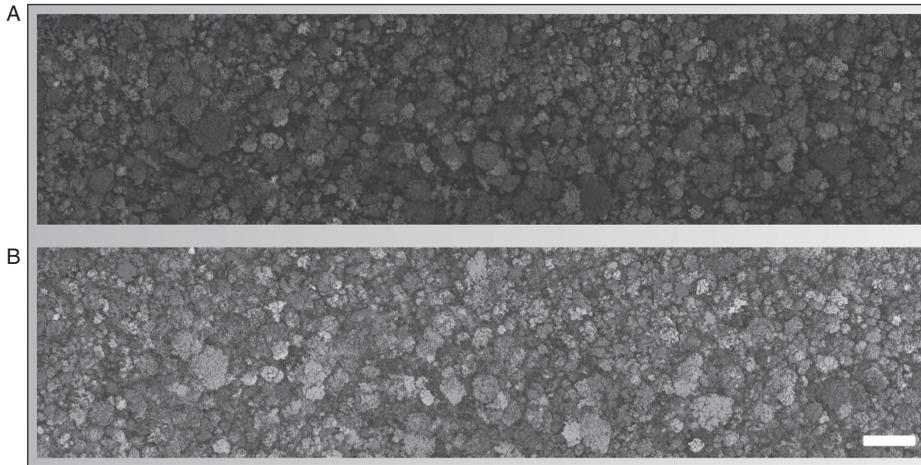


Figure 12.3 This CAO image of the 50-hectare Center for Tropical Forest Science (CTFS) plot on Barro Colorado Island, Panama, shows (A) a natural colour composite as seen by the naked eye, and (B) spectroscopic analysis of three dominant chemical components throughout the canopy. In this case, the image was interpreted in terms of chlorophyll (reds), leaf mass per area (greens) and water content (blues). Note that the expression of chemical variation occurs primarily at the scale of individual crowns. White bar indicates approx. 30 m of distance. See plate section for colour version.

This crown-based pattern in tropical forest spectroscopy can be extended to a taxon-specific interpretation such as shown for an area of lowland rain forest on the Island of Hawaii (Figure 12.4). Combining this image with detailed ground and laboratory analysis, we found that the crowns with similar spectral signatures were of the same species more than 70% of the time (Féret & Asner 2011, 2013). For example, each red crown in Figure 12.4 is the invasive tree *Psidium cattleianum*. Field-based chemical interpretation of the map indicates that the spectra are driven by differences in LMA, chlorophyll, nitrogen, phenols and water content among species.

Finally, evidence suggesting a direct link between spectral and biological diversity in tropical forests is emerging in new comparative analyses of CAO data taken over different forests. For example, a monotypic stand of *Eucalyptus grandis* maintains a nearly constant spectroscopy (Figure 12.5A). Note the expression of low intraspecific variation by near constant colour; where there is variation, it is caused by shadows among crowns. In contrast, a high-diversity Amazonian forest shows a kaleidoscope of spectral variation (Figure 12.5B). Here, it is again observed that the results are expressed at the crown level. Areas of near-constant canopy spectroscopy in the left portion of the image (shown in purple) turn out to be near-monotypic stands of *Mauritia flexuosa* (see also Figure 12.1). That is, even in high-diversity landscapes, one

