A global remote sensing mission to detect and predict plant functional biodiversity change

Walter Jetz* (Yale University), Jeannine Cavender-Bares* (University of Minnesota), Ryan
Pavlick (Jet Propulsion Laboratory, California Institute of Technology), David Schimel (Jet
Propulsion Laboratory, California Institute of Technology), Frank W. Davis (University of
California, Santa Barbara), Gregory P. Asner (Department of Global Ecology, Carnegie
Institution of Washington), Robert Guralnick (Florida Museum of Natural History, University
of Florida), Jens Kattge (Max Planck Institute for Biogeochemisty, Jena), Andrew M. Latimer
(University of California, Davis), Paul Moorcroft (Harvard University), Michael E.
Schaepman (University of Zurich), Mark P. Schildhauer (NCEAS, University of California,
Santa Barbara), Fabian D. Schneider (University of Zurich), Franziska Schrodt (Max-Planck
Institute for Biogeochemisty), Ulrike Stahl (Max-Planck Institute for Biogeochemisty, Jena),
Susan L. Ustin (University of California, Davis).

* Contributed equally. Address for correspondence: <u>walter.jetz@yale.edu</u>; <u>cavender@umn.edu</u>

The world's ecosystems are losing biodiversity fast. A satellite mission designed to track changes in plant functional diversity around the globe could deepen our understanding of the pace and consequences of this change and how to manage it.

The ability to view Earths' vegetation from space is a hallmark of the space age. Yet decades of satellite measurements have provided relatively little insight into the immense diversity of form and function in the plant kingdom in space and time. Humans are rapidly impacting biodiversity around the globe^{1,2}, leading to the loss of ecosystem function³, and the goods and services they provide^{4,5}. Recognizing the gravity of this threat, the international community has committed to urgent action to halt biodiversity loss⁶⁻⁹.

Ecosystem processes^{10–12} are often directly linked to the functional biodiversity of plants, that is, to a wide range of plant chemical, physiological and structural properties, connected to the uptake, use and allocation of resources. The functional biodiversity of plants varies in space and time and across scales of biological organization. Capturing and understanding this variation is vitally important for tracking the status and resilience of Earth's ecosystems, and for predicting how our ecological life support systems will function in the future.

We currently lack consistent, repeated, high-resolution global-scale data on the functional biodiversity of the Earth's vegetation^{2,10–12}. However, the technological tools, informatics infrastructure, theoretical basis, and analytical capability now exist to produce this essential data. Here we suggest that this capability is utilized in a satellite mission supporting a Global Biodiversity Observatory, that tracks temporal changes in plant functional traits across the globe to fill critical knowledge gaps, aid in the assessment of global environmental change, and improve predictions of future change. The continuous, global coverage in space and time such a mission would provide has the potential to transform basic and applied science on diversity and function, and to pave the way to a more mechanistically detailed representation of the terrestrial biosphere in Earth system models.

The data and knowledge gap

Plant functional biodiversity encompasses the wide-ranging variation in the chemical physiological and morphological properties of plants, such as the concentration of metabolites and nonstructural carbohydrates in leaves and the ratio of leaf mass to leaf area. These attributes are related functionally to the uptake, allocation and use of resources, such as carbon and nutrients, within the plant, and to defense against pests and environmental stresses.

Functional properties vary within and among individuals (for instance as determined by the position of a leaf on a plant, or a tree in a forest), populations, species and communities, and may be measured at any of these levels of biological organization. With increasing spatial scale (and thus decreasing spatial resolution of measurement), the capture of functional properties may increasingly represent the aggregate properties of many individuals and species, reflecting the functional biodiversity of whole communities. Aggregate "functional diversity" metrics that characterise the breadth of functional properties of a group of organisms are known to be strongly associated with taxonomic¹³ and phylogenetic¹⁴ measures of biodiversity and their potential decrease under habitat loss¹⁵. Plant functional biodiversity is also closely linked to ecosystem processes such as carbon, water and energy exchange, which enables a direct integration with Earth system models^{16,17}. Global information on the functional composition and diversity of plant communities thus provides a necessary foundation for monitoring,

understanding and predicting the productivity of ecosystems, and for relating productivity and carbon uptake to other critical ecosystem services.

