

## REVIEW

Grime Review: What can remote sensing do for plant ecology?

# Remote sensing of phenology: Towards the comprehensive indicators of plant community dynamics from species to regional scales

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## Funding information

National Aeronautics and Space Administration, Grant/Award Number: 80NSSC18K0755

Handling Editor: Emily Lines

## Abstract

1. Remote sensing of vegetation phenology has long been used to characterize ecosystem functions and responses to climate at spatial and temporal scales unfeasible to field surveys. However, the potential of remote sensing to elucidate mechanistic drivers of phenology and the underlying plant community processes at such scales remains under-discussed.
2. This review synthesizes possibilities to advance this knowledge using multi-temporal remote sensing and discusses remaining challenges and progress in instruments and analytical tools. Recent evidence indicates that, besides documenting vegetation seasonality and responses to climate, remote sensing of phenology can help meet emerging needs for indicators of plant diversity, vegetation structure and ecosystem change.
3. Responses of phenological metrics to stressors over large, heterogeneous regions may provide clues on ecological resilience manifested in asynchronies, recovery of vegetation cycles and stable microrefugia. At the same time, important barriers persist in relation to choosing among phenological estimation methods and paradigms, characterizing phenological events beyond changes in photosynthetically active biomass, and mechanistic interpretation of phenological patterns.
4. *Synthesis.* Increasing temporal frequency of products, opportunities for multi-sensor data fusion, and advances in historically less available hyperspectral, active microwave and lidar instruments promise to help navigate these barriers and enable more comprehensive assessments of seasonality. Progress in customizable local platforms such as unoccupied aerial vehicles and phenocams may further enrich ground-level understanding of phenology and validate satellite-based assessments. However, remote sensing analyses alone are insufficient for mechanistic interpretation of phenology, which can be challenged by artefacts in remote sensing data and sensitivity of estimated metrics to landscape structure and spatial resolution of the inputs. Robust and informative phenological assessments call for rigorous collaborations with field ecological studies, strategic selection of ancillary

environmental and geographic data, and wider adoption of causal inference approaches to address these needs and support novel explorations in plant ecology.

#### KEYWORDS

heterogeneity, phenology, plant diversity, remote sensing, resilience, satellite, spectral vegetation indicators, stability

## 1 | INTRODUCTION

Global change drivers are impacting coverage, composition and diversity of plant communities (Bellard et al., 2012; Sala, 2000) creating profound implications on ecosystem functions and well-being of human populations (Cardinale et al., 2012; Díaz et al., 2006; Hooper et al., 2012). Scientists and conservation organizations alike have called for an urgent increase in our global capacity for monitoring ecological communities and the services they provide to halt species loss and target conservation efforts (e.g. Pereira et al., 2013). Learning how to allocate these efforts and maximize their success becomes critical as we enter the United Nations' decade on ecosystem restoration with ambitious goals for the recovery of degraded ecosystems.

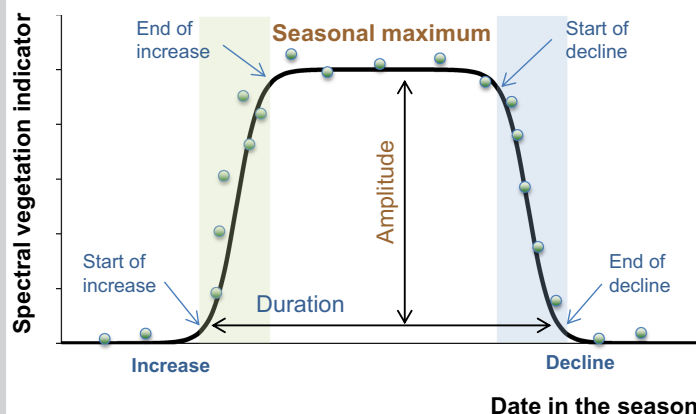
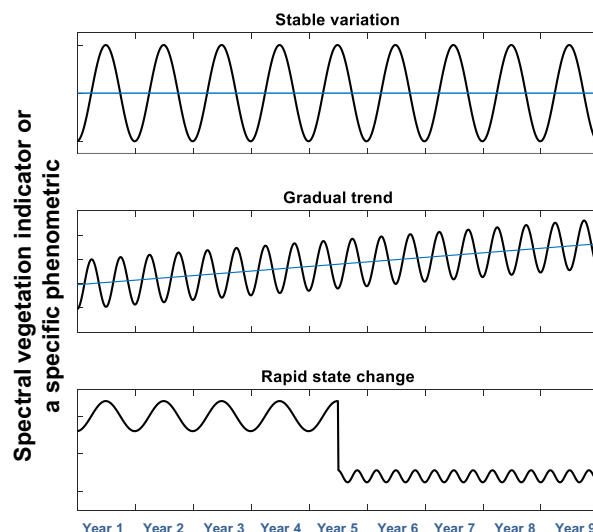
Phenology (i.e. timing of key events in the life cycle of organisms) has been identified as an essential biodiversity variable (Pereira et al., 2013; Skidmore et al., 2015) that can elucidate vegetation responses to environmental change and anthropogenic stressors (Cleland et al., 2007; Parmesan & Yohe, 2003; Wolf et al., 2017; Wolkovich et al., 2014). Phenological timing of plant greening, senescence and reproductive events often strongly responds to climate, including variation in atmospheric and substrate temperatures (Baldocchi et al., 2005; Hüttich et al., 2009; Wolkovich et al., 2012), precipitation (e.g. Clinton et al., 2014; Craine et al., 2012; Crimmins et al., 2011; MacFadyen et al., 2016; Madonsela et al., 2017), and droughts (Barboni et al., 2004; Huesca et al., 2015; MacFadyen et al., 2016; Pilaš et al., 2014; van Rooijen et al., 2015; Wang et al., 2016). These effects become evident in landscape gradients of floristic and phenological similarity that may further respond to topographic, geological and soil factors (Madonsela et al., 2017; Maeda et al., 2014) as well as land use and ecosystem management (Cord, Klein, Gernandt, et al., 2014; Lopes et al., 2017; Viña et al., 2012, 2016). Thus, tracking phenology across landscape, regional or even global scales may offer important clues on changes in diversity, dominance and composition of plant communities and help understand the drivers of their dynamics (Schrodt et al., 2020; Wolf et al., 2017; Wolkovich et al., 2014).

