

## INVITED REVIEW

# Observing terrestrial ecosystems and the carbon cycle from space

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## Abstract

Terrestrial ecosystem and carbon cycle feedbacks will significantly impact future climate, but their responses are highly uncertain. Models and tipping point analyses suggest the tropics and arctic/boreal zone carbon–climate feedbacks could be disproportionately large. *In situ* observations in those regions are sparse, resulting in high uncertainties in carbon fluxes and stocks. Key parameters controlling ecosystem carbon responses, such as plant traits, are also sparsely observed in the tropics, with the most diverse biome on the planet treated as a single type in models. We analyzed the spatial distribution of *in situ* data for carbon fluxes, stocks and plant traits globally and also evaluated the potential of remote sensing to observe these quantities. New satellite data products go beyond indices of greenness and can address spatial sampling gaps for specific ecosystem properties and parameters. Because environmental conditions and access limit *in situ* observations in tropical and arctic/boreal environments, use of space-based techniques can reduce sampling bias and uncertainty about tipping point feedbacks to climate. To reliably detect change and develop the understanding of ecosystems needed for prediction, significantly, more data are required in critical regions. This need can best be met with a strategic combination of remote and *in situ* data, with satellite observations providing the dense sampling in space and time required to characterize the heterogeneity of ecosystem structure and function.

**Keywords:** arctic, boreal, carbon, climate feedback, diversity, fluorescence, spectroscopy, tropics

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## Introduction

Feedbacks from the global carbon cycle contribute substantially to uncertainty about future climates. Twenty years ago, Schimel (1995) summed it up, ‘Lack of knowledge about positive and negative feedbacks from the biosphere is a major limiting factor to credible simulations of future atmospheric CO<sub>2</sub> concentrations’. Despite decades of research since then, and very substantial increases in knowledge, the statement remains true today. Ecosystems take up a significant fraction of carbon released to the atmosphere from fossil fuel burning and deforestation, but if this subsidy declines, the rate of increase in atmospheric CO<sub>2</sub> accumulation will sharply increase for any given emission scenario (Ciais *et al.*, 2013). As a result, the

importance and complexity of the world’s terrestrial ecosystems have come into sharp focus over the past few decades.

Despite the significance of terrestrial carbon storage in the climate system, global ecosystem models persistently diverge on even fundamental predictions of the sign and magnitude of feedbacks (Piao *et al.*, 2013; Friend *et al.*, 2014; Hoffman *et al.*, 2014), contributing substantial uncertainty to the overall accuracy of Earth system prediction (Bodman *et al.*, 2013). Gaps in theory contribute to the failure of models (Wieder *et al.*, 2013), but a lack of critical observations slows to the pace of development of theory, and its implementation into models (Keller *et al.*, 2008). In one recent analysis of observing needs for the carbon cycle, the current state was characterized as a ‘sparse, exploratory framework’ and the need as being a ‘dense, robust, and sustained system’ (Ciais *et al.*, 2014). In this study, we analyze the current state of observations for several critical terrestrial ecosystem variables relative to their known

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patterns, identify systematic issues with the current research efforts and suggest potential solutions. For a comprehensive review of atmospheric, oceanic and human system observing needs, see Ciais *et al.* (2014).

Ecosystem observations provide knowledge about patterns of productivity, species distributions, and other key characteristics and how they are changing. These patterns form an important resource for the development and benchmarking of predictive models, in concert with experiments and process studies. Predicting current patterns is both a crucial test of model skill and a necessary initial condition for forecasts (Luo *et al.*, 2012). Global models and data syntheses have been assembled by international collaboration to meet these requirements and to provide a best estimate of current patterns (Fisher *et al.*, 2014a). Here, we analyze the state of observations of three types of terrestrial ecosystem data, all central to model development, analysis and evaluation. We focus on carbon fluxes—net ecosystem exchange (NEE) and gross primary productivity (GPP), aboveground biomass and plant traits, three data sets covering carbon fluxes, carbon stocks and plant functional diversity.

Flux data represent our best knowledge of the quantity that affects the atmosphere directly and are critical for inferring flux sensitivity to light, water, temperature, nutrients and other factors. Biomass, and related ecosystem structural information, is also critical and integrates information on the growth environment, disturbance regimes and resulting age structures. In ecosystem models, plant traits define some of the most variable, important and poorly constrained model parameters, governing photosynthesis and carbon uptake, resource-use efficiency (light, water, nutrients),

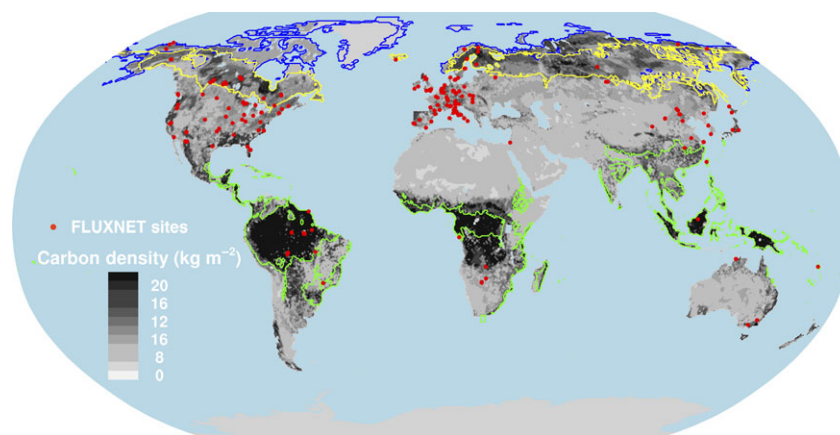
allocation to tissues with different lifetimes and subsequent heterotrophic metabolism.

All three of these types of observations are represented by large global databases widely used by ecosystem modelers and Earth scientists. While there are many other data types for global ecology, these three are represented by large and accessible global data bases, are the focus of substantial and important literature, and represent many of the problems, opportunities and issues that apply to other, less well-developed observation types. We discuss the current state of these data types, the role that remote observations can play and the requirements for sustained observation to detect and understand the change.

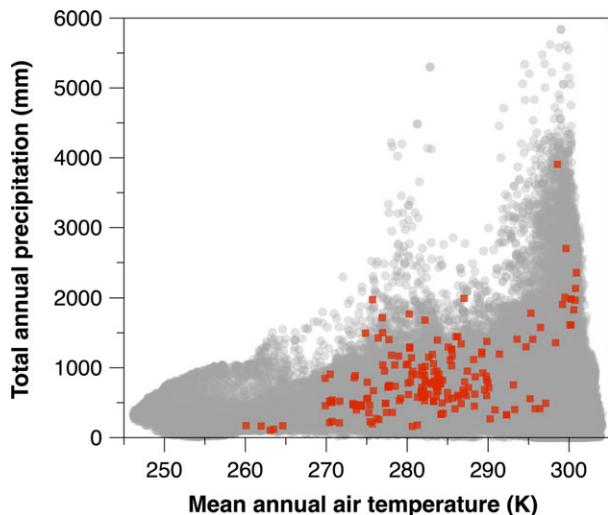
### Carbon cycle tipping points

The terrestrial carbon cycle will play a significant role in future climate change (Friedlingstein *et al.*, 2006). Models of the climate system show large feedbacks from terrestrial ecosystems, including simulated negative feedbacks resulting from increased uptake as northern ecosystems become less temperature limited and positive feedbacks from tropical dieback (Fung *et al.*, 2005). Simulated net positive feedbacks from terrestrial ecosystems can cause atmospheric CO<sub>2</sub> concentrations to be as much as 100 ppmv higher than simulations with no feedbacks for a specified fossil emission level, with accompanying climate effects. However, models disagree wildly about the magnitude of these feedbacks, partly as a result of data gaps described above (Pavlick *et al.*, 2013).