Available global data on plant functional biodiversity are grossly incomplete and nonrepresentative taxonomically, geographically, environmentally, temporally and functionally. While datasets of traits and their connection to function continue to grow^{18,19}, local observations of plant functional traits are limited along multiple dimensions. On average, only around 2% of currently known vascular plant species have any trait measurements available at the regional scale (here defined as a 110 km x 110 km grid cell, N = 11,626), and the portion is even smaller in the species-rich tropical regions (Fig. 1). Data on other biodiversity attributes such as species occurrence, abundance, and biomass hold similar biases^{20,21}. These spatial and environmental data gaps and biases are exacerbated by even scarcer information on temporal variation in plant functional biodiversity. Even in areas in which current data are relatively complete, widespread biodiversity change driven by anthropogenic pressures is rapidly outpacing incremental gains in our knowledge of the Earth's biodiversity afforded by *in situ* biodiversity sampling²². Furthermore, existing "global" datasets have not been collected consistently or systematically, but instead compiled post hoc from thousands of disparate research activities, often not designed to address long-term trends or large-scale patterns²³. These severe sampling inhomogeneities and resulting biases are not readily overcome statistically, and continue to impose severe limits on inference and application in global biodiversity science^{21,24,25}. An integrated system for rapidly and consistently monitoring plant functional diversity globally is thus urgently needed.

Filling the gap

Remote sensing has already proven itself to be a pivotal technology for addressing the global biodiversity data gap. Data on plant productivity, phenology, land-cover and other environmental parameters from MODIS and Landsat satellites currently serve as reasonably effective covariates for spatiotemporal biodiversity models based on *in situ* data^{12,20,26}. However, the coarse spectral resolution of current satellite-borne sensors has so far prevented a more direct capture of biodiversity, and correlative models are limited by the above-mentioned data gaps.

In contrast, imaging spectroscopy is a well-established, continuously advancing technology capable of monitoring terrestrial plant functional biodiversity in a way that is vastly richer and more sensitive than other remote sensing techniques^{22,27,28}. It captures environmental information at extremely fine spectral resolution by simultaneously mapping the reflectance and emission of light from the Earth's surface in hundreds of narrow spectral bands, producing essentially continuous spectra from the visible to infrared wavelengths²⁹. Distinctive features are imprinted in these spectra as light interacts with the chemical bonds and structural composition of plants. Spectra are thus an aggregate signal of the chemical and structural composition of vegetation, and can be directly related to a number of leaf biochemical and morphological functional traits (Table 1; 30-32). Air- or satellite-borne spectrometers are able to measure the aggregate functional traits of plant communities represented in the top layers of vegetation, and even the attributes of single species directly, depending on community spatial and spectral characteristics³³. This capability has been successfully demonstrated using airborne spectrometers for many traits at regional scales across multiple biomes^{34,35}. Similar techniques exist at various stages of development for characterizing freshwater³⁶ and tidal ecosystems³⁷, marine phytoplankton^{38,39} and coral reefs⁴⁰. Satellite technology is now poised to provide global coverage at spatial resolutions sufficiently fine (30 m to 60 m pixel size) to support biodiversity inference and applications.

Linking spectra, traits, phylogenies and distributions across scales

A Global Biodiversity Observatory would integrate remotely sensed information on functional traits together with other remotely sensed information and *in situ* observations of phylogenetic relationships, functional traits and species distributions (Fig. 2). Such an Observatory would not be without challenges. Cloud cover, especially in the tropics, poses constraints for any optical remote-sensing method aiming to be spatially and temporally representative (but see 41 for some encouraging evidence regarding space-based spectrometry). Further, direct measurements of plant traits by imaging spectroscopy are currently limited to only those traits with a clear spectral signature expressed in the canopy layer (Table 1), rendering root and stem traits hard to capture. Finally, the vast quantity of data generated will constrain the spatial resolution a global mission can support, at least initially: envisioned spatial grains of around 30m will limit the direct capture of individuals or stands of single species to select cases.

