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The biogeochemical heterogeneity of tropical forests

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Tropical forests are renowned for their biological diversity, but also harbor variable combinations of soil age, chemistry and susceptibility to erosion or tectonic uplift. Here we contend that the combined effects of this biotic and abiotic diversity promote exceptional biogeochemical heterogeneity at multiple scales. At local levels, high plant diversity creates variation in chemical and structural traits that affect plant production, decomposition and nutrient cycling. At regional levels, myriad combinations of soil age, soil chemistry and landscape dynamics create variation and uncertainty in limiting nutrients that do not exist at higher latitudes. The effects of such heterogeneity are not well captured in large-scale estimates of tropical ecosystem function, but we suggest new developments in remote sensing can help bridge the gap.

Biogeochemical variation in the tropics

In a rapidly changing world, it is critical to understand how tropical forests respond to human perturbations, as their fate is linked to our own [1]. We know that these ecosystems have significant effects on the major biogeochemical cycles and global climate [2], and that they harbor remarkable biological diversity [3]. However, our ability to measure, scale up and predict basic ecosystem function in tropical forests lags behind that of many other biomes. Here we contend that part of this difficulty results from the fact that in addition to high biological diversity, tropical forests house exceptional biogeochemical variation at both local and regional scales (Figure 1). At larger scales, the tropical biome exhibits highly variable combinations of soil age, soil chemistry and rates of erosion and tectonic uplift, and this broad 'abiotic envelope' allows for a suite of potential limiting nutrients that, in turn, have varied effects on ecosystem structure and function. At local to landscape scales, high diversity of plant communities leads to heterogeneity in chemical, structural and functional traits that are known to affect biogeochemical processes. We suggest that capturing the effects of this biogeochemical heterogeneity is important to the study of tropical ecosystem function, and outline how new remote sensing techniques that measure the chemical and structural characteristics of canopies with high fidelity can help achieve this goal.

Abiotic drivers of biogeochemical variation

In 1941, Hans Jenny first proposed that variations in five 'state factors' – climate, organisms, topography, parent material and time – drive differences in soil development [4]. Since that time, a wealth of ecosystem studies have sought to isolate or manipulate all of these state factors and have testified to their importance not only for soil development but also for regulating ecosystem structure and function in general [5]. Of the state factors, the diversity of organisms in tropical rain forests is perhaps most well known. However, a regional-scale view of tropical forests reveals a biome that is also diverse with respect to Jenny's four remaining state factors. Variations in climate, topography, parent material and time undoubtedly contribute to the high biological diversity of the biome

Glossary

Base cations: in ecosystem ecology (and in this paper), the collective term 'base cations' is often used to refer to the macronutrients calcium, magnesium and potassium.

HFIS: high-fidelity imaging spectroscopy. A type of remote sensing that measures the reflectance of the Earth in multiple, narrow spectral bands and at high spatial resolution. In the context of this paper, HFIS can be used to resolve subtle spectral features associated with the chemical composition of vegetation.

Landscape dynamics: used here to refer to geomorphic processes such as erosion and tectonic uplift that can disrupt the vertical structure of a soil profile.

Parent material: one of the state factors of Jenny [4], and formally defined by him as 'the initial state of the soil system.' Typically refers to the original mineral and/or organic material from which soil develops.

Plant polyphenols: a broad class of plant secondary metabolites that contains thousands of different compounds, including relatively simple, low-molecular weight phenols, phenolic acids and flavinoids, as well as more complex, high-molecular weight tannins.

Remote sensing algorithms: the suite of mathematical formulas needed to interpret raw remote sensing data. Distinct from remote sensing platforms, which refers to the combination of physical instruments used to collect the data.

Rock-derived nutrients: those elements essential for plant growth that are originally derived from rock weathering. Examples include (but are not limited to) the macronutrients phosphorus, calcium, magnesium and potassium.

Soil orders: the most commonly used system of soil taxonomy initially divides all soils into 12 major soil orders: alfisols, andisols, aridisols, entisols, gelisols, histosols, inceptisols, mollisols, oxisols, spodosols, ultisols and vertisols.

State factors: in 1941, Jenny [4] proposed that five major 'state factors' control soil development, namely available biota, climate, parent material, topography and time. Jenny's state factor model is often applied to the analysis of ecosystem processes.

Volatile organic compounds (VOCs): in the context of this paper, a class of plant-produced secondary metabolites that have adequate vapor pressures under normal conditions to volatilize from the canopy to the atmosphere. VOCs are important to several aspects of atmospheric chemistry, and include compounds such as isoprene and terpenes.

wLiDAR: waveform light detection and ranging. A type of remote sensing commonly used to measure structural attributes of ecosystems.

