Enhancing global change experiments through integration of remote-sensing techniques

Alexey N Shiklomanov^{1*}, Bethany A Bradley², Kyla M Dahlin³, Andrew M Fox⁴, Christopher M Gough⁵, Forrest M Hoffman⁶, Elizabeth M Middleton⁷, Shawn P Serbin⁸, Luke Smallman⁹, and William K Smith⁴

Global change experiments are often spatially and temporally limited because they are time- and labor-intensive, and expensive to carry out. We describe how the incorporation of remote-sensing techniques into global change experiments can complement traditional methods and provide additional information about system processes. We describe five emerging near-surface remotesensing techniques: spectroscopy, thermal and fluorescence imaging, terrestrial laser scanning, digital repeat photography, and unmanned aerial systems. The addition of such techniques can reduce cost and effort, provide novel information, and expand existing observations by improving their context, accuracy, and completeness. In addition, we contend that use of airborne and satellite remote-sensing data during site selection can improve the ecological representativeness of future experiments. We conclude by recommending a high level of communication and collaboration between remote-sensing scientists and ecologists at all stages of global change experimentation.

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Humans, through their ecological impacts, are conducting an unprecedented global-scale experiment on the Earth's

In a nutshell:

- Global change experiments can help to identify important ecological changes on the horizon, but because they are usually implemented over small spatial scales and short time periods, the applications and inferences drawn from them are relatively limited
- Near-surface remote-sensing techniques offer novel ways to expand and extend global change experiments
- Airborne and satellite data can be used to analyze the representativeness of a site being studied and to search for patterns or early warnings that might reinforce results previously obtained from large-scale experimental manipulations
- Future global change experiments should prioritize extensive communication and collaboration between ecologists and remote-sensing scientists

¹Joint Global Change Research Institute, Pacific Northwest National Laboratory, College Park, MD *(alexey.shiklomanov@pnnl.gov); ²Department of Environmental Conservation, University of Massachusetts– Amherst, Amherst, MA; ³Department of Geography, Environment, and Spatial Sciences, Michigan State University, East Lansing, MI; ⁴School of Natural Resources and the Environment, University of Arizona, Tucson, AZ; ⁵Department of Biology, Virginia Commonwealth University, Richmond, VA; ⁶Climate Change Science Institute, Computer Science & Mathematics Division, and Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN; ⁷NASA Goddard Space Flight Center, Greenbelt, MD; ⁸Environmental and Climate Sciences Department, Brookhaven National Laboratory, Upton, NY; ⁹School of Geosciences, University of Edinburgh, Edinburgh, UK ecosystems (IPCC 2013). Understanding the long-term impacts of human activity on ecosystems is essential for predicting losses of biodiversity as well as changes in biogeochemical cycles and food security. Observational studies, while often broad in scale, rarely uncover the mechanisms driving ecological change; to directly quantify these mechanisms requires controlled ecosystem experiments (Medlyn *et al.* 2015). Unfortunately, the high financial costs and the amount of effort involved in carrying out such experiments limit their quantity, spatial extent, and duration. It is therefore critical that global change experiments provide the largest possible return on investment in terms of data volume generated and ecological representativeness.

Over the past several decades, remote sensing has emerged as an important tool for characterizing changes in ecosystem structure and function across scales. Leaf traits (eg leaf mass per area, nitrogen [N], chlorophyll), vegetation structure (eg height, landscape fragmentation), ecosystem processes (eg phenology, productivity), and measures of ecological disturbances (eg fire, disease, deforestation), all of which can be informed by remote-sensing measurements, have been identified as biodiversity variables that are essential for monitoring and assessing policy initiatives (Pettorelli et al. 2016). Moreover, remote-sensing techniques can complement onthe-ground approaches by reducing effort, offering wider spatial and temporal coverage, facilitating reproducibility, and automating data collection. However, to date, remotesensing techniques have been underutilized in the context of global change experiments; for instance, a Web of Science search (conducted on 31 Jul 2017) revealed that remote-

