Tansley review

Flux towers in the sky: global ecology from space

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Summary

Global ecology – the study of the interactions among the Earth's ecosystems, land, atmosphere and oceans – depends crucially on global observations: this paper focuses on space-based observations of global terrestrial ecosystems. Early global ecology relied on an extrapolation of detailed site-level observations, using models of increasing complexity. Modern global ecology has been enabled largely by vegetation indices (greenness) from operational space-based imagery but current capabilities greatly expand scientific possibilities. New observations from spacecraft in orbit allowed an estimation of gross carbon fluxes, photosynthesis, biomass burning, evapotranspiration and biomass, to create virtual eddy covariance sites in the sky. Planned missions will reveal the dimensions of the diversity of life itself. These observations will improve our understanding of the global productivity and carbon storage, land use, carbon cycle–climate feedback, diversity–productivity relationships and enable improved climate forecasts. Advances in remote sensing challenge ecologists to relate information organised by biome and species to new data arrayed by pixels and develop theory to address previously unobserved scales.

I. Introduction

Global ecology studies the interactions among the Earth's ecosystems, land, atmosphere and oceans: this paper is focused on the study of global terrestrial ecosystems. Global ecology involves the understanding of ecosystems at the global scale, the distribution of productivity, carbon storage, nutrients and energy partitioning over the planet. Global ecology also involves quantifying how ecosystems affect the trajectory of global change, through the carbon and nitrogen cycles, as well as through the Earth's energy budget. Global ecology also studies the response of the Earth's regional ecosystems to global changes in the planet's physics, for example, through changes to rainfall patterns or ocean circulation.

The study of the Earth as a living planet has deep roots in environmental science, for example in Humboldt's classification of ecosystems based on climate factors (Pausas & Bond, 2018), or

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Lovelock's (2000) writings on Gaia. Global ecology was first conceptualized in the early 20th century (Vernadsky, 1926), but remained largely a concept until a few ground-breaking studies began upscaling local measurements during the International Biological Program (Aronova *et al.*, 2010). Global measurements and models emerged at a similar time, with the use of the Normalized Difference Vegetation Index (NDVI) and the first land surface models for coupling to climate models (Dickinson *et al.*, 1993).

Global ecologists have posed counterparts to many of the questions that ecologists have studied locally:

- What is the primary productivity of the globe and how is it controlled?
- How much carbon does the biosphere store and how could it change?
- How does direct human exploitation of the biosphere affect productivity and carbon storage?
- What is the biological diversity of the world and how does it affect the function and stability of ecosystems?

In 1986, Tucker and colleagues showed that the seasonal variation in atmospheric CO_2 was correlated with the seasonal phenology of vegetation by compiling a global record of greenness from the Normalised Difference Vegetation Index, measured from space, and demonstrated conclusively that the land biosphere controls a key aspect of the carbon cycle (Tucker *et al.*, 1986). Fung *et al.* (1987) combined atmospheric CO_2 data and the NDVI with an atmospheric transport model that was able to replicate important features of the surface *in situ* CO_2 observations, laying the foundation for the development of inverse models to estimate the CO_2 fluxes from atmospheric measurements (Tans *et al.*, 1990).

The - inverse models inferred a large sink in the extratropical Northern Hemisphere (Tans *et al.*, 1990; Gurney *et al.*, 2002), instead of the tropical sink expected on ecological grounds. This led to a 2-decade effort to locate, quantify and characterise the 'missing' Northern Hemisphere terrestrial sink (Schimel, 1995; reviewed in; Schimel *et al.*, 2013, 2015b). Early studies have focused on estimating a static or climatological carbon budget, recognising that the cycle was changing, but trying to estimate a stationary budget, and possibly underestimating how fast change could happen (Gaubert *et al.*, 2018).

Early global ecologists relied on extrapolation of local-scale observations, using schemes and models of complexity that have steadily increased with time, from linear regressions to complex simulations and machine learning (Rosenzweig, 1968; Field *et al.*, 1995; Jung *et al.*, 2009) Researchers have studied global patterns of primary productivity since at least 1968 (Rosenzweig, 1968), with exponentially increasing amounts of data. For example, Rosenzweig used 23 sites, and acknowledged that some of these, and all of his tropical sites, had questionable data. Fifty years later Smith *et al.* (2016) used satellite estimates of annual global terrestrial productivity derived from > 900 million spatially resolved pixels and $> 10^{16}$ observations in the entire time series.

There are many sources of data for global ecology (for example Wofsy *et al.*, 1993; Ciais *et al.*, 2005; Stephens *et al.*, 2007), satellite measurements have underpinned many major advances (Thompson *et al.*, 1996). Satellite measurements are increasingly central to understanding trends in the biosphere as a whole, and as described above, now characterise a far wider range of ecosystem properties than just greenness. Today, researchers can begin to see patterns of actual carbon exchange, storage and key controls emerging on seasonal to short interannual times scales (Liu *et al.*, 2017), setting the stage for quantification and explanations of change (Sellers *et al.*, 2018).

Many global calculations have assumed the biosphere to be stable or at least stationary, and characterised global properties such as Net Primary Productivity as stable characteristics, asking what is the global value of NPP? Early observations compiled data from a year or years within fairly long windows and so, while Rosenzweig (1968) was forced to combine data collected over varying time periods over more than a decade into a single regression against evapotranspiration, Myneni *et al.* (1997), Smith *et al.* (2016), Baccini *et al.* (2017), and Gaubert *et al.* (2018) have examined change over decades, identifying strong trends in the behaviour of the biosphere with increasing climate and land use using satellite greenness, laser and microwave remote sensing and atmospheric CO_2.

Studies of both the emerging biospheric multidecadal time series and the paleorecord revealed a dynamic biosphere, responding to climate and other drivers on a range of time scales. Most of these studies began in the early 1990s, although a few have made use of fortuitous data such as Thoreau's notebooks to create longer records (Heberling *et al.*, 2019). Progress in understanding ecological change has more or less paralleled advances in observations and simulation models, while growing in sophistication, have not yet advanced to convergence on even fundamental sensitivities. There has been a steady increase in global ecology data, with new and improved space-based and airborne remote sensing technologies coming on line (Disney, 2019), sensor networks in terrestrial (Richardson, 2019) and marine (Roemmich *et al.*, 2009) systems and growing use of big data compiled from many investigators (Butler *et al.*, 2017).

Here, we review new observations that are expanding the ability to understand global terrestrial ecosystems; some equivalent advances in marine ecology are described elsewhere (Muller-Karger *et al.*, 2018). We focus on space-based measurements and key synergistic surface observing systems. We focus on the suite of flux and ancillary measurements now made at eddy covariance flux sites, as an organising theme. Eddy covariance has enabled breakthroughs by closing local (scales of 10^4–10^6 m^2) carbon budgets, so that photosynthesis, respiration and evapotranspiration could be quantified. Global networks of eddy covariance flux towers elucidated the large-scale (10–1000 km) controls over those fluxes while process studies at flux sites revealed the controls over fluxes. Space-based measurements of ecosystem fluxes and processes now produce data analogous to eddy covariance sites, a virtual network of 'flux towers in the sky' (Fig. 1).