Lenton *et al.* (2008) analyzed potential ‘tipping elements’ in the Earth system, described as regions where



**Fig. 1** Spatial distribution of terrestrial vegetation and soil carbon storage with the three ‘tipping element’ regions identified by Lenton *et al.* (2008). The tipping elements coincide with regions of high storage and hence high potential for losses to influence atmospheric concentrations. Red points show the distribution of carbon flux observations, showing that this network, like the others assessed in this study have sparse coverage in the tipping element regions. Data from Ruesch & Gibbs (2008) and FAO *et al.* (2009).



**Fig. 2** Eddy covariance sites span much of the world's climate variation. FLUXNET sites plotted in climate space (red points), with the distribution of ecosystems in climate space shown in gray. Temperature and precipitation are annual means for 1° latitude-longitude cells. This figure shows the climate-based coverage of the network: Fig. 3 shows its area-weighted coverage, which is quite different.

'a small change in forcing triggers a strongly nonlinear response in the internal dynamics of part of the climate system'. Figure 1 shows Lenton *et al.*'s terrestrial carbon tipping point regions, called tipping elements, superimposed on a map of terrestrial carbon storage. Specifically, they identified the arctic/boreal zone (ABZ) as a region where changes in climate could trigger rapid changes to ecosystem carbon storage, and where, if respiration or combustion were to increasingly dominate over GPP, the massive reserves of carbon stored there (Fig. 2) could cause rapid increases in CO<sub>2</sub> and temperature. Lenton *et al.* also identified the tropics as a tipping element where either reductions in GPP or increases in forest dieback as a result of warmer, drier climates could lead to the release of biomass carbon. This release can be rapid, as wood, the main storage component, can be quickly oxidized to CO<sub>2</sub> if fires increase (Schimel & Baker, 2002).

We evaluate data sets that contribute to basic understanding of tipping elements and aid in monitoring ongoing change through changes to fluxes, biomass carbon storage or plant diversity and functional properties. If the ABZ and the tropics are indeed the location of climate tipping elements, then theory suggests that early detection of change requires dense observations in time and space (Scheffer *et al.*, 2012). *In situ* observations generally provide the most direct measurements of process and mechanism, but are challenged to achieve the density, coverage and longevity to detect and attribute change. In this study, we will evaluate the

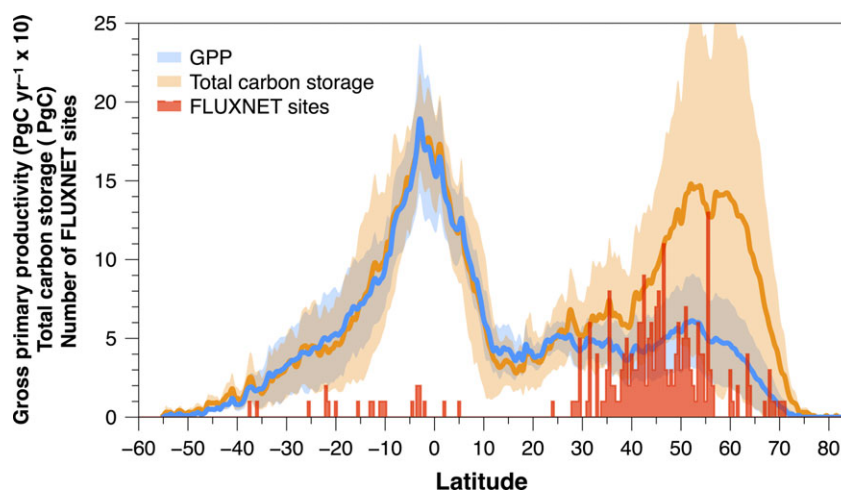
current distribution of three key types of ecosystem data, each represented by a major international database, and the potential of new remote sensing techniques to address sampling issues for these variables. There are many other considerations in using remote observations, including the relationship between the satellite observable and the property in question, calibration, validation and standardization of data products and the length of time series required. Although we touch on many of these issues, we focus on the spatial characteristics of *in situ* and space-based observations relative to the Lenton *et al.* (2008) geography. Below, we evaluate each data type and the potential to complement *in situ* with remote observations.

### Available and required global observations

#### *Carbon stocks and fluxes*

Measurements of carbon fluxes are a foundation for understanding ecosystem carbon balance. Eddy covariance flux measurements are widely used to determine simulated GPP and NEE. An effective global community of researchers has evolved and provides increasingly critical flux data collection, evaluation of data quality and analyses. With more than 500 sites distributed worldwide, FLUXNET provides worldwide sampling of ecosystems and is widely used in model development and evaluation (Bonan *et al.*, 2011). Figure 2 shows the distribution of FLUXNET sites as a function of climate (temperature and precipitation) and biome type. There are now sites spanning the climate range (key drivers for carbon cycling) and covering most biome types. This broad coverage permits the development of empirical models and is central in developing process model parameterizations (Beer *et al.*, 2010; Jung *et al.*, 2011). Figure 3 shows current estimates of the global distribution of GPP and total carbon storage (soils plus vegetation) from a recent multimodel ensemble (Piao *et al.*, 2013).

Figure 3 also presents a histogram of the distribution of FLUXNET sites zonally, resulting in quite a different view of its coverage. Viewed this way, it is apparent that while FLUXNET's coverage extends throughout the world and spans terrestrial climates, the sampling is biased relative to carbon fluxes. About 85% of FLUXNET sites are between 30 and 55 degrees north latitude, in a region of low GPP and intermediate-to-low carbon storage. The broad distribution of FLUXNET sites has demonstrated their value in understanding the principles of ecosystem carbon exchange (Churkina *et al.*, 2005; Baldocchi, 2008; Stoy *et al.*, 2009), but using these data to describe the state of the planet's carbon cycle remain problematic (Beer *et al.*, 2010; Jung *et al.*, 2011).



**Fig. 3** The two ‘poles’ – tropical and arctic/boreal – of the terrestrial carbon cycle. The modeled distribution of GPP and total (soil plus vegetation) carbon storage. FLUXNET sampling spans the latitude range of global land, but sampling is sparse in regions with high flux (GPP) and storage.