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Figure 1. Effect of two leaf traits – (a) nitrogen mass fraction (%N) and (b) chlorophyll content (Chl) – on reflectance of northern red oak (*Quercus rubra*) leaves. Leaves are divided into the 33rd ("lo"), 66th ("mid"), and 100th ("hi") percentiles of the corresponding traits. Within each group, solid lines represent means and dashed lines represent mean \pm standard deviation for all spectra. Higher leaf %N leads to higher reflectance in the near infrared (700–1300 nm) region, whereas higher leaf chlorophyll content leads to lower reflectance in the visible region (<700 nm). These differences in the spectral signatures of different traits allow spectroscopy to be used to non-destructively estimate leaf traits from leaf reflectance observations.

sensing technologies are mentioned in just 30 (2.4%) of the 1271 studies relating to experimental carbon dioxide (CO_2) enrichment.

Here, we review how established and emerging remotesensing techniques can enhance the value of global change experiments, beginning at the organism scale, where vegetation spectra measured by field-portable devices can be used to infer plant chemical and morphological traits; we then advance to the plot scale, where terrestrial laser scanners paint threedimensional (3D) images of vegetation structure and allocation, digital cameras monitor ecological changes, and unmanned aerial systems (UASs) provide detailed imagery; finally, we consider the landscape scale and beyond, where airborne and satellite imagery may inform experimental site selection, and aid in the analysis of site representativeness and expansion of experimental results. Collectively, these approaches encompass a wide range of spatial and temporal scales and provide new insights into a variety of ecological processes relevant to global change. Our primary objective is to demonstrate how these techniques can be applied, both individually and in combination, to improve the accuracy and expand the scale of inference of localscale global change experiments.

Spectroscopy: biochemical and biophysical fingerprinting

One of the fundamental goals of global change experiments is to understand how plants respond to changing environmental conditions. Many aspects of plant function are linked to "traits" (measurable characteristics of plants that directly affect their function; Violle et al. 2007). Because of the fundamental role of leaves in photosynthesis, leaf traits (eg morphology, chemical composition) are particularly important for assessing plant response to environmental change (Gornish and Prather 2014). Conventional approaches to measuring plant traits have several limitations. First, they are typically destructive, which restricts the number of samples that can be collected without affecting a plant's function and is an obstacle to tracking changes to an individual over the course of an experiment; second, analyses based on these techniques often require a full laboratory setting, which limits their applicability in remote and rugged environments.

Spectral observations provide an alternative means of studying leaf traits. Ecologically important leaf components (eg pigments, proteins, structural molecules) interact with light in distinct ways. Field-portable spectroradiometers (offered by companies such as Malvern Panalytical, Spectra Vista Corporation, and Ocean Optics) measure the character of light reflected from and transmitted through surfaces

with high precision and across frequencies beyond the capabilities of the human eye (Figure 1). These spectral measurements can provide estimates of traits as varied as leaf mass per area, N and phosphorus (P) concentrations, and maximum rates of carboxylation and electron transport (Serbin *et al.* 2012).

Compared to traditional trait measurement techniques, spectral measurements are easier, faster, and less expensive for analyzing large numbers of samples. As such, one application of spectroscopy is to establish empirical relationships between spectra and traits for a sample of leaves, and then use spectra to infer traits across larger scales, including experimental manipulations or climatic gradients. For instance, Serbin *et al.* (2012) applied traits derived from spectroscopy to study the temperature sensitivity of photosynthesis across an experimental temperature gradient. A similar approach could be applied to precipitation and nutrient manipulation studies, in which foliar biochemistry is a key focus (Prager *et al.* 2017). The larger sample sizes afforded by spectroscopy also allow for more sophisticated tests of trait–environment relationships (Dahlin *et al.* 2013).