II. Grand challenges in global ecology

New space technologies can measure a much wider range of ecosystem properties. This presents both great opportunity and

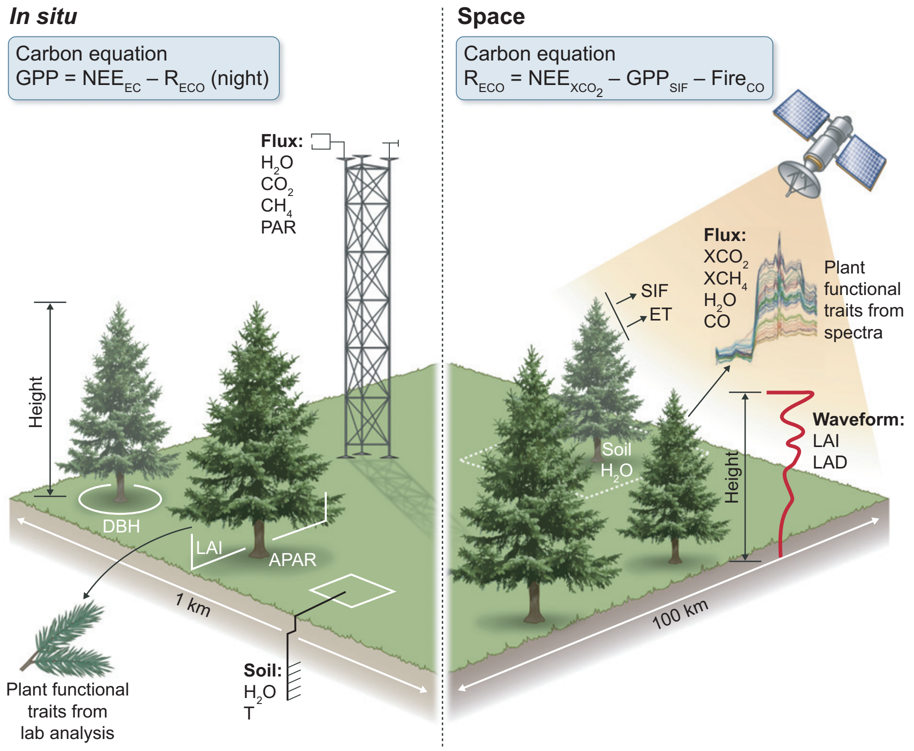

Fig. 1 Flux towers in the sky: carbon exchange can now be measured at flux tower and global scales, but with very different spatial grain and extent, and partition fluxes differently. Flux towers have footprints of *c.* 1 km, while satellite inversions resolve 100s of km. The figure illustrates the variables and data sources for the flux and ancillary measurements *in situ* (left) and from space (right). Flux site-scale measurements are made directly *in situ* (for example, height, diameter breast height (DBH)) or, like soil H_2O and T°, leaf area (LAI) and light interception (APAR), measured with small-scale sensors while from space they are estimates with a variety of remote sensing instruments. See Box 1 for abbreviations.

great challenge for understanding the Earth's ecosystems. The opportunities result from the massive increases in data made available by remote sensing compared with *in situ* data collection, and the reductions in site selection bias as well as the synergistic nature of many of these observations (Saatchi *et al.*, 2015; Schimel *et al.*, 2015a; Shiklomanov *et al.*, 2019).

The challenges arise partly from the newness of the observations. The algorithms to estimate ecological quantities from sensors are not all mature and, in many cases, they have only been tested in a limited range of environments. Their uncertainty may be poorly quantified and all the error sources may not even all be known (Thompson *et al.*, 2018). For some measurements, or for measurements only tested in a few environments, ecological process research may have to wait on several field seasons of *in situ* calibration and validation of the algorithmic approach!

The advent of the plethora of new space-based measurements, across all parts of the electromagnetic spectrum, some active (that is, the sensor emits radiation, not just receives it), means that there is both a need and an opportunity for ecologists interested in building the algorithms and refinements to instruments needed to produce data products with well-quantified uncertainty as well as useful accuracy and precision. For some new observables, empirical calibration may be in advance of a theoretical basis explaining the observed correlations and considerable work will be required before the observations are fully understood!

Ecologists have, however, been grappling with the issue of scale for decades (Risser *et al.*, 1988). The new technologies and algorithms available from space present opportunities for resolving or greatly reducing the uncertainty associated with important questions and hypotheses. Below, we describe a few of the opportunities presented by the array of new observables:

1. What is the primary productivity of the globe and what controls it

Global gross and net primary productivity (GPP and NPP) and how these are changing with climate and human land use are critical for understanding the Earth as a biogeophysical system, for understanding carbon cycle–climate feedback, and for defining limits to sustainability (Vitousek *et al.*, 1986; Running, 2012; Sellers *et al.*, 2018). New remote sensing methodologies provide new constraints on GPP (Frankenberg *et al.*, 2011) and biomass observations over time from radar and LiDAR provide a direct measure of above-ground biomass accumulation and loss (Fatoyinbo *et al.*, 2017).

2. How much carbon does the biosphere store and how could it change

The possibility that carbon cycle–climate feedback currently mitigates climate change, but could eventually weaken or even amplify warming, has long been a concern (Woodwell & Mackenzie, 1995). New, synergistic remote sensing observations (Liu *et al.*, 2017) have the potential to uniquely constrain the effects of changing temperature, rainfall, humidity and incident solar radiation on carbon uptake, respiration and disturbance (Sellers *et al.*, 2018). Understanding how climate affects the carbon cycle requires observations at the scale of climate trends and variation and in the critical, high carbon storage and flux regions of the world (Schimel *et al.*, 2015a). Space-based measurements have their own uncertainties and carbon flux observations will remain at a relatively coarse spatial resolution for some time, but complement *in situ* measurements with their coverage of remote regions and multiple fluxes and controls.

3. How does direct human exploitation of the biosphere affect productivity and carbon storage

Quantifying the direct release of carbon from land use change and deforestation has been a long-term goal of global ecologists (Houghton *et al.*, 1983), but precise estimates have long remained elusive, and trends (decreases or increases) have been difficult to determine with confidence. Combining the top-down measurement of carbon budgets from space (Liu *et al.*, 2017; Sellers *et al.*, 2018) with biomass estimates constrained by LiDAR and radar holds great promise for determining the impacts of deforestation and degradation on continental or subcontinental scales (Bustamante *et al.*, 2016). But besides the direct human impact on the carbon budget, such as through deforestation and biomass burning, there are also indirect effects, for example through forest fragmentation (Brinck *et al.*, 2017) and biodiversity loss (Isbell *et al.*, 2017).

4. What is the biological diversity of the world and how does it affect the function and stability of ecosystems

One of the longest running debates in ecology concerns the effects of changing biodiversity on ecosystem performance (Hooper *et al.*, 2005; Ives & Carpenter, 2007). While consensus may be emerging from large-scale experiments and meta-analysis (Hautier *et al.*, 2015; Oliver *et al.*, 2015), the quantification of large-scale trends in diversity, and their consequences at scale for ecosystem function remains a grand challenge. Remote sensing can contribute to an understanding of the changing ecological diversity and function by linking remote observations of plant functional traits (Asner *et al.*, 2017; Schneider *et al.*, 2017) to remote observations of function, via solar-induced chlorophyll fluorescence (SIF), ET and estimates of GPP, NPP and respiration (Sellers *et al.*, 2018) rather than linking taxonomic identity and function, as done in *in situ* studies. This approach can provide a synoptic view across large regions (Jetz *et al.*, 2016), albeit with higher uncertainty and adrift from taxonomic identity, complementing other sources of data (Schneider *et al.*, 2017).

