Tansley insight

Tracking seasonal rhythms of plants in diverse ecosystems with digital camera imagery

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Summary

Global change is shifting the seasonality of vegetation in ecosystems around the globe. High-frequency digital camera imagery, and vegetation indices derived from that imagery, is facilitating better tracking of phenological responses to environmental variation. This method, commonly referred to as the 'phenocam' approach, is well suited to several specific applications, including: close-up observation of individual organisms; long-term canopy-level monitoring at individual sites; automated phenological monitoring in regional-to-continental scale observatory networks; and tracking responses to experimental treatments. Several camera networks are already well established, and some camera records are a more than a decade long. These data can be used to identify the environmental controls on phenology in different ecosystems, which will contribute to the development of improved prognostic phenology models.

I. Introduction

Shifts in vegetation phenology are among the most robust and tangible examples of the biological impacts of climate change (Settele *et al.*, 2014). Yet, phenological responses to future environmental change remain highly uncertain (Richardson *et al.*, 2013a; Tang *et al.*, 2016; Zohner *et al.*, 2016). The reasons for this include potential interactions among environmental drivers, the validity of space-for-time extrapolation, the scarcity of realistic manipulative phenological experiments, the potential for differing responses among (and within) species, the difficulty of falsifying models with competing process representations, and the challenge of forecasting outside the range of historical environmental variability. Alas, the familiar refrain of 'more data are needed' remains all too common.

In this review I seek not to identify the most pressing questions in contemporary phenological research (see instead: Delpierre *et al.*, 2016; Tang *et al.*, 2016; Singh *et al.*, 2017), but rather to highlight how near-surface remote sensing using digital imaging technology can be applied to 21st century phenological research. My overarching hypothesis is that the urgent need for phenological data can be addressed, in part, using what has become known as the 'phenocam' approach. I provide context for the evolution of this method, review the nuts and bolts of this approach, and provide examples of the derived seasonal patterns. I then identify four specific applications to which the approach is particularly well suited. I conclude with some forward-looking remarks.

II. Evolving modes of phenological study

Phenological science, emphasizing hands-on monitoring of individual organisms, emerged as a branch of natural history in the mid-19th century (Demarée & Rutishauser, 2009). By the late 20th century, satellite remote sensing was being used to observe phenology globally at coarse spatial resolution (Justice *et al.*, 1985). Technological advancements have led to improvements in the spatio-temporal resolution of satellite data. However, the challenge of mixed vegetation types within individual satellite pixels remains a major limitation (Richardson *et al.*, 2018c).

Between these endpoints of on-the-ground and earth-orbiting observation, automated methods have more recently been applied to track vegetation dynamics at fine temporal resolution and at spatial scales from individuals to communities (Richardson *et al.*, 2013b). One approach builds on the idea of using repeat photography to track landscape change over decades (Webb *et al.*, 2003), but is distinguished by the high frequency of image acquisition, and the emphasis on quantitative data calculated from the digital images. For example, Graham *et al.* (2006) used color-based indices derived from digital imagery to monitor the physiological changes associated with desiccation and re-wetting of the moss, *Tortula princeps*, while Richardson *et al.* (2007) used a similar approach to track the progression of springtime green-up in a temperate deciduous forest. The phenocam method is now widely used to characterize vegetation dynamics at time scales from days to years (Fig. 1).