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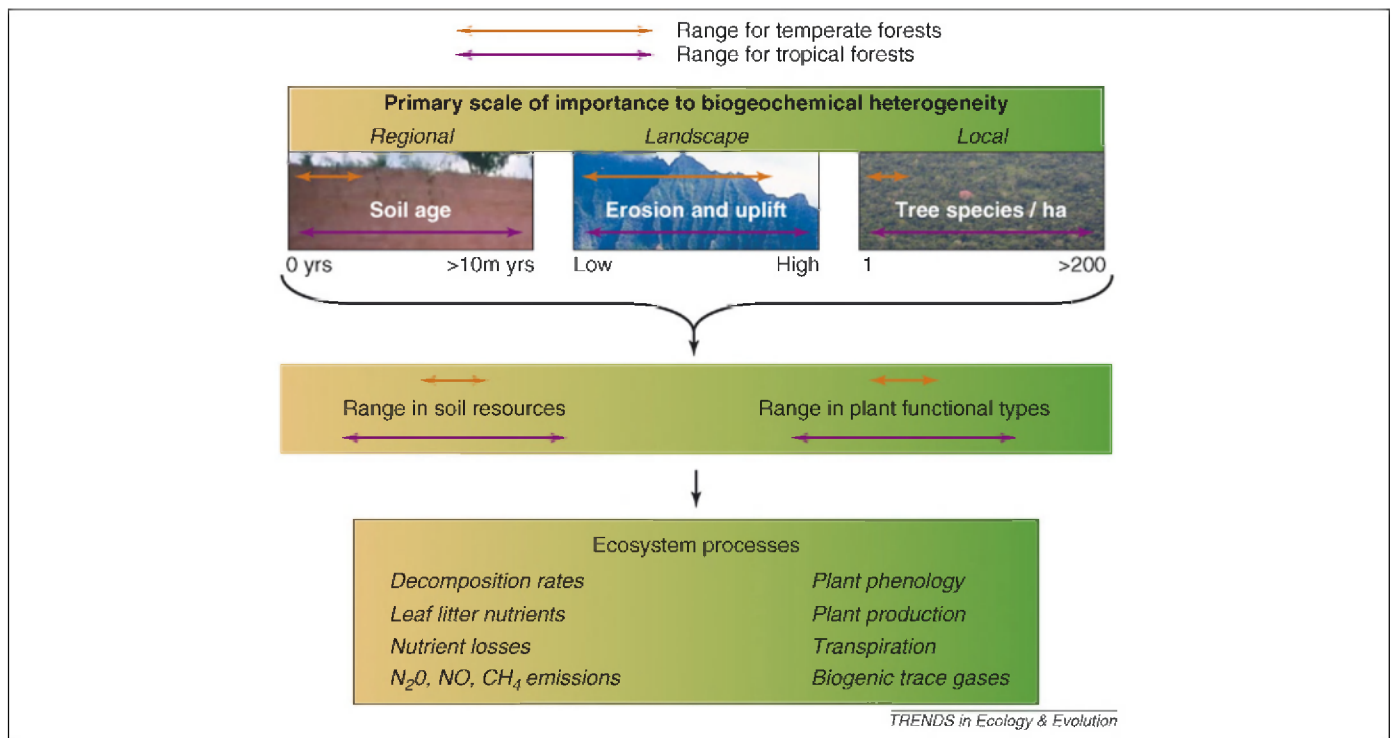
Figure 1. Effects of three major state factors [4] on variation in ecosystem processes in temperate versus tropical forests. Variations in soil age and weathering status lead to differences in the availability of multiple nutrients [5] and, in the tropics, widespread areas of highly weathered soils where primary mineral pools of rock-derived nutrients are essentially depleted [6]. Erosion and tectonic uplift can rejuvenate such soils by bringing weatherable parent material to the surface [13]. Shifts in biotic composition can alter functional traits that affect rates of production, decomposition, nutrient cycling and other ecosystem processes [27]. When compared to temperate ecosystems, tropical forests have far greater ranges in soil age and biotic composition, as well as zones with some of the highest erosion and/or uplift rates on Earth [13]. Here we suggest that variation in these state factors leads to an exceptional level of biogeochemical heterogeneity from local to regional scales.

[3], but also contribute to its uniquely variable and complex biogeochemistry.