Another key advantage of spectroscopy is that it is nondestructive, and therefore allows for repeat sampling of the same plant organs through time. This feature is essential for monitoring plant responses to environmental stress; for example, using repeat reflectance spectroscopy measurements, Bayat *et al.* (2016) monitored phenological changes in pigment content and leaf morphology in grasses subjected to different levels of drought stress.

A final important advantage of spectra is their rich information content. A single reflectance spectrum can provide information on ten or more traits (Asner *et al.* 2015), and spectra from experiments designed to study one set of plant traits can later be re-analyzed with different techniques to examine another set of plant traits.

Fluorescence and infrared thermography: monitoring instantaneous function

Global change experiments offer opportunities for exploring rapid physiological responses to biophysical (eg temperature, precipitation) and biogeochemical (eg nutrients, CO₂) constraints. An active research area involves understanding ecosystem-scale carbon (C) and water fluxes by studying their component parts (eg photosynthesis versus respiration; evaporation versus transpiration). These changes in plant activity can occur within minutes of an environmental change and therefore demand near-real-time detection. Chlorophyll fluorescence (ChlF) and thermal infrared imaging (thermography) are two complementary remote-sensing techniques that capture rapid functional responses related to C uptake and water loss, respectively. ChlF is the re-emittance of energy by photosystems during the light reactions of photosynthesis and is closely linked to vegetation productivity (Baker 2008). Decades of research at the leaf scale provided key insights into the link between ChIF and photosynthesis (Porcar-Castell et al. 2014), but applying these techniques at scales beyond the leaf level has always been problematic. A recently developed method, based on the measurement of sun-induced chlorophyll fluorescence (SIF), has driven a new research frontier in which instruments on towers, aircraft, and satellites measure ChlF. Novel techniques for measuring SIF coupled with growing evidence of a close relationship between SIF and ecosystem productivity (Yang et al. 2015) have generated interest in the application of SIF measurements in experimental contexts (Frankenberg et al. 2016), and SIF measurements have in turn been used to quantify the physiological effects of experimentally induced heat stress (Wang et al. 2016), nutrient limitation (Cendrero-Mateo et al. 2016), and elevated CO₂ (Sekhar et al. 2017).

Whereas SIF measurements capture aspects of plant function associated with C uptake, infrared thermography can measure temperature variations of entire plant canopies (Aubrecht et al. 2016), which can be integrated with additional information on environmental conditions to study canopy transpiration (Leinonen et al. 2006). Stomatal pores on leaf surfaces regulate water and CO₂ exchange, resulting in a complex compromise between leaf C gain and water loss that directly mediates leaf temperature (Figure 2). Loss of heat energy associated with evaporation from stomata (ie transpiration) reduces leaf surface temperature and is detectable with thermography (Figure 2; Costa et al. 2013). A variety of thermal infrared cameras are commercially available (eg FLIR, www.flir.com; ICI, www.infraredcamerasinc.com). Like SIF measurements, thermography has been used in experiments to quantify the effects of drought stress (Santesteban et al. 2017), nutrient limitation (Guo et al.

19 18 17 16 15 Figure 2. Thermography of a sunflower (Helianthus annuus) leaf. Temperature differences reflect the spatial patterns of stomatal density and associated cooling. In this image, the coldest temperatures (blue) are

in the leaf lamina, which have the highest stomatal density, whereas leaf veins (green) and petioles (orange), as well as developing inflorescences (orange), do not have stomata and are therefore warmer. The rim of the pot in the background (red) has the highest temperature.

2016), and elevated CO₂ (Leuzinger and Körner 2007) on plant function.

SIF and thermography can be used in combination to assess vegetation water-use efficiency (WUE; a measure of the relative amount of water lost through transpiration per unit C gained through photosynthesis). Changes in atmospheric CO₂ concentrations and vapor pressure deficit are expected to differentially impact rates of photosynthesis and transpiration, resulting in increases or decreases in WUE with profound ecosystem-scale consequences (Lemordant et al. 2018). Largescale experimental manipulations that include these techniques are therefore urgently needed to improve understanding of how changes in these processes will feed back to influence rates of global change.