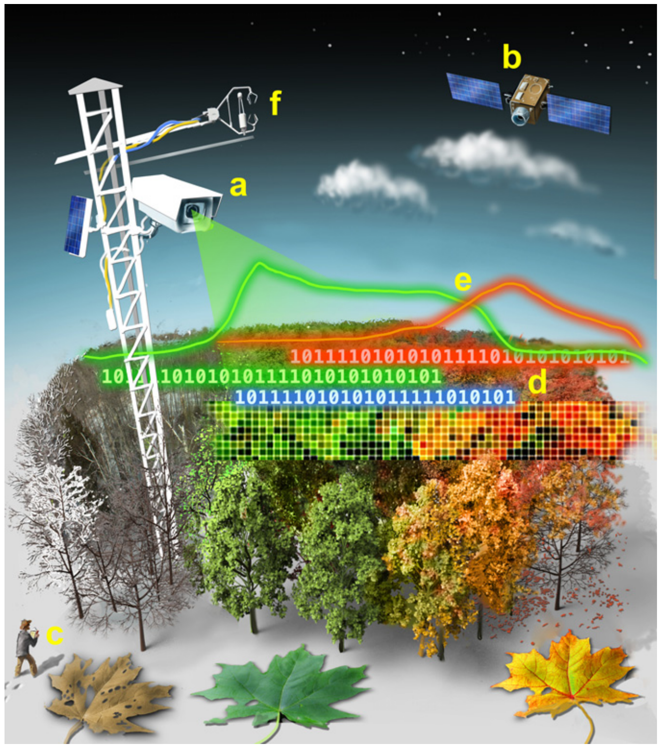

Fig. 1 Digital camera – or 'phenocam' – imagery serves as a bridge between comparatively coarse-scale satellite remote sensing and fine-scale direct human observation of vegetation phenology. Quantitative data on vegetation color, in three wavebands (red, green and blue – following the RGB additive color model), can be extracted directly from the imagery and transformed to vegetation indices analogous to those used in satellite remote sensing. The seasonality of those indices (e.g. green and red chromatic coordinates, G_{CC} and R_{CC}, respectively) provides a direct measure of vegetation phenology, and a means by which specific phenophase transition dates – onset of green-up, peak autumn color – can be quantified. This analysis can be done separately for individual organisms, or at the canopy level, integrating across multiple individuals or species. The canopy-scale perspective is particularly valuable for contextualizing seasonal variation of ecosystem–atmosphere fluxes of CO_2 (and other trace gases), as well as latent and sensible heat, as measured by the eddy covariance approach. The method can be applied to a range of vegetation types, and not just deciduous forests. Image elements: (a) tower-mounted phenocam; (b) satellite sensor; (c) human observer; (d) RGB data; (e) seasonal variation in G_{CC} and R_{CC} for the deciduous forest illustrated; (f) eddy covariance instrumentation.

III. The phenocam approach

Implementation of the basic phenocam method is described by Richardson *et al.* (2018a) and Nasahara & Nagai (2015). In a typical set-up, a consumer-grade digital camera is installed overlooking the vegetation of interest and set to record time-lapse images. Buildings, meteorological towers and antenna masts all provide suitable mounting points, and cameras are usually directed to minimize shadows and forward scattering off the canopy (Richardson *et al.*, 2013b). A wide variety of camera models have been shown to be suitable (Sonnentag *et al.*, 2012).

In most cases, images are acquired at least once per day. Images are commonly stored in minimally compressed JPEG format, which has been shown to be satisfactory for phenological studies (Sonnentag *et al.*, 2012; but see Verhoeven, 2010). Depending on the camera being used, images can be recorded locally or sent to a remote server. The latter has the advantage that an off-site researcher is always able to access the imagery in real-time and ensure system functionality. This is particularly important during periods of active change in the state of the canopy.

Image processing

While the recorded images can be visually inspected to identify phenological transition dates, they can also be processed in a manner analogous to multi-channel satellite images. This processing retrieves quantitative information about the color of specific pixels in the image. Software tools to facilitate these steps are publicly available (Filippa *et al.*, 2016; B. Seyednasrollah *et al.*, unpublished, https://github.com/bnasr/xROI).

When a JPEG image file is loaded for processing, it is converted to a three-layer array. Those layers correspond to the red, green and blue primary colors of the RGB additive color model. The color of each pixel is thus defined by a vector (R_{DN}, G_{DN}, B_{DN}), where DN denotes digital number, and the elements of this RGB triplet are a measure of the intensity of each primary color for that pixel. Image processing consists of extracting color information for a region of interest that corresponds to the portion of the image under study.

RGB triplets can be converted to vegetation indices (e.g. canopy 'greenness' as measured by the green chromatic coordinate, G_{cc})

which yield an easily interpreted representation of seasonal changes in canopy status (Fig. 2). These indices provide a consistent metric for characterization of vegetative (green leaf) phenology across different ecosystem types. Other indices, including a green–red vegetation index (Anderson *et al.*, 2016), textural metrics (Almeida *et al.*, 2014) and alternative color spaces (Richardson *et al.*, 2013b), have also been applied to extract phenological data from digital camera imagery. Methods have been developed to characterize reproductive phenology (e.g. flower counts) from camera images (Crimmins & Crimmins, 2008).

Camera-based ecosystem monitoring is not limited to what can be seen by the human eye: the semiconductor-based imaging sensors used in most digital cameras are also sensitive to near-infrared (NIR) wavelengths. This sensitivity has been leveraged to calculate an approximation of the well-known normalized difference vegetation index (NDVI; Petach *et al.*, 2014; Filippa *et al.*, 2018), as well as the newer NIRv index (Luo *et al.*, 2018). Alternatively, selective filtering could be used to target specific wavelengths in the visible–NIR spectrum. This approach would permit continuous, high-frequency imaging of narrowband spectral indices without the high cost of a hyperspectral camera.