For example, tropical forests contain all but one of the major soil orders, and exhibit ranges of soil age and weathering status that far exceed those found in more temperate biomes [6]. In young and lightly weathered soils, nitrogen (N) limitation of primary production is most common [7], in part because readily weatherable primary minerals maintain an adequate supply of 'rock-derived' nutrients such as phosphorus (P) and the major base cations. As a result, nitrogen limitation of primary production dominates the geologically younger temperate zone [8]. However, tropical forests occupy a soil continuum ranging from young, N-poor soils to those where old age and a warm, wet climate have exhausted primary mineral pools of the rock-derived elements [6]. As such, defining the nature of nutrient limitation in tropical forests is complex [9]; in a single Panamanian forest growing on highly weathered oxisols, at least four different nutrients appeared to control rates of litterfall and decomposition [7].

Three major processes can counteract the effects of parent material age, further enhancing soil nutrient heterogeneity. Two of these, erosion and tectonic uplift, are often grouped under the term 'landscape dynamics' for their broadly similar tendency to disrupt otherwise stable soil profiles. The third process is atmospheric deposition. The traditional view of tropical nutrient limitation suggests that the soil environment is relatively static, and that long-term weathering depletes rock-derived nutrients (*sensu* [10]). However, research now suggests that transport of parent material from deeper layers to surface soils can occur in regions long-removed from original parent material sources, resulting in higher quantities of rock-derived nutrients than would be predicted from soil age and climate alone. Such transport can occur via erosion [11] or tectonic uplift [12], both of which have notably high rates in some tropical regions [13].

The effects of interaction between climate, soil age and landscape dynamics on soil nutrient conditions are perhaps best seen in the Hawaiian Islands. There, the ability to isolate a given state factor has revealed, for example, that time alone causes a relatively rapid transition from N limitation on young soils, to nutrient-rich conditions at intermediate soil ages, and eventually to P limitation as the warm, wet conditions rapidly weather initial stocks of rock-derived elements [5]. However, sharp gradients in both climate and topography in Hawaii have been used to show that the speed at which ecosystems transition among these nutrient states is a function of rainfall [5], and that soil erosion in 'old' sites can cause shifts in nutrient availability that equal those produced by millions of years of soil development [14]. Thus, even within the relatively species-poor tropical forests of the Hawaiian Islands, one finds remarkable heterogeneity in basic biogeochemical traits, including changes in the nature of plant nutrient limitation [5].

In addition, in areas with significant maritime influence on the atmosphere, rapid weathering and loss of calcium, magnesium and potassium from the original parent material can be attenuated by significant deposition of all three elements from marine sources [15]. Hawaii again provides a clear example; along a long soil age gradient,

base cations weather out of surface soils more rapidly than P, but high atmospheric inputs of calcium, magnesium and potassium are sufficient to drive eventual limitation by P rather than by any of the base cations [15]. By contrast, forests on highly weathered soils in the central and western Amazon basin – hundreds to thousands of kilometers from the nearest ocean – are more likely to experience cation limitation [15]. Although the transport of mineral dust from arid regions to tropical forests can replenish losses of rock-derived nutrients even in forests far from oceans, that transport process in itself is quite variable across the entire biome [16].

Thus, gradients in soil age, landscape stability and atmospheric deposition combine to create exceptional landscape-to-regional scale heterogeneity in soil nutrient availability in tropical forests. Yet that heterogeneity is not well captured in current projections of how the tropical biome will respond to human-induced environmental change. Research in temperate sites has demonstrated the importance of knowing the identity and extent of nutrient limitation when assessing the effects of varied global change scenarios on ecosystems; for example, soil N availability regulates responses to changes in atmospheric CO_2, N deposition and climate [17]. Some tropical forests are already experiencing significant changes in climate and nutrient deposition [18,19], and thus it is imperative that we understand how the complex soil environment of this biome will determine its responses to change.

Finally, although perceptions of the tropics as warm and wet might be broadly accurate, such generalizations belie the gradients in temperature and rainfall that they experience [20]. Unlike the other state factors (Figure 1), the tropical climate is perhaps less variable than in many higher-latitude ecosystems. However, given the high rates of processes such as CO_2 uptake and loss in the tropics, small variations in temperature or rainfall can have significant implications for large-scale biogeochemistry [21]. For example, relatively subtle warming in lowland tropical forests could drive globally significant increases in soil carbon (C) efflux [21], and perhaps increase tree mortality in mature forests [22]. Likewise, both seasonal and spatial variations in rainfall drive shifts in light availability and net ecosystem production that can have measurable effects on the C cycle at multiple scales [23,24].