Terrestrial laser scanning: mapping structure and function in 3D

Where and how much C accumulates and is stored in biomass, and how vegetation structure relates to ecological processes, are as important for ecologists to answer as are questions regarding plant physiology. To this end, global change experiments frequently track plant biomass stocks, production, and allocation among leaves and stems (Wu et al. 2011). Direct measurements of plant biomass by weighing are often undesirable because they are destructive, impractical for large plants, and time- and labor-intensive

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(Kloeppel *et al.* 2007). On the other hand, non-destructive approaches for inferring biomass stocks, production, and allocation based on allometric relationships that predict wood and leaf mass from height or stem diameter can be biased or uncertain (Clark *et al.* 2001).

Terrestrial laser scanning (TLS; also known as groundbased LiDAR or T-LiDAR) uses infrared lasers on a fixed rotating platform to measure the 3D characteristics of surfaces, including individual trees and whole canopies (Figure 3). Raw 3D scans (Figure 3a) contain an enormous amount of information about the physical distribution and quantity of biomass, and when repeated from a fixed location over time, the accumulation or loss of biomass within an area. TLS instruments are therefore useful for non-destructive, plot-level forest inventories of plant species, stem density, height, biomass, and leaf area, as well as characterization of the physical structure of trees and canopies (Dassot et al. 2011). Moreover, TLS allows for more rapid and accurate assessment of these structural parameters than conventional methods (Stovall et al. 2018). Recently, the highly detailed mapping capabilities of TLS have led to the development of novel structural metrics that could predict functional responses to global change (Juchheim et al. 2017).

In the context of global change experiments, TLS enables detailed studies of plant structural changes in response to shifts in environmental conditions and biotic changes (eg invasive species, disturbances). Many global change experiments employ conventional inventory and meteorological-based methods to quantify changes in ecosystem biomass and productivity (eg Wu et al. 2011). Greater reliance on TLS may therefore lead to improvements in the accuracy of biomass quantity and distribution estimates (Figure 3c), and support the development of novel descriptions of ecosystem structure (eg branching order; Figure 3b; Hackenberg et al. 2015) to predict ecosystem function. For example, in precipitation manipulations, high-resolution measurements of canopy structure provided by TLS could improve our understanding of canopy interception, a process that is poorly represented in current ecosystem models (Medlyn et al. 2015).

While first-generation TLS instruments measure only the phase or timing of reflected light, an emerging class of TLS instruments leverages aspects of spectroscopy by also measuring the intensity of returns (the strength of laser pulses reflected off an object) at multiple wavelengths. This enables paired mapping of plant functional (eg nutrient concentrations, chlorophyll fluorescence) and structural (eg leaf and



Figure 3. Terrestrial laser scanning (TLS) enables sophisticated analyses of individual tree and stand structures. (a) TLS returns from La Selva Biological Station, Costa Rica. Color indicates distance from scanner and saturation indicates laser reflectivity. Reproduced from Palace *et al.* (2016). (b) Processed TLS returns from a single *Prunus avium* individual, with colors indicating branching order (primary, secondary, tertiary, etc). Reproduced from Hackenberg *et al.* (2015). (c) Allometric relationships of stem diameter (left) and diameter² × height (right) to biomass estimated from TLS scans. Each colored line represents a different species, and the black line is the combined fit for all species. Reproduced from Stovall *et al.* (2018).

branch sizes and angles) characteristics with extremely high spatial resolution (~5 mm) in 3D (Eitel *et al.* 2016). Coupled with experiments, next-generation TLS instruments that record laser return intensity can concurrently quantify photosynthetic pigments and canopy structure, enabling simultaneous evaluation of physiological and structural responses to global change events (Zhang *et al.* 2017).