The convergence of imaging spectroscopy with other remote sensing advances, together with prominent developments in plant biology and biogeography, can pave the way to a more integrated global assessment of plant functional biodiversity. Specifically, spectroscopic trait measurements combined with LiDAR data on ecosystem vertical structure at similar spatial resolutions may dramatically enhance the ecological interpretation of the spectral imagery and help overcome its limitation to surface signals only^{42,43}. In addition, the continuing development of a global plant trait database should provide a means to both directly and indirectly connect, through models, spectral observations from the top layer of vegetation to a variety of plant traits¹⁸. While significant gaps remain (Fig. 1), select trait data has now been collected *in situ* for more than 100,000 vascular plant species, providing a means to both directly and indirectly connect, through models, spectral observations from the top layer of vegetation to a variety of plant traits. And the global phylogeny (tree of life) for plants is becoming ever more complete⁴⁴, enabling researchers to trace the evolutionary history of plant traits within lineages⁴⁵. While for some traits and functions convergent evolution has pulled disparate, and often geographically distant, lineages into functional similarity^{46–49}, traits and associated functions are in many cases conserved to relatively deep phylogenetic levels^{50–52}. In combination, this provides several relevant opportunities. For example, advances in macroevolutionary models and data gap-filling techniques⁵³⁻⁵⁵ when coupled with increasingly complete phylogenies can allow for the prediction of traits for species lacking observations. Further, the strong phylogenetic signal in the individual traits that make up overall functional biodiversity means that spectral observations of aggregate species may in some cases still be meaningfully connected to specific functional properties or clades, and interpreted or monitored as a unit⁵⁶.

The increasing volume of online species occurrence data is a fourth synergistic development that supports the predictive modeling and mapping of species' and plant community distributions⁵⁷. Combined with trait and phylogenetic data, and potentially other ecological information (such as typical stand density), hierarchical statistical models and downscaling techniques^{58,59} may, with some uncertainty, allow the pinpointing of particular species and the make-up of communities. We hypothesize that such predictions will generally be much more effective at coarser levels of biological organization, such as higher-level clades or other well-characterized species groups that can be associated with the aggregate functions of the spectral signal of a pixel.

The envisioned imaging spectroscopy mission will naturally provide only some of the data required for global biodiversity monitoring and modeling. Nevertheless, the model-based

integration of detailed and global spectral information with other remote sensing data and rapidly growing *in situ* biological information points to an array of transformative new opportunities for monitoring plant functional biodiversity through space and time.

Toward a Global Biodiversity Observatory

Scaling up processes from fine-grained local studies to large regions and the globe is an urgent challenge for all of the Earth sciences. Environmental understanding at larger scales requires observations that capture dimensions of the entire system to place the microscale measurements in context. Plant functional biodiversity observations from space have the potential to provide a global context for biodiversity science, and to link the evolutionary and functional diversity of plants at local scales to ecosystem function around the globe. Such information would link key dimensions of diversity to ecosystem processes including the carbon cycle, the water cycle and the provisioning of ecosystem services. And it would revolutionize large-scale research on the stability and resilience of ecosystems to shocks such as drought, fire and pathogen outbreaks. Several space missions planned for launch within this decade ⁶⁰, such as EnMAP ⁶¹ (DLR/GFZ, Germany) and HISUI⁶² (JAXA, Japan), will have some capability for mapping plant functional diversity over limited geographic areas. However, none of these will provide the spatial coverage, repeat frequency or mission duration needed to monitor ecosystem relevant changes in global plant functional biodiversity through time. Satellites technology such as that proposed for HyspIRI⁶³, a mission called for in the 2007 NRC Decadal Survey⁶⁴, would be able to serve the initial remote sensing capabilities of the envisioned Global Biodiversity Observatory, but no satellite development process or launch date has vet been determined.

