



Integrating remote sensing with ecology and evolution to advance biodiversity conservation

Jeannine Cavender-Bares¹✉, Fabian D. Schneider², Maria João Santos³, Amanda Armstrong⁴, Ana Carnaval⁵, Kyla M. Dahlin⁶, Lola Fatoyinbo⁴, George C. Hurtt⁷, David Schimel², Philip A. Townsend⁸, Susan L. Ustin⁹, Zhihui Wang¹⁰ and Adam M. Wilson¹¹

Remote sensing has transformed the monitoring of life on Earth by revealing spatial and temporal dimensions of biological diversity through structural, compositional and functional measurements of ecosystems. Yet, many aspects of Earth's biodiversity are not directly quantified by reflected or emitted photons. Inclusive integration of remote sensing with field-based ecology and evolution is needed to fully understand and preserve Earth's biodiversity. In this Perspective, we argue that multiple data types are necessary for almost all draft targets set by the Convention on Biological Diversity. We examine five key topics in biodiversity science that can be advanced by integrating remote sensing with in situ data collection from field sampling, experiments and laboratory studies to benefit conservation. Lowering the barriers for bringing these approaches together will require global-scale collaboration.

The conservation community is at a pivotal moment, with recent international efforts advancing a new set of ambitious global and regional biodiversity targets¹ through the Conference of the Parties (CoP) to the Convention on Biological Diversity (CBD). Any effort to meet these targets requires monitoring dimensions of biodiversity (for example, ref. ²). While it is now possible to remotely observe a suite of biodiversity variables^{3–5} and ecosystem services (or nature's contributions to people)⁶, the information required for understanding how close we are to meeting most of the CBD targets—or other regional targets—goes well beyond the biodiversity variables that can be monitored remotely (Table 1).

Here, we argue that for humanity to understand, monitor and protect biodiversity, a synthesis of information that comes from many kinds of observations, obtained using myriad tools, is necessary (Fig. 1). We present insights on how new remote sensing capabilities can be integrated with process-based approaches to understand the ecological and evolutionary processes that support biodiversity. Because the recent advances in remote sensing of biodiversity and biodiversity-related variables have been extensively discussed elsewhere (for example, refs. ^{3,7–13}), we only review these in brief (Box 1). To explore how the use of remote sensing can go beyond monitoring, we structure the remainder of the paper around five key research topics as examples of where remote sensing can be integrated with other kinds of biodiversity knowledge to advance ecology and evolutionary biology and contribute to conservation.

Several insights emerge from the consideration of these topics for how integrative biodiversity research can be conducted in the service of understanding and managing biodiversity. We argue that

the impact of remote sensing investments will be broadened by lowering the barriers to data access and usability. Inclusive efforts to connect scientific disciplines and subdisciplines and link investigators and practitioners will be critical to ensure rich syntheses of differing kinds of biodiversity data and enhance humanity's capacity to transform biodiversity knowledge to action.

From monitoring to deciphering processes

Detection of pixel content from remote sensing contributes to monitoring needs and complements other kinds of biological knowledge. Yet remotely sensed biodiversity variables do not replace the continued discovery of species, an understanding of genetic composition and diversity of the biota, specimen archival, functional characterization, natural history documentation, evolutionary processes across the tree of life or understanding the ecological role of organisms in the web of life.

Many key aspects of understanding origins and maintenance of biodiversity require methodological tools focused on biological processes. Phenotypic, life history and evolutionary information is most reliably captured at the scale of the individual organism: organisms are better measured and more completely understood through on-site collection, DNA sequencing techniques and comparisons with archived samples^{14,15}. Even as spectroscopic imagery has enhanced our ability to detect intraspecific variation^{16,17}, experiments are necessary to understand how genes interact with the environment to give rise to organismal phenotypes and for linking phenotypes to fitness to understand how natural selection operates on organisms^{18,19}. Plant life history and trait data collected in situ are needed to connect the broad-scale ecosystem responses observed

¹Department of Ecology, Evolution and Behavior, University of Minnesota, St Paul, MN, USA. ²Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA, USA. ³Department of Geography, University of Zurich, Zurich, Switzerland. ⁴Biospheric Sciences Laboratory, NASA Goddard Space Flight Center, Greenbelt, MD, USA. ⁵Department of Biology, Ph.D. Program in Biology, City University of New York and The Graduate Center of CUNY, New York City, NY, USA. ⁶Department of Geography, Environment, and Spatial Sciences, Michigan State University, East Lansing, MI, USA. ⁷Department of Geographical Sciences, University of Maryland, College Park, MD, USA. ⁸Department of Forest and Wildlife Ecology, Univ. of Wisconsin-Madison, Madison, WI, USA. ⁹Department of Land, Air and Water Resources and the John Muir Institute of the Environment, University of California, Davis, CA, USA. ¹⁰Key Lab of Guangdong for Utilization of Remote Sensing and Geographical Information System, Guangdong Open Laboratory of Geospatial Information Technology and Application, Guangzhou Institute of Geography, Guangdong Academy of Sciences, Guangzhou, China. ¹¹Department of Geography, University at Buffalo, Buffalo, NY, USA. ✉e-mail: cavender@umn.edu

Table 1 | An examination of the kinds of scientific tools and data types that are necessary for monitoring and evaluation of progress towards goals A and B and associated milestones delineated by the CBD post-2020 framework draft (CBD/WG2020/3/3/5 July 2021)

Goals and milestones of the CBD/ WG2020/3/3/5 July 2021 relevant to biodiversity and ecosystem assessment	Scientific tools/type of data collection			
	Laboratory	In situ	Remote sensing	Socioeconomic
Goal A. The integrity of all ecosystems is enhanced, with an increase of at least 15% in the area, connectivity and integrity of natural ecosystems, supporting healthy and resilient populations of all species; the rate of extinctions has been reduced at least tenfold and the risk of species extinctions across all taxonomic and functional groups is halved and genetic diversity of wild and domesticated species is safeguarded, with at least 90% of genetic diversity within all species maintained.				
Milestone A1. Net gain in the area, connectivity and integrity of natural systems of at least 5%.	Contributing (for example, microbial community analysis)	Contributing (for example, soil sampling for nutrients and microbes)	Required (for example, ecosystem extent and connectivity)	Contributing (for example, road and infrastructure data)
Milestone A2. The increase in the extinction rate is halted or reversed and the extinction risk is reduced by at least 10%, with a decrease in the proportion of species that are threatened and the abundance and distribution of populations of species is enhanced or at least maintained.	Contributing (for example, genetic analysis)	Required (for example, biodiversity surveys and environmental DNA)	Contributing (for example, environmental data at global extent for habitat suitability models)	Not applicable
Milestone A3. Genetic diversity of wild and domesticated species is safeguarded, with an increase in the proportion of species that have at least 90% of their genetic diversity maintained.	Required (for example, genetic analysis)	Required (for example, tissue samples from wild and domesticated populations)	Contributing (for example, airborne or satellite hyperspectral imagery to identify hot spots of diversity for directed field reconnaissance)	Contributing (for example, livestock distribution data)
Goal B. Nature's contributions to people are valued, maintained or enhanced through conservation and sustainable use supporting the global development agenda for the benefit of all.				
Milestone B1. Nature and its contributions to people are fully accounted and inform all relevant public and private decisions.	Contributing (for example, genetic analysis of germ plasm in storage banks)	Required (for example, water quality assessment)	Required (for example, landscape to regional scale ecosystem services assessment)	Required (for example, analysis of stakeholder preferences, people's relations with nature)
Milestone B2. The long-term sustainability of all categories of nature's contributions to people is ensured, with those currently in decline restored, contributing to each of the relevant Sustainable Development Goals.	Contributing (for example, monitoring of genetic variation within and among populations)	Required (for example, water quality monitoring)	Required (for example, landscape to regional scale ecosystem services monitoring)	Required (for example, assessment of demand for ecosystem services)
The matrix provides a summary of whether laboratory, in situ, remote sensing and/or socioeconomic tools and data collection are either required, contribute to or are not applicable to quantifying components of biodiversity relevant to the milestones under each goal. The authors present examples (in parentheses) of data collection activities within each data category to illustrate how it is required or contributes to the milestone. Laboratory, in situ, remote sensing and socioeconomic data are explicitly examined but other types of data are relevant as well. Remote sensing includes sensors on satellites, planes, unmanned aerial vehicles and other platforms. CBD goals C and D are not considered because they are less directly relevant to assessing biodiversity and ecosystems.				