The ability of these data to benchmark global models depends on extending process-level validation from the better-sampled to the under-sampled regions, and given the differences in biotic and abiotic conditions, this is unlikely to reduce uncertainty sufficiently for skillful prediction.

The FLUXNET sites span a wide range of variability in *drivers* of carbon exchange, but do not sample the full range of likely variability in *rates* of carbon exchange. FLUXNET coverage is severely limited in the high GPP/high carbon storage tropics, and in the low GPP but high storage ABZ. Current sampling of the variability of ecosystem fluxes is lowest in the regions with high flux or storage. Extremely low tropical and ABZ coverage implies near-certain biases, contributing to uncertainty in model parameterization (Galbraith *et al.*, 2010; Fisher *et al.*, 2014a,b). Perhaps even more serious, the ability of such a biased global observing system to serve as an early warning system for carbon cycle or ecosystem change may be compromised by low coverage in critical regions.

While model development and evaluation have historically focused on *in situ* data, new remote sensing technologies are expanding the number of ecosystem properties that can be quantified from space. Many of the key stocks and fluxes in Fig. 3 above can, or will soon, be estimated using remote sensing. Given the challenges of long-term *in situ* observations in tropical and ABZ regions, satellite measurements can make an increasingly important contribution. Remote sensing complements the detailed information available *in situ* by providing broad spatial and temporal coverage.

Photosynthetic carbon uptake or GPP has been mapped, somewhat indirectly, from satellite estimates

of light interception using light-use efficiency models (Sellers *et al.*, 1996), and this product has produced an increasingly clear view of the distribution of GPP over the planet, agreeing well spatially with eddy covariance estimates (Verma *et al.*, 2014). These calculations are based on the light-use efficiency model where:

$$\text{GPP} = \varepsilon_{\text{PAR}}(\text{PAR} \times \text{FPAR}) \quad (1)$$

where  $\varepsilon_{\text{PAR}}$  is the intrinsic light-use efficiency, FPAR is the fractional photosynthetically active radiation absorbed by the canopy and PAR is the incident amount. Additional terms are typically included to describe reductions due to stress (water, high temperature) not captured by the observables. In remote sensing-based approaches, the observables are APAR and PAR. The actual GPP is constrained by these observations but can only be calibrated and validated locally using eddy covariance or other methods (Verma *et al.*, 2014). These satellite-constrained models of GPP also show trends (Hasenauer *et al.* 2012), but the accuracy of these trends is hard to assess, as few independent data exist.

A new, related method uses solar-induced fluorescence (SIF) to estimate GPP. SIF can be described by:

$$\text{SIF} = \varepsilon_{\text{F}}(\text{PAR} \times \text{FPAR}) \quad (2)$$

where  $\varepsilon_{\text{F}}$  is the ratio between fluorescence photons emitted and light absorption. As a result, the two approaches are related by:

$$\text{GPP} = \frac{\varepsilon_{\text{PAR}}}{\varepsilon_{\text{F}}} \text{SIF} \quad (3)$$

The combination of SIF and FPAR observations provides information on both the right-hand side and the



left of the carbon balance equation. As a result not only is the driver (FPAR) constrained by observation (e.g., from MODIS), the responses (SIF and GPP) are as well. SIF is important, first, because the efficiencies ( $\epsilon_F$  and  $\epsilon_{PAR}$ ) are now also constrained by earth observations and, second, because, during stress, rates of GPP and hence SIF may respond before leaf area (the control over FPAR) changes.

The scaling between fluorescence and photosynthesis from seconds to seasons is complex, and the observed linear global relationship is not well understood (Van der Tol *et al.*, 2009; Frankenberg *et al.*, 2011). The satellite measurement is made consistently at mid-day, under high light conditions and with repeat intervals of days to weeks (Frankenberg *et al.*, 2012). The satellite measurement also reflects the canopy SIF response to absorbed PAR, and so its variation in time and space reflects incident and absorbed radiation, adding many factors not usually present in the laboratory. *In situ* studies show clear positive correlations between canopy SIF and GPP. The efficiency ( $\epsilon_F$ ) is determined from the slope of the SIF: (PAR  $\times$  FPAR) relationship, and this efficiency seems to vary systematically with stress (Flexas *et al.*, 2002). While considerable research is required to fully understand these new observations, early indications are very promising (Joiner *et al.*, 2012; Lee *et al.*, 2013). Solar-induced fluorescence can provide observations and estimates of vegetation stress responses in regions where flux sites are sparse (Fig. 4).

The space-based technique for measuring SIF makes use of high spectral resolution remote sensing (Frankenberg *et al.*, 2012; Joiner *et al.*, 2012). Solar-induced fluorescence photons are emitted in proportional response to photosynthesis and can be observed by

appropriate instruments in saturated absorption features where no reflected sunlight is present (Berry *et al.*, 2012). SIF measurements are now available, by serendipity, from orbiting sensors like GOSAT and the OCO-2 satellite, launched in July 2014, but only at low spatial resolution and coverage (Fig. 5).

This new measurement already shows high correlation with other measures of GPP (Frankenberg *et al.*, 2011) and has provided information on previously unknown variability in global photosynthetic rates (Guanter *et al.*, 2014). While leaf-level relationships between fluorescence and photosynthetic rates are complex, available data show predictable scaling between variability in space-based SIF and GPP. SIF complements the inference of NEE from gradients of CO<sub>2</sub> in the atmosphere from sensors such as GOSAT and OCO-2 (Miller *et al.*, 2007; Crisp *et al.*, 2008). No direct measurement of respiration is currently available, but it could be constrained by simultaneous estimates of GPP from SIF and NEE from spaceborne measurements of CO<sub>2</sub>.

Global estimates of carbon storage are uncertain (Fig. 3). We assessed the distribution of forest inventory data compared to a recent space-based estimate of global biomass stocks (Fig. 5). Today's forest inventory data are biased globally toward the mid-latitudes, with limited coverage in the high biomass tropical and boreal forests. The distribution of total carbon stored in live woody vegetation (above- and belowground) along with the samples of *in situ* measurements from national forest inventories (Fig. 5) shows that forests in temperate and boreal regions dominate observations, with 5–15 plots 1000 km<sup>-2</sup>. Tropical regions are grossly undersampled by comparison, with <1 plot 1000 km<sup>-2</sup>