Predicting how ecosystems and the services they provide will respond to accelerating environmental change requires more comprehensive, globally-consistent and repeated data on the patterns and dynamics of functional biodiversity. Advanced observing technology, available but not yet deployed at scale, integrated with *in situ* measurements⁶⁵ could transform this situation. The envisioned Global Biodiversity Observatory offers vastly more biologically relevant and spatially and temporally highly resolved information about vegetation than any existing or otherwise planned global sampling or observation scheme. Rates of change today are so high that the longer a global spectroscopic mission is delayed, the more biological information is irretrievably lost²². The earliest possible launch of a mission able to spectroscopically monitor key plant functional traits globally is an urgent priority for understanding and managing our changing biosphere.

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Table 1: Key functional plant traits that are remotely observable from space (see Table S1 for additional traits).

Trait	Trait definition	Trait functions	Trait role	Remote observation
Leaf Mass Per Area (LMA) [g m ⁻²]	One-sided area of a fresh leaf divided by its dry mass. The reciprocal is specific leaf area (SLA.	A primary axis of the global leaf economics spectrum ¹¹	49,66,67	34,35,68–70
Nitrogen (N) [%]	Concentration of elemental nitrogen in a leaf or canopy.	Important for photosynthesis and other metabolic processes as a constituent of plant enzymes.	67,71,72	34,35,73–75
Non-structural carbohydrates (NSC) [%]	Direct products of photosynthesis (sugars and starches), not yet incorporated into plant structural components and thus readily assimilable	Useful as an indicator of tolerance to environment stress	76	77
Chlorophyll [mg g ⁻¹]	Green pigments	Responsible for capturing light in the process of photosynthesis.	78,79	35,80,81
Carotenoids [mg g ⁻¹]	Orange and yellow pigments	Involved in the xanthophyll cycle for dissipating excess energy and avoiding oxygen radical damage under stress conditions (drought, chilling, low	82,83	31,35

		nutrients).		
Lignin [%]	A complex organic polymer	Provides mechanical support and a barrier to pest and pathogens; negatively correlated with tree growth rate and microbial decomposition.	84,85	32,35,73,86

Figure 1: The data gap in regional species trait measurements. Latitudinal variation in the number of vascular plant species for which at least one trait has been measured regionally (white, left axis) in relation to all species expected for that region (right, black axis). Regions are here defined as 110 km x 110 km grid cells (N = 11,626), their expected richness is from 25 , and region trait data comes from TRY¹⁸ (version June 2015). Regions are analyzed at the grid cell level and their variation is summarized in latitudinal bands of five degrees width. On average, only ca. 2% of species have any such regional measurements, and the data gap is largest in the tropics, limiting understanding of both biodiversity and of ecosystem function and services.

Figure 2: The Envisioned Global Biodiversity Observatory. Space-based imaging spectrometer sensors capture global spatial data on key functional attributes in time, including leaf mass per area (LMA), nitrogen (N), and non-structural carbohydrates (NSC) and others (Table 1). Other sensors may contribute measurements such as LiDAR. An informatics infrastructure and appropriate modeling techniques connect this information with trait, evolutionary and spatial biodiversity information collected *in situ* worldwide at different spatial scales and levels of biological organization.