through remote sensing with the ecological processes happening on the ground²⁰. They allow scientists to identify which physiological, morphological, reproductive or dispersal characteristics enable species to persist locally, to be resilient in the face of environmental shifts or to become locally extinct^{21,22}. Mechanistic explanations for the ecosystem-level responses to climate and landscape changes that can be detected remotely require the collection of physiological, microbial and chemical flux data in controlled experiments that tease apart their drivers and test specific hypotheses about the ecological and evolutionary processes behind them^{23–25}. Legacies from deep time have enormous consequences for biodiversity patterns and processes on Earth today. Calibrating the tree of life, which is essential to understand the time scales across which the history of life on our planet has evolved, requires fossil data obtained from on-site sampling^{26,27}. Whenever palaeoclimatic models or data are available to describe the environmental conditions formerly experienced by a species (often thousands of years ago), it is then possible to project their correlative distribution models into those time periods and identify regions that were probably suitable for them^{28,29}.

Towards an integrative biodiversity science

To understand, monitor and protect biodiversity, an integrative biodiversity science is necessary that extends knowledge of processes at local scales, on the basis of experiments and longitudinal observations, to much larger extents over physiological, ecological and evolutionary time via remote sensing (Fig. 1). Within the remote sensing community, integration often implies validating remotely sensed products and variables with in situ (ground-truth) data or data integration across multiple sensors. Integration in the context of EBVs focuses on selecting remote sensing products from satellite imagery that can contribute to the variables necessary for monitoring biodiversity across scales³. Here, we expand on this level of integration to include synthesis of biological information to understand local processes at larger extents, generation of information not accessible or missing from in situ observations, forecasting dynamics into the future based on understanding of processes from experiments and models and connecting deep-time evolutionary and biogeographic processes to global-scale patterns. Integration may require bridging spatial and temporal scales across hierarchical

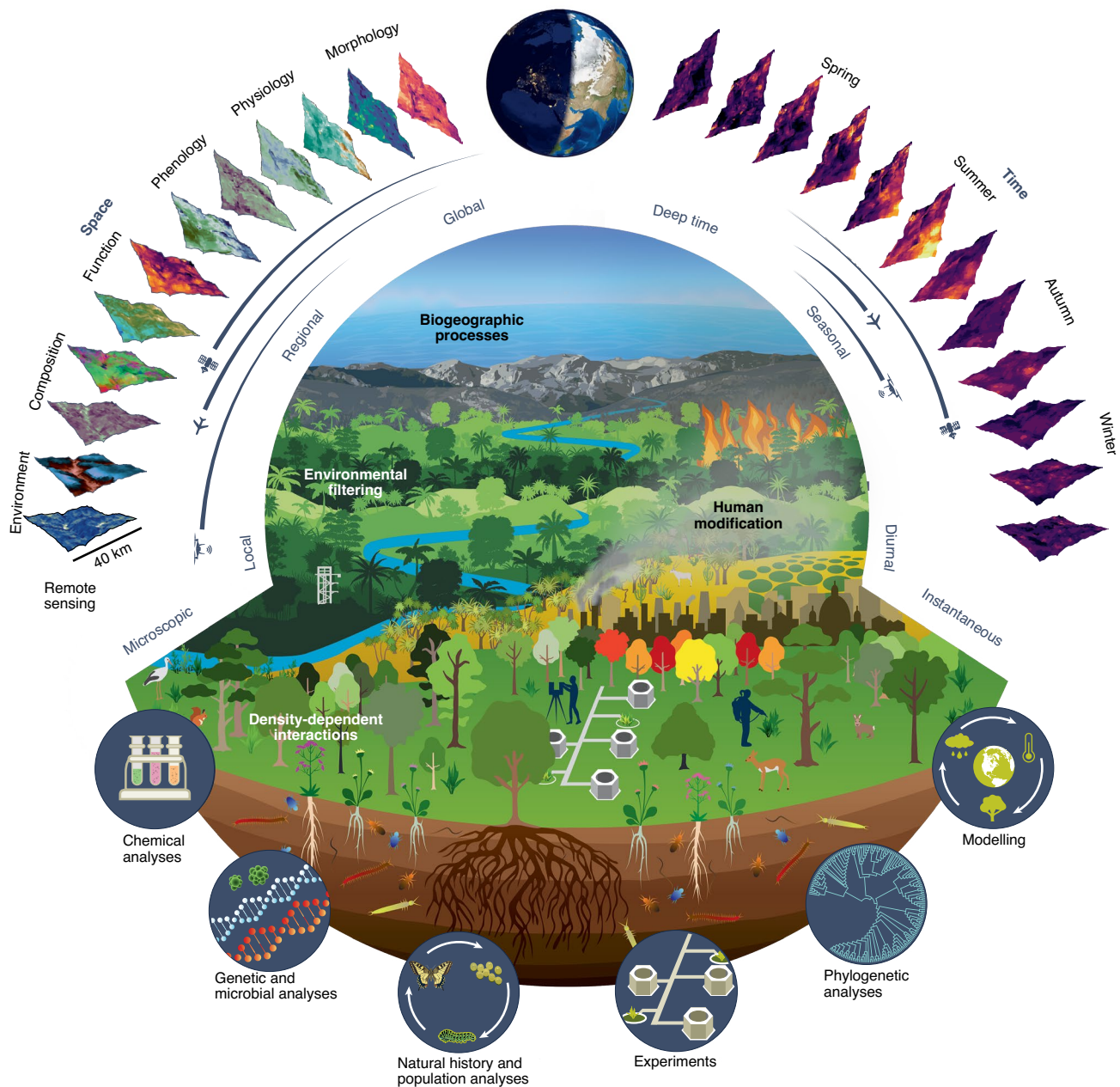


Fig. 1 | The integration of remote sensing and in situ observations, experiments and models as tools to understand biodiversity in the Earth system.