Camera calibration, settings and field deployment

A potential concern is that inexpensive digital cameras have typically not been calibrated (in the classic sense) to a radiometric standard, and hence are of unknown accuracy. This is true to the extent that calibration coefficients to convert DNs to radiometric quantities are generally not readily available. Moreover, the spectral response of the imaging sensor is often not documented (but see Wingate *et al.*, 2015). However, the demands of the consumer market are such that even the most inexpensive cameras are highly sophisticated and sensitive instruments, capable of rendering impressively consistent images of a scene (in daylight conditions) with remarkable reliability. For many researchers, this trade-off between unknown accuracy but demonstrated repeatability is considered acceptable, given the low cost, ease of use, compact size and minimal power requirements. Indeed, a range of analyses by Richardson *et al.* (2018a) give high confidence in the technical quality – comparable to calibrated, narrow-band radiometric sensors – of the data derived from digital imagery.

The capacity to detect landscape changes is greatest when exogenous variation is minimized. Consistency is vital. Paramount is keeping the field of view as stable as possible. Almost as important is minimizing the effects of diurnal and day-to-day variation in lighting conditions resulting from changes in illumination geometry and weather. Automatic exposure is desirable because this gives the best chance of avoiding a poorly exposed image. But, other automatic settings should be disabled to minimize within-camera image processing and associated artifacts (Richardson *et al.*, 2013b). Critically, automatic color balancing (also referred to as automatic white balancing) is one setting that *must* be disabled to avoid confounding variation in sensor response.

Following standard methods used in satellite remote sensing, extraction of phenological transition dates, for example 'onset of green-up', is based on curve-fitting approaches (Klosterman *et al.*, 2014; Filippa *et al.*, 2016). Because these methods mimic the *shape* of the seasonal greenness trajectory – with dates extracted based on *relative* changes in greenness – they are essentially insensitive to camera calibration. In addition, while the derived transition dates typically correlate with biologically relevant and visually obvious changes in vegetation state, they do not always correspond directly to the phenophase transitions that might be recorded by an observer on the ground (Wingate *et al.*, 2015; Kosmala *et al.*, 2016). Although there is a similar challenge with interpretation of satellite data products, an advantage with phenocam data is that visual inspection of imagery can provide biological context.

IV. Applications of the phenocam method

Potential applications of camera data to phenological science are diverse. Recent studies have used camera imagery to characterize seasonal changes in leaf-level physiology, including linking changes in pigmentation and photosynthetic capacity to indices of canopy color (Bowling *et al.*, 2018; Liu *et al.*, 2018). Other studies have proven the usefulness of camera imagery for identifying phenological differences among coexisting species or plant functional types (Browning *et al.*, 2017; Luo *et al.*, 2018), which is of importance for improving scaling relationships and interpreting remote sensing imagery. Camera data have been used extensively for validation of satellite data products. These analyses indicate good agreement for deciduous forests but less strong agreement in heterogenous environments and evergreen systems (Richardson *et al.*, 2018c; Zhang *et al.*, 2018). And even when phenology is not the main focus of a particular study, relatively short (1–3 yr) image time series from a single site offer a convenient means of characterizing plant phenological patterns, providing context for interpretation of other ecological data, such as insect, bird or animal abundance. However, there are four applications to which the phenocam method is exceptionally suited: these are illustrated in Fig. 3 and described below.

Close-up observations of individual plants

Cameras mounted in close proximity to specific plants of interest can be used for visual assessment of phenological phenomena at the bud-to-branch scale, particularly those phenomena that might be difficult to identify from color-based vegetation indices. Such an approach is well suited to remote or inaccessible sites where frequent ground surveys are impossible. And, in an extension of closely related methods used in controlled lab-based settings for high-throughput plant phenotyping (Araus *et al.*, 2018), phenocam approaches could be similarly applied in outdoor common gardens or provenance trials to quantify genotypic variation as manifest by differences in the timing of phenological events across phenotypes or populations.