In sum, abiotic drivers alone create regional-scale biogeochemical heterogeneity that likely exceeds most, if not all other, major biomes. But the last of the state factors of Jenny [4], namely organisms, further enhances the biogeochemical complexity, creating a suite of patterns and challenges that we believe are unique to tropical forests.

Taxonomic diversity enhances biogeochemical variation

The patterns in both local and regional diversity of tropical flora, most notably canopy trees, have received considerable attention [25]. Briefly summarized, we know that most indices of diversity are high in tropical forests, but that considerable local and regional variation still occurs. For example, tree species richness across the Center for Tropical Forest Science global plot network (CTFS; http://www.ctfs.si.edu) ranges from 22 species per ha in India to

254 species per ha in Ecuador [26]. In addition, we know that across the CTFS network, changes in species richness outpace those of family-level richness by 300% [26]. Together, these results highlight the fact that in most portions of the tropical biome, forests are taxonomically diverse even at local scales, and that the specific contributors to (and thus effects of) that diversity likely will change across landscape-to-regional scales.

Unfortunately, although the links between species diversity and ecosystem processes have received substantial attention in other biomes [27], our understanding of analogous relationships in tropical forests lags behind. This is not surprising, as species manipulations are difficult in any forest setting, but in the tropics, where forests often contain more than 100 species ha^{-1} [3], they are practically infeasible at a level that is representative of the native ecosystem. The limited number of manipulative studies that do exist suggest that shifts in tropical tree species composition can alter a range of ecosystem properties, including soil C storage, rates of N turnover and loss, and soil chemistry [28,29]. We also know that tropical forest canopies are among the most chemically diverse on earth [30], and that differential species-loss scenarios – for example, species with low wood density versus those that reach the largest stature in mature forests – would likely create substantial variation in total C storage [31].

Although still not well understood, we contend that the effects of high tree diversity on biogeochemistry and ecosystem function are likely to be significant. Phylogenetic diversity translates into chemical, physiological and structural variation (Box 1), all of which have the potential to affect the uptake, storage and turnover of carbon and nutrients in multiple ways. For example, structural differences among species alter the distribution of photosynthetically active radiation, and chemical differences typically include shifts in photosynthetic enzymes (Box 1). In addition, between-species differences in structural, physiological or chemical traits can drive variations in biogeochemical processes beyond those involved in photosynthesis.

For example, in the lowland forests of Costa Rica, P availability limits a variety of microbial processes, including organic matter decomposition and free-living N fixation [32]. More recently, data from these same sites have shown that species-level variation in foliar P and C chemistry is associated with tree-specific differences in both free-living N fixation and soil respiration [33,34], suggesting that variation in the quantity and quality of carbon and nutrients in the canopy can regulate processes at and beneath the forest floor. Similarly, in a Panamanian forest, litter decomposition rates among neighboring tree species were highly species specific, and correlated with indices of litter chemistry [35]. In addition, interspecific variation in the production of plant polyphenols can be high among tropical species, and can have greater influence on litter decomposition rates than commonly measured metrics such as leaf N or lignin concentration [36]. Tropical forests are also large sources of volatile organic compounds to the atmosphere, but rates of emission are highly species specific [37]. Finally, lianas are an important component of most tropical forests, but their

Box 1. Canopy chemical and structural diversity in tropical forests

Multiple measures of tropical canopies suggest that high taxonomic diversity creates significant chemical and structural variation in the canopy. For example, even at the local scale, neighboring species display marked differences in leaf area, mass and light use, as well as in the three-dimensional structure of the tree itself [47]. These structural differences lead to variation in the proportion of incident radiation that is absorbed by the canopy and the quality of the radiation as it penetrates to lower leaf layers, and hence affects gross and net primary production of the forest [47].