All of these challenges build towards a critical capability.

5. Can we predict the future of terrestrial carbon storage and the role of ecosystems in the Earth system

Accurately predicting the future trajectory of a system requires knowing its current state and recent past (May 2001). Earth system models have attempted to predict the future trajectory of the Earth's ecosystems, and their carbon storage using very simple representations of initial conditions, estimated by running models to a steady state, and constrained by a very limited number (of order < 30) of plant functional types representing the world's *c.* 400 000 functionally distinct species. Above-ground and below-ground processes are linked (as are species), so characterisation of above-ground dynamics may better enable the constraint of below-ground processes. Fungal species are thought to outnumber plants by *c.* 6 to 1, and recent estimates suggest as many as 1 trillion microbial species (Locey & Lennon, 2016). This means that parameters governing plant function are dramatically simplified from their underlying complexity. While most current models were built in the greenness era, modellers are responding to the advent of more global observation types. Remote sensing of plant functional traits, biomass (capturing some aspects of disturbance history) and plant function (SIF and ET) can add substantial texture to the current schematic representations of the diversity of life in current models, and have already shown an ability to improve prediction (Fox *et al.*, 2018).

III. Current advances and capabilities for global ecology from space

1. Ecosystem carbon balance: ecosystem productivity and carbon storage

Ecosystem carbon balance has long formed a framework for understanding ecosystems (Woodwell *et al.*, 1973). Eddy covariance is used to quantify carbon, sensible and latent heat fluxes over ecosystems. It is the current observational method for understanding the exchange of CO_2 and water at the ecosystem scale and approximating Net Ecosystem Carbon Balance. (NECB) is most simply summarised as:

$$\mathrm{NECB} = \mathrm{d}C/\mathrm{d}t, \qquad \text{Eqn 1}$$

or, the change in total ecosystem carbon storage per unit time (Chapin *et al.*, 2006). Some fluxes contribute to NECB, including the uptake by photosynthesis, and numerous losses or horizontal transfers, including respiration, methane production, erosion, and emission of volatile organic compounds (Unger, 2014). NECB may be approximated by net ecosystem exchange (NEE) at eddy covariance spatial scales:

$$\mathrm{NEE} = \mathrm{GPP} - R_{\mathrm{eco}}, \qquad \text{Eqn 2}$$

where GPP is gross primary productivity (photosynthesis) and $\mathrm{R}_{\mathrm{eco}}$ is ecosystem respiration, itself the sum of autotrophic and heterotrophic respiration, the largest fluxes at the scale of a flux tower (Fig. 1). As will be discussed below, NECB may also now be estimated from space, but in a very different framework.

Observationally, NEE can be decomposed, approximately, into the largest fluxes, GPP and R_{eco} in a number of ways. When NEE is measured using eddy covariance, R_{eco} can be measured at night, when no photosynthesis occurs and then daytime R_{eco} estimated by fitting models to the nighttime data (Reichstein *et al.*, 2005). Extrapolating nighttime $\mathrm{R}_{\mathrm{eco}}$ to daytime conditions is challenging and leads to uncertainties resulting from the measurement itself, deviation from the meteorological conditions or physiological response assumed and from the fitted nighttime model (Wehr *et al.*, 2016; Keenan *et al.*, 2019).

Remote sensing also allows inverse models to constrain estimates of NECB, NEE, GPP and $\mathrm{R}_{\mathrm{eco}}$ as well, albeit at very different scales. This finding is in contrast with inversions of flask data that only estimate the net flux of carbon. Classically (Smith *et al.*, 2016) NPP was estimated by modelling the conversion efficiency from absorbed photosynthetically active radiation (APAR) to accumulation of carbon as NPP, an approach grounded in theory and local empirical studies (Monteith, 1972; Running *et al.*, 2004) using an expanded version of the Light Use Efficiency (LUE) equation, and estimating APAR from the MODIS sensor:

$$\mathrm{GPP} = \varepsilon\ \mathrm{APAR}, \qquad \text{Eqn 3}$$

where ε is light use efficiency or carbon fixed per unit light absorbed (Running *et al.*, 2004). This approach has been shown to have great value when implemented globally but depends on independent estimates of ε, as well as requiring empirical adjustment for moisture and temperature stress, as well as other factors and so requires complex tuned models for application.

NECB can be estimated from global gradients of atmospheric CO_2, measured by precise and accurate surface analysers or in flasks, by inverting atmospheric transport models to estimate regional sources and sinks (Tans *et al.*, 1990; Gaubert *et al.*, 2018). These 'inverse' models are now applied to space-based observations of atmospheric CO_2 (technically the column averaged CO_2 dry air mole fraction, typically denoted X_{CO_2}; see Eldering *et al.* (2017), Liu *et al.* (2017)). These models generate global gridded estimates of NECB, corrected for other fluxes from fossil fuels and the ocean, albeit at relatively coarse spatiotemporal resolutions, for example monthly at 4° × 5°.

However, the spectrometers used for greenhouse gas measurements from space provide an additional benefit (Gu *et al.*, 2019): By measuring light with very high spectral resolution ($\Delta\lambda/\lambda$ *c.* 20 000) in the chlorophyll red edge (740–780 nm), they capture SIF (Fig. 2), the waste light produced by chlorophyll during photosynthesis regulation (Frankenberg *et al.*, 2011; Joiner *et al.*, 2011) SIF provides a measurement that has been shown to be largely and surprisingly linearly related to GPP as measured at flux sites (Frankenberg *et al.*, 2011; Verma *et al.*, 2017). As SIF is related to photosynthetic activity, it responds to stress directly, in contrast with LUE models, in which APAR, driven by leaf area, responds more slowly. SIF therefore captures aspects of photosynthesis that must be modelled in LUE approaches.

Using space-based observations, we can close the carbon budget but quite differently than with eddy covariance, estimating R_{eco} as the residual of NECB from X_{CO_2}, GPP from SIF and including an additional disturbance component, fire emissions estimated from atmospheric CO (Liu *et al.*, 2017; Sellers *et al.*, 2018):

$$R_{eco} = \mathrm{NECB}(X_{CO_2}) - \mathrm{GPP}(\mathrm{SIF}) - \mathrm{Fire}(\mathrm{CO}). \qquad \text{Eqn 4}$$

The space-based X_{CO_2} measurement is considered NECB rather than NEE, as it includes the disturbance flux from fire, and covers large enough regions that horizontal (erosion) export largely occurs within the grid cell, while the global flux to rivers is corrected in the inverse model calculation. While the typical footprint of an eddy covariance tower is in the order of 1 km^2, the typical resolution of a carbon cycle inverse model is 10 000 km^2 or even coarser! The information content of the satellite measurements does not support arbitrary resolution, even if the transport model were perfect (Liu & Bowman, 2016).