References:

- 1. Pereira, H. M., Navarro, L. M. & Martins, I. S. Global Biodiversity Change: The Bad, the Good, and the Unknown. *Annu. Rev. Environ. Resour.* **37**, 25–50 (2012).
- 2. Tittensor, D. P. *et al.* A mid-term analysis of progress toward international biodiversity targets. *Science* **346**, 241–244 (2014).
- 3. Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
- 4. Dobson, A. *et al.* Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology* **87**, 1915–1924 (2006).
- 5. Quijas, S., Schmid, B. & Balvanera, P. Plant diversity enhances provision of ecosystem services: A new synthesis. *Basic Appl. Ecol.* **11**, 582–593 (2010).
- 6. Convention on Biological Diversity. *Decision X/2, The Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets, Nagoya, Japan, 18-29 October 2010.*
- 7. Inouye, D. W. IPBES: global collaboration on biodiversity and ecosystem services. *Front. Ecol. Environ.* **12**, 371–371 (2014).
- 8. Cadotte, M. W., Carscadden, K. & Mirotchnick, N. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* **48**, 1079–1087 (2011).
- 9. Díaz, S. *et al.* The IPBES Conceptual Framework connecting nature and people. *Current Opinion in Environmental Sustainability* **14**, 1–16 (2015).
- 10. Pereira, H. M. et al. Essential biodiversity variables. Science 339, 277-278 (2013).
- Geijzendorffer, I. R. *et al.* Bridging the gap between biodiversity data and policy reporting needs: An Essential Biodiversity Variables perspective. *J. Appl. Ecol.* (2015). doi:10.1111/1365-2664.12417
- 12. Skidmore, A. K. *et al.* Environmental science: Agree on biodiversity metrics to track from space. *Nature* **523**, 403–405 (2015).
- 13. Petchey, O. L. & Gaston, K. J. Functional diversity (FD), species richness and community composition. *Ecol. Lett.* **5**, 402–411 (2002).
- 14. Flynn, D. F. B., Mirotchnick, N., Jain, M., Palmer, M. I. & Naeem, S. Functional and phylogenetic diversity as predictors of biodiversity--ecosystem-function relationships. *Ecology* **92**, 1573–1581 (2011).
- 15. Keil, P., Storch, D. & Jetz, W. On the decline of biodiversity due to area loss. *Nat. Commun.* **6**, 8837 (2015).
- 16. Scheiter, S., Langan, L. & Higgins, S. I. Next-generation dynamic global vegetation models: learning from community ecology. *New Phytol.* **198**, 957–969 (2013).
- Yang, Y., Zhu, Q., Peng, C., Wang, H. & Chen, H. From plant functional types to plant functional traits: A new paradigm in modelling global vegetation dynamics. *Prog. Phys. Geogr.* (2015). doi:10.1177/0309133315582018
- 18. Kattge, J. *et al.* TRY--a global database of plant traits. *Glob. Chang. Biol.* **17**, 2905–2935 (2011).
- 19. Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J. & Kattge, J. The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 13690–13696 (2014).
- 20. Jetz, W., McPherson, J. M. & Guralnick, R. P. Integrating biodiversity distribution

knowledge: toward a global map of life. Trends Ecol. Evol. 27, 151–159 (2012).