Addressing the challenges of monitoring biodiversity change, understanding its root causes and effectively cogenerated biodiversity knowledge for decision-making requires complementary and collaborative research that integrates tools (remote and in situ observations and analyses, experimentation and modelling) and knowledge of biological, biogeographic and anthropogenic processes across spatial and temporal scales. Remote sensing is a tool that is particularly helpful to characterize the Earth's biophysical environment (including variables related to habitat, climate change and human modification of the Earth system), as well as vegetation composition, function, phenology, physiology and morphology. These observations require integration with the biological understanding gained from the vast advances in biological methods and tools for observing the many dimensions of life above- and below-ground. Example remote sensing data layers are shown at a spatial grain of 1 km and extent of 40 km, for (from left to right): environment—topographic wetness¹⁶⁴ and temperature seasonality¹⁶⁵; composition—variation and average principal components of AVIRIS¹⁶⁶; function—evapotranspiration¹⁶⁷ and sun-induced fluorescence (adapted from ref. ¹⁶⁸, CC BY 4.0); phenology—dynamic habitat index¹⁶⁹ and growing season duration (USGS eMODIS Remote Sensing Phenology, 10.5066/F7PC30G1); physiology—leaf mass per area²⁰ and leaf nitrogen; and morphology—functional beta diversity and richness (adapted from ref. ¹⁶⁴, CC BY 4.0). An example of remotely sensed temporal variation is shown for sun-induced fluorescence at monthly scale¹⁶⁸. Globe: Earth viewer by J. Walker, combining Earth imagery derived from the NASA Blue Marble Terra/MODIS cloudless Earth and NASA Black Marble night lights images. Colour maps: ref. ¹⁷⁰. Figure drawn by D. Tschanz and F.D.S. with J.C.-B. and M.J.S.

levels of biological organization^{30,31} and bringing together data and concepts from different disciplines, cultures and contexts^{32,33}. We also consider integration to mean connecting people and disciplines,

which requires lowering barriers to entry by making data and algorithms easily accessible and usable and building networking opportunities to transfer technology, exchange information and enhance

Box 1 | Advances in global monitoring of biodiversity change

Remote sensing technologies quantify the reflection and emission of radiation from the Earth surface with active sensors such as radar and lidar (that emit energy and receive its reflection) or passive sensors such as imaging spectrometers (that measure reflected or emitted energy over hundreds of adjacent spectral bands)¹⁵⁹.

New satellite capabilities

Satellites, such as Sentinel 1 and 2, Planet and Worldview, have higher spatial resolution than those launched in earlier decades¹⁶⁰. Imaging spectroscopy allows derivation of plant functional traits, functional diversity and spectral measures of vegetation diversity at unprecedented spatial scales^{20,178–183}. New lidar and radar satellites provide a foundation to measure the diversity of primary producers¹⁸⁴ and vegetation canopy structure^{164,185,186} and relate it to other dimensions of biodiversity¹⁸⁷. Multiband thermal imagers and new imagers that measure chlorophyll fluorescence provide information about plant and ecosystem function, composition and response to stress¹⁸⁸. Building on long-term satellite records of vegetation greenness¹⁸⁹, space agencies are planning many new missions for launch by the decade's end that will provide data freely and openly (for example, NASA's SGB, NISAR or ESA's CHIME, BIOMASS).

Essential biodiversity variables

Biological scientists are developing a suite of essential biodiversity variables (EBVs) that capture the attributes of life on Earth to provide the basis for global biodiversity monitoring systems worldwide¹⁹⁰. Some are in advanced levels of development, including species populations¹⁹¹, species traits¹⁹² and species distribution and abundance¹⁹³. EBVs have been increasingly embraced by the remote sensing community^{7,10}, led by the Group on Earth Observations Biodiversity Observation Network (GEO BON), which has developed a pipeline for prioritizing global remote sensing products that can observe EBVs³. These products can be used to monitor some EBV classes quite well and can

contribute to the measurement of others, such as species or populations. Animal tracking from space has also seen major advances^{3,11}. Animal-borne tags are now far smaller and the number of animals that may be tracked much greater, allowing space-based sensing to address animal populations and movement (for example, refs. ^{194–196}).

Current limitations of remote sensing

At the same time, some EBV classes require entirely different observational approaches and some aspects of biodiversity are not yet fully considered by the EBV community, such as macroevolutionary dimensions that capture phylogenetic relationships among species and their origins in deep time. For the great majority of species in the world, statistical relationships, which require in situ data from the field or archived in museums and herbaria to constrain and develop robust predictive models—known as species distribution models or ecological niche models—are the basis for predicting where species are likely to be found. These predictive models can be scaled up and used to characterize in situ diversity^{197,198}. Remote sensing products can provide detailed information on habitat change and loss that provide an indirect means to predict species range shifts^{27–30}. Reliance on these models can be risky, however, especially when species are under pressure from many stressors. Extirpation or even extinction is possible even when correlative models suggest that suitable conditions remain. While remote sensing can fill spatial and temporal gaps and identify areas of conservation concern, in situ data provide biological information not detectable from above. The identity of plant species—often essential to management—can be inferred from remote sensing only in the emergent canopy with sufficient spatial resolution^{97,199}. Even as remote sensing for monitoring plant diversity has improved dramatically in recent decades—with advances in fine-grain mapping of canopy structure and chemistry^{97,200}—detection of understory plants, animals and small organisms such as fungi, bacteria and soil microorganisms remains challenging.

human capacity in respectful and inclusive ways. If we intend to understand how and why biodiversity is changing and what the impacts of biodiversity change are on society, our efforts to integrate and synthesize biological information need to combine biodiversity knowledge with that of Earth and human systems. To extend efforts globally, cogeneration of knowledge among local communities, including Indigenous groups and international science teams and organizations is critical³⁴.

To demonstrate the value of this integrative biodiversity science, we present five fundamental ecology and evolution topics, as example research focal areas, that depend on remote sensing and integration with in situ data. Our focus is on terrestrial systems but parallel considerations can be addressed for marine and aquatic systems. For each topic, we examine why integration of in situ and remote sensing is important, how it can be operationalized and what new understanding of ecological and evolutionary processes or advances toward conservation goals emerge from it.

Influences of evolutionary and biogeographic legacies on ecosystem functioning. Scientists have long pondered how biological change over time has interacted with climate and geology to generate the variation in biota we now observe across the globe^{35–37}. The origins, diversification and long-term expansion and displacement of distinct lineages have led to contrasting floras and faunas across continents³⁸ (Fig. 2). Contemporary and past climatic gradients, the

formation of continents and their position and distribution on the planet have set a range of constraints that have influenced where and how organisms evolved and migrated and the functioning of ecosystems³⁹. The environmental conditions under which species evolved left legacy effects on their functional traits, through phylogenetic conservatism⁴⁰. These traits, in turn, influence their dispersal, species interactions and current ecosystem processes and biomes globally^{41,42}. When interpreting ecological functions from remote sensing, the role of biogeographic history in determining ecosystem functioning is a critical factor, independent of what might be deterministically predicted from the abiotic environment^{41,43}.

