REPORT

Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation

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Functional biogeography may bridge a gap between field-based biodiversity information and satellite-based Earth system studies, thereby supporting conservation plans to protect more species and their contributions to ecosystem functioning. We used airborne laser-guided imaging spectroscopy with environmental modeling to derive large-scale, multivariate forest canopy functional trait maps of the Peruvian Andes-to-Amazon biodiversity hotspot. Seven mapped canopy traits revealed functional variation in a geospatial pattern explained by geology, topography, hydrology, and climate. Clustering of canopy traits yielded a map of forest beta functional diversity for land-use analysis. Up to 53% of each mapped, functionally distinct forest presents an opportunity for new conservation action. Mapping functional diversity advances our understanding of the biosphere to conserve more biodiversity in the face of land use and climate change.

Global ecology and conservation are challenged by a disconnection between two scale-dependent views of Earth's biota. One view, based on spatially discontinuous field inventories of species composition, has generated local- to global-scale estimates of biological diversity (1). The other view, from spatially continuous satellite observations, partitions the world into vegetation classes, such as forests and grasslands (2), with further analysis of vegetation properties, such as leaf cover and biomass (3, 4). An example of the disconnection between these two views is that forest cover and biomass are weak indicators of biological diversity (5).

The concept of functional diversity can bridge the disconnection between biological diversity and ecosystem processes (6). Functional diversity is the value and distribution of traits among organisms that simultaneously influence their individual fitness and ecosystem functioning. Studies of traits among communities of coexisting plant species have shown that plant floristic and functional composition can track one another in space and time (7). In turn, the functional diversity of plant communities affects ecosystem functioning, and vice versa (8). Despite growing understanding of this interaction, spatially continuous, multivariate plant trait data are lacking for large portions of the biosphere. As a result, little is known about ongoing changes in the functional biogeography of the Earth system, which hampers

spatially explicit strategies to conserve functional diversity in the face of land use and climate change.

Tropical forests, such as in the Andes-to-Amazon region in Peru, are a critical case in point. Beginning with von Humboldt (9), numerous field surveys have generated an enormous bank of plant and animal specimen data for this region, revealing that it harbors the highest biological diversity in the terrestrial biosphere (10, 11). Yet compilations of field taxonomic data do not provide the information needed to construct a geography of forest functional composition or its underlying human and environmental controls. Consequently, there has been no way to assess the portfolio of current protections or the rise of new threats with respect to the functioning of this or other high-diversity regions.

To map tropical forest functional diversity as an indicator of biological diversity and ecosystem processes, the target traits must be (i) functionally relevant, (ii) linked to spatial variation in species and communities, and (iii) accessible using remote sensing approaches. A candidate suite of plant canopy traits may meet these criteria. Foliar nitrogen (N) and water and leaf mass per unit area (LMA) underpin photosynthesis, primary production, and plant responses to climate change (12, 13); are organized by canopy species in tropical forests (14); and have proven to be remotely measureable (15). Foliar defense compounds, such as polyphenols and lignin, are tied to both phylogeny and forest compositional patterns (16) and can be remotely sensed (17). Last, foliar phosphorus (P) and calcium (Ca), which can also be mapped (18), are related to species community turnover in tropical forests (19) and are mediated by topo-edaphic patterns

and biogeochemical processes (20). Mapping these seven canopy traits may offer a new window into the functional diversity of forests, with linkages to biological diversity and ecosystem processes.

Recent methodological advances in airborne laser-guided imaging spectroscopy have made it possible to map these seven canopy foliar traits (21). We used this technique, combined with computational machine learning, to generate multivariate forest functional composition and diversity maps for a large portion of the tropical biosphere (22) (figs. S1 to S8 and table S1). Peruvian tropical forests cover 76 million ha, from hot Amazonian lowlands to cool Andean treelines, and harbor thousands of canopy species. This biodiversity hotspot provides a model system to explore forest functional biogeography across a global range of tropical conditions, and it is under both increasing land-use pressure and conservation focus. With this mapping of forest canopy functional diversity, combined with government land-use data, we assess conservation threats, protections, and opportunities to sustain functional diversity throughout this region.