- 21. Schimel, D. *et al.* Observing terrestrial ecosystems and the carbon cycle from space. *Glob. Chang. Biol.* (2015). doi:10.1111/gcb.12822
- 22. Schimel, D. S., Asner, G. P. & Moorcroft, P. Observing changing ecological diversity in the Anthropocene. *Front. Ecol. Environ.* **11**, 129–137 (2013).
- 23. Scholes, R. J. *et al.* Ecology. Toward a global biodiversity observing system. *Science* **321**, 1044–1045 (2008).
- 24. Sandel, B. *et al.* Estimating the missing species bias in plant trait measurements. *J. Veg. Sci.* (2015). doi:10.1111/jvs.12292
- 25. Kreft, H. & Jetz, W. Global patterns and determinants of vascular plant diversity. *Proc. Natl. Acad. Sci. U. S. A.* **104,** 5925–5930 (2007).
- 26. de Jong, Schaepman, M. E., Furrer, R., Bruin, S. & Verburg, P. H. Spatial relationship between climatologies and changes in global vegetation activity. *Glob. Chang. Biol.* **19**, 1953–1964 (2013).
- Homolová, L., Malenovský, Z., Clevers, J. G. P. W., García-Santos, G. & Schaepman, M. E. Review of optical-based remote sensing for plant trait mapping. *Ecol. Complex.* 15, 1–16 (2013).
- 28. Schaepman, M. E. *et al.* Advanced radiometry measurements and Earth science applications with the Airborne Prism Experiment (APEX). *Remote Sens. Environ.* **158**, 207–219 (2015).
- 29. Schaepman, M. E. *et al.* Earth system science related imaging spectroscopy—An assessment. *Remote Sens. Environ.* **113, Supplement 1,** S123–S137 (2009).
- 30. Asner, G. P. & Martin, R. E. Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. *Front. Ecol. Environ.* **7**, 269–276 (2009).
- 31. Ustin, S. L. *et al.* Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. *Remote Sens. Environ.* **113, Supplement 1,** S67–S77 (2009).
- 32. Serbin, S. P., Singh, A., McNeil, B. E., Kingdon, C. C. & Townsend, P. A. Spectroscopic determination of leaf morphological and biochemical traits for northern temperate and boreal tree species. *Ecol. Appl.* **24**, 1651–1669 (2014).
- 33. Roth, K. L. *et al.* Differentiating plant species within and across diverse ecosystems with imaging spectroscopy. *Remote Sens. Environ.* **167**, 135–151 (2015).
- 34. Singh, A., Serbin, S. P., McNeil, B. E., Kingdon, C. C. & Townsend, P. A. Imaging spectroscopy algorithms for mapping canopy foliar chemical and morphological traits and their uncertainties. *Ecol. Appl.* **25**, null (2015).
- 35. Asner, G. P., Martin, R. E., Anderson, C. B. & Knapp, D. E. Quantifying forest canopy traits: Imaging spectroscopy versus field survey. *Remote Sens. Environ.* **158**, 15–27 (2015).
- 36. Hestir, E. L. *et al.* Measuring freshwater aquatic ecosystems: The need for a hyperspectral global mapping satellite mission. *Remote Sens. Environ.* **167**, 181–195 (2015).
- 37. Turpie, K. R., Klemas, V. V., Byrd, K., Kelly, M. & Jo, Y.-H. Prospective HyspIRI global observations of tidal wetlands. *Remote Sens. Environ.* **167**, 206–217 (2015).
- Palacios, S. L. *et al.* Remote sensing of phytoplankton functional types in the coastal ocean from the HyspIRI Preparatory Flight Campaign. *Remote Sens. Environ.* 167, 269–280 (2015).
- Moisan, T. A. H., Moisan, J. R., Linkswiler, M. A. & Steinhardt, R. A. Algorithm development for predicting biodiversity based on phytoplankton absorption. *Cont. Shelf Res.* 55, 17–28 (2013).
- 40. Hochberg, E. J. in Coral Reefs: An Ecosystem in Transition 25-35 (Springer Netherlands,

2011).