GPP is estimated from SIF using the Berry equation (Sellers *et al.*, 2018):

$$\mathrm{GPP} = \varepsilon\ \mathrm{SIF}, \qquad \text{Eqn 5}$$

where this ε is the amount of photosynthesis per unit SIF emitted, or the SIF efficiency (Sellers *et al.*, 2018). While ε is a variable at the molecule and leaf level, it appears surprisingly invariant globally when SIF is measured vs GPP at flux sites, combining the surface network with remote sensing (Sun *et al.*, 2017), except perhaps under extreme stress (Verma *et al.*, 2017). These approaches allow quantification of a few additional ecosystem characteristics, notably

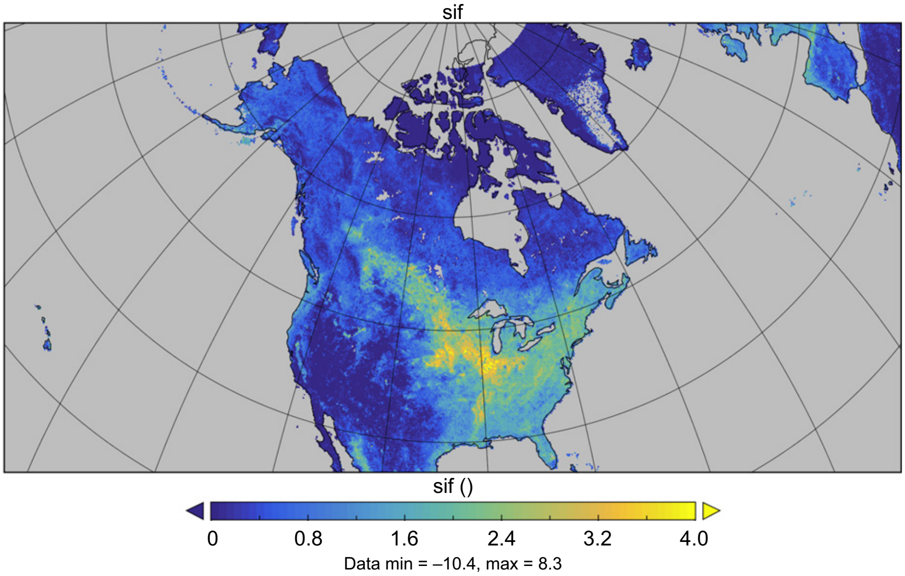

Fig. 2 High resolution image of solar-induced chlorophyll fluorescence (SIF) for North America, capturing patterns of primary productivity, using early data from the TROPOMI mission (Köhler *et al.*, 2018). TROPOMI has a wider swath and smaller pixels than most previous missions capable of measuring SIF, and so provides more frequent (nearly daily) and high resolution (3.5 × 7 km) coverage than previously available. Image courtesy of Nicholas Parazoo, Troy Magney, Philipp Köhler and Christian Frankenberg.

LUE from SIF and APAR (Verma *et al.*, 2017; Zhang *et al.*, 2018). So, for example, LUE may be estimated as:

$$\mathrm{LUE} = \mathrm{GPP(SIF)}/\mathrm{APAR(MODIS)}. \qquad \text{Eqn 6}$$

As we will see later, see section 4.2 estimates of water use efficiency (WUE) and even nutrient use efficiency (NUE) are also now possible, though not yet widely implemented (Stavros *et al.*, 2017).

Satellite measurements of CO_2, X_{CO_2}, complement the surface observing network by providing many more measurements (*c.* 10^4 more usable measurements per day), and coverage in poorly covered areas, especially in the tropics, but arguably the new science enabled by satellite X_{CO_2} results as much from synergism with SIF, and as we will see from other new measurements, as it does from the improved coverage (W. Smith *et al.*, unpublished).

How confident can we be of new satellite estimates of the carbon cycle? There are many uncertainties in estimates from our flux towers in the sky and not all of these are even understood (Liu *et al.*, 2018b). Are they comparable with our other sources of insight? Even this question is difficult. For example, the uncertainties of eddy covariance compared with remotely observed carbon budget estimates are quantitatively and conceptually different. The two approaches are similar in that they both begin with an estimate of NECB that is itself quite uncertain, and must partition it into component fluxes by integrating other uncertain estimates. Satellite estimates may avoid some of the uncertainty issues discussed by Lasslop *et al.* (2010) as the NECB and GPP estimates are independent, while for eddy covariance, they are not. However, the two estimates are at very different inherent scales. Each eddy covariance site captures a footprint of *c.* 1 km^2 while assimilation model grid cells are > 100 km^2. To bring uncertainties together at a common scale could be done by 'upscaling' flux towers (Jung *et al.*, 2009), in which case the uncertainty at 100 km^2 is likely to be dominated by sampling error and ecosystem heterogeneity, increasing the uncertainty as increasing aspects of the landscape not sampled by the flux tower are included.

Alternatively, an assimilation model grid cell or ensemble of grid cells could be 'downscaled', perhaps by assuming a SIF-NECB correlation, taking advantage of the smaller pixel size for SIF. The uncertainty then would likely be dominated by a number of factors: such as noise in the SIF-NECB relationship and NECB uncertainty, which grows as unresolved fine scales of atmospheric motion are approached. In either case, if eddy covariance fluxes are upscaled to assimilation model resolution, or assimilation model fluxes are downscaled to flux tower resolution, the uncertainty grows, making finding the right scale to which to compare the estimates a research challenge (Desai *et al.*, 2011; Liu *et al.*, 2018a). SIF itself may be more readily compared with flux tower scales, as current satellites have pixels 3–7 km on a side, comparable with the *c.* 1 km^2 footprint of a flux tower.

The uncertainty of our flux towers in the sky, and the component fluxes of the carbon cycle derived from these towers, has another impact on addressing grand challenges, specifically when building models to predict future carbon fluxes. Carbon cycle assimilation models work by combining observations and theory within simulation models. The relative impact of observations vs 'theory' (as embodied in the model equations) is determined by the uncertainty assigned to the data vs the model at each location and time step when they are compared (Dietze, 2017). Observational uncertainty is therefore critical when data are used to inform a forecast, and to the extent that it is poorly understood, the ability to use observations in prediction is reduced.

2. Water balance

Water fluxes are key to understanding ecosystem processes and quite central to understanding the carbon cycle. In fact, early extrapolations of site-level NPP data relied on far more spatially extensive estimates of actual evapotranspiration, and used the estimates of AET to estimate NPP (Rosenzweig, 1968; Running *et al.*, 2004), essentially estimating water use efficiency and extrapolating via WUE (as opposed to the more recent LUE based models). Countless analyses show the sensitivity of ecosystem carbon flux and storage to water availability (Damm *et al.*, 2018) and recent all-satellite analyses have confirmed the sensitivity of ecosystem fluxes to drought (Saatchi *et al.*, 2011; Parazoo *et al.*, 2013; Liu *et al.*, 2017).

As with flux towers, scientists can now study watersheds from the sky. Some ecosystem water variables can now be measured from space. First, and directly relevant to carbon fluxes, is evapotranspiration itself. ET is estimated from imaging land surface temperature (LST) measuring in the thermal infrared portion of the spectrum (Fig. 3 and reviewed by Courault *et al.*, 2005). If LST is known, along with energy available (downwelling shortwave, modelled or estimated from other sensors), and the surface to air temperature gradient is known, then ET comprises the majority of the remaining energy balance (Anderson *et al.*, 2011; Bonan, 2015). By closure, using a small number of satellite observations, ET can essentially be estimated through the cooling effect of water use. This approach, implemented for a number of sensors, and in a number of specific algorithms, is now widely used for estimates of ET, and has been implemented in an innovative sensor, ECOSTRESS, currently on the International Space Station (Hulley *et al.*, 2017).