Digital repeat photography: continuous monitoring

Digital repeat photography is a relatively simple and inexpensive method for continuously observing individual plants and whole canopies over time. An important and effective application of this technology is high-frequency (sub-daily) monitoring of ecological events, such as phenological transitions and disturbances (Figure 4; Brown *et al.* 2016). The fine spatial resolution of digital photographs facilitates detection of subtle differences between individuals within a canopy, as well as monitoring canopy structural variables like leaf area index, leaf angle distribution, and clumping factor (Ryu *et al.* 2010).

Although most research involving digital repeat photography focuses on observational studies, this technique was used successfully to detect differences in phenology among experimental treatments. For example, Knox *et al.* (2015) deployed a cluster of phenocams (Brown *et al.* 2016) to track phenological differences among five sites in California's Sacramento–San Joaquin Delta with various agricultural practices. Phenocam "greenness" supplemented destructive sampling so that field measurements could be extended to a high temporal resolution. In a study focusing on grasslands, Hufkens *et al.* (2016) linked phenocam data from North American grasslands to climate projections and found that future climate scenarios could substantially increase both grassland cover and length of growing season. Most global change experiments have historically focused on long time-series and interannual variability (eg Zhu *et al.* 2016), but digital repeat photography has the potential to add an important dimension of intraseasonal variation.

The utility of digital repeat photography is enhanced when it is combined with other measurements. For example, Wingate *et al.* (2015) combined digital repeat photography with meteorological tower measurements of CO_2 across Europe to identify and explain temporal lags between peak canopy greenness and vegetation primary productivity. Tang *et al.* (2016) reviewed the critical roles that digital repeat photography, fluorescence measurements, satellite imagery, and other measurements play in advancing phenological research, and emphasized the importance of integrating these data with direct observations to improve our understanding of the mechanisms driving phenology.

The majority of digital repeat photography cameras capture light in three visible bands (red, green, and blue) but occasionally include a near-infrared band. However, cameras with



Figure 4. Time-series of mean daily green chromatic coordinate (Sonnentag *et al.* 2012) of a phenocam at a field station in the Bartlett Experimental Forest, in Bartlett, New Hampshire, illustrating how repeat photographs can monitor the timing of phenology. Photographs were taken at noon on (a) 25 Apr 2016, (b) 17 May 2016, and (c) 30 May 2016. Data available at https://phenocam.sr.unh.edu/data/archive/bartlettir/ROI/bartlettir_DB_0001.html.

higher spectral resolution are becoming more common and are now commercially available (eg www.specim.fi). As described in the Spectroscopy section above, such "hyperspectral" images could enable high-frequency measurements of the phenology of additional leaf traits, such as pigment and nutrient contents.

Unmanned aerial systems: precision and flexibility

A primary objective of many global change experiments is to expand plot-level observations to landscape scales, which requires knowledge of local landscape features such as land cover, soil characteristics, and topography. UASs provide a cost-effective platform for extrapolating measurements to landscape levels (Anderson and Gaston 2013).

Because UASs can fly very close to measurement targets, they are able to collect imagery at exceedingly high spatial resolutions (<1 cm). By photographing targets at high resolution from different angles, UASs are effective at quantifying detailed canopy structural variables, such as leaf angle distributions (McNeil et al. 2016) and canopy clumping (Chianucci et al. 2016). Moreover, high-resolution images obtained from UASs can map plant composition by classifying the shapes of tree crowns (Michez et al. 2016). Programmable flight paths greatly improve on the capabilities of manually piloted UASs, enhancing the effectiveness for repeat monitoring because they collect measurements over the same configuration multiple times. Detailed photogrammetry missions are a powerful example of the application of programmable flight paths. For instance, "structure from motion" is a popular photogrammetry technique whereby a 3D surface model of an object is constructed from repeat two-dimensional (2D) images collected from different sides. For mapping structure and estimating biomass, UAS-based photogrammetry can achieve accuracy comparable to or better than airborne LiDAR at a fraction of the cost, even at multi-hectare scales (Messinger et al. 2016). Cunliffe et al. (2016) generated canopy height maps of tundra tussock vegetation at sub-centimeter resolutions over a 10-ha area; on the basis of those maps, they then predicted biomass and aboveground C stocks.