Long-term observations at individual sites

Long-term phenocam observations at individual sites are particularly useful for studying phenological trends and variability of

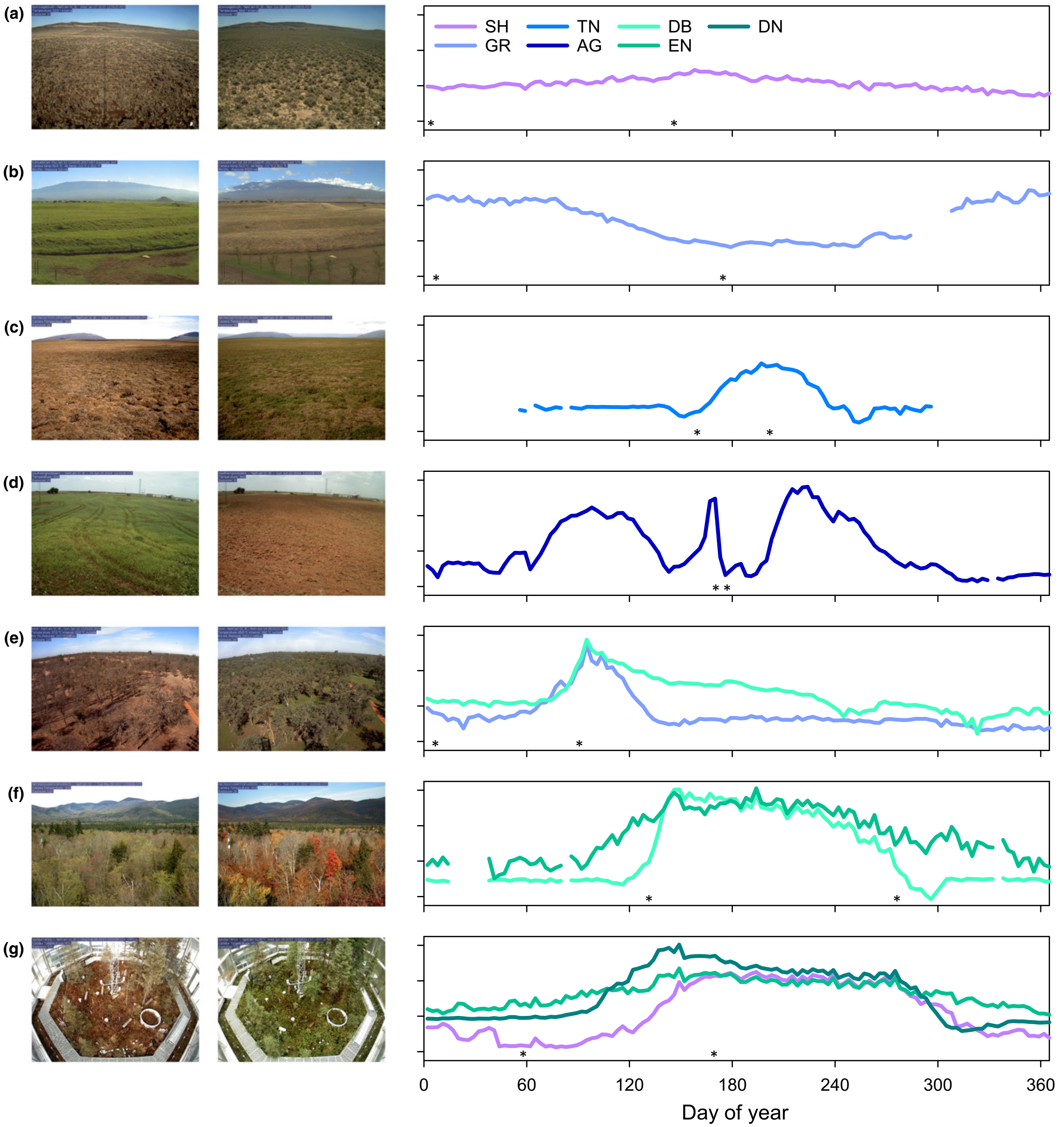

Fig. 2 Seasonal variation in canopy greenness of different ecosystem types, as derived from PhenoCam Network camera imagery. Greenness is characterized by the green chromatic coordinate (G_{CC}), calculated as $G_{CC} = G_{DN}/(R_{DN} + G_{DN} + B_{DN})$. Here *R*, *G* and *B* refer to the red, green and blue color channels, respectively, and DN is the mean pixel value (as a digital number) for each color channel, calculated across a user-defined region of interest. The *y*-axis range is 0.14 G_{CC} units in all plots. (a) Shrub vegetation in Oregon; (b) tropical grassland in Hawaii; (c) Arctic tundra in Alaska; (d) managed agricultural field in Oklahoma; (e) Mediterranean savannah in California; (f) mixed temperate forest in New Hampshire; (g) experimental temperature manipulation in a Boreal peatland in Minnesota. See Table 1 for additional site details. Vegetation type abbreviations: AG, agricultural; DB, deciduous broadleaf; DN, deciduous needleleaf; EN, evergreen needleleaf; GR, grassland; SH, shrubland; TN, tundra. Asterisks indicate when the sample photographs were recorded.