The Earth's gravity field provides another measure of the water cycle, allowing total water storage to be estimated. From 2002 to 2017, the GRACE (Gravity Recovery and Climate Experiment) mission, two satellites (dubbed *Tom* and *Jerry*), built jointly by NASA and the German Aerospace Agency (DLR) orbited in tandem, the distance between these was measured with great precision. This measurement continues with GRACE-Follow-On (GRACE-FO). Local variations in mass on the Earth cause the satellites to accelerate relative to each other, and the distance between these can be measured to within 10 µm over 220 km, allowing a measurement of the gravity field 1000 times finer than previous estimates (Tapley *et al.*, 2004). As the total amount of water stored varies with time, due to precipitation, runoff or groundwater addition or depletion, the mass of a region changes, and GRACE was able to measure those changes.

GRACE has been used to study the terrestrial water cycle in a number of ways. For example, it is well known that the El Niño−La Niña cycle affects precipitation over land. Boening *et al.* (2012)

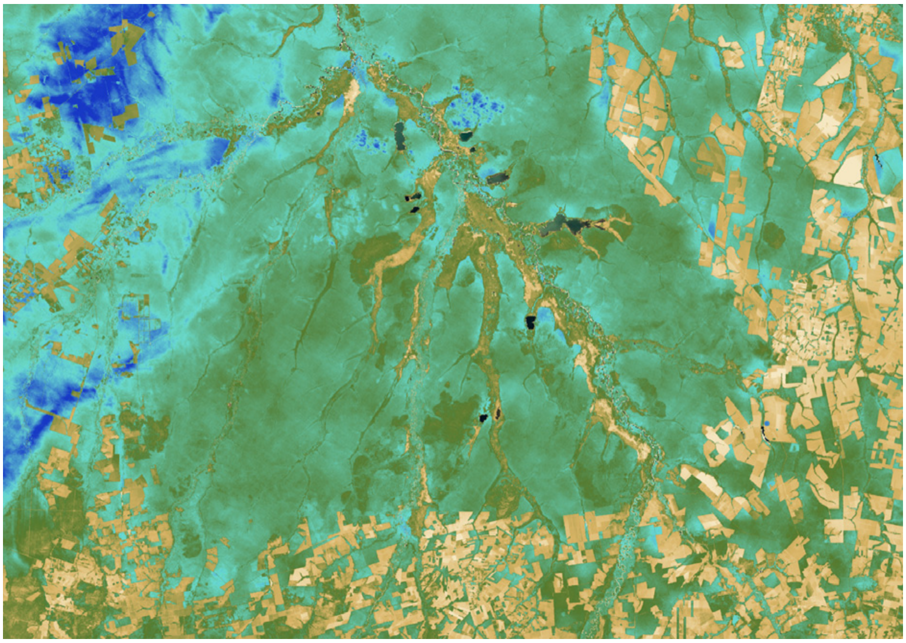

Fig. 3 Evapotranspiration (ET) estimated from ECOSTRESS on the International Space Station, for a portion of the Brazilian Amazon, showing subtle texture in the intact forest and stark contrasts between intact and deforested areas. Blue is open water, darker greens are higher ET, and tans are areas of deforestation. Image courtesy of Joshua Fisher.

showed that precipitation over Australia increased so much during the 2011 La Niña that it had a discernible effect on sea level globally by affecting soil water storage, measured by satellite altimeters. At the same time, Poulter *et al.* (2014) demonstrated that the effects of this water anomaly enhanced carbon uptake, connecting the carbon and water cycles as they co-varied with climate. Bloom *et al.* (2010) combined satellite measurements of methane and gravity to infer large-scale controls over methanogenesis in the tropics, showing correlations between gravity anomalies and CH_4 concentrations to diagnose the influence of the water cycle on CH_4 production, and extending the use of total water storage to a direct estimate of water cycle controls over biogeochemistry.

Several components of water storage are constrained by satellite observations. Passive and active microwave observations can be used to estimate soil moisture, although these measurements may be limited to water near the soil surface and in the absence of extremely dense vegetation (Entekhabi *et al.*, 2010), and this measure of water availability for growth is being used to inform estimates of carbon fluxes (Jones *et al.*, 2017).

Saatchi and co-workers have estimated canopy water storage or vegetation optical depth (VOD), yet another water cycle measurement made from space (Konings *et al.*, 2019). Water in the plant canopy interacts strongly with microwave radiation, allowing an estimate of canopy water separate from other forms of water in the soil or groundwater (Saatchi *et al.*, 2013). Saatchi *et al.* (2013) described this in a seminal paper to show that drought in the Amazon has persistent impacts for multiple years after the actual drought. Specifically, drought reduced the average VOD and increased the amplitude of the diurnal cycle in VOD, suggesting long-term canopy die-back and greater daily water losses with drought. Lee *et al.* (2013) then showed that reductions in VOD and changes to the magnitude of its diurnal cycle (Konings *et al.*, 2019) were well correlated with reductions in SIF, implying a direct relationship between canopy water changes and photosynthesis (Damm *et al.*, 2018).

Having addressed water storage and water flux, evapotranspiration, what else might be observed globally and from space? The Surface Water and Ocean Topography mission, to launch in 2021, will use highly precise radar interferometry to measure water surface heights and quantify, over time, changes to river stage for estimates of runoff, closing an additional flux in the land surface water budget. SWOT will improve the quantification of runoff down to midsized rivers (down to 100 m width) and provide a major additional constraint on continental and watershed scale water budgets.

The terrestrial water budget is:

$$\text{Storage} = \text{Precipitation} - \text{Evapotranspiration} - \text{Runoff}, \qquad \text{Eqn 7}$$

with storage partitioned into:

$$\begin{aligned}\text{Storage} = {} & \text{Plant} + \text{Soil} + \text{Ground} + \text{Surface Inundation} \\ & + \text{Snow and ice}.\end{aligned} \qquad \text{Eqn 8}$$

New water cycle measurements will deliver global measurements for all of the terms in Eqns 7, 8 and , all of which influence ecosystems. There will be some remaining gaps in time and space scales, but with far more coverage than available from upscaling sparse surface data. Storage is constrained by both gravity and VOD, and partitioned into soil moisture, canopy water (VOD), surface inundation in wetlands and groundwater. Snow cover can be estimated from MODIS; algorithms exist to estimate its water content. ET can be estimated in thermal and runoff from radar altimetry. Some methods exist for measuring inundation, most recently using 'bistatic' radar, or analysis of Global Positioning System signals by special receivers (Jensen *et al.*, 2018) (Fig. 4).

The water cycle links to the carbon cycle through total water storage, affecting soil moisture, wetlands and soil moisture, through ET, a direct link to photosynthesis and via VOD, which is indicative of water stress to the vegetation. Just as eddy covariance sites measure water flux and a host of correlates with other sensors, new water cycle measurements extend the flux towers in the sky to observe terrestrial water cycle. As with the carbon cycle, watersheds in the sky provide information at scales larger than those typically studied on the ground, with attendant scale mismatches for validation, and mismatched uncertainties.