To fully understand the influence of these evolutionary legacies on global ecosystems, integrating remote sensing data that describes spatial variation in ecosystem functions with knowledge of the evolutionary history of the flora and fauna and of the functional attributes of the biota, is essential. To infer evolutionary history, scientists combine proxy data such as chemical analyses of cave deposits^{44,45}, fossil information⁴⁶ or palaeoclimatic models⁴⁷ with species inventories and sequencing of DNA from voucher specimens¹⁵. By comparing the number and placement of genetic mutations within a species of interest relative to those of other closely related species, DNA sequencing allows us to generate phylogenetic information to understand the long evolutionary history of all life on Earth^{48,49}. These genetic, phylogenetic and fossil information as well plant functional data and symbiotic, multitrophic associations

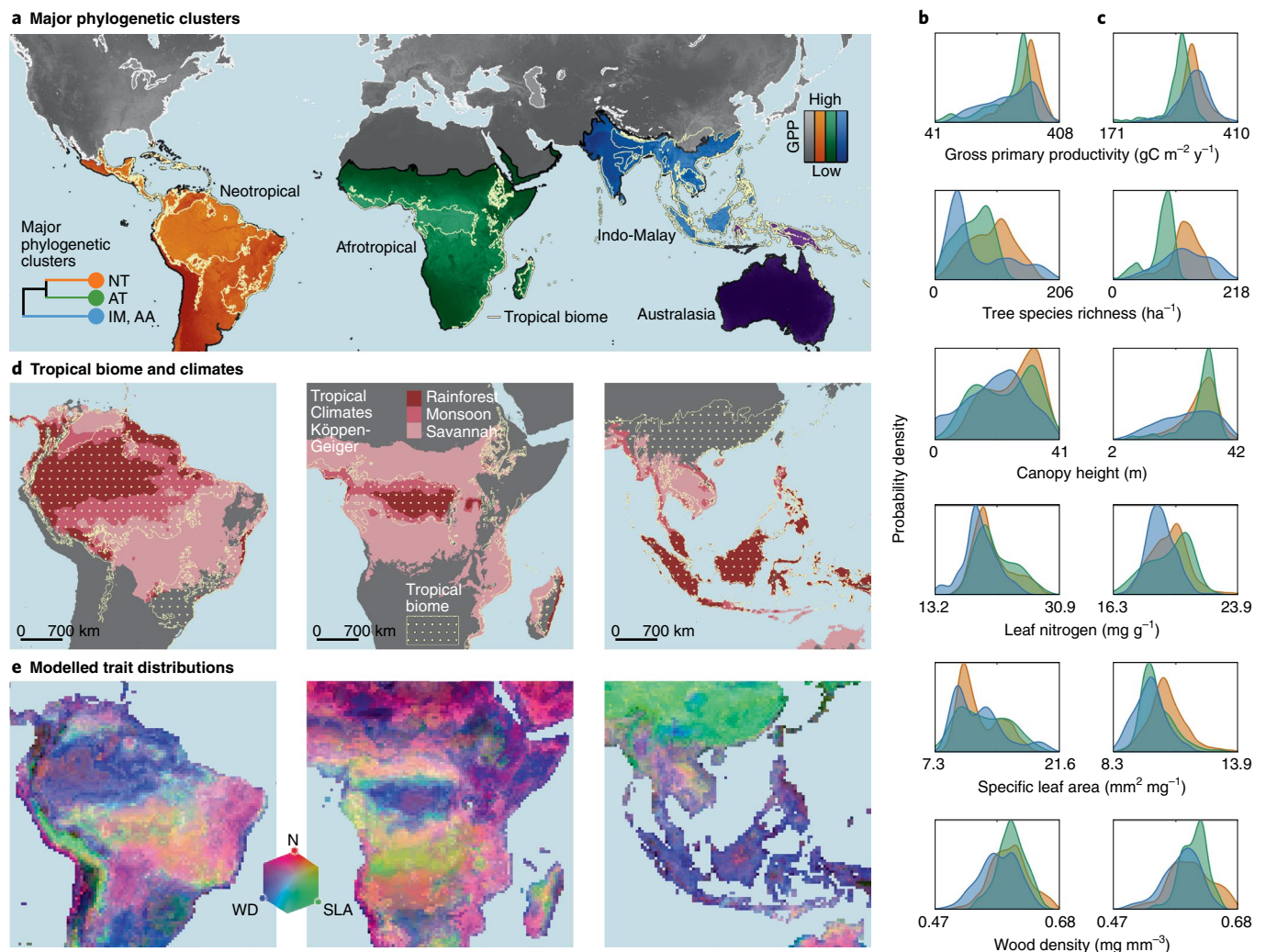


Fig. 2 | Remote sensing can contribute to uncovering the legacies of evolutionary history and human activity that influence the variation in composition and function of ecosystems across tropical floras (Neotropical, Afrotropical and Indo-Malay/Australasia). **a**, Reconstruction of the phylogenetic history across the major tropical floras by Slik et al.³⁸ shows that dominant lineages differ among them as a consequence of long-term biogeographic processes³⁸ such that deep splits in the angiosperm tree of life are associated with different continents. Phylogenetic radiations within continents form major phylogenetic clusters—a pattern that dominates over migration from other continents. Contrasting floras are hypothesized to result in differences in how tropical ecosystems function, even within the same biome or climate zone. Brightness indicates GPP, gross primary productivity by Li and Xiao¹⁷¹. **b,c**, The histograms show differences among major floras in terms of their continental-scale distributions of ecosystem function (gross primary productivity¹⁷¹), modelled tree species richness¹⁷², forest structure (tree canopy height¹⁷³) and plant functional traits (leaf nitrogen (N), specific leaf area (SLA) and wood density (WD), upscaled at 0.5-degree scale¹⁷⁴). The between-continent distributions within the tropical biome are shown in **b** and within the humid tropical rainforest climate zone are shown in **c**. **d**, Outlines of the tropical biome defined by Olson et al.¹⁷⁵ and the climate zones defined by Beck et al.¹⁷⁶. **e**, Globally upscaled in situ trait distributions by Boonman et al.¹⁷⁴ indicate considerable variation in N, SLA and WD across the pantropical region but may lack accuracy, detail and local variability due to currently limited availability of remotely sensed traits and data gaps in in situ sampling. GPP panels in **a–c** adapted from ref. ¹⁷¹, CC BY 4.0; tropical biome boundaries in **a,d**, adapted from ref. ¹⁷⁵; trait distributions in **b,c,e** adapted from ref. ¹⁷⁴, CC BY 4.0; climate zones in **d** adapted from ref. ¹⁷⁶, CC BY 4.0.

above- and below-ground help to determine how and why lineages and ecosystem functions differ across continents. Remote sensing can then enable global detection of how life has unfolded differently across continents by quantifying the contrasting structure and function of distinct floras. It has the ability to capture multiple data layers that can be interpreted as a time series of ecosystem function and structure³, including estimates of productivity⁵⁰, canopy nutrient content⁵¹, functional composition, structural composition and diversity (Fig. 2). The contrasting morphophysiological attributes of forests remotely detected across wet tropical biomes lead to the hypothesis that ecosystem functions differ across continents, even

in the same climatic zone, as a consequence of contrasting historical biogeographic and phylogenetic histories (Fig. 2).