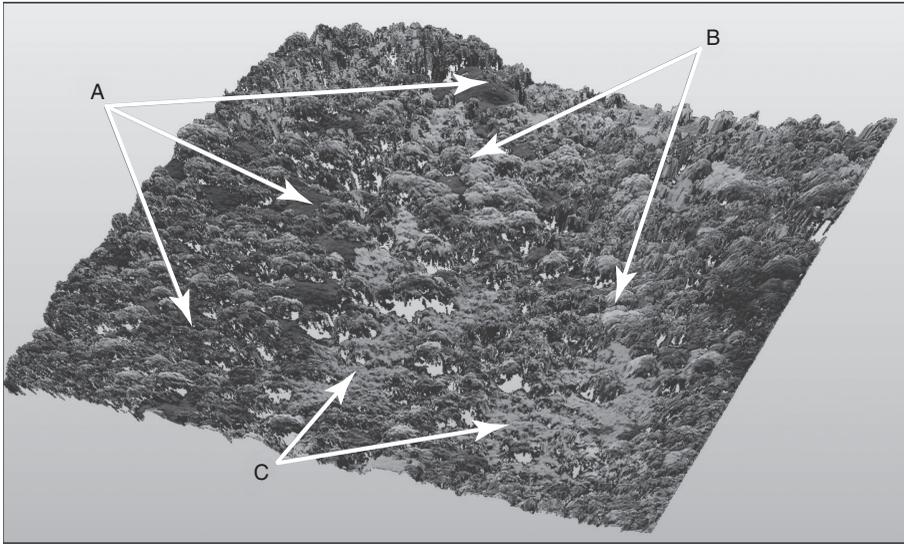


Figure 12.4 This three-dimensional CAO image of a Hawaiian tropical forest indicates that canopy chemical traits are differentially expressed among species, including (A) *Psidium cattleianum*, (B) *Mangifera indica* and (C) *Trema orientalis*. Species-level chemical signatures are created by low intraspecific variation, low inter-trait correlation and phylogenetic organisation in chemical traits. See plate section for colour version.

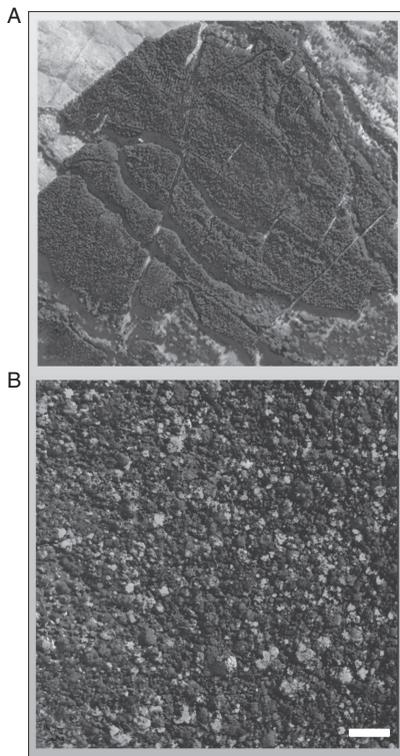


Figure 12.5 CAO imagery taken over (A) *Eucalyptus grandis* plantation and (B) high-diversity lowland Amazon forest indicates the role of chemical diversity in expressing biological diversity. Chemicals expressed here include chlorophyll, water and phenols. Notice the near-constant chemistry (colour) in the plantation canopy and the crown-scale variation in chemical signatures in the Amazon case. The near-constant purple canopies in the left portion of the Amazon image are small monotypic stands of *Mauritia flexuosa* as seen in Figure 12.1. White bar indicates 100 m of distance. See plate section for colour version.

can find cold spots of spectral diversity expressing local areas of lower canopy biodiversity in the CAO imagery.

Although for years we have known that spectral properties are directly controlled by the foliar chemical properties in forest vegetation, only now are we getting a top-down look at the degree to which these patterns occur and how they may be related to tropical forest biodiversity. These are the first quantitative glimpses, and the degree to which species dictate the chemistry and spectroscopy of forest canopies is still far from understood. Much more study is needed to advance the role of this new observational capability in scientific, conservation and forest management contexts.

12.5 Ecological and evolutionary causes for chemical signatures

What ecological and evolutionary processes give rise to individual canopies and species having unique spectral and chemical signatures within a community? Some new information, combined with long-standing theories, provides important clues.