3. Ecosystem carbon storage, structure and diversity

Saatchi *et al.* (2011) characterised carbon stocks by combining LiDAR (laser ranging) and radar measurements of vegetation structure. Researchers have been exploring for some time the ability of active remote sensing to quantify above-ground biomass, and the earlier literature was replete with case studies at site or landscape scales. The Saatchi *et al.* paper not only established a baseline estimate based on millions of observations, rather than a few hundred plots extrapolated globally, but also captured important systematic differences in canopy height and biomass between tropical regions, starting to erode the notion portrayed in models that tropical forests are uniform across the continents, despite their considerable evolutionary, geological and climatic differences.

In 2010, no space mission had been specifically designed for biomass and forest structure measurements, so researchers have exploited general-purpose radar missions and the GLAS LiDAR (Box 1), built to measure ice sheet elevations, combined with optical remote sensing for extrapolation between the relatively sparse GLAS measurements of canopy height. Importantly, the spaceborne approach to measuring biomass is fundamentally the same as measurements on the ground. Canopy height is observed and converted to biomass using allometric equations (Fischer *et al.*, 2019) capturing stem architecture with assumed wood densities.

The spaceborne measurement of height is similar to, or better than, ground-based estimates and involves many more samples, albeit with fewer corresponding measurements of stem diameter and other quantities useful for refining allometry. While many researchers have a higher degree of comfort with estimates made on field plots, the far greater volume of data, with its ability to both reduce sampling error and to quantify regional variation not captured in models for extrapolation, lends remote sensing of biomass singular advantages (Saatchi *et al.*, 2015).

At this time, substantial investments in measuring biomass from space have been made. The Global Ecosystem Dynamics Investigation (GEDI), a multilaser LiDAR on the International Space Station (ISS) is currently on orbit (Fig. 5) and two radar missions have partial or primary focused on biomass, the European Space Agency's BIOMASS mission, and NASA and the Indian Space Research Agency's NISAR (NASA-ISRO Synthetic Aperture Radar), to fly in the early 2020s. GEDI, on orbit from 2018, will cover the world's temperate and tropical forests from the ISS orbit (bounded at 50N to 50S) while NISAR and BIOMASS will be nearly global, limited by restrictions on the use of active radar in some regions of the world.

Active remote sensing inherently provides some measure of forest structure, as well as biomass, if only by characterising the horizontal variability of canopy height. However, LiDARs provide more information returning a waveform that captures the vertical structure of foliage within the canopy, and so provide both vertical and horizontal aspects of forest ecosystem structure (Lefsky *et al.*, 2002; Morsdorf *et al.*, 2006), a capability implemented for space by GEDI (Stavros *et al.*, 2017).

Beyond simply characterising biomass and aspects of forest structure, such as disturbance, that affect carbon storage, LiDAR and radar have a great potential to characterise habitat for other creatures (Zellweger *et al.*, 2013). For example, Goetz *et al.* (2010) used LiDAR to map breeding habitats for a migratory bird and the

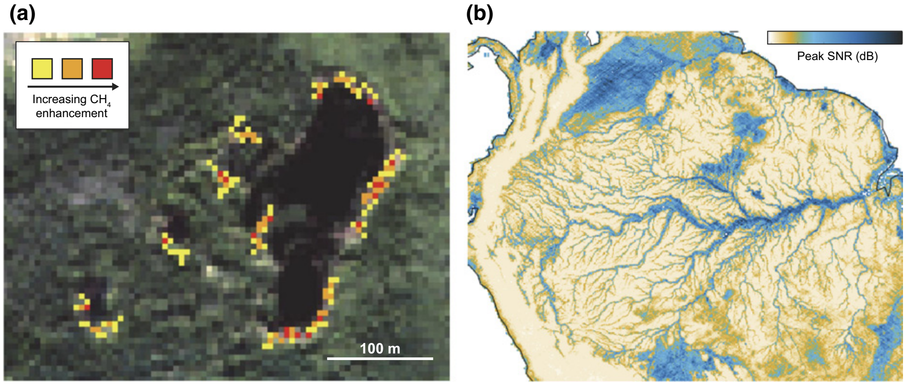

Fig. 4 Methane and wetland source region mapping. (a) CH_4 in high latitude landscapes. Image from the ABoVE Field campaign, collected with the AVIRIS instrument, showing strong and very localised enhancements surrounding an Arctic lake, occurring in inundated areas with high carbon availability. While this instrument does not quantitatively retrieve these enhancements as fluxes, it allows metre-squared mapping where in a landscape fluxes are most intense, critical for trace gases whose fluxes are extremely patchy. (b) Tropical CH_4 source regions, wetland extent in the Amazon, derived from bistatic radar using the Cyclone Global Navigation Satellite System (CYGNSS) constellation of satellites, with a high signal to noise ratio (SNR) in blue indicating primarily open water (water without any standing vegetation) or inundated wetlands and low SNR in tan colours indicating noninundated vegetation. Images courtesy of (a) Clayton Elder and (b) Erika Podest and Nereida Rodriguez-Alvarez.

Box 1Glossary

ABoVE	Arctic Boreal Vulnerability Experiment
AET	Actual EvapoTranspiration
APAR	Absorbed Photosynthetically Active Radiation
AVIRIS	Airborne Visible/Infrared Imaging Spectrometer
BIOMASS	European Space Agency mission
CO	Carbon Monoxide
DBH	Diameter at Breast Height
DLR	Deutsches Zentrum für Luft- und Raumfahrt, Germany
ECOSTRESS	ECOsystem Spaceborne Thermal Radiometer Experiment on Space Station
EMIT	Earth Surface Mineral Dust Source Investigation
ESA	European Space Agency
ET	EvapoTranspiration
GEDI	Global Ecosystem Dynamics Investigation LiDAR
GLAS	Geoscience Laser Altimeter System
GPP	Gross Primary Productivity
GRACE	Gravity Recovery and Climate Experiment
HISUI	HyperSpectral Imager Suite
ISRO	Indian Space Research Agency
LAD	Leaf Area Distribution, or leaf area by height
LAI	Leaf Area Index
LST	Land Surface Temperature
LUE	Light Use Efficiency
MODIS	MoDerate Resolution Imaging Spectroradiometer
NECB	Net Ecosystem Carbon Balance
NEE	Net Ecosystem Exchange
NISAR	NASA-ISRO Synthetic Aperture Radar
NPP	Net Primary Productivity
PAR	Photosythetically Active Radiation
R_{eco}	Ecosystem Respiration
SIF	Solar (or Sun)-Induced Fluorescence
SBG	Surface Biology and Geology
TIR	Thermal InfraRed
TROPOMI	TROPOspheric Monitoring Instrument
VSIR	Visible and Shortwave InfraRed
VOD	Vegetation Optical Depth
XCH_4	Column mole fraction of methane
X_{CO_2}	Column mole fraction of carbon dioxide

use of radar and LiDAR for mapping habitat was reviewed by Bergen *et al.* (2009). Remote sensing of structure, coupled with other measures used *in situ* and now available from space, to characterise habitat, such as productivity, may allow the study of migration and habitat use widely and in remote areas, especially in conjunction with new animal tracking technologies (Wikelski & Tertitski, 2016).