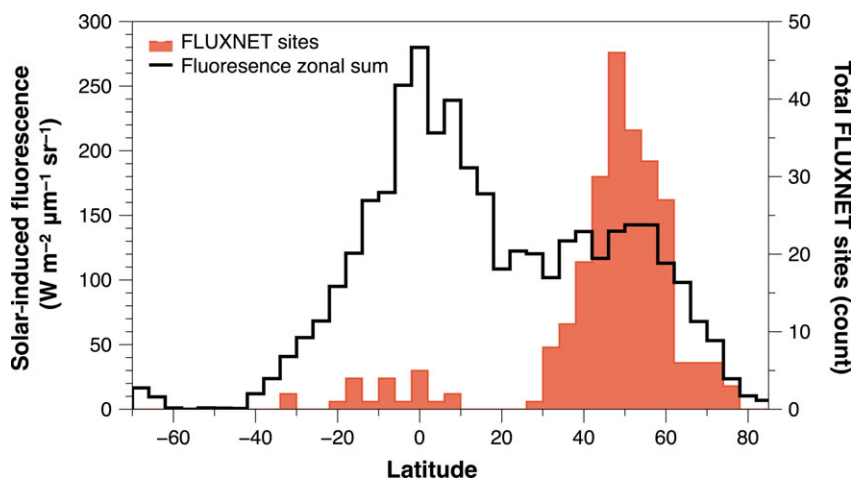
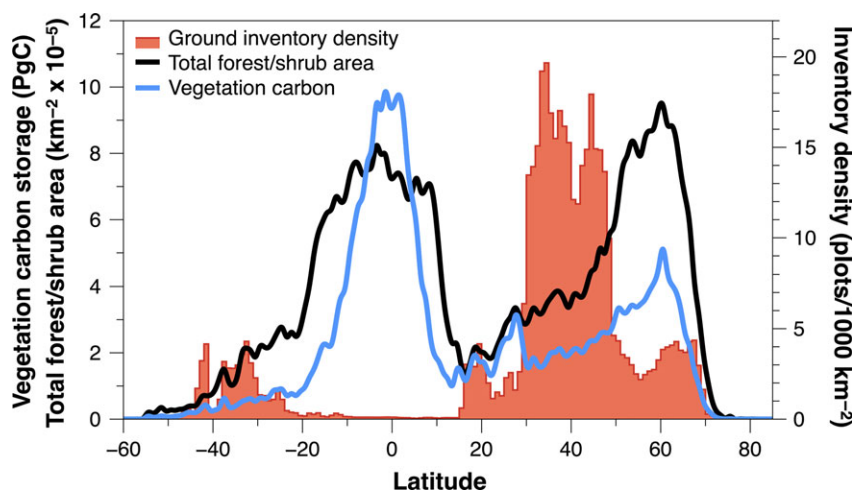


Fig. 4 The global distribution of solar-induced fluorescence, showing its strong correlation to modeled GPP (Fig. 3), compared to FLUXNET's distribution. SIF may provide global coverage of GPP, with extensive data in high flux regions, but using existing and planned satellites, it will provide low resolution in space and time compared to eddy covariance.



**Fig. 5** The distribution of woody (forest and shrub land) area and biomass, estimated by radar–LiDAR fusion compared to data availability from forest inventory. The red histogram shows forest inventory plot density in plots  $1000 \text{ km}^{-2}$ . Similar to flux observations, biomass data is sparse in regions of maximum storage.

or about 1000 tropical plots globally. As a result, maps of tropical carbon do not agree more than suggested by chance and biases could easily be as high as 30% (Mitchard *et al.*, 2014). Brazil is developing a new forest inventory which will bring coverage to about 2 plots  $1000 \text{ km}^{-2}$  (de Freitas *et al.*, 2009). Because of the sparse plot coverage in the tropics, where much of the world's forest biomass is concentrated, spaceborne measurements are critical to expand sample sizes and reduce bias error (Asner *et al.*, 2014a,b; Saatchi *et al.*, 2014). Repeat space coverage may also be the best means for assessing long-term changes to forest carbon stocks, if sufficient accuracy and length of record can be achieved to enable quantification of change over time. Despite the significant aboveground biomass concentrated in boreal forests, ABZ carbon storage is dominated by vast stocks of soil carbon (Fig. 5). Because high-latitude carbon storage is dominated by soils whose dynamics are controlled by the growing season length and moisture availability, biomass measurements will be a weaker constraint on the ecosystem model predictions compared to that in the tropics (Kimball *et al.*, 2000; Kim *et al.*, 2012; Barichivich *et al.*, 2013).

Total and soil carbon storage cannot be observed directly using remote sensing with current or proposed technology, but aboveground carbon storage (particularly in wood) can be estimated using active remote sensing techniques from a combination of radar and light detection and ranging (LiDAR) sensors globally (Saatchi *et al.*, 2011). Both radar and LiDAR (Lefsky *et al.*, 2005; Saatchi *et al.*, 2011; Asner *et al.*, 2012) have proven extremely useful, although each technology has somewhat different strengths and weaknesses. LiDAR measurements provide the most direct estimate of for-

est structure and can be used to estimate forest biomass (Drake *et al.*, 2002; Lefsky *et al.*, 2005; Asner & Mascaro, 2014). Previous spaceborne LiDAR provided systematic but sparse sampling of the world with high spatial resolution ( $\sim 0.25 \text{ ha}$ ) (Lefsky *et al.*, 2005), measuring canopy height (Simard *et al.*, 2011), which can be related statistically to biomass (Saatchi *et al.*, 2011; Baccini *et al.*, 2012). The recently selected GEDI mission could update this record with optimized LiDAR sampling for biomass using the International Space Station as a platform.

Radar observations at long wavelengths (20–80 cm) are sensitive to the amount of biomass present at landscape scales ( $\geq 1\text{-ha}$ ), by indirectly measuring forest structure (volume and height) (Shugart *et al.*, 2010). Radar sensors, unlike LiDAR, provide comprehensive coverage, and because of their ability to penetrate through clouds, radar sensors complement LiDAR and will be used for global observation of forest carbon storage and changes from disturbance and recovery processes as part of ESA's Earth Explorer mission concept (BIOMASS) and NASA's Decadal Survey mission (previously called DESDynl-R, now called NISAR) (Hall *et al.*, 2011; Le Toan *et al.*, 2011).

Remote sensing complements *in situ* observations by providing more extensive and less biased sampling, while *in situ* calibration and validation are required to define allometric ratios and wood density. However, data from spaceborne sensors overcome the statistically biased sampling of research plots, particularly in tropical forests where national forest inventory is not available and substantially reduce or eliminate spatial undersampling (Asner & Mascaro, 2014; Saatchi *et al.*, 2014). LiDAR, radar and even *in situ* sampling

approaches require information about wood density and/or regional variations of biomass allometry to quantify the vegetation carbon storage accurately, but these limitations apply to *in situ* and remote sensing approaches, emphasizing the need for close coordination of ground and space-based data collection.