Our seven mapped forest canopy traits proved to be largely uncorrelated (Fig. 1 and fig. S9), indicating the multidimensionality of derived biogeographic information. These trait maps make no a priori assumptions about forest type or composition, instead expressing top-down, remotely sensed variation in functional composition. Environmental modeling subsequently indicated that geologic substrate and elevation [and thus temperature (23)] are the dominant controls on canopy trait composition (Fig. 1). Secondary drivers include topographic slope, local hydrology, and solar insolation.
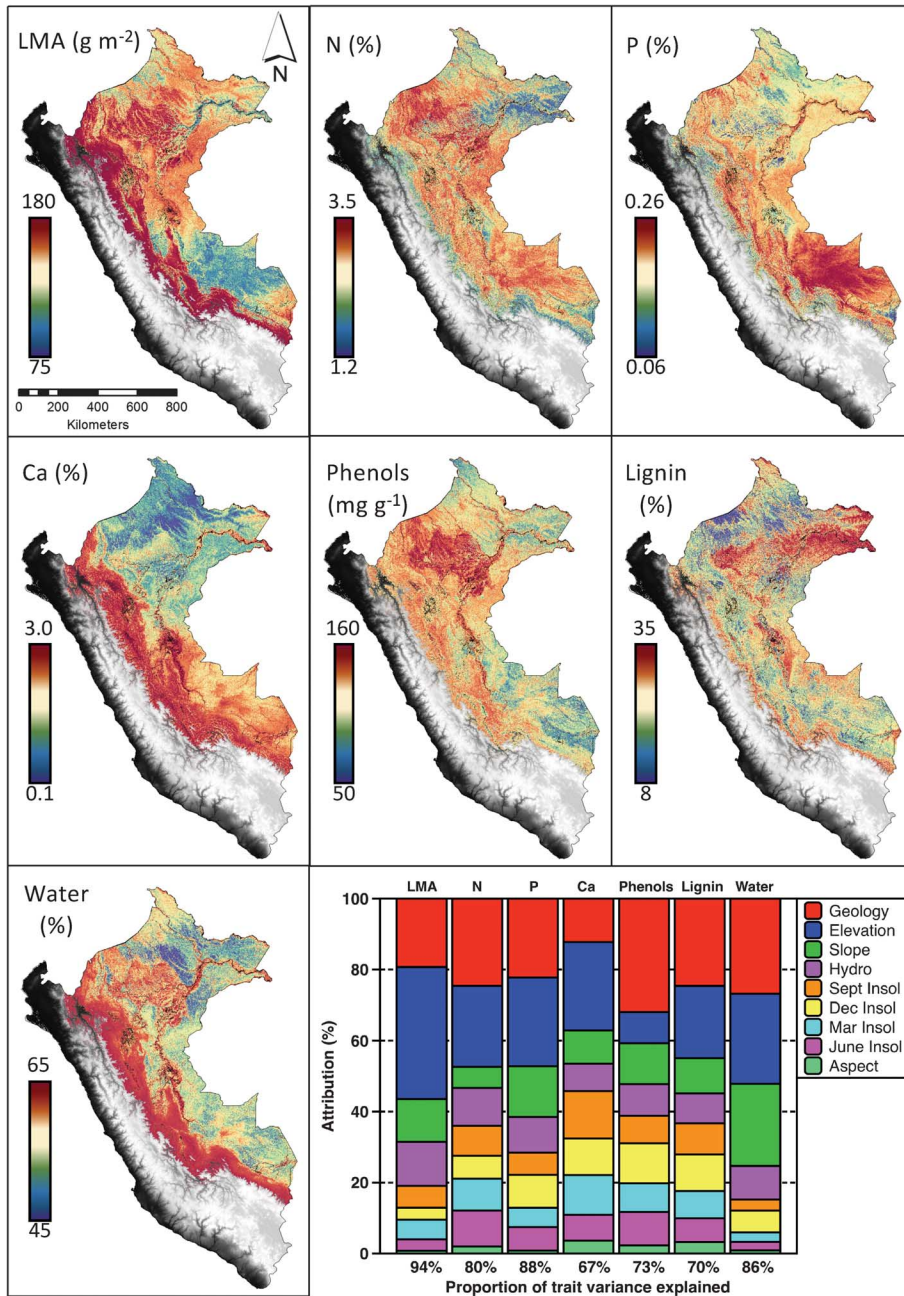
We used 301 forest inventory plots in the Peruvian Andes and Amazon to draw connections between mapped canopy traits and measured floristic composition and community turnover (figs. S14 and S15 and tables S2 to S6). There is a highly significant relationship between canopy functional composition, computed by principal components analysis of the individual trait maps (Fig. 1), and canopy floristic composition, calculated from field inventory data (coefficient of determination R^2 = 0.43, P < 0.001) (fig. S16). Building on this finding, we used cluster analysis to integrate the seven mapped canopy traits into 36 forest functional classes (FFCs), each representing a common suite of functional properties among coexisting species (Fig. 2). The seven traits accounted for 78% of variation among FFCs (fig. S15), and the FFCs mirrored field-based changes in functional traits and floristic composition.