In humid tropical forests, geologic and topographic variation is often associated with changes in plant species composition (Gentry 1988; Higgins *et al.* 2011; Phillips *et al.* 2003), and in some regions such as Amazonia, floristic changes are connected to differences in soil cations, phosphorus availability and texture (ter Steege *et al.* 2006; Tuomisto *et al.* 1995, 2003). Floristic variation also occurs with geographically varying climate regimes. Critically, the observed compositional turnover is often paralleled by changes in average (community-level) chemical concentrations in canopy foliage (Asner & Martin 2011; Fyllas *et al.* 2009). That is, we see both a change in floristics and a change in the average chemical make-up of the canopies when crossing soil- and climate-mediated thresholds and boundaries. On either side of these thresholds, convergence in the canopy chemical signatures among coexisting species can be viewed as a syndrome, and we know that soil-mediated chemical syndromes occur among growth-related traits, especially for leaf nitrogen and phosphorus. For example, high-fertility soils harbour species with higher nutrient concentrations in their foliage; opposite patterns are often found in species found in low-nutrient conditions (Townsend *et al.* 2007; Townsend, Asner & Cleveland 2008). We also see community-scale shifts in foliar trait syndromes related to longevity-defence and maintenance-metabolism (e.g. phenols and carbon fractions), although these patterns can be more subtle (Asner & Martin 2011). Moreover, plant species tend to display suppressed levels of phenotypic plasticity in foliar longevity-and-defence compounds in resource-poor conditions (Stamp 2003). It seems that abiotic resources are key factors mediating plant evolutionary strategies, setting spatially explicit templates for the types of defence that may evolve (Kursar & Coley 2003). Furthermore, although growth (e.g. nitrogen) and defence (e.g. lignin) traits are often viewed as correlated in

temperate forest ecosystems (Melillo, Aber & Muratore 1982), we can find a clear disconnect between them in tropical canopies (Asner & Martin 2011; Fyllas *et al.* 2009). This provides a critical insight: it suggests that evolution in highly competitive, high-production environments, such as humid tropical forests, leads to highly diverse, uncorrelated foliar chemical strategies. Why?

The environmental factors supporting elevated productivity in tropical forests (abundant nitrogen, light, water) are also correlated with pest and pathogen pressure (Ayres 1993; Mattson 1980), and the diversity of herbivores, parasites, viruses and other leaf-attacking lifeforms may well have led to the pronounced radiation of host strategies designed to combat, accommodate and outlast these threats in order to increase survival and fitness. This builds directly on the seminal work of Janzen (1970) and Connell (1970), who argued for the existence of pest- and pathogen-mediated density dependence in plant seedling establishment and recruitment. They suggested that, by host-specific co-evolution, herbivores and other leaf-threatening lifeforms maintain very low densities of conspecific plants locally. Janzen also proposed that tropical plants found in low-nutrient environments allocate heavily to chemical defences to protect foliage, whereas plants found on higher-nutrient soils invest more in chemicals yielding higher growth rates. Key work by Coley (1983) also suggests that light-gap species maintain chemical traits that are different from those found in shaded understorey environments. So while soil nutrient status fosters the community-scale foliar chemical syndromes described earlier, host-specific growth and defence strategies create unique chemical signatures among plant species coexisting within a community. Add to this the possibility for highly competitive plant-to-plant interactions and evolved syndromes for light and nutrients (Coley 1993; Coley & Barone 1996; Fine, Mesones & Coley 2004), and a multi-scale kaleidoscope of chemical traits emerges, as we observe in CAO imagery of humid tropical forests.

How diverse are chemical signatures among coexisting canopy species? Does each have a unique combination of chemical traits? At some level, the answer is yes, but intraspecific variation – as low as it can be at times – still leaves a buffer of chemical variability for each species, making it hard to answer these questions. Species-specificity is also dependent upon the number of traits considered within a chemical signature: combining traits results in increased differentiation among species, but does this have ecological or evolutionary meaning? The CAO imagery again provides some clues. In the Hawaiian image example (Figure 12.4), the forest is dominated by a relatively recent compilation of exotic species introduced from forests of Oceania, Asia, Central and South America (Mascaro *et al.* 2008; Zimmerman *et al.* 2007). The forest thus harbours species with chemical traits established in far-flung communities evolved under diverse environmental conditions and biogeographic

histories. Perhaps as a result, each canopy species is very distinct and separable in the imagery. In the Peruvian Amazon image, the canopy comprises species evolved in similar, late-Holocene climate conditions (Williams, Jackson & Kutzbach 2007). There was thus a shared environment for chemical trait evolution, but the species also come from differing pre-Holocene biogeographic origins (Horn *et al.* 2010). Chemical diversity is high and many species are chemically distinct, yet the imagery suggests greater overlap among coexisting canopies (i.e. a shared syndrome) than we find in the Hawaiian forest canopy occupied by species from very diverse evolutionary and biogeographic backgrounds.