However, field observations of phenology are often sparse in space and time due to logistical and financial constraints, making it difficult to generalize evidence from species and plant community levels to broader climatic, geographic and administrative units (Pereira et al., 2013; Thackeray et al., 2016; Wolkovich et al., 2012, 2014). Recent advances in land surface phenology based on remote

sensing can help navigate these challenges and support phenological monitoring at unprecedented spatio-temporal scales (Brooks et al., 2020; Oehri et al., 2017; Radeloff et al., 2019). Such opportunities include increasing public access to long-term satellite time series and cloud-based platforms for their processing (Bolton et al., 2020; Gorelick et al., 2017; Wulder et al., 2012), enhanced spatial, temporal and spectral detail of recent observation systems (Claverie et al., 2018; Dash & Ogutu, 2016), and a growing variety of customizable in situ sensors such as time-lapse cameras (phenocams) and unoccupied aerial vehicles (UAVs) (Anderson & Gaston, 2013; Brown et al., 2016; Coops et al., 2019; Xie et al., 2018). These prospects allow assessments of various indicators of vegetation seasonality (Box 1) and their connections with plant diversity, ecological functioning, and resilience to change drivers (Brooks et al., 2020; Klosterman et al., 2014; Madonsela et al., 2017; Rheault et al., 2020; Viña et al., 2016; Wolkovich et al., 2014; Zeng et al., 2020).

However, despite growing availability of data and analytical tools (Gorelick et al., 2017; Rocchini et al., 2017), the potential of phenological remote sensing to advance the frontiers of plant ecology remains under-utilized. Most applications to date have focused on specific phenological events at the plant community level (e.g. leaf emergence and senescence) and their impacts on land surface phenology observed by remote sensors, often detected via indicators of spectral greenness (Box 1) sensitive to plant biomass, coverage, and photosynthetic function (e.g. Keenan et al., 2014; Wu et al., 2017). Such analyses have provided valuable insights into plant and ecosystem responses to short-term climate anomalies (Friedl et al., 2014; Hufkens et al., 2012), long-term climate change (e.g., Myers-Smith et al., 2020; Zeng et al., 2013), and regional microclimatic gradients (e.g. Melaas, Wang, et al., 2016). Remote sensing of phenology has become fundamental to understanding the role of vegetation in carbon, water, and energy exchange (Keenan et al., 2014; Knox et al., 2017; Magney et al., 2019; Sturtevant et al., 2016). Finally, seasonal spectral contrasts among vegetation types have facilitated mapping of both natural and anthropogenic landscapes (Hüttich et al., 2009; Schwieder et al., 2016).

Fewer studies have used phenology to understand how diversity, dominance and interactions within plant communities affect their responses to climate and other change drivers and land surface phenology patterns over large regions prohibitive to dense field surveying. For example, despite numerous studies on spectral indices of plant diversity based on discrete-time and snapshot observations (Asner & Martin, 2009; Cavender-Bares et al., 2016; Gholizadeh

**BOX 1 Remote sensing assessments of vegetation phenology from the time series of greenness****(a) Single growing cycle of deciduous vegetation****(b) Multiple growing cycles (seasons)**

Time series of remote sensing observations can be used to estimate phenological characteristics of vegetation over single seasons (a) and multiple years (b) by interpolating discrete observations of spectral vegetation indices (SVIs), often by design related to coverage, biomass and chemistry of photosynthetically active vegetation. Panel (a) shows a generalized SVI curve over one growing cycle, where a mathematical function (dark line) is fitted to discrete observations (small circles); the specific curve functions vary among studies (Zeng et al., 2020). Estimated curve parameters ('phenometrics') may represent both the **timing of changes** (e.g. start and end dates of greening and senescence determined by function curvatures, or duration of the growing cycle between start of increase and end of decline) and **magnitude of SVI values** at specific transition dates or seasonal amplitude (difference between the seasonal maximum and the start of increase values). Panel (b) shows different examples of long-term trajectories that could be evaluated for SVIs or specific phenometrics to assess presence and frequency of cycles, their inter-annual variability, or rapid shifts. Three scenarios shown indicate stable fluctuations of a single growing season system (top), gradual increasing trend in a system with two cycles per year (middle) and an abrupt shift from a single-year season system to a state with greater number of cycles and lower amplitude of spectral variation (bottom).