As in the case of structural differences, differences in leaf chemistry correlate with significant variation in leaf carbon uptake and water use [48], and the chemical environment of the tropical canopy is exceptionally diverse. In the case of foliar nitrogen (N) and phosphorus (P), the N:P ratio of species within individual tropical sites or families frequently exceeds that of a biome-wide database on all temperate trees [38] (Figure Ia; boxes denote median, 75th and 95th percentiles. Redrawn with permission from the Ecological Society of America). Similar results are found when comparing foliar $\delta^{15}N$ values in tropical versus temperate forests; ranges in $\delta^{15}N$ both in single sites and biome-wide are considerably larger in the tropics [49,50]. In two Amazonian forests, the range of foliar N or P values begins to level out asymptotically at 30–40 species, but never reaches saturation, even at 150 tree species [51] (Figure Ib; reproduced with permission from the Taylor and Francis Group). Moreover, in rain forest sites on Kauai Island where diversity approaches that of many continental forests, a multiparameter index of leaf chemistry in which pigments, water and nutrients are combined, the range of chemical 'signatures' among species never reaches a saturation point [47] (Figure Ic; reproduced with permission from the Taylor and Francis Group). Chemical indices such as this one are typically the weighted and squared sum of each chemical constituent, with the weighting based on the value range of each constituent among all species. Taken as a whole, it is clear that even local-scale variation in canopy structure, nutrient pools and photosynthetic pigments in tropical forests tends to exceed that for most, if not all, other biomes.
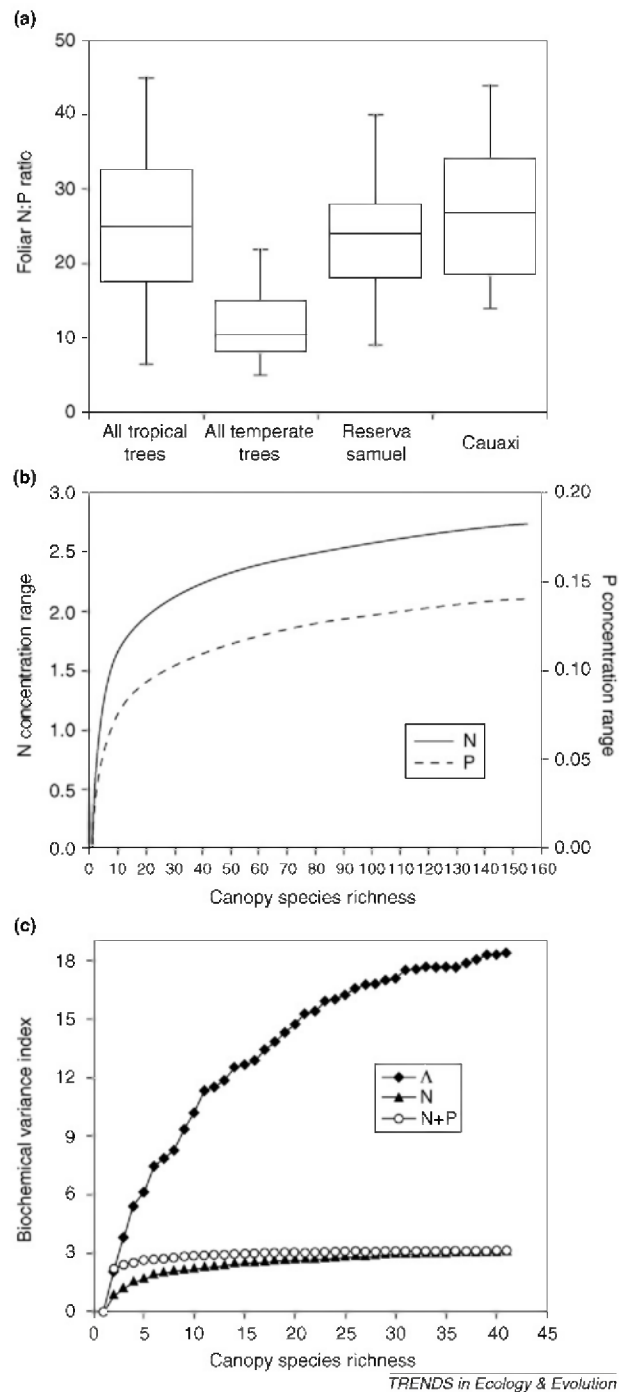
Figure I. Examples of canopy chemical diversity in tropical forests. Explained as part of box.

distribution even at local scales is highly dependent on that of structurally suitable hosts [38]. Where present in high abundance, lianas can influence ecosystem-level processes and alter the hydrologic regime by altering both the amount and distribution of carbon storage and whole-forest transpiration rates [39].

Thus, even in highly diverse tropical forests, individual species might create tree-specific 'biogeochemical foot-prints' that extend from the canopy to the soil. The fact that an individual species can alter biogeochemical function is not surprising [40]. However, in tropical forests, some have argued that despite local-scale variation in canopy chemistry, structure and phenology, inputs to the forest floor are quickly mixed among species, thereby diluting or even removing the influence of individual trees on the forest floor [41,42]. Yet, one study [41] showed significant associations between local-scale variation in soil chemistry and tree species composition in forests of Panama, Colombia and Ecuador. Although the authors concluded that the soil variation drives community

assembly, we suggest that a more parsimonious explanation is that the substantial variation in the chemistry of the canopy creates much of the observed, small-scale differences in soil nutrient content. We note, for example, that most of the correlations reported in Ref. [41] are for nutrients unlikely to limit plant production, suggesting that the canopy drives patterns in soil nutrients at this local scale, as opposed to the reverse.