These tantalising hints suggest that canopy biodiversity maps based on chemical plant traits could unlock doors to understanding forest function and community assembly, and how species have evolved under contrasting environmental regimes. Far more work is needed to measure the spectral patterns and to interpret them chemically and in terms of biological diversity. Yet this early evidence suggests a novel pathway forward to unravelling the secrets of the ecology and evolution of tropical forest communities.

12.6 Biodiversity mapping and global change

There is a pressing need to take biodiversity mapping and monitoring beyond the plot or transect scale. The velocity of climate and land-use changes is now likely to exceed the migration potential of many species and functional groups of species (Asner, Loarie & Heyder 2010; Loarie *et al.* 2009), and this process has already begun to rearrange the composition of our biosphere (Parmesan 2006; Wake, Hadly & Ackerly 2009). In short, our biosphere is in a state of non-equilibrium change (Biggs, Carpenter & Brock 2009; Schimel, Asner & Moorcroft 2013). Without leaps forward in the area of biodiversity monitoring, changes in biospheric composition will go unaccounted, and thus will have unknown impact on prognostic studies of the future global environment. New technologies such as imaging spectroscopy are key to making sure biodiversity change is quantified, but technology represents only part of the solution going forward. New and innovative approaches are needed to take advantage of the developing technologies. I propose that the best approaches will be seated in an understanding of the underlying evolutionary drivers of trait-based diversification among species. More generally, mapping compositional and functional changes at the regional level will require effort among experts from multiple fields including engineering, chemistry and evolutionary biology. The required interdisciplinary links still need forging, yet the effort is central to advancing biodiversity monitoring for conservation planning, ecosystem management and resource policy development in this century of rapid global change.

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Figure 12.1 As in much of Amazonia, lowland forests of Madre de Dios, Peru appear as vast expanses of green canopy, incised by water bodies and deforestation (gold mining at A). Even a careful eye will pick out only the most basic variation in forest composition, such as swamp areas dominated by *Mauritia flexuosa* palm trees (B).

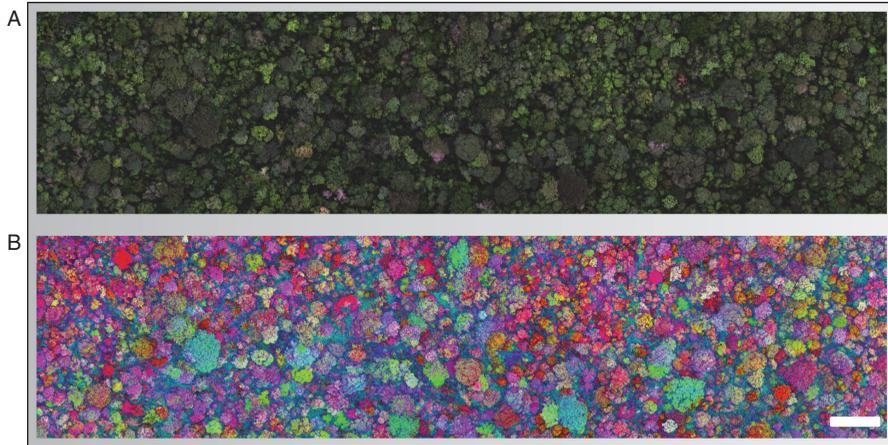


Figure 12.3 This CAO image of the 50-hectare Center for Tropical Forest Science (CTFS) plot on Barro Colorado Island, Panama, shows (A) a natural colour composite as seen by the naked eye, and (B) spectroscopic analysis of three dominant chemical components throughout the canopy. In this case, the image was interpreted in terms of chlorophyll (reds), leaf mass per area (greens) and water content (blues). Note that the expression of chemical variation occurs primarily at the scale of individual crowns. White bar indicates approx. 30 m of distance.