both individual organisms and the canopy as a whole (Hemming *et al.*, 2018). Decade-long image archives are available for some sites, and are most valuable when environmental drivers and ecosystem response variables are also measured simultaneously on-site, facilitating interpretation of environmental effects on phenology, and phenological effects on ecosystem function. These data

Table 1 List of PhenoCam network sites used in Fig. 2, and standard site metadata.

Site name	Burnssagebrush	Kamuela	NEON.D18.TOOL	Southern Great Plains	Tonzi	Bartlettir	SpruceT4P13
Location	Eastern Oregon Agricultural Research Center, Burns, Oregon	Parker Ranch, Waimea, Hawaii	NEON Site – D18 (Tundra) Toolik, Alaska – tower top	ARM Southern Great Plains Central Facility, Billings, Oklahoma	Tonzi Ranch, Amador County, California	Bartlett Experimental Forest, Bartlett, New Hampshire	+5°C/aCO_2, Marcell Experimental Forest, north of Grand Rapids, Minnesota
Latitude (°N)	43.4712	20.015	68.6611	36.6058	38.4309	44.0646	47.5057
Longitude (°W)	119.6909	155.6613	149.3705	97.4888	120.9659	71.2881	93.453
Elevation (m asl)	1398	850	827	314	177	268	410
Start date	2012-10-12	2000-01-01	2017-02-24	2012-05-16	2011-10-26	2008-04-18	2015-08-23
Camera orientation	N	SSE	N	N	NW	N	N
UTC offset (h)	−8	−10	−9	−6	−8	−5	−6
Site type	I	I	I	I	I	I	I
MAT (°C)	7.45	19.1	−9.95	15.15	16.5	6.35	4.05
MAP (mm)	305	1024	237	898	680	1284	717
Dominant species	*Artemesia tridentata* var. *Wyomingensis*, *Festuca idahoensis*, *Pseudoroegneria spicata*, *Poa secunda*	*Cenchrus* spp., *Senecio madagascariensis*	*Eriophorum vaginatum*, *Vaccinium vitis-idaea*, *Betula glandulosa*	*Triticum aestivum*	*Quercus douglasii*, *Brachypodium distachyon*, *Hypochaeris glabra*, *Trifolium dubium*, *Trifolium hirtum*, *Dichelostemma volubile*, *Erodium botrys*	*Acer rubrum*, *Betula papyrifera*, *Fagus grandifolia*	*Larix laricina*, *Picea mariana*, *Rhododendron groenlandicum*, *Chaedaphne calyculata*
NA Ecoregion	10	N/A	2	9	11	5	5
WWF Biome	13	2	11	8	8	4	4
Koeppen Geiger	BSk	Af	Dfc	Cfa	Csa	Dfb	Dfb
IGBP Landcover	10	10	7	12	9	5	5
Acknowledgments	This site was supported by the NOAA Earth System Science Program (grant. no. NOAA-OAR-CPO-2012-2003041)	The Kamuela PhenoCam is made possible by logistical support and internet access provided by Richard and Linda Carbone, with additional thanks to the Board of Directors at Holo Holo Ku	The NEON Data Usage and Citation Policy can be found at: http://data.neonscience.org/data-policy. NEON is a project sponsored by the National Science Foundation and operated under cooperative agreement by Battelle	Research at the site is supported by the Office of Biological and Environmental Research of the US Department of Energy under contract no. DE-AC02-05CH11231 as part of the Atmospheric Radiation Measurement Program (ARM)	Funding for AmeriFlux core site data was provided by the US Department of Energy's Office of Science	Research at the Bartlett Experimental Forest tower is supported by the National Science Foundation (grant DEB-1114804) and the USDA Forest Service's Northern Research Station	The SPRUCE project is supported by the US Department of Energy (DOE), Office of Science, Office of Biological and Environmental Research

MAP, mean annual precipitation (climate data from Daymet); MAT, mean annual temperature. For definitions of site types, ecoregions, biomes, Koeppen Geiger Classifications and IGBP Landcover types, see Richardson *et al.* (2018a). asl, above sea level; N/A, not available.