**Relevant terms and definitions:**

<b>Phenology</b>	Timing of key events in the life cycle of organisms
<b>Phenological phase (stage)</b>	Temporal frame corresponding to a specific life cycle event, e.g., flowering or greening
<b>Phenometric</b>	Quantitative measure describing the timing or magnitude of phenological change
<b>Spectral vegetation index (SVI)</b>	Mathematical combination of spectral reflectance in two or more electromagnetic regions sensitive to certain physiological and structural properties of vegetation
<b>(Spectral) greenness</b>	An umbrella term referring to SVIs more specifically representing solar energy utilization and reflectance by photosynthetically active plant matter, which enables their use as proxies for biomass and coverage by green vegetation
<b>Seasonal maximum SVI</b>	Maximum SVI value in a single growing cycle or season, for greenness indices often interpreted as a proxy for peak photosynthetically active biomass or plant coverage
<b>Passive remote sensing</b>	Remote sensing systems measuring ambient energy that is reflected and/or emitted by Earth surface elements (such as reflected energy of the Sun)
<b>Active remote sensing</b>	Remote sensing systems which use their own energy source to investigate Earth surface elements and measure the returned (reflected) portions of their emitted signals
<b>Multispectral sensor</b>	Sensor measuring surface reflectance using few bands representing broader portions of the electromagnetic spectrum (often exceeding 20nm)
<b>Hyperspectral sensor</b>	Sensor measuring surface reflectance using a large number of bands representing narrow portions of the electromagnetic spectrum (e.g. 10–20nm)
<b>Synthetic aperture radar (SAR)</b>	Active remote sensor that transmits microwave energy and records its return backscatter
<b>Light detection and ranging (lidar)</b>	Active remote sensing systems using pulsed laser scanning to target landscape objects and measuring the time taken by the reflected signal to return back and its intensity

et al., 2020; Meireles, Cavender-Bares, et al., 2020; Schweiger et al., 2018; Wang et al., 2016), the role of diversity in seasonality of vegetation spectra and ecosystem functions remains little understood. Progress in very high spatial resolution sensors now allows studying phenomena requiring high level of landscape detail yet also spatial extents that are too large for field surveys of individual organisms and patches (Dixon et al., 2021; Dronova et al., 2017; Klosterman et al., 2018). However, studies linking phenology to plant community ecology, species interactions and biodiversity at such scales are still not common.

This synthesis discusses how remote sensing indicators of phenology and vegetation dynamics can allow us to better understand factors mediating plant responses to change drivers at multiple scales, from the plant community to broader geographical extents. We especially highlight the potential of phenological remote sensing in three under-discussed areas: the connections between phenology and plant diversity, the relevance of phenological analyses to studies of resilience to disturbance and stressors and the ability of phenological information to measure vegetation structure and its effects on ecosystem functions. We also summarize key knowledge gaps concerning limited guidance on choosing among phenological estimation approaches, under-representation of important phenological phenomena in studies to date and the challenges of mechanistic interpretation of remotely observed phenological patterns. We then discuss emerging opportunities and future research needs to address these gaps based on the advances in remote sensing systems, products and data analysis strategies.

## 2 | PHENOLOGICAL INFERENCE FROM REMOTE SENSING DATA—AN OVERVIEW

Phenological analyses at landscape scales often use time series of remote sensing data (Box 1) that ideally should be calibrated for consistency and corrected to minimize the influence of atmospheric effects (e.g. clouds, pollution and aerosols). Higher frequency of usable observations improves the chance of detecting seasonal transitions and capturing short-term events such as flowering and fruiting. Not surprisingly, until the last decade, most relevant data have come from satellite platforms (Table 1) providing repeated and usually sun-synchronous (i.e. collected at consistent time of the day at each visit) observations. Such datasets, however, may need to be calibrated for seasonal changes in sun and viewing angles, while their actual data frequencies may depend on geographic location affecting overlaps between satellite tracks and cloudiness. Advances in geostationary satellites such as GOES-16 and -17 (Table 1) discussed in more detail in Section 4.2 can greatly improve temporal richness of datasets for phenological studies.

Local-scale analyses of phenology have increasingly adopted in situ time lapse phenocam imagery, particularly to assess the seasonality of plant-based ecosystem functions (Dronova et al., 2021; Klosterman et al., 2014; Knox et al., 2017). Rapidly advancing UAV technology also provides detailed, spatially comprehensive

observations at landscape levels unfeasible to extensive field sampling, and is increasingly incorporated in phenological studies (e.g. Park et al., 2019). We discuss other, more recent emerging sensors and data opportunities in Sections 4.2 and 5.3, and additionally refer the reader to recent comprehensive reviews on phenological remote sensing (Bajocco et al., 2019; Berra & Gaulton, 2021; Matongera et al., 2021; Zeng et al., 2020).