What do we gain from integration? Because all variation in life is the outcome of evolution, understanding the conditions experienced by species over their evolutionary history provides clues about how they came to be, where they are and why they react to shifts in the environment the way they do⁵². The integration of models of palaeoclimates with spatial patterns of biodiversity and DNA sequence data, for instance, demonstrate how present-day species have tracked changes in climate over the past 100,000 years and achieved their current distributions on Earth^{28,53}. Because past

environmental changes have impacted the demography of natural populations, they are central to understanding the distribution of species and lineages, especially those that are narrowly distributed and endemic. While the distribution of present-day climates explains general patterns of species richness globally, endemism is often best understood by looking at the deeper history of climate and landscape changes, at the scale of millions to several thousands of years past^{54,55}. Moreover, the contrasting climatic histories experienced in distinct parts of the globe have differentially affected regional biodiversity patterns, with ecological consequences. Regions that have experienced more stable climates over the Late Quaternary, for instance, have accumulated more species and genetic diversity. By contrast, areas that have witnessed drastic environmental changes often have a recent history of colonization and lower levels of intra-specific diversity^{28,53}.

Acknowledging biogeographic changes at even deeper evolutionary time scales is also relevant for remote sensing. Deep splits in the evolution of plant flora, for instance, coincide with continental divisions³⁸ and these lineages carry with them contrasting ancestral traits that have the potential to lead to very different ecosystem functions—productivity, nitrogen content, flammability and fire dynamics, microbial community associations (ectomycorrhizal and arbuscular mycorrhizal fungi alternative stable states), decomposition and nutrient cycling^{41,56}. Idiosyncrasies in the origins and dispersal of lineages thus have consequences for ecosystem functioning. These differences in genetic and/or phylogenetic diversity have consequences for metrics of functional composition and diversity that have the potential to be captured from remote sensing (Fig. 2).

When legacy effects are revealed, they inform our understanding of the resilience and vulnerability of ecosystems in a changing world and demonstrate that alternative ecosystem functions and services can be managed for. By acknowledging the role of the past in current patterns of biodiversity, management options can then be designed for the purpose of fostering ecosystem functions and services (goal B, milestone B2 in Table 1), including system resilience and enhancement of evolutionary potential in the face of rapid climate change^{57,58}. These options are complementary to conservation approaches that focus on protecting biodiversity and preventing extinction.

Changing global distributions of plant functional traits and trait diversity. Plant functional traits—attributes of individual plants that impact fitness⁵⁹ through carbon, water and nutrient uptake as well as defence, stress tolerance, growth and reproduction—can be measured at the scale of individuals or communities and ecosystems (for example, on the basis of species mean traits and abundances⁶⁰) to characterize plant functional composition and diversity. Functional diversity refers to the variation of functional traits along one or multiple trait axes and can be derived at various spatial or organismal scales, within or between species, communities, ecosystems or biomes. It “generally involves understanding communities and ecosystems based on what organisms do, rather than on their evolutionary history”⁶¹ and influences ecosystem functions and their response to environmental change^{62,63}. At any given site, the variation in functional traits is associated with evolutionary variation among species and genetic and plastic variation within species⁶⁴. Convergence in relationships between plant traits and their ecosystem functions can be seen across biomes⁶⁵, while high trait variation is observed within climatic regions and even at single sites⁶⁶. Major advances in understanding the range of plant functional trait variation on Earth have been accomplished through contributions of plant trait data for species across the globe by broad networks of ecologists^{64,67,68} (Fig. 3a–c).

In situ measurements show that only a small number of axes of trait variation describe trade-offs in plant functions at the global scale. Ecologists interpret these trade-offs as evidence that natural

selection and biophysical constraints on the form and function of plants prevent certain combinations of traits (Fig. 3d, recreated from ref. ⁶⁹). For example, low photosynthetic rates have not evolved in plants with high leaf nitrogen concentrations and large seeds have not evolved on short plants. However, the trade-off space may not be fully characterized given that plant functional ecologists generally follow protocols for consistency that tend to capture trait measurements at peak function and mature phenological stages. Spatial bias in the distribution of researchers and research effort has resulted in some of the most biodiverse parts of the world being chronically under-sampled on the ground⁶⁷ (Fig. 3a–c). Multidimensional functional variation measured from individual plants may therefore miss important variation due to limitations of sampling efforts, either spatially or through traits that are unmeasured in some locations.

Instruments that measure reflected and emitted light capture key trait variation and trait combinations that are associated with physiological functioning. More than 25 traits can be mapped from imaging spectroscopy data based on the linkage of in situ samples to imagery^{20,70}. Traits derived from spectroscopic imagery covering all North American biomes⁶⁹ capture comparable, although not identical, patterns in trait variation as those identified from in situ data (Fig. 3d,e).

Remote sensing can complement field-based discoveries and potentially broaden our understanding of constraints on plant function by expanding the spatial and temporal range of sampling²⁰ and capturing variation that might be left unmeasured using other approaches. Particularly poorly understood in existing databases, both in situ and remote, is how traits vary phenologically⁷¹ and how trait–trait and trait–environment relationships vary with phenology. Remote sensing will offer the capacity for unravelling these relationships in a manner that is not practical with in situ data collection.

At the same time, spaceborne or airborne instruments cannot capture all of the critical attributes of functional variation that can be measured in situ. For example, attributes of roots and wood, flowering and seed traits, pollinator or reproductive traits, fungal symbionts or pathogens and hydraulic architecture are only partially captured by reflected photons, although some can be inferred from relationships with traits that are detectable. Traits such as seed mass can be readily measured in situ at the species level but cannot be remotely detected, yet they covary with other traits such as height, which can be remotely sensed using lidar. Remote sensing techniques also predominantly capture only the dominant growth forms in a plant community, leaving understory plants and new growth undetected, thus missing important components of plant diversity. The most extensive and realistic understanding of plant functional trait variation will come from integrating in situ and remotely sensed data. However, the extent to which remotely sensed spectroscopic measurements of plants can reliably predict plant functional composition and diversity across spatial and temporal scales is an active area of investigation for statistical (for example, ref. ⁷²), physical (for example, ref. ⁷³) and hybrid (for example, ref. ⁷⁴) modelling. Physical models estimate plant traits through the inversion of leaf or canopy reflectance using radiative transfer equations from electromagnetic theory for the interaction of radiation with foliar constituents, while statistical or machine learning models are based on empirical relationships between measured variation in reflectance spectra and traits⁷⁵. In all cases, while remotely sensed traits can capture important chemical and structural traits across all ecosystems on Earth, they can be difficult to capture at the scale of individual organisms, as the spatial grain of many sensors is larger than an individual.