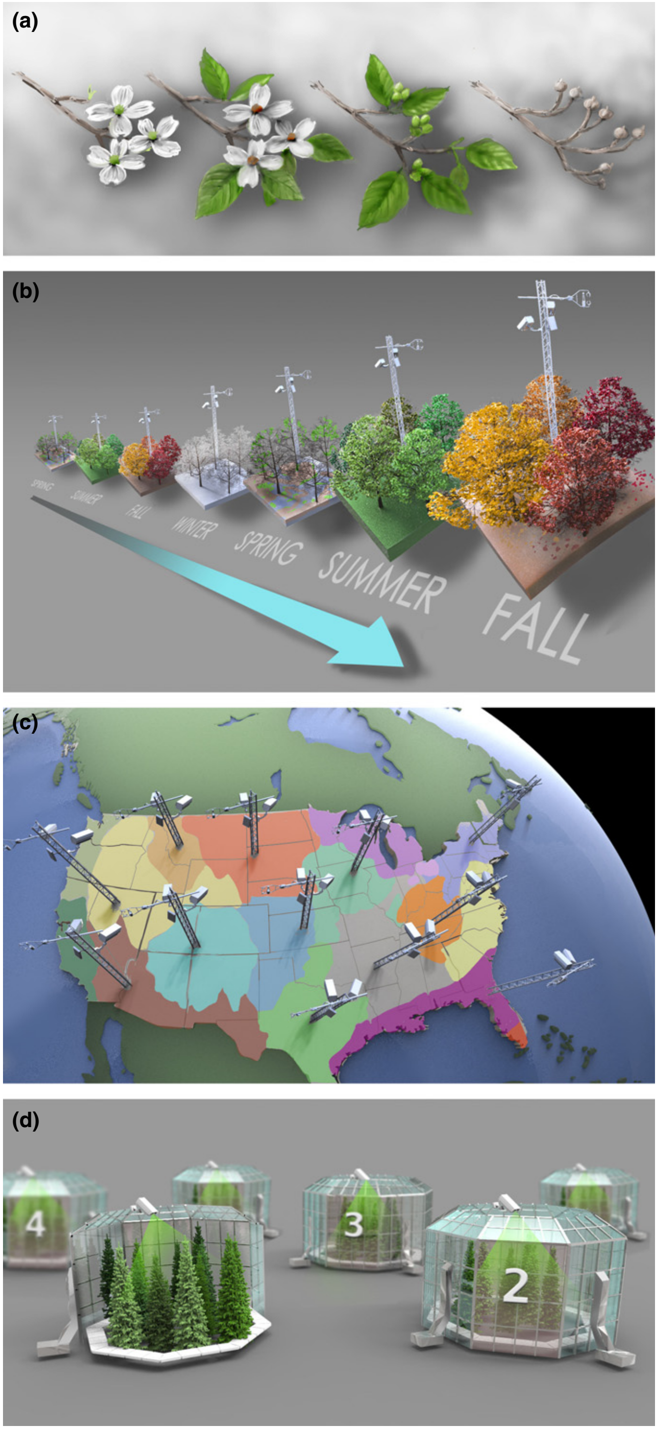

Fig. 3 The phenocam method is particularly well suited to four specific applications. (a) Close-up observations of individual organisms, particularly at remote sites where regular direct observation is not feasible, and when phenological phenomena might be difficult to identify from color-based indices, such as the production of white or inconspicuous flowers, the initial stages of bud swell and break in advance of full leaf emergence by deciduous broadleaf species, and the production of new leaves and turnover of old leaves by evergreen species; (b) long-term observation of phenology at individual sites, especially where other ecosystem-scale measurements (e.g. CO_2 flux) are simultaneously conducted, and links between environmental factors, phenological responses and ecosystem processes can be investigated; (c) phenological observations across a network of sites, for example spanning different ecoregions, vegetation types or climate zones, where a regional-to-continental scale perspective would be valuable; (d) experimental installations, where phenologically relevant factors (e.g. temperature, precipitation or water availability, and CO_2) are manipulated, and where the long-term trajectory of the experiment is of interest.

also offer the potential to observe and document successional processes and disturbance, and to relate phenology to other measures of ecosystem activity, such as ecosystem–atmosphere fluxes of CO_2 and water (Hufkens *et al.*, 2012; Stephens *et al.*, 2018). Detection of changes in community composition, for example resulting from invasive species, may also be facilitated by corresponding phenological shifts if the phenology of the novel species differs from that of the uninvaded community (e.g. Fridley, 2012).