Most phenological applications to date have used passive remote sensing products, i.e., images of spectral reflectance in electromagnetic regions (bands) sensitive to plant coverage, physiology, and stress (Helman, 2018; Zeng et al., 2020). Studies have also used various multi-band spectral vegetation indices (SVIs; Box 1) designed to capture certain aspects of plant foliar chemistry, vigour, photosynthetic capacity (Ollinger, 2011; Ustin & Gamon, 2010) or life stages such as flowering (Chen et al., 2019; Mahmud et al., 2020). Some SVIs have become especially common in phenological analyses, particularly, Normalized Difference Vegetation Index (NDVI; (Rouse et al., 1974) and Enhanced Vegetation Index (EVI; Huete et al., 2002; Melaas, Sulla-Menashe, et al., 2016). Certain phenological events, such as flowering, may be characterized by temporary reductions in greenness (e.g. Chávez et al., 2019; Van Doninck et al., 2020; Wang et al., 2016) or by specialized SVIs emphasizing flower spectra (Chen et al., 2019; Dixon et al., 2021; Mahmud et al., 2020). Hyperspectral datasets (Box 1) are especially promising for such efforts, as they can be sensitive to unique flower pigments (Mahmud et al., 2020), chemical traces of flowering events (Carvalho et al., 2013), and spectral differences between flowers and other plant parts (Duan et al., 2021; Landmann et al., 2015; Paz-Kagan et al., 2019). Thermal remote sensing may also assist in spatial analyses of blooms for species with non-conspicuous flowers, particularly in heterogeneous landscapes (Bogawski et al., 2019).

Progress in active remote sensing also opens new prospects for phenological assessments, particularly with synthetic aperture radar (SAR) instruments in the microwave electromagnetic range (Box 1). Active SAR sensors provide data in the form of a backscatter, i.e., intensity of a return signal, which in some instruments can be also measured in different wavelengths and signal polarizations. Such signals are often responsive to volume, biomass and structure of plant canopies, as well as terrain, soil moisture and flooding (Frison et al., 2018; Laurila et al., 2009). Limited sensitivity of SAR to clouds provides robust observations in regions with highly sparse time series from passive sensors. Challenges of SAR analyses include specialized corrections for terrain effects, removal of speckle and noise, and signal calibration. Publicly available products historically have been also limited in spatial and temporal resolution. This has changed with the launch of Sentinel-1 satellites and open-access products by the European Satellite Agency's Copernicus program, and advances in other SAR systems, including unoccupied UAVSAR which has been used in several locations across the globe (Li et al., 2019). Prominent studies of SAR-based or combined SAR-passive phenology have emerged in croplands (Liu et al., 2019), forests (Frison et al., 2018; Rüetschi et al., 2017) and flooded regions (Chen et al., 2020; Niculescu et al., 2020).

TABLE 1 Examples of remote sensing satellite systems used in vegetation phenology analyses

Type	Sensor or mission	Temporal scope	Frequency	Spatial resolution	Spectral bands	Examples of studies
Broadband, passive, sun-synchronous	Moderate Resolution Imaging Spectrometer (MODIS)	1999–Present	Daily	250–1000m	36	John et al., 2008; van Rooijen et al., 2015
	Landsat	1972–Present	16days	15–120m	4–11	MacFadyen et al., 2016; Maeda et al., 2014; Melaas et al., 2013
	Sentinel-2A,B	2015–Present	5–10days	10–20m	13	John et al., 2020; Melaas, Sulla-Menashe, et al., 2016
	Satellite Pour l'Observation de la Terre (SPOT)	1986–	26days	1.5–20m	4–5	Nightingale et al., 2008
	Pléiades	2009–	Daily	0.5–2 m	4	Niculescu et al., 2020
Specialized solar induced chlorophyll fluorescence	WorldView- series	2007–	1–6days	0.3–2.4 m	8–16	Westergaard-Nielsen et al., 2013
	RapidEye & PlanetScope	2008–	1–6days	3–5 m	5	Dronova et al., 2021; John et al., 2020; Schuster et al., 2015
	IKONOS	1999–2015	3days	0.82–4 m	5	Madonsela et al., 2017
	Advanced Very High Resolution Radiometer (AVHRR)	1979–2019	Daily	1000m	4–6	Kariyeva & Van Leeuwen, 2011
	TROPOMI (Sentinel-5P), OCO-2	2017–2019–	Daily	3500–28,000m	7	Magney et al., 2019
Broadband passive geostationary	Geostationary Operational Environmental Satellites (GOES-16 and -17)	2016–	~5–10 min	500–4000m	16	Hashimoto et al., 2021; Wheeler & Dietze, 2021
	Earth Observing One (EO-1)—Hyperion	2000–2017	16days	10–30 m	196	Somers & Asner, 2013
	Precursore IperSpettrale della Missione Applicativa (PRISMA)	2019–	29days	30m	240	Vangi et al., 2021
	Hyperspectral Imager Suite (HISUI)	2019–	2–60days	30m	185	—
	DLR Earth Sensing Imaging Spectrometer (DESI)	2018–	3–5days	30m	235	—
Synthetic aperture radar (SAR, active)	Sentinel-1A,B	2014–	~6–12days	5–20m	5	Frison et al., 2018; Rütschi et al., 2017; Tran et al., 2021
	Radarsat-1	1995–2013	~24days	10–100m	1	Laurila et al., 2009
	ENVISAT ASAR	2002–2012	Location-dependent, up to 35days	150m	1	Laurila et al., 2009
	ERS-1	1991–2000	35days	6–30m	1	Laurila et al., 2009