If chemically and structurally diverse canopies do promote significant local-scale variation in biogeochemistry, it suggests some intriguing connections between multiple areas of ecology and evolutionary biology. For example, classic ecosystem theory holds that varying soil nutrient conditions result in predictable plant–soil feedbacks: nutrient-poor conditions tend to cause high nutrient use efficiency, low nutrient concentrations in litter and thus low rates of nutrient turnover that the plant characteristics help maintain [43]. Yet, the high species diversity of many tropical forests might lessen soil nutrient constraints to a greater degree than is seen in many other biomes. For example, mean foliar P concentrations in tropical forests are typically lower in P-poor oxisols and

ultisols than in more P-rich soils, but the range for any given site – and thus the local-scale, species-driven variation – often exceeds the range measured across soil types [30]. Thus, tropical forests might harbor both 'hot' and 'cold spots' of canopy nutrient content that exist independent of soil type, and could create islands of fertility in more nutrient-poor locales. Intriguingly, the creation of local-scale chemical variation in the canopy seems largely a product of varying evolutionary histories, life-history strategies and community assembly dynamics, rather than soil type. Yet, whereas the soils themselves might not have a strong influence on local-scale chemical patterns in the canopy, some evidence [33–37] suggests the canopy, in turn, could drive variation in biogeochemical function of the soil.

The view from above: scaling up the effects of high diversity

The effects of locally high biological diversity, coupled with the regional-scale effects of variations in climate, soil age and landscape stability (Figure 1), challenge our ability to both measure the effects of diversity on ecosystem


Box 2. New airborne taxonomic mapping systems

The potential ties between the taxonomic and chemical diversity of tropical tree species are driving new efforts to combine advanced remote sensing technologies to map the composition of forests from aircraft. One contributing technology called high-fidelity imaging spectroscopy (HFIS) measures the reflectance of the Earth in narrow spectral bands and at high spatial resolution ($\ll 1.0$ m), thereby resolving the subtle spectral features associated with the chemical composition of each canopy and even branches within canopies. A complementary technology – waveform light detection and ranging (wLiDAR) – is providing a means to measure the three-dimensional