To support our forest functional conservation assessment, we applied a hierarchical clustering algorithm to the 36 FFCs to generate six forest functional groups (FFGs) (Fig. 2C and figs. S10 to S13). These FFGs were recognizable against known regional topo-edaphic and geomorphological features (fig. S12). FFG-1 covers a part of the southern Amazonian lowlands that is centered on the Fitzcarrald Arch geologic feature, and it is characterized by high canopy foliar N and

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Fig. 1. Seven forest canopy traits mapped throughout the Peruvian Andes-to-Amazon region by using airborne imaging spectroscopy and modeling. The graph indicates the attribution of environmental factors and the total variance explained for each canopy trait mapped with airborne imaging spectroscopy. LMA, leaf mass per unit area; hydro, hydrology; insol, solar insolation.

ern lowland Peruvian Amazon, has undergone a 500% increase in deforestation since 2010. Cattle ranching and illegal gold mining are the main drivers of these forest losses (*24, 25*). Additional forest functional groups have been lost at an average 1000 ha yr^{-1} since 2000.

Government land allocation data indicate that petroleum oil exploration and logging together threaten 33% of FFG-1 and 27% of FFG-3 in the southern and northern lowlands, respectively (Fig. 3, Table 1, and table S7). In contrast, 28 to 32% of FFG-2 and FFG-4 are threatened primarily by petroleum activities. Andean forests in FFG-6 are proportionally less threatened (12%) by these activities. However, these threat tallies do not include the explosive rate of deforestation associated with gold mining and oil palm expansion under way in FFG-1 and FFG-3, respectively. Although these sources of loss contribute to the deforestation results, government land-use allocation data do not exist for these activities to support threat analyses.

Between 32 and 46% of each mapped FFG is currently protected (Fig. 3, Table 1, and table S7), of which about two-thirds are under government control and one-third is on indigenous lands. The largest current protections are in FFG-1 and FFG-2, followed by FFG-4 and FFG-6. The massive peat forests of FFG-5, however, are afforded less government protection, relying more on the efficacy of indigenous occupancy for protection. Our analysis also revealed large tracts of officially unallocated forest functional diversity arrayed throughout the region, including 21 to 53% of the mapped FFGs and their contributing functional classes. Of these opportunities for conservation, lowland Amazonian forests in northern Peru, consisting primarily of FFG-2 and FFG-3, offer more than 12 million ha. An additional 3 million ha of northern peatland forest (FFG-4) could be protected. Perhaps most critically, 6.4 million ha of submontane and high Andean forests today go without officially reported land tenure and are highly threatened by unofficial uses. These mountain forests contain distinct functional compositions relative to forests in the western Amazon (*26*), thus offering important opportunities for protection.

Our maps uncover previously unknown variation in functional composition, geographically sorted by elevation (temperature), geology, and hydrology and with quantifiable linkages to forest canopy floristic composition. Previous work revealed the high beta floristic diversity of the Andes-to-Amazon region, along with several key environmental controls over it (*11*). We found equally high levels of intercommunity functional trait variation, or beta functional diversity, which may eventually provide the spatially explicit context needed to connect floristic composition and biospheric processes.

A recent Amazon modeling study suggests that strong within-community variation in canopy traits begets resilience to climate change by allowing some functional types to flourish while others decline with increasing temperature (*27*). Although field studies agree that high forest

low defense compound investment. FFG-2 extends over portions of the northern lowlands on very low-fertility clay substrates harboring canopies with low foliar P and Ca and high phenol- and lignin-based defense investments. FFG-3 is found in the lowland Amazonian floodplains in areas of high rock-derived cation deposition. FFG-4 is located in P-rich colluvial deposition zones at the base of the Andes. FFG-5 is found in anoxic swamp regions of the Pastaza-Maranon foreland basin, where canopy foliar N and P are

low and defenses are high. Last, FFG-6 covers the submontane to montane reaches of the Andes, where LMA and leaf water content are high, and foliar N and Ca are low in concentration.