Light detection and ranging (lidar) active sensors are also appealing for tracking seasonality of vegetation structure, particularly in ecosystems with sparse plant distribution prone to background effects in passive sensor images (Sankey et al., 2014). Lidar datasets can help study phenological responses of understory species, which are often obscured by taller, dominant species (Calders et al., 2015) or track seasonal changes in evergreen plant communities (Griebel et al., 2015). However, phenological applications of lidar are often still limited by the cost and sparsity of observations. Advances in UAV-based lidar show promise for local-scale surveying; for example, phenological changes in vegetation can affect the error in digital terrain models derived from UAV observations (Goodbody et al., 2018). Satellite-based lidar instruments such as recently launched Global Ecosystem Dynamics Investigation (GEDI) mission do not yet provide fully contiguous data that would allow tracking vegetation seasonality at frequencies similar to passive and SAR systems. However, such data can improve phenological inference when used with passive data time series in regions with varying canopy structure (Di Tommaso et al., 2021).

Most phenology analyses from remote sensing to date have focused on seasonal changes in photosynthetically active biomass and foliar chemistry (Bajocco et al., 2019; Zeng et al., 2020; Box 1), which affect the shape and curvatures in seasonal trajectories of SVIs (Box 1). Phenometrics marking dates and spectral values of important seasonal transitions (Box 1) can be estimated by fitting multi-parameter mathematical curve functions to the spectral time series (e.g. Bolton et al., 2020; Elmore et al., 2012; Klosterman et al., 2014; White et al., 1997; Zeng et al., 2020; Zhang et al., 2003). Remote sensing literature offers multiple examples of studies estimating phenological events from such models fitted to a time series of satellite or phenocam observations. Such events include start and end of growing season (e.g. Melaas et al., 2013), rate of greening and senescence (e.g. Bolton et al., 2020; Klosterman et al., 2014; Toomey et al., 2015; Vrieling et al., 2018), and flowering (e.g. Chen et al., 2019). These phenological metrics are commonly used to study ecosystem response to climate change, extreme climatic events, and recovery from disturbance. Other remote sensing studies use temporal aggregates, which can still correspond to phenological processes without necessarily relying on a fitted phenological model. For example, seasonal maximum greenness (Box 1), which should roughly correspond to the timing at which a plant community reaches peak biomass, has been shown in several studies to significantly correlate with plant diversity (e.g. Hernández-Stefanoni et al., 2012; Taddeo, Dronova, & Depsky, 2019).

Quantifying phenometrics for individual pixels within larger landscapes covered by image products provides a way to characterize spatial variability and dynamics of phenological cycles. This information, in turn, may reveal phenological sensitivity of plant communities to various environmental gradients (Cord, Klein, Gernandt, et al., 2014; Oehri et al., 2017; Pilaš et al., 2014; Viña et al., 2016) and help predict future vegetation trajectories (Cord, Klein, Gernandt, et al., 2014). Long-term variation in phenometrics may signal both short-term responses to anomalies, such as droughts

and extreme temperatures (Friedl et al., 2014; Hufkens et al., 2012; Pilaš et al., 2014), and progressive, directional ecosystem changes (Hilker, Lyapustin, et al., 2014; Melaas et al., 2013; Myers-Smith et al., 2020; Zeng et al., 2013).