#### *Diversity and functional diversity*

Uncertainty about key plant and ecosystem properties, captured today in plant functional type (PFT) distributions, is high. Models include a small number of plant traits to capture functional differences and focus on, for example, nitrogen concentration, leaf mass per unit area, the maximum velocity of photosynthesis, lignin concentration as an index of decomposability and root : shoot ratios. These plant traits influence growth, competition, environmental sensitivity and carbon storage, and many of these can be estimated from remote sensing (Table 1). Traits influence plant's interactions

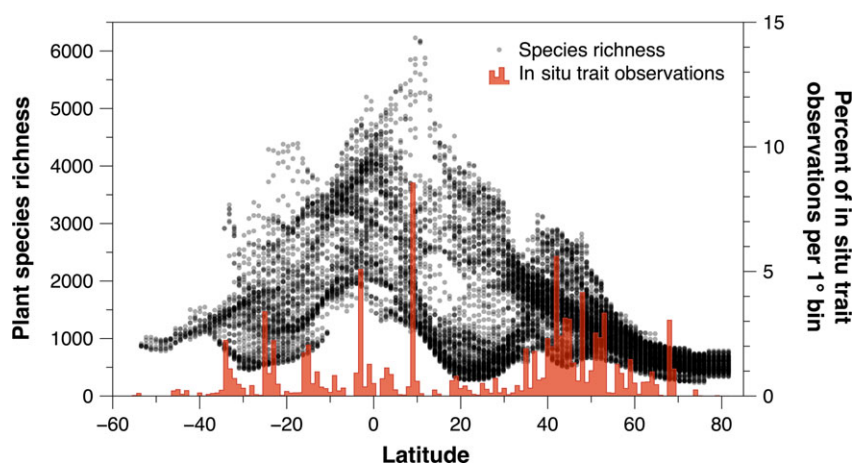
with each other, and with other trophic levels, and determine trajectories of change as competition and other successional processes occur. These processes cannot be understood without characterizing the range of these properties within regions or biomes, and mean values, as are used in today's models, are not sufficient.

Today, models use extremely reduced descriptions of functional diversity to simulate processes. The roughly 250 000 vascular plant species worldwide are represented in models by 7–22 PFTs (Poulter *et al.*, 2011). Disaggregation of the information today lumped into a small number of global PFTs is needed to understand how ecosystem carbon storage and climate sensitivity will evolve into the future, and this requires more, and more systematically collected, knowledge of plant traits. Models group vegetation into a small number of PFTs and assign parameter values to each PFT. The majority of biome-specific parameters in ecosystem models reflect plant traits affecting photosynthesis, carbon allocation, decomposability and other processes.

**Table 1** Certain key plant traits may be estimated from spaceborne sensors

Trait name	Units	Description/ significance	Global range	Measurement accuracy from remote sensing	Corresponding model quantity/ function	Citation
Foliar nitrogen concentration	mg g <sup>-1</sup>	Rubisco content, CO <sub>2</sub> fixation, GPP, decomposition	3–64 mg g <sup>-1</sup>	<20% RMSE	Foliar N, model state variable and control over GPP	Wright <i>et al.</i> (2004) [GLOPNET database]; Reich & Oleksyn (2004)
Leaf mass per area	g m <sup>-2</sup>	Leaf structure/density, leaf physiological strategy, leaf longevity	12–1516 g m <sup>-2</sup>	<3% RMSE	LMA, model state variable and control over leaf longevity	Wright <i>et al.</i> (2004); Poorter <i>et al.</i> (2009)
Chlorophyll (a + b)	mg cm <sup>-2</sup>	Light harvesting, ATP/NADPH synthesis, RuBP regeneration	1–150 mg cm <sup>-2</sup>	<10% RMSE	Chlorophyll, leaf optical properties, albedo, V <sub>cmax</sub>	Coste <i>et al.</i> (2010); Asner & Martin (2008)
Lignin concentration	%	Decomposition, leaf water transport	2–65%	2 < 5% RMSE	Lignin, model state variable and control over decomposition	Asner & Martin (2011)
Maximum rate of RuBP carboxylation	μmol m <sup>2</sup> s <sup>-1</sup>	Photosynthetic capacity/performance, CO <sub>2</sub> uptake,	0–200 μmol m <sup>2</sup> s <sup>-1</sup>	<15 μmol m <sup>2</sup> s <sup>-1</sup>	V <sub>cmax</sub> , model parameter, regulates GPP	Singh <i>et al.</i> (in press); Kattge <i>et al.</i> (2011)

The table describes the traits, their global ranges, their measurement accuracy from remote sensing and their role in terrestrial carbon models.



**Fig. 6** Global plant diversity and functional diversity data. The black dots show the estimated number of vascular plant species per equal area grid cell ( $\approx 12,000 \text{ km}^2$ ,  $\approx 1^\circ$  latitude  $\times$   $1^\circ$  longitude near the equator) from a statistical model (Kreft & Jetz, 2007). The red histogram shows the number of existing *in situ* measurements of leaf nitrogen concentration in a global trait database (Kattge *et al.*, 2011) per degree latitude. Most data on plant functional diversity come from regions of low to intermediate overall diversity.

To assess the data available to characterize plant functional diversity and PFTs, we examined currently available data for overall plant diversity (as a measure of how many PFTs might be required) and functional diversity, or the data available to estimate parameter values of an increased number of PFTs. Figure 6 shows the output of a statistical model of global vascular plant biodiversity (Kreft & Jetz, 2007), with diversity given in estimated species per unit area ( $\alpha$  diversity, or richness). The model predicts diversity as a function of climate, orography (some data sets span a wide range of altitudes) and evolutionary history. The figure shows the estimated diversity for each  $\sim 1^\circ$  grid cell within a latitude band and indicates the zonal heterogeneity of diversity at that latitude.

Plant diversity is highest in the tropics, with secondary maxima in both hemispheres. High-latitude regions have low diversity in both hemispheres. Figure 6 also shows the distribution of observations of important plant functional traits (used to estimate model parameters) from a major international database (TRY; Kattge *et al.*, 2011). The figure shows the proportion of all data on a set of key traits needed by models (Table 1) at any given latitude. While the total number of observations is quite large (millions), the observations are most limited, particularly relative to the level of diversity found there, in the diverse tropics. The distribution of observations is biased to the northern hemisphere mid-latitudes, from regions of intermediate-to-low diversity, while regions of high diversity are under-sampled.

The tropics, containing the bulk of the world's plant species, are the most sparsely sampled region. Sampling challenges are worse than might appear from the plot as the data are dominated by observations from a

few well-studied sites. For example, the large number of observations at  $10^\circ\text{N}$  all come from a single site (the Smithsonian Tropical Research Institute's Barro Colorado site in Panama:  $9.15^\circ\text{N}$ ,  $79.85^\circ\text{W}$ ), and so sample a single cell of the many cells at that latitude. Other grid cells in that latitude have entirely different species and significantly different climates: the latitude includes lands in Africa and Indonesia. This sampling outcome results in the lowest number of trait observations per unit diversity where diversity is highest. The lack of coverage in tropical trait data may contribute to current asymmetries in model parameterization: the species-rich tropics are represented in the widely used IGBP system by two forest types (Eidenshink & Faundeen, 1994), while the far less-diverse temperate and boreal zones have three forest PFTs each. This distribution of PFTs is determined more by what can be observed with moderate resolution remote sensing than the actual levels of functional diversity in these regions. Experiments and models suggest that representation of diversity influences the way in which ecosystems respond to change, and so limited representation of heterogeneity affects system behavior and predictive skill (Hooper *et al.*, 2005; Alton, 2011; Pavlick *et al.*, 2013; Antonarakis *et al.*, 2014).