Conserving the Earth's biodiversity and enhancing ecosystem integrity (goal A, Table 1) requires knowledge of how diversity is distributed in its various dimensions—including functional diversity within and among ecosystems—and where it is changing most rapidly. One of the schemes used to identify biodiversity hot spots^{76,77} estimates their extent to cover 24.9 million km² or 18.5% of

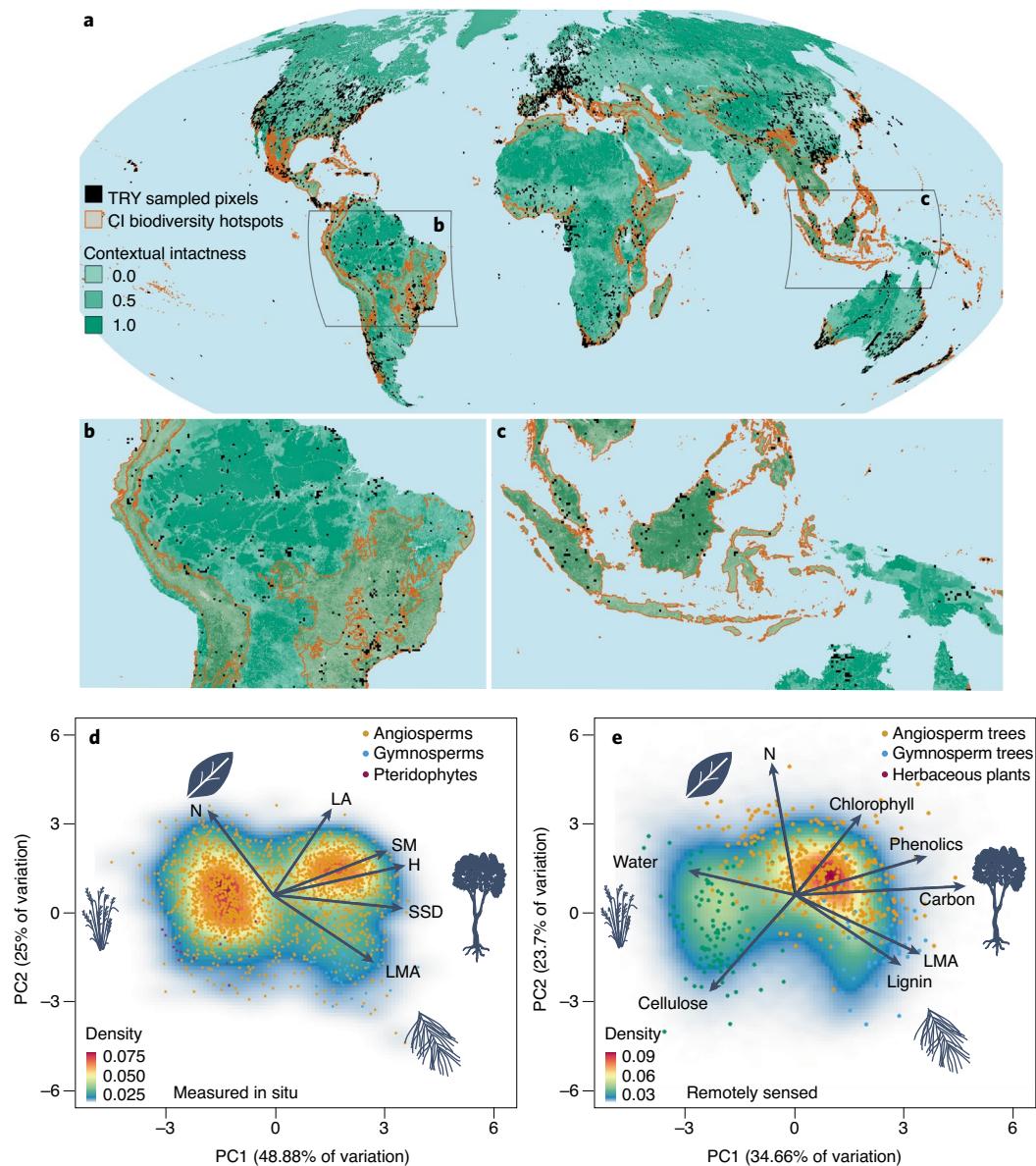


Fig. 3 | Field sampling and remote sensing are complementary approaches for capturing functional diversity across the globe. Critical areas for biodiversity conservation are often very large and remain under-sampled with ground-based approaches. **a**, Global map showing where plant traits have been measured in the TRY trait database⁶⁷ with Conservation International (CI) biodiversity hot spots⁷⁶ and contextual intactness¹⁷⁷; higher contextual intactness indicates high-value biodiverse areas that are currently under threat. **b,c**, Highlighted examples of areas of biodiversity importance in South America (**b**) and Southeast Asia (**c**). **d,e**, Plant functional trait variation projected in two dimensions using the first two principal components. **d**, Traits measured in situ at the species level from the TRY plant trait database⁹⁶ include leaf area (LA), seed mass (SM), stem specific density (SSD), maximum height (H), leaf mass per area (LMA) and leaf nitrogen (N); dots show species means, colours show phylogenetic groupings (angiosperms, gymnosperms and pteridophytes). Red colouring in the heatmap indicates highest density of samples. **e**, Readily observed remotely sensed traits at the ecosystem level from the National Ecological Observatory Network (NEON) sites in the USA²⁰ include LMA, foliar water, chlorophyll, N, cellulose, phenolics, carbon and lignin concentration; dots show plot means from NEON sites, colours show plant physiognomic types (angiosperm trees, gymnosperm trees and herbaceous plants). Both approaches show similar trade-offs. For example, the trade-off between N and LMA captures the separation between angiosperms and gymnosperms (depicted by silhouettes of a broad leaf or needles). TRY data in **a–c** adapted from ref. ⁶⁷, CC BY 4.0; CI biodiversity hotspot data in **a–c** adapted from ref. ⁷⁶, Springer Nature Limited; contextual intactness data in **a–c** adapted from ref. ¹⁷⁷, CC BY 4.0; **d** adapted from ref. ⁶⁹, Springer Nature Limited.

the terrestrial land area excluding Antarctica; far too large an area to monitor with ground exploration alone (Fig. 3a–c). Pinpointing hot spots of biodiversity and rapid change at a fine grain and global extent, within and beyond priority areas, can only be achieved with satellite data. Widespread linkage of in situ and satellite data to identify the relationships between remotely sensed measurements and functional traits will enable more specific predictions about

where biodiversity hot spots are, how fast they are changing and where to target additional in situ monitoring. Understanding the relationships between remotely detected signals and the functional attributes of vegetation that can be predicted from them, especially in under-studied or new environments and in no-analogue climates, will be central to future conservation efforts that incorporate remotely sensed functional information.

Ecosystem resilience to global change. Another longstanding topic within ecology and evolution relates to the resilience of ecosystems that differ in dimensions of biodiversity. Resilience is the “capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure and feedbacks”⁷⁸. Resilience includes both the ability of the system to ‘resist’ change and to ‘recover’ following perturbation. Evidence shows that the capacity of ecosystems to recover from disturbance and stress is linked to the composition, structure and function of the underlying biodiversity^{79,80} and that it is highly scale dependent⁸¹. Yet many open questions remain about the factors that influence ecosystem resilience, including its scale dependency⁸¹ and where limited conservation resources should be first deployed to increase resilience of regions with greatest need and impact^{79,82}.

Analysis of remote observations through time to make inferences about ecosystem resilience has been applied in ecosystems ranging from boreal⁸³ to Mediterranean⁸⁴ and to tropical forests⁸⁵, shrubland⁸⁶ and even dryland river systems⁸⁷. Typically these approaches use a long time series of satellite imagery to characterize decadal-scale temporal variability. Space-for-time substitutions can enable inferences to be made about changes on time scales longer than the available data. In some cases, the spatial distribution of organisms or ecosystems on the landscape may offer clues into the stability of an ecosystem⁸⁸. Coupling variability in space-borne measurements with ongoing in situ observations and experiments enables careful evaluation of ecosystem function, dynamics and the factors that contribute to them⁸⁹. For example, tropical forests cleared and replaced with palm oil plantations can appear to satellites as ‘recovered’ forests⁹⁰, yet these altered ecosystems have lower biodiversity^{91,92} and decreased ecosystem function⁹³. Invasive species can invade ecosystems following fire, increasing local biomass and quickly recovering some remotely measured ecosystem functions—but with major costs to local biodiversity⁹⁴.