### 3 | THE POTENTIAL OF PHENOLOGICAL REMOTE SENSING TO ADVANCE PLANT ECOLOGY

#### 3.1 | Remotely sensed phenology as an indicator of plant diversity and its change

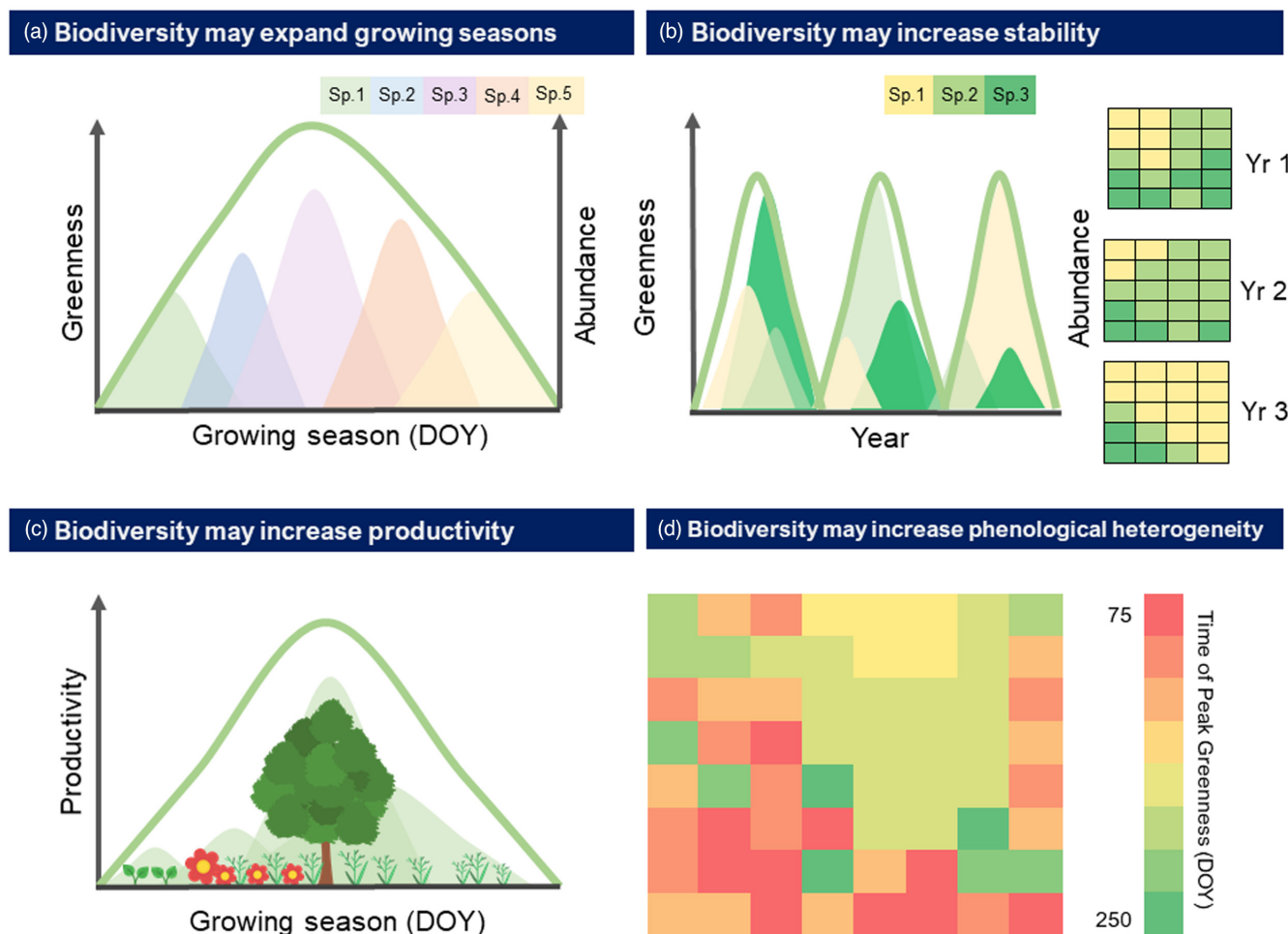
##### 3.1.1 | Plant diversity-phenology relationships

Besides climatic factors, changes in composition and diversity of plant communities can impact the seasonality of their life cycles and remotely sensed phenometrics (Figure 1), which appeals to critical needs in biodiversity monitoring (Bellard et al., 2012; Cardinale et al., 2012; Díaz et al., 2006; Hooper et al., 2012; Pereira et al., 2013; Sala, 2000). Evidence to date suggests several potential links between diversity and phenology of plant communities that call for further research (Figure 1). First, phenological contrasts among species in diverse communities can favour co-existence by enabling resource harvesting during times of decreased competitive pressure (Fargione & Tilman, 2005), which can lengthen the growing season measured by remote sensors (Figure 1a; Oehri et al., 2017; Wilsey et al., 2014). Second, the diversity of species responses to environmental fluctuations favours compensatory dynamics in which the decline of one species following a disturbance allows others to increase their abundance (Isbell et al., 2009; Loreau & de Mazancourt, 2013). This may reduce variability in phenometrics over time (Figure 1b; Oehri et al., 2017; van Rooijen et al., 2015), though such stabilizing effects can be context-dependent (García-Palacios et al., 2018; Rheault et al., 2020).

Third, increased resource use efficiency in highly diverse ecosystems (Hooper et al., 2012; Loreau & Hector, 2001) can enhance production of plant biomass, which may increase the magnitude and seasonality of SVIs (Figure 1c; Castillo-Riffart et al., 2017; Feeley et al., 2005; Hernández-Stefanoni et al., 2012; Taddeo, Dronova, & Harris, 2019). Finally, plant diversity may increase phenological asynchronies due to niche differentiation in time (e.g. adaptations to different conditions within the growing season; Gotelli & Graves, 1996) or in space (differential adaptations to local environmental gradients; Cord, Klein, Mora, & Dech, 2014; Pilaš et al., 2014; Viña et al., 2012). This may lead to positive correlations between vegetation diversity and spatial heterogeneity of measured phenometrics (Figure 1d; Cabezas et al., 2016; Huesca et al., 2015; Maeda et al., 2014; Rocchini et al., 2004; Tomaselli et al., 2017).