Imaging spectroscopy can quantitatively map plant diversity because structural and chemical traits influencing spectral reflectance are often distinctive to species and have lower variability within species than between species (Asner *et al.*, 2014a,b; fig. 7). Remotely observable traits include chemical composition (nitrogen and other elements), leaf mass per unit area and chlorophyll content. This technique, long under development, is now routinely applied using aircraft sensors



(Asner *et al.*, 2012, 2014a,b), and spaceborne application is proposed for the 2020s through NASA's HypSPIRI mission concept (<http://hypspiri.jpl.nasa.gov/>). Remote estimates of plant traits are quite different from *in situ* estimates, like other remote sensing techniques. Spectroscopic estimates of traits integrate over pixels, are influenced most by the upper canopy and typically have precision ( $R^2$ ) of 60–90%, with accuracy from 10% to 20% RMSE (Asner *et al.*, 2014a,b). These uncertainties are comparable to the precision needs of ecosystem models (Papale *et al.*, 2006). These are comparable to estimates from chemical analyses of individual leaves scaled to canopies (Serbin *et al.*, 2014).

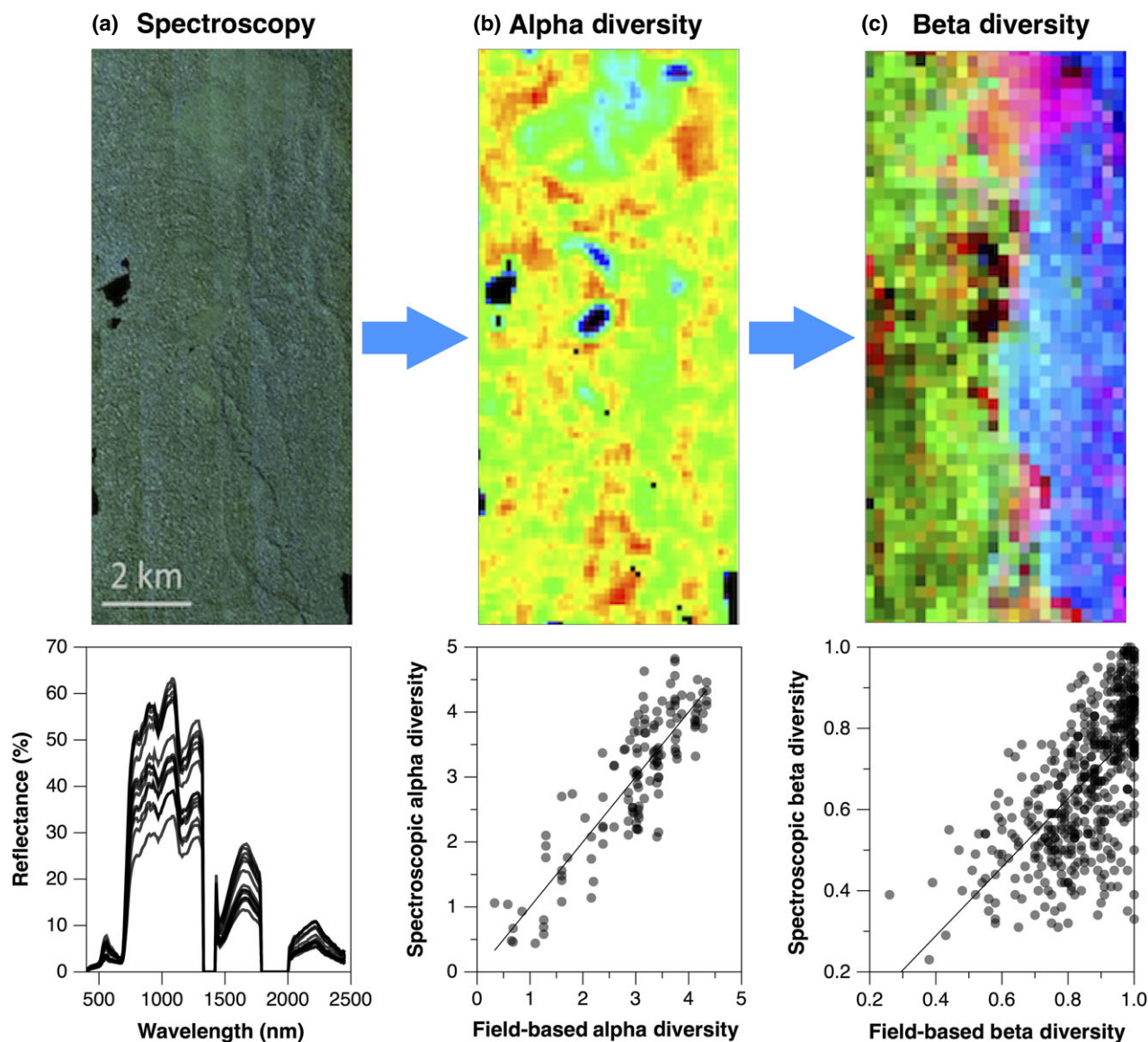
Imaging spectroscopy can estimate the variety, relative abundance and community turnover of plant species at large scales because of the spectral uniqueness of many plant species (corresponding to species-specific chemical and leaf structural properties), resulting in an estimate of diversity parallel to ground-based estimates. This allows estimation of biological diversity without direct reference to taxonomic identity and so complements traditional field techniques, but on a spatially explicit basis (Féret & Asner, 2014). Figure 7 shows an image from the humid tropics, converted first into  $\alpha$  diversity and then into  $\beta$  diversity, or turnover, using the methods of Féret & Asner (2014). Figure 7d shows the range of spectra collected within this region. Plant traits influencing the observed spectral reflectance include nitrogen, which in this ecosystem ranges from ~1% to more than 5%, chlorophyll and other pigments.

The low number of PFTs used in the tropics implies that all the species there are functionally equivalent: these results suggest functional diversity as great or possibly much greater than in other ecosystems. Canopy reflectances at a benchmark wavelength of 1000 nm range from 30% to 60%, similar to the range observed globally across all vegetated biomes. The wide range of canopy traits observed suggests potentially high functional diversity: the range of N contents in this one forest span nearly the global range (Table 1). Plant traits influencing growth rate tend to be correlated with wood density (Chazdon, 2014), so improved mapping of plant traits may also reduce uncertainty in aboveground biomass estimates. This all suggests that the classification of the tropical biome as a single functional type reflects the limitations of current remote sensing instruments and sparse *in situ* data, and not the relative functional diversity of tropical forests.