structure of tree crowns and, critically, to isolate comparable sections of each tree crown for chemical analysis using HFIS (Figure I). A combined HFIS–wLiDAR system has only recently been deployed to make remote chemical determinations of specific plants from the air (Figure II [52]). Although this type of airborne mapping instrumentation has come of age technologically, the methods for extracting chemical and taxonomic information from the images have only been developed in a few small regions of the world [45]. The challenge of mapping species in continental tropical forests remains particularly daunting, given the high diversity of these regions.
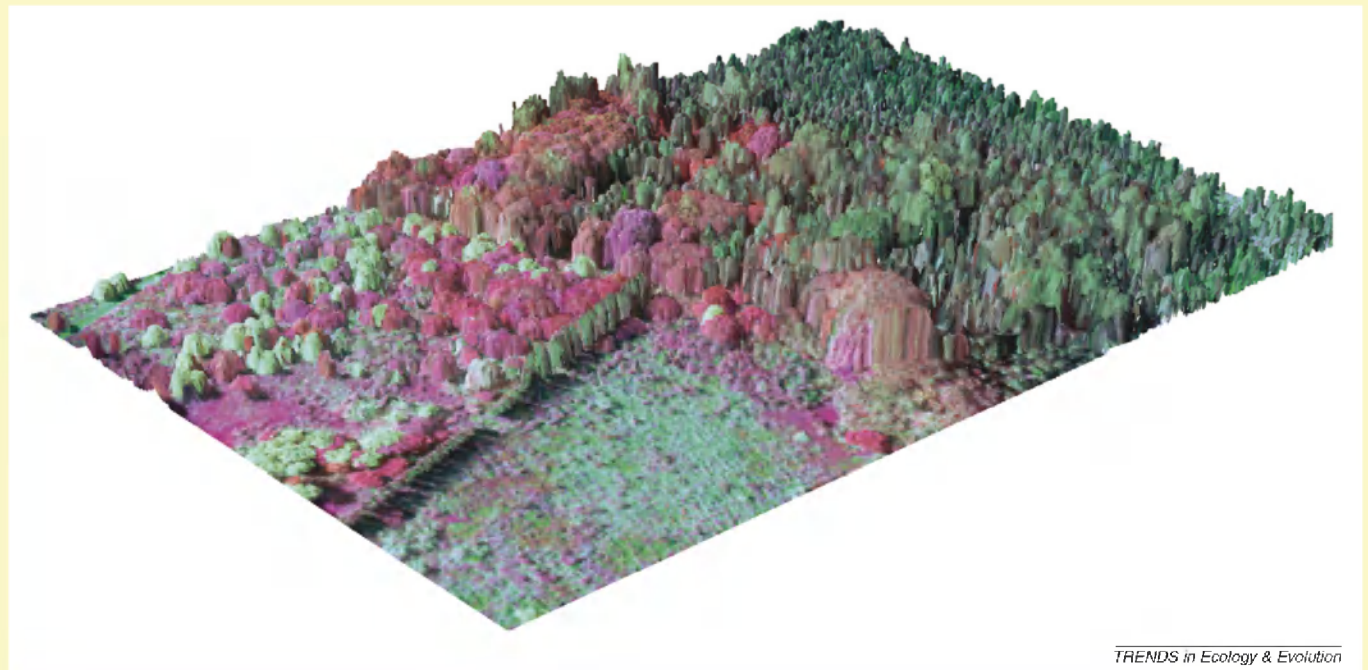
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Figure I. New airborne three-dimensional mapping techniques can provide canopy chemical information for rain forests. This image, taken over an area composed of lowland rain forest and cleared lands on the Island of Hawaii, highlights the distinct chemical signatures of trees and other vegetation in colors ranging from reds to greens. In the foreground, trees and shrubs with high foliar pigment and nutrient concentrations have hyperspectral signatures that convert to red and pink colors and, in this particular case, are composed of fast-growing invasive taxa including *Falcataria moluccana*, *Psidium cattleianum* and *Melastoma* spp. Slow-growing, native hardwoods in greens and blues include *Metrosideros polymorpha* and *Psychotria* spp. Canopy heights and crown sizes show the relative size and aboveground biomass of the species.
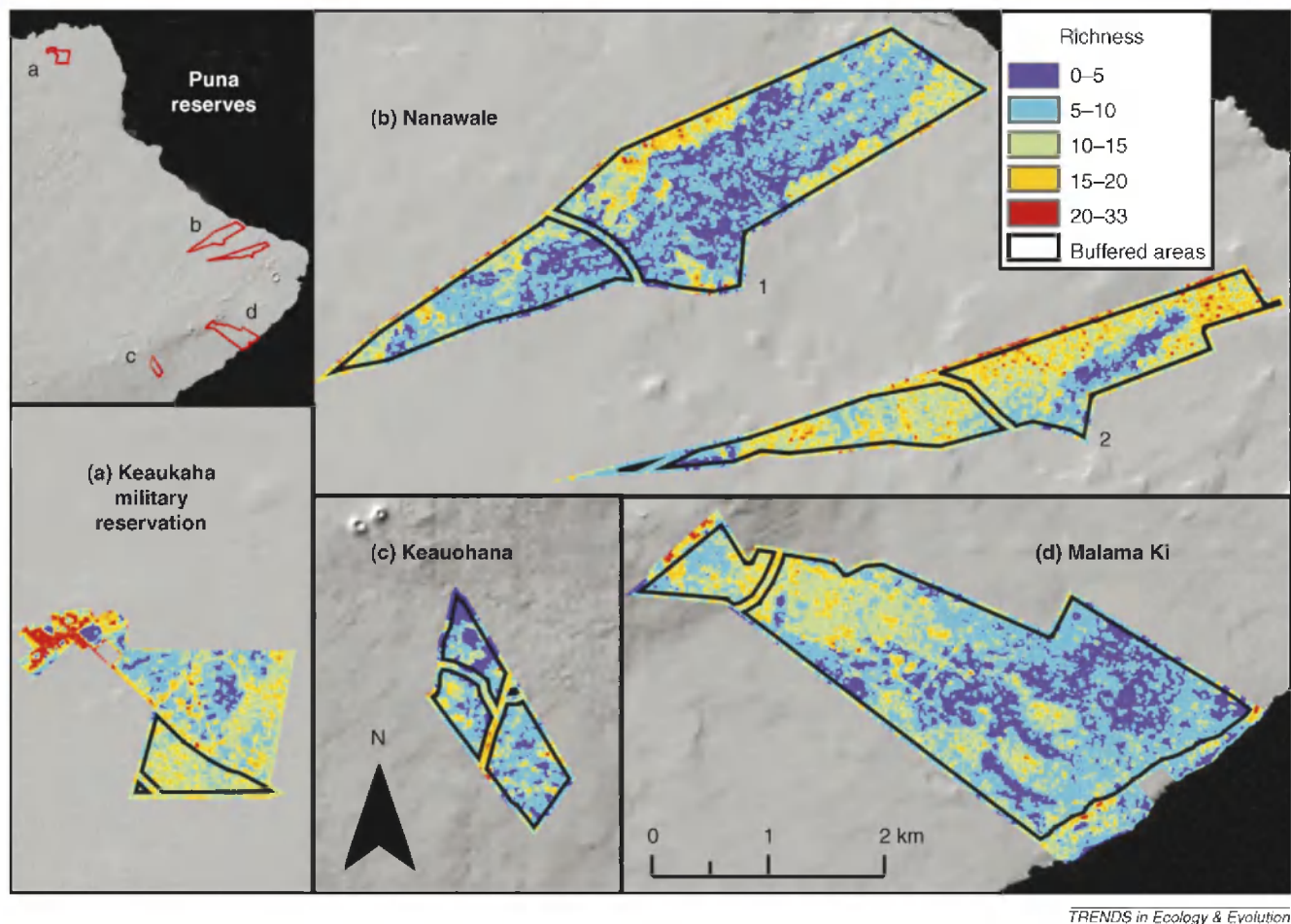
Figure II. New airborne imaging technologies and analytical methods provide a way to detect and map canopy species richness based on biochemical variation across landscapes. In this image, high-fidelity imaging spectroscopy and biochemical detection techniques were used to map canopy species richness (number of species per 0.1 ha) throughout lowland rain forest reserves on the Island of Hawaii [46]. Colors denote species richness levels; black lines indicate the buffered areas within which field measurements were collected, showing that remotely sensed species richness was highly correlated with field-measured richness [46]. The technique relies on the fact that canopy species often maintain unique chemical signatures composed of nutrients, pigments, water and secondary compounds. These chemical signatures translate to spectroscopic signatures that vary with species richness, as shown in Box 1, Figure Ic. New spectroscopic variance approaches such as this one might facilitate canopy species richness mapping over other tropical forests, but additional field and airborne research is needed to test these approaches from the leaf to landscape level. Reproduced with permission from Springer Science and Business Media.