Applying government deforestation data (fig. S17) to the FFG map, we found that the highest deforestation rates of up to 7000 ha yr^{-1} occurred in FFG-4 (fig. S18), which contains five FFCs found in the high-fertility colluvial deposition region at the base of the Andes. We also found that FFG-1, which includes six FFCs in the south-

canopy functional diversity exists within tree communities (*28*), our maps reveal large-scale beta functional diversity mediated by nested, overlapping biogeophysical controls, occurring in a pattern expressing combinations of threshold-type (i.e., abrupt changes in underlying geology) and gradient-type (i.e., decreasing temperature at progressively higher elevation) environmental filters. Understanding this pattern will allow the investigation and perhaps forecasting of the differential resilience of functionally distinct forest communities to changing climate.
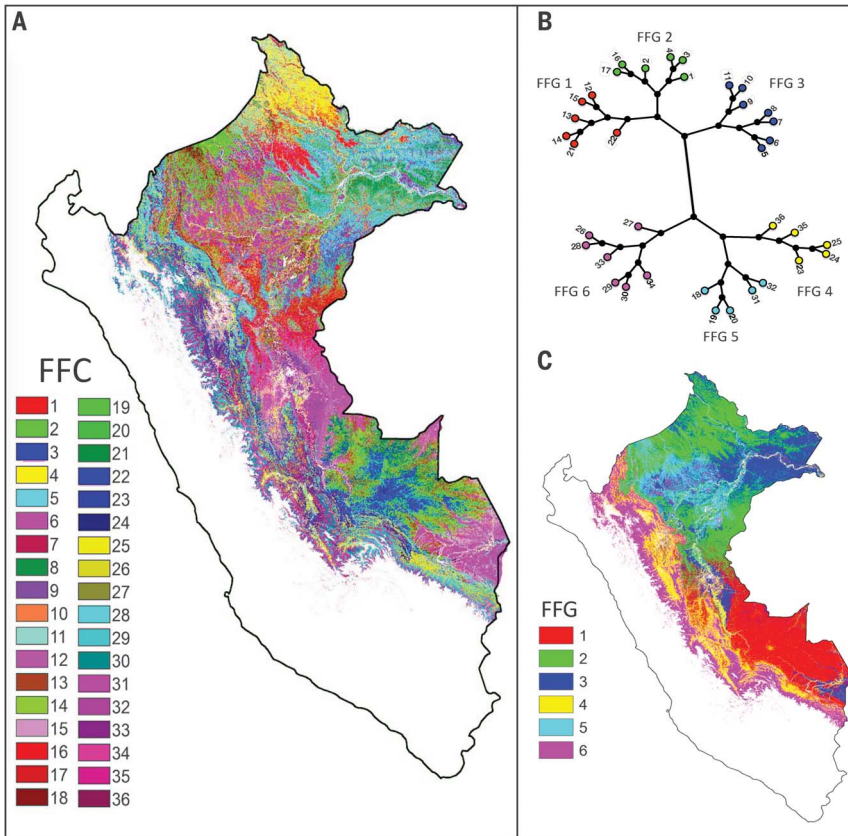
Fig. 2. Forest functional diversity of the Peruvian Andes-to-Amazon region. (**A**) Classification based on seven forest canopy traits derived from airborne imaging spectroscopy, yielding 36 forest functional classes (FFCs). (**B**) Clustering of FFCs based on mapped canopy traits (Fig. 1) into six associated forest functional groups (FFGs). (**C**) The six FFGs used for land-use analyses.
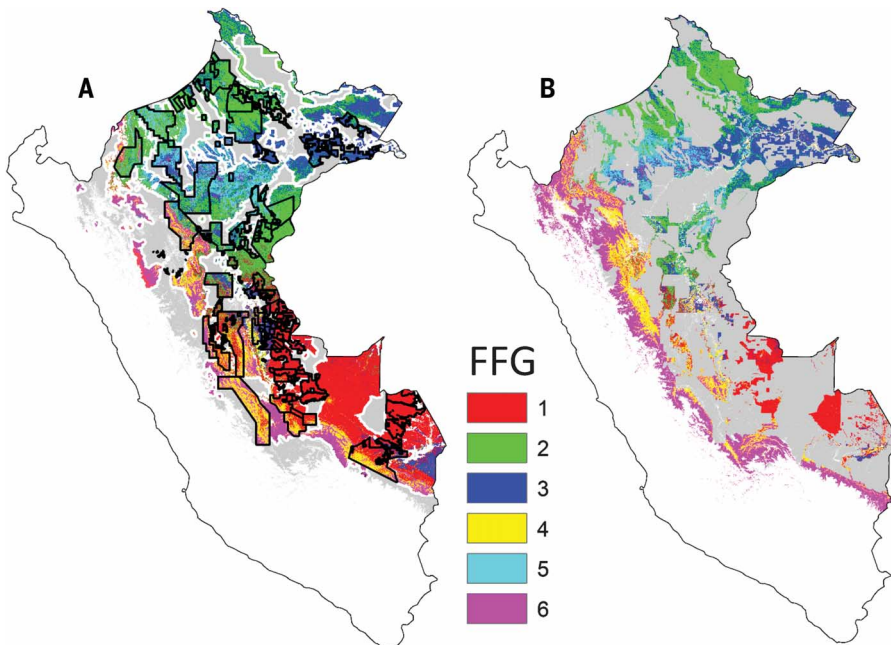
Fig. 3. Threats, protections, and conservation opportunities for forest functional diversity in the Peruvian Andes-to-Amazon region. (**A**) Geographic distribution of threats (outlined in black) and protections (outlined in white) for each FFG. (**B**) Officially unallocated lands representing opportunities for conservation in each FFG.