Over the past several decades, the capability to measure canopy water, nitrogen (N), and phosphorus (P) composition, correlates of vegetation function, has been developed (Ustin *et al.*, 1991) to the point at which it is now operational for airborne sensor retrievals (Kampe *et al.*, 2010, Fig. 6). This technology will soon be available from space, initially from the ISS (instruments from Germany, DESIS, Japan, HISUI and the US, EMIT) and later, globally, via the US SBG concept (National Academies, 2018).

Visible and Shortwave InfraRed (VSWIR) imaging spectroscopy can map vegetation and other surface properties over terrestrial domains. Most studies analyse the properties of the spectral surface reflectance, related to the fraction of light reflected from the surface (Schaepman-Strub *et al.*, 2006). Remote sensors do not measure this value directly, but instead observe the radiance incident at the aperture. An atmospheric correction is required to compensate for the spectral radiance loss between the surface and the satellite sensor due to atmospheric absorption and scattering (Thompson *et al.*, 2017). The radiative transfer theory required for atmospheric correction is a mature science and current algorithms perform well for nadir-looking observations in clear sky conditions (Fig. 6).

Once VSWIR data are corrected for the effects of the atmosphere, and aspects of the scene such as topography, the spectra can be used to estimate a wide range of plant functional traits (Butler *et al.*, 2017). Commonly measured traits are those closely related to photosynthesis, growth and subsequent decomposition of leaf material (Singh *et al.*, 2015) (Table 1).

As a critical element in enzymes such as rubisco, amino acids and chlorophyll, nitrogen has long been considered a key control over terrestrial carbon uptake and storage (McGuire *et al.*, 1995) and a target for remote sensing (Schimel, 1995). The combination of nitrogen and lignin is an important control over decomposition (Aber & Melillo, 1982) while phosphorus may be limiting in some ecosystems with highly weathered soils or where nitrogen is abundant, for example through anthropogenic deposition. Detection of additional compounds (sugars, starches, phenolics) from imaging spectroscopy may further enable the characterisation of plant economic investment strategies, for example in defence, reproduction, etc. Just as *in situ* measurements of canopy N may be related to GPP and NEE at sites where carbon fluxes are measured *in situ*, the large-scale relationships between canopy chemistry and plant function may be assessed globally when canopy nutrients are measured from space in conjunction with SIF, ET and other new space-based measurements.

Remote observations of plant functional traits allows finer distinctions geographically than the use of a small number of plant functional types based on greenness, phenology and other attributes accessible with multispectral sensors such as MODIS (Asner *et al.*, 2017). As with remote sensing of canopy structure, the implications of remote sensing of canopy chemistry go far beyond an understanding of the carbon balance of ecosystems, as chemical traits may influence the export of nutrients to receiving waters, defence against herbivory, food quality for herbivores and other aspects of habitat.

Recently, it has been shown that VSWIR imaging spectroscopy can even quantify plant diversity across landscapes and directly contribute to the understanding of biodiversity (Féret & Asner, 2014; Dahlin, 2016). Biodiversity analyses exploit the high dimensionality of spectroscopic data: in which multispectral sensors typically have around three significant principal components, spectroscopic data may have 15–50, depending on methodology and scene (Schimel *et al.*, 2013; Thompson *et al.*, 2017). This extraordinarily high information content suggests that current algorithms may just have scratched the surface of the biological information inherent in spectroscopy, much less in combination with other remote sensing modalities (Asner *et al.*, 2012; Cawse-Nicholson *et al.*, 2013).

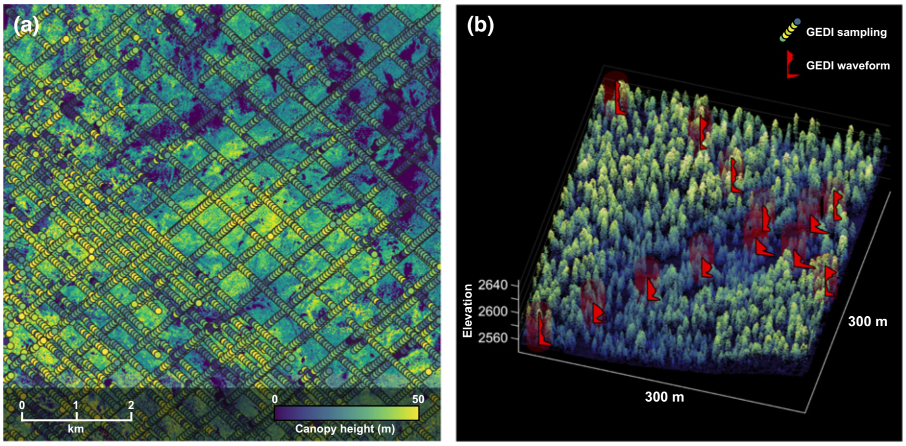

Fig. 5 Simulated GEDI observations, using data collected by an airborne LiDAR and algorithmically converted to emulate GEDI to characterise a Sierra Nevada forest using the method of Hancock *et al*. (2019) to characterise it as would be observed from space. (a) GEDI sampling over imaging LiDAR, with each circle showing a GEDI sample, colour-coded to indicate the corresponding height. (b) An inset image, showing the simulated waveform GEDI would retrieve at each sample point over a 2-yr observation period, over the reconstructed canopies from imaging LiDAR. The image shows mapped canopy height over a complex mountain landscape. Image courtesy of Fabian Schneider and Antonio Ferraz.

Table 1 Targeted observables (specific quantities identified as priorities for new NASA observing systems): plant functional traits and their estimated uncertainty after retrieval, based on independent validation.

Functional trait	Units	Normalised uncertainty, retrieved (Singh *et al*., 2015)
LMA	$\mathrm{g\,m^{-2}}$	11%
Nitrogen	% dry mass	16%
Chlorophyll	$\mathrm{ng\,mg^{-1}}$	8%
Lignin	% dry mass	12%
Phosphorus	% dry mass	16%

Normalised uncertainty, uncertainty in original units/mean value (Serbin *et al*., 2014). LMA, leaf mass per unit area.

While most current spectroscopic data have been acquired from aircraft, or from sensors more limited than the emerging generation capable of retrieving a wide range of plant functional traits, data sets now exist that can show how functional diversity may be characterised across widely divergent ecosystems (Martin *et al.*, 2018) and various estimates related to plant functional diversity are shown in Fig. 6. In concert with massive crowd-sourced data sets, next-generation imaging spectroscopy retrievals will not only allow plant functional traits to be related to plant function (photosynthesis, respiration, evapotranspiration), but are also poised to make contributions to biogeography and macroecology (Butler *et al.*, 2017).

4. CH_4, the other carbon

Methane emissions (CH_4) are an important ecosystem flux, and CH_4 has been observed from space since the mid-1980s (Atmospheric Trace Molecule Spectroscopy (ATMOS), Michelsen *et al.*, 2000). While, as noted above, Bloom and others have used global CH_4 estimates from space and other Earth observations to model its flux, CH_4 can also be imaged at very high resolution using imaging spectroscopy, making use of its very strong absorption features in the shortwave infrared (Kort *et al.*, 2014). This capability is being used to map aspects of the human carbon cycle, such as CH_4 leaks (Kort *et al.*, 2014), but can also be used to visualise patterns of CH_4 flux at the landscape scale, scales not practical to survey with *in situ* techniques, and obscured by the low resolution of global sensors (Fig. 4). This new capability, available on aircraft, but feasible from space, promises to address scaling challenges that have plagued trace gas research for decades (Matson *et al.*, 1989). Methane, notoriously produced in small regions of the landscape, as in Fig. 4(a), also benefits from am ever-improving mapping of wetlands, as in Fig. 4(b).