Such relationships between plant diversity and phenology (Figure 1) support the potential of remote sensing to monitor and predict plant dynamics at broad ecological, geographic, and administrative scales. For example, spatial heterogeneity in satellite-derived





**FIGURE 1** Potential effects of plant diversity on phenology of plant communities suggested by earlier experimental and remote sensing studies including (a: Oehri et al., 2017; Steinaker et al., 2016; b: Oehri et al., 2017; van Rooijen et al., 2015; c: Castillo-Riffart et al., 2017; Feeley et al., 2005; Hernández-Stefanoni et al., 2012; Taddeo, Dronova, & Harris, 2019; d: Viña et al., 2012).

phenometrics, possibly related to asynchronies among plant types, has shown positive associations with vegetation composition and diversity in multiple biomes (Cabezas et al., 2016; Huesca et al., 2015; Maeda et al., 2014; Rocchini et al., 2004; Tomaselli et al., 2017). Relatedly, floristic similarity may correlate with phenological similarity even after controlling for confounding landscape effects, e.g., gradients of human activity (Viña et al., 2012, 2016). However, strength of such associations varies among diversity metrics (Maeda et al., 2014; Taddeo, Dronova, & Harris, 2019) and among the input remote sensing products (John et al., 2008; Maeda et al., 2014; Taddeo, Dronova, & Harris, 2019; Viña et al., 2012).

Plant diversity often correlates with SVIs measured at specific points in the growing season or statistically integrated over the latter. Single-date and seasonal maximum SVIs have shown significant associations with plant diversity of wetlands (Castillo-Riffart et al., 2017; Taddeo, Dronova, & Harris, 2019), savanna woodlands (Madonsela et al., 2017), tropical dry forests (Feeley et al., 2005; Hernández-Stefanoni et al., 2012), boreal forests (Parviainen et al., 2009) and alpine communities (Dedieu et al., 2016), among others (Wang & Gamon, 2019). However, such correlations only rarely

explain more than 45%–50% variation in plant diversity (Feilhauer & Schmidtlein, 2011) and tend to be stronger near the peak growing season (e.g. Feilhauer & Schmidtlein, 2011; Gholizadeh et al., 2020; John et al., 2008; Maeda et al., 2014; Wang et al., 2016), possibly due to representation of species complementarity at high biomass stages (Davidson & Csillag, 2001; Wang et al., 2016). Specific forms of diversity-SVI relationships and their transferability also vary depending on redundancy in functional traits and competition within communities (Brun et al., 2019; Wang et al., 2016), saturation of spectral signals with increasing biomass (Huete et al., 2002), sampling effects of site selection (Davidson & Csillag, 2001), and landscape characteristics (Feilhauer & Schmidtlein, 2011).

Phenometrics derived from multi-date remote sensing observations may show more robust associations with plant diversity than snapshot measures. For example, a USA-wide study of forest tree diversity (Nightingale et al., 2008) found a significant relationship between satellite-derived annual gross primary productivity and tree species richness, accounting for 51%–77% variation in the latter depending on satellite product. In another USA-wide study relating annual maximum and median SVI to structural, functional,

geographic and site-specific characteristics of wetlands, associations with vegetation composition and diversity were stronger for annual median greenness than for annual maximum (Taddeo, Dronova, & Depsky, 2019). However, strength of such relationships may vary across different analysis units, e.g., floristic, bioclimatic or administrative regions (e.g. Fairbanks & McGwire, 2004; John et al., 2008), which calls for more research on factors influencing their scaling.

### 3.1.2 | Phenological insights on plant diversity change

Shifts in phenology detected by remote sensing may provide important signals of biodiversity changes (García-Palacios et al., 2018; Huesca et al., 2015; Oliver et al., 2015; Wolkovich & Cleland, 2011) in response to climate, stressors and land use (Cord, Klein, Gernandt, et al., 2014; Polley et al., 2013; Revermann et al., 2016). For example, phenological strategies of some invasive plant species provide competitive advantages in resource and space acquisition (Bolch et al., 2020; Wolkovich & Cleland, 2011) and produce unique spectral dynamics such as earlier greening, later senescence or unique flowering patterns (e.g. Bolch et al., 2020; Dronova et al., 2017, p. 201; Paz-Kagan et al., 2019; Tian et al., 2020). Similar effects may result from the expansion of plant species with  $C_4$  photosynthetic pathway (Davidson & Csillag, 2001; Pau & Still, 2014), or forest succession (Bergen & Dronova, 2007; Greig et al., 2018; Huesca et al., 2015). Novel 'azonal' and 'extra-azonal' plant communities emerging in response to gradual climate shifts may differ in spectral phenological characteristics from their surroundings, which facilitates their detection and monitoring (Pilaš et al., 2014; Revermann et al., 2016; Schwieder et al., 2016). Such effects make remote sensing of phenology of high interest to species distribution models, i.e., models studying the association between environmental variables and current distribution of a species to identify its potential habitats under climate change scenarios (Andrew & Warrener, 2017; Bobrowski et al., 2018; Cord, Klein, Mora, & Dech, 2014; Gonçalves et al., 2016).