processes at small scales and to extrapolate those measurements to large scales. Fortunately, a range of airborne and space-based remote sensing technologies hold real promise for overcoming the challenges posed by the biogeochemical complexity of the tropical biome. Although some broad-scale phylogenetic differences are likely to be discernible in basic color–infrared images, spectral differences among specific tropical forest canopy species are often very subtle [44]. However, recent work suggests that the foliar chemical signatures of individual canopy species might be accessible using new airborne instruments and techniques (Box 2). Early steps in this effort show that even a handful of key chemicals within the forest canopy can denote the presence of species and/or plant functional types [45], and can even provide information about the species richness of tropical forest canopies [46].

Despite this early progress, it is still unclear how plant canopy chemical signatures are expressed taxonomically, that is, whether they vary at individual, species, genera or family levels. The data available today suggest that chemical and spectral variation is pronounced among species

(http://spectranomics.stanford.edu), which both helps and hinders the effort to map canopies. If chemical–spectral signatures are species specific, then the remotely sensed data should be useful for determining species diversity in the canopy [46]. However, extremely high taxonomic diversity, as found in some of the CTFS plots in Malaysia and Ecuador [26], would likely limit the utility of the remote sensing algorithms available today. New databases and algorithms are needed in combination with the new remote sensing instrumentation to make the linkages between chemical, spectral and taxonomic diversity in tropical forests [47].

If and when these remote sensing challenges can be met, high-resolution maps of canopy chemistry, structure and perhaps taxonomy hold tremendous promise for improving our ability to accurately estimate biogeochemical processes at multiple scales. In combination with targeted, on-the-ground campaigns, such maps could possibly resolve the effects not only of high chemical and structural variation on carbon uptake at the scale of individual trees but across multiple (often remote) regions as well. Moreover, the

potential importance of canopy chemistry on driving litter and soil processes creates another opportunity for the remote sensing approaches, in that it might be possible to use them to better estimate not only canopy function but also some key processes that occur at and beneath the forest floor. A coordinated acquisition of more on-the-ground data in tropical environments with the development of new remote sensing platforms and algorithms is both a grand challenge and a significant opportunity for modern ecology.

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