Figure 5. Unmanned aerial systems (UASs) are able to collect a variety of observations at high spatial and temporal resolutions. (a) An octocopter (8 motor, CarbonCore Cortex) platform can be equipped with multiple instrumentation, in this case a high-resolution digital camera (Canon M6), dual spectrometer system (Ocean Optics FLAME spectrometers to measure upwelling and downwelling radiation for calculating surface reflectance), and a thermal infrared (TIR) camera (ICI 9640P). (b) Centimeter-scale orthorectified digital imagery of a tundra landscape near Council, Alaska. Such imagery can be used to identify species cover types and distributions, as well as to create surface elevation and vegetation canopy height models based on the Structure from Motion (SfM) approach. (c) Thermal image of the landscape shown in (b) with superimposed average chlorophyll content estimated from the dual spectrometer retrievals of surface reflectance (R Meng *et al.* unpublished data). This type of imagery highlights both the cooling effect of vegetation and its functional variability.

UASs can also be equipped with more advanced instruments, such as spectrometers or thermal imagers (Figure 5). UASs equipped with spectrometers can map leaf traits (eg pig-





Figure 6. Global representativeness of three sampling networks using the site-based metric described by Hoffman *et al.* (2013). Colors indicate bioclimatic similarity to sites in the FLUXNET (red), RAINFOR (blue), and CTFS-ForestGEO (green) networks. For instance, patches of light green across Canada and Russia indicate locations well represented by the CTFS-ForestGEO network, but not by the RAINFOR or FLUXNET networks. Darker shades (eg montane and boreal regions) highlight locations with characteristics not captured by any existing networks.

ment contents) at high spatial resolutions, facilitating detection of plant degradation due to prolonged stress conditions (Figure 5c; Zarco-Tejada *et al.* 2013). Similarly, UASs equipped with thermal cameras (Figure 5c) can provide high-resolution (<9 cm) monitoring of plant water status at multi-hectare scales, identifying drought-stressed plants within minutes of stress onset (Santesteban *et al.* 2017). These capabilities mean UASs are well suited to enhancing the results of experimental manipulations performed at plot and site scales. Moreover, the ability of UAS platforms to repeatedly sample the same area over time aids in examinations of temporal variations in plant function.

Airborne and satellite remote sensing: site selection and representativeness

The effort and expense required to conduct global change experiments limits their spatial extent. Results from such experiments are therefore often extrapolated to larger areas, making the assumption that one site is representative of a larger landscape or biome. Moreover, global syntheses of experimental results require that experiments sample the full range of environmental conditions observed worldwide, and failure to sample certain conditions (or oversampling others) can introduce substantial biases (Beier *et al.* 2012). "Representativeness" analyses can evaluate the similarity of sites based on a suite of environmental variables, and can therefore help to optimize sampling designs by targeting locations that are the most dissimilar from one another (Hoffman *et al.* 2013). For example, using the same methods as Hoffman *et al.* (2013), we estimated the global representativeness of the ForestGEO, RAINFOR, and FLUXNET observational networks. These maps highlight considerable sampling biases for certain networks (eg tropical rainforests are well-represented by RAINFOR, but not temperate or boreal forests) and revealed large regions (eg montane environments) that are not represented by any network (Figure 6).