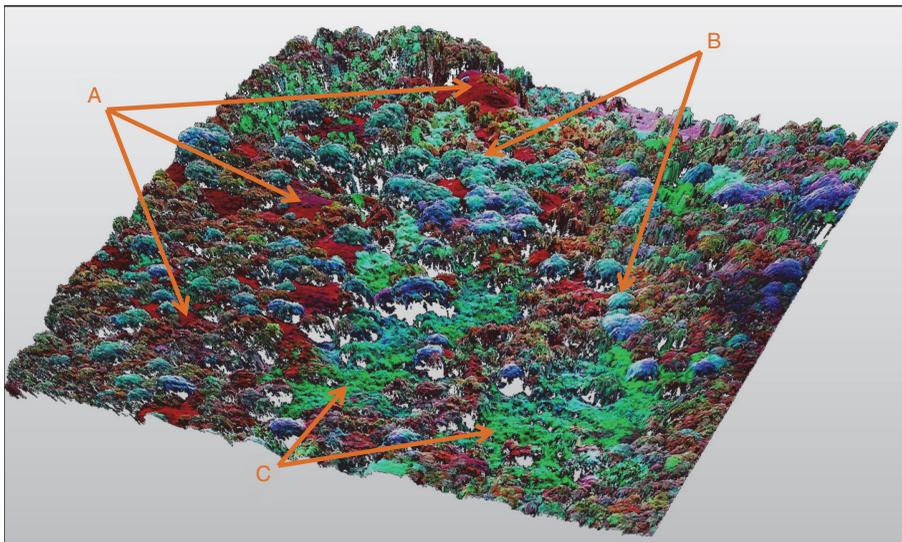


Figure 12.4 This three-dimensional CAO image of a Hawaiian tropical forest indicates that canopy chemical traits are differentially expressed among species, including (A) *Psidium cattleianum*, (B) *Mangifera indica* and (C) *Trema orientalis*. Species-level chemical signatures are created by low intraspecific variation, low inter-trait correlation and phylogenetic organisation in chemical traits.

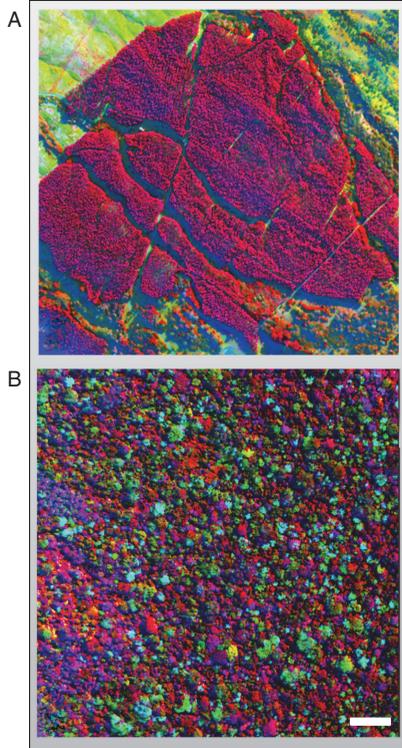


Figure 12.5 CAO imagery taken over (A) *Eucalyptus grandis* plantation and (B) high-diversity lowland Amazon forest indicates the role of chemical diversity in expressing biological diversity. Chemicals expressed here include chlorophyll, water and phenols. Notice the near-constant chemistry (colour) in the plantation canopy and the crown-scale variation in chemical signatures in the Amazon case. The near-constant purple canopies in the left portion of the Amazon image are small monotypic stands of *Mauritia flexuosa* as seen in Figure 12.1. White bar indicates 100 m of distance.