In addition to quantifying patterns of plant diversity, imaging spectroscopy can be used to quantify aspects of plant functional diversity. Imaging spectroscopy allows a number of key plant parameters to be estimated (Table 1). These parameters largely define plant growth strategies and can be used to understand plant responses

to climate, competition and herbivory (Coley & Kursar, 2014). Particularly, powerful results can be achieved by integrating estimates of chlorophyll, nitrogen, LMA and  $V_{\text{cmax}}$  (Wright *et al.*, 2004), which may reveal trade-offs in canopy growth traits associated with climate change over time. Table 1 shows the ability of remote sensing to estimate the key traits described above. Models must resolve global gradients in these traits, and these global gradients can be well resolved with anticipated accuracy and precision. As HypSPIRI's launch is not even scheduled yet, and no analogous global mission has ever flown, this technology cannot be demonstrated in the same way as GPP (MODIS, GOSAT) and biomass (ICESat) can, and so is a crucial new Earth observation. However, space-based hyperspectral sensors are technologically mature: instruments with similar performance to that needed for remote sensing of terrestrial ecosystems have successfully flown around Mars (Pelkey *et al.*, 2007) and the Moon (Pieters *et al.*, 2009).

The increase in knowledge of plant functional diversity data that would result from space-based observations is extraordinary. As Fig. 6 demonstrates, current observations of plant traits are sparse and biased on their distribution and the most diverse ecosystems have the most limited data. Figure 8 shows the increase in plant trait data that could be obtained via an imaging spectrometer housed on NASA's International Space Station (ISS), the most likely location for a near-term instrument deployment. The simulation assumes 30 m<sup>2</sup> pixels, and a swath width of about 30 km, and an 18-month mission, typical for the ISS. The simulation takes into account the ISS orbital altitude and path, as the ISS is in an inclined orbit with varying overpass times, and cloud statistics to generate an estimate of cloud-free pixels. The simulation includes only land pixels. The typical number of plant trait records per degree of latitude is about 10, with maxima around 1000. For each degree of latitude, a mission like this could collect 500 million pixels, for a 500 000-fold increase in coverage. As in many cases, the underlying *in situ* data are measurements of a few individual plants or leaves, scaled to the canopy, and the remote observations are of areas of 10 s of m<sup>2</sup>, the information difference is actually hard to compare outside of a formal modeling framework. The actual increase in information is less because of spatial autocorrelation, redundancy and measurement uncertainty, but would allow characterizing many more PFTs and the spatial distributions of traits within biomes and environmental correlations in far more detail than available now. Global coverage of plant trait distributions data would fundamentally change the vegetation modeling paradigm from its current data-poor to a data-rich framework (Luo *et al.*, 2012).



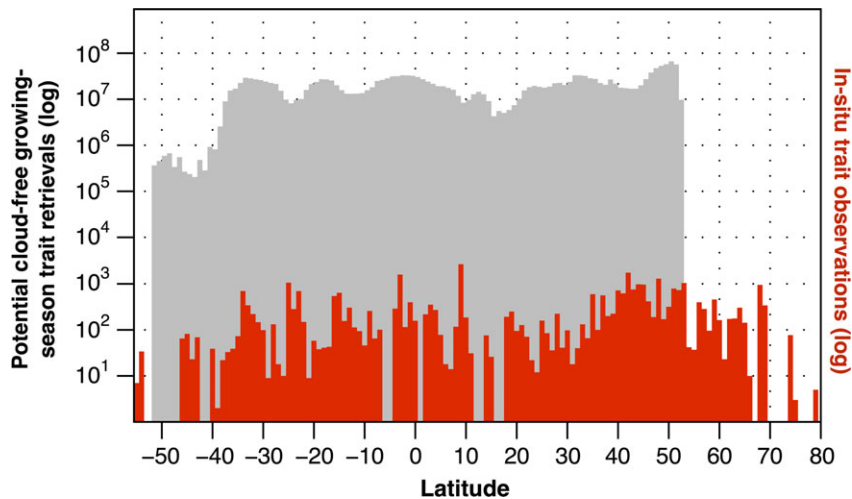
**Fig. 7** Airborne high-fidelity imaging spectroscopy provides a direct path to estimation of vegetation diversity. In this example, (a) visible-to-shortwave infrared (VSWIR; 400–2500 nm) imagery over an Amazonian rainforest was acquired using the Carnegie Airborne Observatory. The spectral diversity of the forest canopy has been translated into estimates of local-scale (alpha) and landscape-scale (beta) diversity using the concept of spectral species distributions (Féret & Asner, 2014). (b) Alpha diversity is shown as the evenness of canopy species relative abundances within one-hectare grid cells based on the Shannon index. (c) Beta diversity is shown as the dissimilarity of canopy species composition among grid cells based on the Bray–Curtis index. The remotely sensed alpha and beta diversity were well validated with an extensive field plot network (Féret & Asner, 2014).

The suite of measurements and mission opportunities described here does not do justice to the full range of spaceborne data contributing to global ecology, which covers a far wider range of properties than described here, including climate drivers of ecological processes, land use and land cover change and the hydrological cycle. An overview of some of these capabilities, focused on climate and hydrological correlates of carbon cycle processes, is provided in Table 2. The full range of capabilities related to land imaging of land

use and land cover change is outside the scope of this perspective, but see NRC (2013).

## Conclusions

Important gaps exist in our observations of the terrestrial carbon cycle, resulting from sparse and biased sampling of high flux and high storage regions. Scientists have a sense of these gaps: here, we present an in-depth analysis of sampling relative to current



**Fig. 8** Simulated gain in information from *in situ* relative to spaceborne plant trait data. Spaceborne data could increase the amount and coverage of plant trait data by many orders of magnitude. The red histogram shows log of the number of existing *in situ* measurements of leaf nitrogen concentration in a global trait database (Kattge *et al.*, 2011) per degree latitude on a log scale. The gray histogram shows the potential number of cloud-free retrievals possible with a proposed 2-year imaging spectroscopy investigation to be flown aboard the International Space Station. Each retrieval would provide data for four critical traits (leaf mass per unit area, chlorophyll concentration, nitrogen concentration and photosynthetic capacity).

**Table 2** The range of quantities available or soon to be available from missions which are either on-orbit or well along in planning and funding

Model variable type and identity	Technology	Current missions and mission concepts*	Status	Quantity retrieved	Key references
Soil water, plant water stress (canopy water content, vegetation optical depth, land surface temperature)	Passive and/or active microwave. Thermal	SMOS, SMAP, Aquarius, ECOSTRESS	On orbit (SMOS) 2015 (SMAP), ECOSTRESS (2017–18)	Soil moisture, plant canopy water content, evapotranspiration, soil freeze/thaw, surface inundation	Entekhabi <i>et al.</i> (2010), Lee <i>et al.</i> (2013)
Precipitation	Radar	GPM	On orbit	Rainfall	Hou <i>et al.</i> (2014)
Land surface temperature	Thermal	MODIS, VIIRS, LANDSAT 8, Sentinel-2, ECOSTRESS*	On orbit or planned (Sentinel-2) 2015, proposed 2018 (ECOSTRESS)	Temperature	Wan (2008)

\*denotes a mission concept.