To date, representativeness analyses have been primarily based on climate, soil characteristics, and coarse vegetation or biome types. Airborne and satellite remote sensing provide continuous, quantitative indices of vegetation composition and condition that can enhance these analyses. Furthermore, the time dimension of data collected by satellites (eg Landsat, MODIS imagery) can be useful for selecting sites based on ecological context, such as disturbance history. Meigs et al. (2011) used Landsat imagery to identify insect-disturbed forest patches in the US Pacific Northwest, and then supplemented these with field surveys to characterize the effects of the disturbances on subsequent recovery. Sites can also be selected on the basis of spectral signatures or their derived data products. For instance, airborne imaging spectroscopy (eg AVIRIS) can produce maps of plant traits at landscape scales (Singh et al. 2015). These maps can then help investigators select experimental locations that best sample the functional trait space. Airborne and satellite measurements can also accurately characterize sites where representative field sampling is difficult, such as in heterogeneous, remote, or rugged environments. In a comparison of field- and airborne LiDAR-based biomass inventories in Peru, for instance, Marvin et al. (2014) identified biases as high as 98% in biomass measured in the field; due to landscape heterogeneity, Marvin *et al.* (2014) estimated that a logistically infeasible number of field plots would be required for robust biomass estimates across this region.

The same techniques that are useful for selecting sites for new experiments may also be helpful for post-hoc upscaling of earlier experimental results. Past studies have successfully combined remote-sensing data products with climate data to empirically scale observations from observational networks like FLUXNET (Jung *et al.* 2011). However, to our knowledge, similar analyses have not been attempted with major experimental networks such as DroughtNet, or with the airborne and satellite observations described above.

Conclusions

In a time of unprecedented planetary-scale change, the mechanistic understanding that can be provided only by global change experiments is essential for accurate forecasting and preparation for a future in the Anthropocene. Given how costly and time consuming these experimental manipulations often are, ecologists must employ every tool at their disposal to measure the outcomes of such large-scale experiments. To that end, the emerging remote-sensing technologies we outline above can provide unique ecophysiological and ecological insights, often for relatively little effort and cost.

The impacts of global change on individual plants and whole ecosystems are usually multifaceted and span a wide range of spatial, temporal, and ecological scales. In combination, the remote-sensing techniques we have presented can allow researchers to traverse these different domains and scales. For instance, although the concurrent effects of global warming on foliar biochemistry, photosynthetic metabolism, and biomass have been observed indirectly (Gornish and Prather 2014), a warming experiment integrating spectroscopy, fluorescence, and terrestrial LiDAR would measure all three of these variables simultaneously and dynamically. Similarly, the detailed information on vegetation physiological dynamics provided by integration of near-surface digital repeat photography, spectroscopy, and fluorescence measurements offers important opportunities for phenological research, especially in experimental contexts where the contributions of different environmental drivers (eg light, temperature) can be isolated (Tang et al. 2016). A final example of a large-scale global change experiment being potentially limited by the absence of remote-sensing techniques is the Free Air CO₂ Enrichment Model-Data Synthesis Project, which found on multiple occasions that its experimental data were insufficient for informing ecosystem models (Medlyn et al. 2015). The integration of some of the remote-sensing techniques described above could prevent similar data limitations in future experiments. For instance, measuring leaf photosynthetic activity (via fluorescence), transpiration (via thermal imagery), and biochemistry (via spectroscopy) would show how CO₂

enrichment differentially affects these processes to alter plant resource-use efficiency.

The advent of off-the-shelf instruments and processing software is likely to make remote-sensing approaches more accessible to the ecological community, but for these techniques to reach their full potential, additional collaborations between experimental ecologists and terrestrial remotesensing experts are needed. We predict that the additional data and insight generated by such collaborations will markedly improve the cost-effectiveness, depth, inference, and reach of global change studies, by providing additional data as well as by increasing the precision of inference beyond the boundaries of the experiments. Such collaborations will also advance remote-sensing and ecosystem models by improving our understanding of the physical links between ecosystem processes and remote-sensing signals. Ultimately, bidirectional feedbacks between remote sensing and global change ecology will be critical for enhancing our ecological forecasting capabilities.

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