- 41. Mercury, M. *et al.* Global cloud cover for assessment of optical satellite observation opportunities: A HyspIRI case study. *Remote Sens. Environ.* **126**, 62–71 (2012).
- 42. Torabzadeh, H., Hossein, T., Felix, M. & Schaepman, M. E. Fusion of imaging spectroscopy and airborne laser scanning data for characterization of forest ecosystems A review. *ISPRS J. Photogramm. Remote Sens.* **97**, 25–35 (2014).
- 43. Asner, G. P. *et al.* Carnegie Airborne Observatory-2: Increasing science data dimensionality via high-fidelity multi-sensor fusion. *Remote Sens. Environ.* **124**, 454–465 (2012).
- 44. Zanne, A. E. *et al.* Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**, 89–92 (2014).
- 45. Cornwell, W. K. *et al.* Functional distinctiveness of major plant lineages. *J. Ecol.* **102,** 345–356 (2014).
- 46. Reich, P. B., Walters, M. B. & Ellsworth, D. S. From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. U. S. A.* **94**, 13730–13734 (1997).
- 47. Meinzer, F. C. Functional convergence in plant responses to the environment. *Oecologia* **134**, 1–11 (2003).
- 48. Reich, P. B. *et al.* The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies. *Int. J. Plant Sci.* **164**, S143–S164 (2003).
- 49. Wright, I. J. et al. The worldwide leaf economics spectrum. Nature 428, 821-827 (2004).
- 50. Kerkhoff, A. J., Fagan, W. F., Elser, J. J. & Enquist, B. J. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *Am. Nat.* **168**, E103–22 (2006).
- 51. Edwards, E. J. & Still, C. J. Climate, phylogeny and the ecological distribution of C4 grasses. *Ecol. Lett.* **11**, 266–276 (2008).
- 52. Cavender-Bares, J., Ackerly, D. D. & Kozak, K. H. Integrating ecology and phylogenetics: the footprint of history in modern-day communities. *Ecology* **93**, S1–S3 (2012).
- 53. Swenson, N. G. Phylogenetic imputation of plant functional trait databases. *Ecography* **37**, 105–110 (2014).
- 54. Jetz, W. & Freckleton, R. P. Towards a general framework for predicting threat status of data-deficient species from phylogenetic, spatial and environmental information. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **370**, 20140016 (2015).
- 55. Schrodt, F. *et al.* BHPMF a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. *Glob. Ecol. Biogeogr.* (2015). doi:10.1111/geb.12335
- 56. Asner, G. P. *et al.* Amazonian functional diversity from forest canopy chemical assembly. *Proc. Natl. Acad. Sci. U. S. A.* **111,** 5604–5609 (2014).
- 57. Jetz, W., McPherson, J. M. & Guralnick, R. P. Integrating biodiversity distribution knowledge: toward a global map of life. *Trends Ecol. Evol.* 27, 151–159 (2012).
- 58. Gelfand, A. E. *et al.* Modelling species diversity through species level hierarchical modelling. *J. R. Stat. Soc. Ser. C Appl. Stat.* **54**, 1–20 (2005).
- 59. Keil, P., Belmaker, J., Wilson, A. M., Unitt, P. & Jetz, W. Downscaling of species distribution models: a hierarchical approach. *Methods Ecol. Evol.* **4**, 82–94 (2013).
- 60. Staenz, K., Mueller, A. & Heiden, U. Overview of terrestrial imaging spectroscopy missions. in *Geoscience and Remote Sensing Symposium (IGARSS), 2013 IEEE International* 3502–3505 (ieeexplore.ieee.org, 2013).
- 61. Stuffler, T. et al. The EnMAP hyperspectral imager-An advanced optical payload for

future applications in Earth observation programmes. Acta Astronaut. 61, 115–120 (2007).