Table 1. Area in hectares of six FFGs in threatened, protected, or unallocated (conservation opportunities) land-use categories. The percentage of each FFG (Fig. 2) assigned to threats, protections, and opportunities is also shown.

		1	2	FFG 3	4	5	6	Total area
Threats								
Logging concessions*		3,147,800	1,171,625	1,735,016	467,877	242,229	327,048	7,091,595
Petroleum concessions†		3,064,724	5,097,269	2,096,483	2,392,255	1,922,711	1,204,911	15,778,437
	Total threatened	6,212,524	6,268,894	3,831,499	2,860,132	2,164,940	1,531,959	22,870,032
	% FFG threatened	33%	32%	27%	28%	27%	12%	
Protections								
Government-protected areas‡		4,960,816	4,527,071	2,820,643	2,031,961	1,329,202	3,080,210	18,749,903
Nongovernment-protected areas§		143,865	14,225	126,613	3104	4401	568	292,776
Indigenous lands		2,664,384	2,655,862	1,593,469	2,033,783	1,575,443	1,400,778	11,923,719
Brazil nut concessions		790,084	1509	53,953	16,438	1013	2213	865,210
Rubber concessions		15,056	—	226	303	—	—	15,610
	Total protected	8,574,205	7,198,689	4,594,904	4,085,589	2,910,062	4,483,769	31,847,218
	% FFG protected	46%	37%	32%	40%	36%	35%	
Opportunities								
Lowland Amazonia (<500 m)		3,720,909	6,222,913	5,961,815	1,147,344	2,915,631	546,039	20,514,651
Submontane forests (500 to 2000 m)		107,212	14,141	12,579	2,114,397	30,141	2,730,367	5,008,837
High Andean forests (>2000 m)		—	—	—	3395	6453	3,593,827	3,603,680
	Total unallocated	3,828,121	6,237,054	5,974,399	3,265,136	2,952,225	6,870,233	29,127,168
	% FFG unallocated	21%	32%	41%	32%	37%	53%	

*Peruvian Ministry of Environment (http://geoservidor.minam.gob.pe). †PetroPeru (www.perupetro.com.pe). ‡Includes national parks and reserves, communal reserves, protected forests, national sanctuaries, wildlife refuges, and similar designations. §Includes ecotourism, conservation, wildlife, and reforestation concessions.

The threats and conservation opportunities revealed through mapping forest beta functional diversity could guide initiatives to further mitigate ongoing losses in the Andes-to-Amazon case or any other region. Conservation strategies often attempt to secure differing portfolios of biological diversity, yet such efforts have been blind to the geography of functional diversity, which may be more prognostic of climate change sensitivity (29). By emphasizing functional composition, conservation plans can be crafted to address challenges such as the size, location, and connectivity of protected areas required to support forest functional migration in response to climate change and shrinking habitat. At the biospheric scale, a refocus on the protection of functional diversity is likely to save species anyway, because biological and functional composition are interdependent (7, 8). Given the rapid pace of environmental change, accelerated mapping of global functional diversity is critically needed.

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Editor's Summary

Airborne spectroscopy for forest traits

The development of conservation priorities in the tropics is often hampered by the sparseness of ground data on biological diversity and the relative crudeness of larger-scale remote sensing data. Asner *et al.* developed airborne instrumentation to make large-scale maps of forest functional diversity across 72 million hectares of the Peruvian Andes and Amazon basin (see the Perspective by Kapos). They generated a suite of forest canopy functional trait maps from laser-guided imaging spectroscopy and used them to define distinct forest functional classes. These were then compared with government deforestation and land allocation data, which enabled an analysis of conservation threats and opportunities across the region.

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