Regional-to-continental scale networks

Phenocams are increasingly seen as critical components of large-scale ecological observatory networks (Brown *et al.*, 2016). Data collected in this manner are highly useful for studying the broad geographic patterns of canopy-level (community) phenology. Additionally, these data have been shown to be well suited to the investigation of environmental controls on vegetation phenology, and phenological model development and testing. For example, 80 site-years of camera data were used to parameterize a range of candidate models for leaf emergence across the extensive eastern deciduous forest of North America (Melaas *et al.*, 2016). Similarly, 34 site-years of data were used to parameterize a coupled plant growth–soil hydrology model for the grasslands of North America (Hufkens *et al.*, 2016). These analyses have shown the viability of developing relatively simple phenological models that generalize well in time and space. An extension of this type of approach would be to use camera network data for evaluating or benchmarking the phenological subroutines in Earth system models. These subroutines are known to poorly represent spatiotemporal phenological variation under current climate conditions, and in all likelihood perform even worse under future climate scenarios (Richardson *et al.*, 2013a).

In many observatory networks, additional measurements are conducted to characterize ecosystem functional responses to climate variability and change. These include biometric inventories to quantify ecosystem productivity, eddy covariance measurements of land–atmosphere fluxes of matter and energy, and watershed measurements of hydrological and biogeochemical cycling. There is tremendous potential to use these data – in conjunction with data from co-located phenocams – for regional-to-continental scale analyses of relationships between environmental factors, phenology and ecosystem function. While there are already many fine examples of this kind of analysis being conducted at site level, the high-impact synthesis studies to emerge from FLUXNET in the last two decades show the power of a network-based approach (Baldocchi *et al.*, 2001; Pastorello *et al.*, 2017).

Tracking manipulative experiments

Experiments are critical for pushing systems outside the range of historical variability and rigorously testing hypotheses in ways that are not possible with observational studies. Phenocam deployments in experimental settings are valuable for two reasons. First, they are useful for high-frequency observation of phenological responses to manipulative treatments. Second, the imagery serves as an unique document with which to track the long-term progression of the experiment. For example, at the 10-yr SPRUCE (Spruce and Peatland Responses Under Changing Environments) experiment in a boreal peatland forest, phenocam data were used to test – and reject – the hypothesis that the phenological response to increasing temperatures would be constrained by photoperiod (Richardson *et al.*, 2018b). However, in the long term the camera imagery will also facilitate detection and quantification of changes in ecosystem structure and community composition. Archived camera imagery permits analysis of these changes to be conducted retrospectively.

V. Looking forward

The PhenoCam Network (http://phenocam.unh.edu/) serves as a continental-scale phenological observatory focused on the vegetation of North America. Established in 2008, the network's image archive currently includes imagery from almost 550 sites, located from tundra to tropics (Fig. 4). PhenoCam is just one of several similar networks worldwide: other efforts focus on Asia (Nasahara & Nagai, 2015), Europe (Wingate *et al.*, 2015) and Australia (Moore *et al.*, 2016). Imagery and data from these monitoring networks is increasingly being made publicly available (Nagai *et al.*, 2018; Richardson *et al.*, 2018a). There is also a trend towards publishing transparent and reproducible workflows for phenological analysis and modeling (Hufkens *et al.*, 2018). Together, these efforts should contribute to a better understanding of the environmental controls on vegetation phenology, and hence improvements to both phenological models and projections of phenological responses to future climate change. With the larger phenological data sets becoming available, it should be possible to falsify competing model formulations, and refine our understanding of the underlying processes and mechanisms.

Although substantial progress has been made, there is also considerable potential to better understand how phenological transition dates derived from spectral data (cameras, satellite remote sensing) align with those recorded by human observers in different ecosystems. Efforts to develop a plant phenology ontology (Stucky *et al.*, 2018) may provide a useful starting point.

There are still untapped opportunities to use phenocam data to investigate the complex interactions that occur between environment, phenology and ecosystem function at regional to continental scale. This could be extended to investigate the role of phenology in mediating biosphere–atmosphere interactions, specifically related to seasonal changes in the surface energy budget.