Remote sensing can increasingly quantify drivers of ecosystem response, such as land surface temperature, precipitation, soil moisture and freeze/thaw at spatial and temporal scales useful for model development and in simulations. The range of quantities available or soon to be available from missions that are either on-orbit or well along in planning and funding. Combining information on drivers (temperature, precipitation, etc.) with responses (GPP, NEE, NBP), sensitivities or the derivatives of carbon variables with respect to climate variables can be estimated at large scales, for example,  $\Delta(\text{GPP})/\Delta$  (water stress). Remote sensing is routinely used for quantifying land use, land cover and land cover change. We do not address remote sensing of land use and land cover change in detail, an area of long-term success using remote sensing approaches.

knowledge of carbon geography. Networks or data sets assembled *post hoc* will almost always contain sampling bias that will limit, or at least influence the inferences that may be drawn (Lindenmayer & Likens, 2013). New

space-based observations can strongly complement *in situ* observations in providing required quantitative ecosystem information globally. While spaceborne measurements have uncertainty and bias errors of their

own, they can aid greatly in reducing bias errors associated with relatively sparse *in situ* systems through their coverage and large sample size and can be used to assess bias and extrapolate limited local information. A number of questions remain:

*What is the minimum observing system needed to understand and detect change in terrestrial carbon dynamics?* Whatever that minimum is, current networks do not reach it. Gaps exist in knowledge of the terrestrial carbon cycle, resulting from sparse and biased sampling of high flux and high storage regions. Sampling of fluxes is sparse in regions of potentially high fluxes, sampling of biomass is next to nonexistent in the highest biomass regions of the world, and plant traits are least known where their diversity may be highest. Networks or data sets assembled *post hoc* will almost always contain sampling biases that will limit, or at least influence the inferences that may be drawn (Lindenmayer & Likens, 2013). Formal network design studies should become a required precursor to large or even individual investment in site selection and infrastructure development (Schimel *et al.*, 2007; Hoffman *et al.*, 2013).

*Can adequate coverage realistically be achieved by increasing the investment in *in situ* observations of fluxes, biomass and plant properties?* Although it is tempting to see a simple explanation for the current distribution of terrestrial research sites and data in the distribution of wealth globally, and the tendency of funding agencies to support research within their own territories, the reality is different. The tropics and ABZ face serious access challenges, with limited or no roads, and restricted access to electrical power. Complex terrain in some of the most productive and diverse parts of the tropics, for example, the western Amazon and much of southeast Asia, further complicates access and adds to the challenge of implementing eddy covariance sites. Installing large towers is expensive and may be in conflict with conservation objectives. The incessant biological activity of tropical plants and animals and mechanical effects of ABZ temperatures, freezing and wind create maintenance issues of their own. Logistical constraints will limit the number and distribution of site locations, even if financial resources were available to achieve sampling density similar to the mid-latitudes. Other approaches must be used to obtain sufficient coverage.

*Can remote sensing provide quantitative and compelling information on ecosystem structure, function and functional diversity?* New space-based observations of structural variables such as biomass, function, captured in flux estimates, and key plant traits and functional diversity, estimated from the spatial variability of fluxes and

traits, can strongly complement *in situ* observations and provide quantitative ecosystem information globally, beyond that available from remote sensing traditional indices. Spaceborne measurements can reduce bias errors associated with relatively sparse *in situ* systems through their spatial coverage and large sample size and can be used to assess bias and extrapolate limited local information. Space-based systems can also measure drivers of ecological change (Table 2). The evolution of remote sensing systems that combine estimates of drivers of ecological change (Table 2) and carbon cycle responses (Table 3) can, in concert with appropriate and coordinated *in situ* and calibration/validation efforts, allow the testing of ecological theory at previously inaccessible scales.

*Can combining *in situ* and remote observations reduce sampling bias?* Assembling networks and data sets *post hoc* carries with it the near certainty of biases: for global models where calculating the correct integral or average value is critical, this is a particularly serious issue (Lindenmayer & Likens, 2013; Soranno and Schimel 2014). In some cases, more data may provide less insight than the right data from a careful design. Remote observations, while containing biases of their own, provide a largely independent reference for assessing bias in *in situ* networks and identifying potential covariates for correction of spatial sampling bias.

*What about variables that cannot be sensed remotely?* Using remote sensing for key properties of the biosphere may allow redirection of *in situ* emphasis to equally important measurements and experiments, on soil properties, microbial processes, genomics and trophic processes that cannot be sensed remotely and that are equally important to prediction. This may be particularly important at high latitudes where soil processes dominate potential tipping element processes. Coordination of *in situ* and remote observations is critical and helps with calibration and validation.

*Without a coherent set of observations of terrestrial ecosystems and the carbon cycle, can we achieve early warning and prediction of carbon cycle–climate feedbacks?* Most ecosystem observations are initiated for project purposes and, unlike meteorological observations, not as part of a global design to inform or evaluate models and predictions. As a result, and as a consequence of logistical issues, the current *in situ* network is sparse in the regions where carbon cycle feedbacks are most likely, making detection of changes difficult. Detection alone is not sufficient: to enable prediction, attribution of changes to quantified mechanisms is also essential. To know carbon stocks and fluxes always and everywhere, coordination of *in situ* and remote observations is needed.



**Table 3** Variables, technologies and missions/mission concepts for carbon fluxes, stocks and parameters

Variable type and identity	Technology	Current missions and mission concepts*	Status	Quantity retrieved	Key references
Ecosystem Flux					
GPP	Spectroscopy	GOSAT, OCO-2	GOSAT: on orbit OCO-2: launch 2014	Solar-induced Fluorescence	Frankenberg <i>et al.</i> (2012)
Net Ecosystem Exchange	Spectroscopy and inverse modeling	GOSAT, OCO-2	GOSAT: on orbit OCO-2: launch 2014	Column CO <sub>2</sub> , followed by inverse or assimilation modeling	Crisp <i>et al.</i> (2008), Baker <i>et al.</i> (2006)
Ecosystem state variable					
Biomass	Radar or LIDAR	BIOMASS, ICESAT II GEDI*	BIOMASS: launch 2020 ICESat-2: launch 2016, GEDI: proposed >2018	Canopy height or volume scattering	Saatchi <i>et al.</i> (2011)
Ecosystem parameters					
Biological Diversity	Imaging spectroscopy	HyspIRI*	Proposed, no date	Distinct spectra per unit area	Feret and Asner <i>et al.</i> (2014a,b)
Functional diversity (plant traits)	Imaging spectroscopy	HyspIRI*	Proposed, no date	LMA, Chlorophyll, nitrogen concentration, V <sub>cmax</sub> , other chemicals	Kokaly <i>et al.</i> (2009)

\* denotes a mission concept.

The table shows the model fluxes, state variables, parameters and drivers that may be informed by existing or near-term space missions, together with the missions, time frames and geophysical data products corresponding to model requirements.

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