Integration of field and remote sensing observations is also necessary to allow systematic comparison of how different ecosystems respond to stress. Biodiversity and related ecosystem functions are dynamic at scales ranging from minutes to millennia. Remote sensing can provide globally and temporally consistent observations through time, at scales from daily to decadal and at resolutions from metres to kilometres, for monitoring ecosystem dynamics and responses to events such as wildfire, land-use change or climate extremes such as drought, heat waves or hurricanes^{95,96}. However, the multidecadal satellite archive is insufficient to infer underlying processes—field-based studies are critical to understanding the mechanistic basis of change. Field experiments, for example, enable us to understand how species composition and interactions affect ecosystem-level function^{97,98} and stability⁹⁹, whether there are non-linear or threshold responses that lead to abrupt shifts in function¹⁰⁰ and the extent to which components of ecosystems fail to recover following disturbance^{91,101}. We know from field-based studies and experiments that biodiversity can enhance an ecosystem’s ability to both resist perturbations and recover from them⁹⁹. Furthermore, as remote sensing data products are typically based on calibration, continuous collection and integration with field data is necessary to produce reliable estimates through time. Doing so effectively across the globe requires partnerships and networking so that all ecosystems are included^{102,103}. Building mechanistic understanding will enable us to forecast, and potentially manage, how ecosystems will respond to future environmental change.

Understanding ecosystem resistance, recovery and resilience is fundamental to the CBD goal A of integrity of ecosystems, of restoration and reducing ecosystem degradation (Table 1)¹⁰⁴. Application of our understanding of ecosystem dynamics and resilience will be important in implementing conservation strategies to restore or enhance ecosystem functioning under various disturbance regimes to generate dynamic working landscapes and to mitigate

biodiversity loss or invasive species recovery (for example, ref. ¹⁰⁵). For instance, better understanding of the factors that contribute to resilience and resistance can advance static spatial conservation planning towards more dynamic conservation measures, such as assisted migration or stepping-stone conservation areas. Finally, improved knowledge of ecosystem resilience through the integration of remote sensing and in situ data to monitor and understand transition pathways towards more sustainable outcomes is fundamental to CBD in aspects related to sustainable use of ecosystems (goal B, milestone B2 in Table 1) and to the ways humans interact with and benefit from nature.

Past and present human modifications of the land and their consequences. Changes in land-use extent and intensity have driven changes in land systems—from hunting and gathering to low-intensity shifting cultivation, and intensive agriculture and logging that includes fire-use and fragmentation—that are now entering a new phase of global simplification¹⁰⁶. Most of our planet has been modified by human presence such that our so-called natural systems are arguably human-modified systems with differing levels of land-use intensity¹⁰⁷. The impact of long-term human presence on ecosystems such as the Amazon has motivated much debate about human legacies on biodiversity^{108–110}, given that some of our most biodiverse regions globally have a long history of human occupation¹¹¹. Yet land-use change is a major driver of biodiversity loss. Reconstruction of past land system changes enables better understanding of long-term human impacts on biodiversity patterns and current Earth system processes^{106,112}, which in turn advance predictions of future change.

Integration of remote sensing data with land-use, socioeconomic and social processes not directly sensed with satellite data is advancing understanding of human impacts on the biosphere and human and Earth system processes that depend on the biosphere¹¹³. Mapping and monitoring land-use/land-cover change (LULCC) has traditionally been a problem addressed with remote sensing, yet remote sensing data alone are unable to disentangle land-cover from land use. Auxiliary data—such as censuses, gazetteers or other inventory data, as well as modelling products—have been used to annotate land-cover data to decipher, for example, whether a forest is a natural forest or human-managed or if a grassland is grazed or not¹¹⁴. More recently, satellite data have been used in conjunction with field and auxiliary data to uncover unexpected processes, with some studies showing the greening up of the Earth due to land abandonment and migration¹¹⁵. The powerful combination of satellite and ground data to reveal that the dynamics of land systems over time has changed our understanding of social-ecological processes¹¹⁶. The integration of satellite, socioeconomic and field data is contributing to a growing understanding of the role that systemic racism has played in the patterns of urban green space, biodiversity, heat islands and environmental pollution^{117,118}, with consequences for human well-being¹¹⁹. These advances have exposed how social inequalities limit access to forest land¹²⁰, often due to existing poverty traps¹²¹. Models that integrate remote sensing data with censuses, field surveys, historical archives, games and choice experiments or that combine land-use processes with biophysical processes to understand and forecast consequences of human activities require bridging disciplines and forms of knowledge to inform management choices.

Integration of data is important for understanding the primary drivers of LULCC and how land-use planning can be geared towards conservation objectives¹²². For instance, the integration between remote sensing and socioeconomic indicators might be operationalized by using night-time lights to measure human presence and linking this information with indicators of development¹²³, using modelled indicators such as human appropriation of net primary productivity based on remotely sensed products to estimate

ecosystem services¹²⁴ or using field surveys and remote sensing to predict poverty levels¹¹⁶. Alongside these types of integration, gamification approaches and choice experiments use remote sensing as a baseline to identify cultural ecosystem services (for example, ref. ¹²⁵) that, together with agent-based models, contribute important information about the feedbacks between natural ecosystem dynamics and human land-use choices¹²⁶. Emerging Earth system and integrated assessment models already connect LULCC processes and project their effects on climate or on biodiversity¹²⁷. These examples have integrated information from seemingly distant disciplines—bringing together ecology, hydrology, Earth system and remote sensing science with economics, history, anthropology and human geography.

Coupling social-ecological dynamics and land system dynamics is fundamental to many of the CBD targets (Table 1). Doing so will help scientists and practitioners to understand how to “reduce threats to biodiversity” through an understanding of the feedbacks between ecosystem processes and human choice, current and historical. Integration of social-ecological data with knowledge of land systems can inform strategies for meeting CBD goals, such as spatial planning of land and sea conservation actions, identifying management options for restoration and mitigation or that minimize trade-offs between human resource use and biodiversity. Advancing our knowledge of land and sea use is fundamental to reducing climate change impacts on biodiversity with the possibility of using nature-based solutions to concurrently meet biodiversity and livelihood goals. Dramatic land system changes are occurring in high biodiversity regions in some of the lowest income nations³⁴. Answers to questions about land system dynamics are fundamental to “meeting people’s needs through sustainable use and benefit sharing”, the main targets of the CBD as well as the Sustainable Development Goals¹²⁸. Greater understanding of land and sea use allocation, equality and sharing of benefits can also be gained from integration of remote sensing and other data types¹²⁹. These are challenging issues and we are only in the infancy of integrating remote sensing and in situ data to answer questions regarding resource use, nature’s contributions to people and sustainable use (for example, ref. ¹³⁰).