IV. Meeting the challenge

Meeting the challenges of global ecology by integrating the plethora of new observations to build a system of flux towers in the sky requires addressing some outstanding issues. Key areas for effort include:

1. Uncertainty quantification

To distinguish real phenomena, and combine observations from multiple sources in model statistical and data assimilation models, the uncertainty of each observation must be well quantified, to balance its influence against other sources of information (Fox *et al.*, 2018). Individual satellite observations often have complex sources of random and systematic errors (Hobbs *et al.*, 2017) therefore correctly computing the uncertainty becomes all the more complex when using multiple satellite observation records (Liu *et al.*, 2017; Fox *et al.*, 2018). At the same time, the extraordinary coverage and detail from satellite remote sensing data reduces sources of error that may dominate inference from *in situ* methods (Saatchi *et al.*, 2015; Schimel *et al.*, 2015a). However, independent validation of satellite estimates remains a serious challenge, in part because of the mismatch in scale between *in situ* and remote estimates, and novel techniques involving aircraft (Desai *et al.*, 2011) and networks (Jung *et al.*, 2009) are needed.

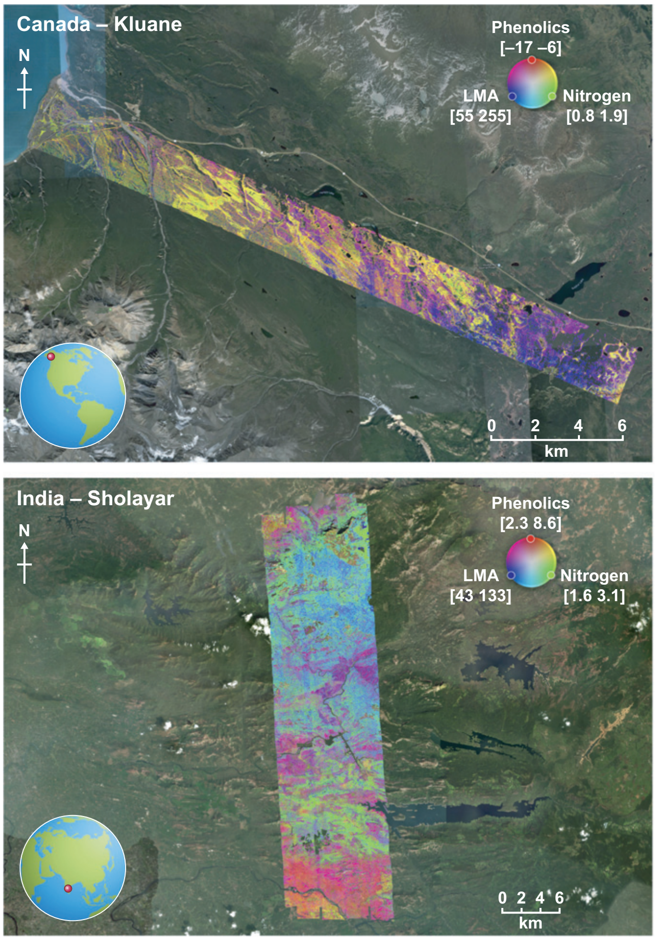

Fig. 6 Algorithms for canopy composition are approaching maturity for global application and can provide comprehensive information on plant functional traits and their diversity within biomes. Retrieved patterns of canopy nitrogen in Red–Green–Blue (RGB), phenolics and leaf mass per unit area in two contrasting ecosystems, Kluane, Yukon, Canada and Sholayar, Kerala, India, retrieved with the same algorithm from AVIRIS airborne data. The three traits are combined in the image using a Red–Green–Blue algorithm. The inset maps show the site locations. Figure courtesy of Fabian Schneider and Philip Townsend.

2. Algorithm development

Algorithms – the mathematical procedures that convert sensor measurements, usually counts of photons at a detector, into meaningful biogeophysical quantities – for new satellite observables can be extraordinarily complex, and their development constitutes a field in itself. In many cases, the usability of satellite data products depends directly on how the data were processed. Yet, for new satellite observables, a relatively small community is engaged in developing and testing these procedures, and, in contrast with the recognised subfield of satellite meteorology, few programmes teach the foundational techniques. The mathematics and computation underlying most satellite algorithms are well within the experience of current ecology graduates, save perhaps for the sheer data volumes that may be involved.

3. Modelling and data integration

The seamless fusion of new global satellite observations, *in situ* measurements and modelling of biology is key to the success of global ecology, combining observations of different processes and at different scales (Wikle *et al.*, 2001). Remote sensing can observe over large scales and down to fairly fine detail while uniquely observing landscape change, but the fundamental units of biology are organisms or even genes, and these are not usually observable from space since satellite observations usually characterise plant canopies. Learning to combine the power of space-based global observations with increasingly massive compilations of biological measurements is a grand challenge, and the basis for predicting the impacts of global change on the world's ecosystems (Jetz *et al.*, 2016).

Measurements from satellites now on orbit and planned in the near future open a second golden era of terrestrial remote sensing, following the successes of the MODIS/LANDSAT era. MODIS, LANDSAT and their international counterparts, saw the living planet in shades of green, while the following generation of sensors observed terrestrial ecosystems in terms of fluxes (SIF, GPP, CO_2 and CH_4), ecosystem state variables (height and biomass, canopy chlorophyll and chemistry) and water variables (precipitation, total storage, soil moisture, canopy moisture and runoff). The transition is analogous to the transition from monochrome black-and-white (or green-and-white) TV to full colour: with multispectral sensors we observe the world in shades of green; with the new generation of sensors we begin to observe a full spectrum of ecosystem states and fluxes.

In parallel, models greatly simplify the diversity of life and the legacy of disturbance. Current Earth system models paint the Earth as having 10–30 plant functional types, although, in fact, the Earth hosts $> 350\,000$ plant species. Global models spin up initial biomass to levels in equilibrium with climate and fail to capture the fine-grained mosaic of disturbance, degradation and regrowth, as well as cohorts of less-disturbed vegetation affected by wind, fire, insects, pests and pathogens and other influences that affect biomass and species distribution. These factors are well known by ecologists and have been addressed in local studies (Bürgi *et al.*, 2017) but data have simply been inadequate to address the complexity of global ecosystems.

New observations from space as described above can potentially provide huge volumes of synergistic data on ecosystem fluxes, state variables and parameters. The new measurements are more informative in combination, forming a virtual flux tower site, and allowing flux partitioning and the analysis of relationships of carbon flux to the water cycle, to ecosystem structure and composition and to disturbance. Taken together, the suite of new observations form an enhanced basis for prediction (Fox *et al.*, 2018). The 'Blue Marble' image of the view of the Earth emphasises the role of life on Earth (Mayer, 2016) while new measurements will expose the diversity of life on our living planet (Merow *et al.*, 2017). As physical flux tower sites do locally, flux towers in the sky provide an integrative view of the Earth's ecosystems.

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