Finally, it is worth considering how technological advances may further enhance the potential for phenological monitoring using digital imagery. In many ways, the existing technology is not a limiting factor. However, expansion of existing monitoring efforts will no doubt result from ever-increasing capabilities at ever-lower cost (and improvements in low-cost, real-time data transfer for remote geographic locations would be advantageous). At current camera resolution, storage and processing of camera imagery are

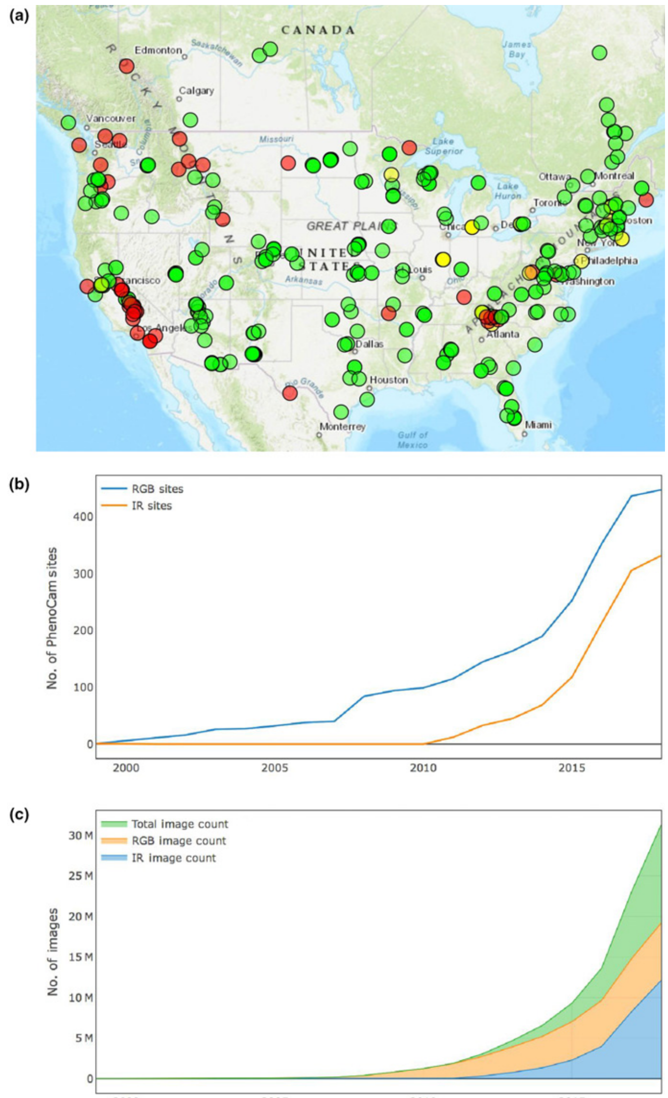

Fig. 4 The PhenoCam Network serves as a continental-scale phenological observatory, focused on vegetation of North America. (a) Site locations in the conterminous USA and adjacent Canada (https://phenocam.sr.unh.edu/webcam/network/map/), as of 5 September 2018. Green dots indicate 'Type I' cameras (Richardson *et al.*, 2018a), that is those deployed following a common protocol and with ongoing collaboration of site personnel. Yellow dots indicate 'Type II' cameras (protocol not strictly followed, but site personnel are active collaborators) and red dots indicate 'Type III' cameras (protocol not strictly followed; site personnel not active collaborators). Note that in some cases, multiple cameras are installed at a given site. Approximately 20 cameras in Alaska, Hawaii and Puerto Rico are not shown. (b) Increase in the number of active camera sites over time (although almost 450 sites are currently designated 'active', the archive includes imagery from almost 550 sites in total). The network was formally established in 2008, but previously archived imagery from a small number of cameras was available back to 2000. The method to take successive visible (red–green–blue, RGB) and infrared (IR) images was developed in 2010, and since then almost all new cameras deployed have been configured to implement the method of Petach *et al.* (2014). Imagery from cameras deployed by the National Ecological Observatory Network (NEON) was integrated into PhenoCam beginning in 2016. (c) Increase in the total number of archived images over time (on the *y*-axis, M denotes million). Each day, *c.* 18 000 new RGB images and 16 000 new infrared images are added to the archive. In (b) and (c), graphs have been generated automatically (https://phenocam.sr.unh.edu/webcam/archive/) with data up to 5 September 2018.

not bottlenecks, although fog, precipitation and camera field-of-view shifts increase the difficulty of fully automated extraction of high-quality data (Richardson *et al.*, 2018a). Both brute force ('crowdsourcing', Kosmala *et al.*, 2016) and artificial intelligence ('deep learning') methods have the potential to facilitate the extraction of more sophisticated phenological data from both new and previously archived camera imagery. This approach – synergistically looking forward and backward – will undoubtedly lead to new avenues of research, guided by emerging questions as the science of phenology advances.

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