- 62. Iwasaki, A., Ohgi, N., Tanii, J., Kawashima, T. & Inada, H. Hyperspectral Imager Suite (HISUI) -Japanese hyper-multi spectral radiometer. in *Geoscience and Remote Sensing Symposium (IGARSS), 2011 IEEE International* 1025–1028 (ieeexplore.ieee.org, 2011).
- 63. Green, R. O. *et al.* The HyspIRI decadal survey mission: update on the mission concept and science objectives for global imaging spectroscopy and multi-spectral thermal measurements. in *Proceedings of the International Geoscience and Remote Sensing Symposium (IAGARSS'12)* (ntrs.nasa.gov, 2012). at http://ntrs.nasa.gov/archive/nasa/casi.ntrs.nasa.gov/20120014260.pdf>
- 64. National Research Council, Space Studies Board. *Earth Science and Applications from Space: National Imperatives for the Next Decade and Beyond*. (National Academies Press, 2007).
- 65. Turner, W. Conservation. Sensing biodiversity. Science 346, 301–302 (2014).
- 66. Reich, P. B., Ellsworth, D. S. & Walters, M. B. Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: evidence from within and across species and functional groups. *Funct. Ecol.* **12**, 948–958 (1998).
- 67. Walker, A. P. *et al.* The relationship of leaf photosynthetic traits V cmax and J max to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *Ecol. Evol.* **4**, 3218–3235 (2014).
- Fourty, T. & Baret, F. On spectral estimates of fresh leaf biochemistry. *Int. J. Remote Sens.* 19, 1283–1297 (1998).
- 69. Riaño, D., Vaughan, P., Chuvieco, E., Zarco-Tejada, P. J. & Ustin, S. L. Estimation of fuel moisture content by inversion of radiative transfer models to simulate equivalent water thickness and dry matter content: analysis at leaf and canopy level. *IEEE Trans. Geosci. Remote Sens.* **43**, 819–826 (2005).
- Vohland, M., Mader, S. & Dorigo, W. Applying different inversion techniques to retrieve stand variables of summer barley with PROSPECT + SAIL. *Int. J. Appl. Earth Obs. Geoinf.* 12, 71–80 (2010).
- 71. Evans, J. R. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* **78**, 9–19 (1989).
- 72. Loomis, R. S. On the utility of nitrogen in leaves. *Proceedings of the National Academy of Sciences* **94**, 13378–13379 (1997).
- 73. Serrano, L., Peñuelas, J. & Ustin, S. L. Remote sensing of nitrogen and lignin in Mediterranean vegetation from AVIRIS data. *Remote Sens. Environ.* **81**, 355–364 (2002).
- 74. Martin, M. E., Plourde, L. C., Ollinger, S. V., Smith, M.-L. & McNeil, B. E. A generalizable method for remote sensing of canopy nitrogen across a wide range of forest ecosystems. *Remote Sens. Environ.* **112**, 3511–3519 (2008).
- 75. Knyazikhin, Y. *et al.* Hyperspectral remote sensing of foliar nitrogen content. *Proc. Natl. Acad. Sci. U. S. A.* **110**, E185–92 (2013).
- O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J. & Hector, A. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nat. Clim. Chang.* 4, 710–714 (2014).
- 77. Asner, G. & Martin, R. Spectroscopic Remote Sensing of Non-Structural Carbohydrates in Forest Canopies. *Remote Sensing* **7**, 3526–3547 (2015).
- 78. Govindjee & Rabinowitch, E. Two forms of chlorophyll a in vivo with distinct photochemical functions. *Science* **132**, 355–356 (1960).

- 79. Grimm, B. in eLS (John Wiley & Sons, Ltd, 2001).
- 80. Gitelson, A. A. & Merzlyak, M. N. Remote estimation of chlorophyll content in higher plant leaves. *Int. J. Remote Sens.* **18**, 2691–2697 (1997).
- 81. Siebke, K. & Ball, M. C. Non-destructive measurement of chlorophyll b : a ratios and identification of photosynthetic pathways in grasses by reflectance spectroscopy. *Funct. Plant Biol.* **36**, 857 (2009).
- 82. Björkman, O. & Demmig-Adams, B. in *Ecophysiology of Photosynthesis* 17–47 (Springer Berlin Heidelberg, 1995).
- 83. Demmig-Adams, B. & Adams, W. W., 3rd. Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. *New Phytol.* **172**, 11–21 (2006).
- 84. Melillo, J. M., Aber, J. D. & Muratore, J. F. Nitrogen and Lignin Control of Hardwood Leaf Litter Decomposition Dynamics. *Ecology* **63**, 621 (1982).
- 85. Austin, A. T. & Ballaré, C. L. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proc. Natl. Acad. Sci. U. S. A.* **107,** 4618–4622 (2010).
- 86. Martin, M. E. & Aber, J. D. High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes. *Ecol. Appl.* **7**, 431–443 (1997).