Inferring below-ground processes from above-ground information. Studies of ecosystem processes—often conducted using experimental approaches—show strong linkages between primary producers and their biotic interactions with soil organisms. These linkages are often highly dependent on species or ecosystem-level characteristics, such as foliar chemistry of trees, and on phylogenetically defined associations, such as host plant–fungal symbioses. Particular evolutionary lineages have biochemical similarities, such as nitrogen fixation in legumes and C_4 photosynthesis in some monocot lineages, that may be linked to below-ground processes and symbioses^{131,132}. Variation in the chemistry and quantity of above-ground inputs to microbial communities can lead to contrasting soil processes, such as decomposition and nutrient cycling¹³³, which in turn affect primary production, species composition and carbon storage^{134,135}. The composition and diversity of vegetation canopies determine the chemical composition and diversity of litter, which affects soil microbial community composition and function^{134,135}. In turn, plant communities can be influenced by symbioses and below-ground associations. Ecosystem and taxon-specific linkages between above- and below-ground properties and processes thus provide a basis for understanding below-ground dynamics at large spatial scales from above-ground data when drivers of below-ground processes are well-characterized¹³⁶.

Given these linkages, remote sensing can help to tackle the difficult problem of understanding the variation across continents in soil processes and microbial interactions that influence global biogeochemical cycles. The chemical and structural

compounds synthesized by plants and other organisms contribute to the chemical composition and abundance of inputs below-ground that influence symbionts and the microbial community composition and dynamics^{134,137}. Spectral reflectance may be diagnostic of the presence of symbiotic⁵⁶ or pathogenic¹³⁸ organisms, whether soil-borne or aerially transmitted. Similarly, spectral reflectance can correlate with foliar characteristics that are not directly sensed (for example, isotopic concentrations) that themselves may be indicators of below-ground processes¹³⁹. Remotely sensed phenology, canopy chemistry and foliar signatures of species composition can complement other ground-based measurements to understand patterns and dynamics of biotic or biogeochemical variation across landscapes¹⁴⁰. Contrasting fungal symbionts—ectomycorrhizal or vesicular-arbuscular mycorrhizae—that drive nutrient uptake and soil carbon and nutrient dynamics are tightly coupled to plant phylogenetic lineages¹⁴¹. As a consequence of the tight coupling between spectroscopic signatures of plants and their evolutionary history¹⁴², remote sensing has the potential to categorize vegetation into phylogenetic-functional groups^{143,144} to predict below-ground processes^{133,145}.

Unlike other aspects of ecosystem function, few indices relating canopy reflectance to remotely unobservable biotic interactions are universal or easily captured algorithmically. However, reflectance measured in the context of in situ studies can be related physically or by correlation to the phenomenon under study and can aid in understanding the spatial dimension of the process. Remote sensing at the landscape or larger scale may thus allow drivers of edaphic processes to be inferred¹⁴⁶. While spectral indicators of biotic interactions are often context-dependent and should be interpreted with care, they can greatly expand the geographic scope of process studies and potentially reveal dynamics not evident in necessarily limited in situ studies and experiments.

There is growing recognition of the need to understand soil microbial processes at global scale and how they are influenced by the interactions of plants with their soil environment, symbionts and antagonists¹⁴⁷. The ability to scale-up would improve capabilities for soil carbon management¹⁴⁸ and ecosystem restoration focused on beneficial soil microbial processes¹⁴⁹. Remote sensing of vegetation chemistry and productivity could be used to extend predictions of microbial processes to larger spatial extents if specific knowledge of each ecosystem and soil type were available¹⁴⁵.

Understanding species and ecosystem specific^{150,151} relationships between vegetation canopies and below-ground processes requires knowledge of species interactions across trophic levels in connection with soil processes at the level of ecosystems and biomes. If these relationships could be systematically determined from in situ analyses and modelled for different ecosystems, soil types and climates globally, the potential exists to predict below-ground processes and biogeochemical cycling at greater spatial extents and with greater accuracy than has been possible previously. Comprehensive understanding of the variation and changes in below-ground processes could be achieved through thorough and strategic integration of remotely sensed and extensive in situ measurements across time and space. Developing this knowledge would require collaborations between remote sensing scientists and scientists who study soil, microbial and ecosystem processes across different terrestrial ecosystems.

All hands are needed to safeguard biodiversity globally

Advancing the synergy of remote and in situ data for biodiversity does not depend on further advances in technology as much as on collaboration between people bringing together diverse talents and knowledge to fully harness existing technologies and monitoring networks. Opportunities to bring diverse scientific experience, disciplines and perspectives together will enhance opportunities for discovery. Measurements from above will provide vast streams of

data; developing useful biodiversity information to understand and protect biodiversity requires cogenesis of knowledge from these data between scientists and practitioners and engaging local communities to incorporate traditional knowledge¹⁵².

Some of the world's highest biodiversity regions under threat from rapid global change are in low income countries³⁴, where ground-based observations are difficult to obtain owing to lack of financial support, political instability or lack of capacity. The geographic scope of biodiversity research that integrates remote sensing data continues to expand. Yet scientists with the skills, background and internet access necessary to use these emerging data and tools remain concentrated in a small number of countries. Reducing barriers to entry for groups not well represented in science and expanding stable broadband internet connections will help¹⁵³. Programmes like NASA's Applied Remote-Sensing Training¹⁵⁴, which provides free online and in-person training in both English and Spanish, show that there is a strong demand for these tools and data around the world.

A substantial fraction of protected lands globally are managed by or belong to Indigenous Peoples¹⁵⁵. Ignoring the knowledge, rights and perspectives of these communities perpetuates scientific colonialism¹⁵⁶. Applications of remote sensing tools for mineral discovery¹⁵⁷ or oil and gas exploration¹⁵⁸ suggest that such criticisms are not unfounded. Tools for monitoring biodiversity change should thus be implemented by and cocreated with the local communities who will be most impacted by biodiversity and ecosystem change and are making decisions that could counteract biodiversity loss trends.

Applied research that responds to the needs of local communities, practitioners and under-represented groups will increase stakeholder involvement in biodiversity conservation and ensure equitable access to knowledge. Strong institutions are necessary to enable efforts to expand human capacity and implement long-term place-based research in under-studied regions, so that biodiversity monitoring and understanding can become a global endeavour.

Conclusion

We argue that the promise of remote sensing data capabilities should be tempered by the recognition that the patterns of variation they reveal do not translate to processes and mechanisms without integration. Major collaborative efforts have already begun, embraced in particular by GEO BON, which is leading a global discussion and series of working groups to develop and implement EBVs. These efforts are increasing capacity to integrate remotely sensed observations with biodiversity research and models to provide a more synthetic understanding of biodiversity that can be directly applied to management efforts^{3,159–163}. No one group of elite scientists in a small region of the globe can address the challenges we face. Biodiversity science, monitoring and conservation require the full range of human potential and collaboration to manage our planet. Remote sensing-based biodiversity data need to be both openly and equitably available to regions including those with less current capacity. The data collected from above need to allow for both flexibility—to address the many kinds of scientific questions emerging in biodiversity science—and usability to be easily accessible and readily integrated into applications by decision-makers, resource managers and a wide range of users at all scales across the globe. Efforts to integrate ecology and evolutionary biology with remote sensing science must also invite broad participation and build trust within the global biodiversity conservation community so that humanity can make informed management decisions, forecast outcomes and stem the current trajectory of massive biodiversity loss.

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Author contributions

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Competing interests

The authors declare no competing interests.

Additional information

Correspondence should be addressed to Jeannine Cavender-Bares.

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