Novel phenological patterns observable at broad spatial scales can also indicate irreversible shifts and tipping points in plant communities. For example, widespread decline of greenness in central African rainforests (Zhou et al., 2014) provided evidence of broad-scale vegetation response to persistent droughts. Such responses are early warning signals of future changes including increasing deciduousness (Fauset et al., 2012), losses of plant diversity, and homogenization (Aguirre-Gutiérrez et al., 2020) reported in other African regions. Satellite observations have also revealed novel patterns of the pre-rain green-up across southern tropical Africa, manifested in new leaf growth during the dry season (Ryan et al., 2017). This phenomenon likely reflects local phenological adaptations resulting from competition among trees and may even involve non-weather related cues, such as insolation (Ryan et al., 2017).

## 3.2 | Phenological perspective on stability and resilience of plant communities

### 3.2.1 | Phenological stability and asynchronies

Experimental and theoretical studies have highlighted several mechanisms by which plant diversity can promote stability and resilience (Gonzalez et al., 2020; Oliver et al., 2015), including niche partitioning, functional redundancy, response diversity (Loreau & de Mazancourt, 2013; Mori et al., 2013; Yachi & Loreau, 1999), and overyielding (Isbell et al., 2009; Zhang et al., 2017). Sensitivity of phenometrics to both plant community composition and stability of ecosystem functions offers a unique opportunity to assess these mechanisms across space and time to understand factors promoting stability (Barbosa et al., 2006; Hodgson et al., 2015; Oliver et al., 2015). With some datasets extending over 30 years, remote sensing archives can help devise indicators of stability and resilience in response to climate change, extreme events, management and biodiversity loss (Cleland et al., 2006; García-Palacios et al., 2018; Madonsela et al., 2017; Oehri et al., 2017; van Rooijen et al., 2015). For example, García-Palacios et al. (2018) observed a significant relationship between taxonomical and functional diversity and ecosystem stability of drylands measured as mean-to-standard deviation ratio of satellite-derived NDVI. Oehri et al. (2017) observed a positive impact of plant diversity on ecosystem stability across an altitude gradient using the coefficient of variation in the growing season length estimated from EVI time series. Mazzochini et al. (2019) observed a stabilizing effect of functional plant diversity in drylands on mean-to-standard deviation ratio for EVI at different spatial resolutions even after controlling for relevant climatic factors.

While such examples illustrate a positive impact of diversity on stability, more research is needed to compare the relative contributions of community processes and landscape factors in promoting resilience. For instance, a study of wetlands in Canada (Rheault et al., 2020) found that growing season length estimated from satellite data responds more strongly to edaphic, climatic and geographic contrasts between wetland plant assemblages than to their plant diversity. Losses of species and environmental changes following disturbance can decrease remotely assessed length and consistency of growing seasons and increase phenological heterogeneity in space (Dronova et al., 2021; Steinaker et al., 2016). More research is also needed on how the key stability-promoting mechanisms—including niche partitioning, functional redundancy and response diversity (Loreau & de Mazancourt, 2013; Mori et al., 2013; Yachi & Loreau, 1999)—operate at different levels of spatial heterogeneity, connectivity, landscape legacies and trophic interactions (Gonzalez et al., 2020; Oliver et al., 2015; Vogel et al., 2019), particularly in managed landscapes (Kremen & Merenlender, 2018; Lopes et al., 2017; Manning et al., 2019). Remote sensing can help assess more in-depth the specific and combined impacts of these drivers by comparing phenometrics across broader abiotic, biotic and management gradients than possible with field efforts alone.



An interesting question arising from the research to date is whether phenological complementarity and asynchrony among and within species impact the resilience of plant community vegetation cycles observed by remote and in situ sensors (e.g. Cleland et al., 2006; Rathcke & Lacey, 1985; Stevens & Carson, 2001; Zhao et al., 2007). Phenological asynchronies can be hypothesized to promote resilience as an outcome of species co-existence, spatio-temporal niche differentiation and enhanced ecosystem function (Cord, Klein, Mora, & Dech, 2014; Gonzalez & Loreau, 2009; Gotelli & Graves, 1996; Lasky et al., 2016; Mason et al., 2013; Viña et al., 2012; Vitasse, 2013). They may result both from intraspecific genetic diversity (e.g. Doi et al., 2010) reflecting gradients of flowering times, pollen dispersal, and limitations to genetic connectivity (Hirao & Kudo, 2008; Rossetto et al., 2011; Tuomisto, 2003; Viña et al., 2012), and from intra-specific diversity capturing species adaptations to local environmental heterogeneity (Huesca et al., 2015; Pilaš et al., 2014; Wolkovich et al., 2014) and relationships with pollinators (e.g. Donoso et al., 2016; Leong & Roderick, 2015; Olliff-Yang et al., 2020). Regional asynchronies in phenometrics can also identify microrefugia, i.e., stable regions of quality habitat and unique microclimates that help buffer the effects of climate in dynamic landscapes and promote species persistence (Andrew & Warrener, 2017; Bobrowski et al., 2018).

At the same time, field studies do not universally corroborate the stabilizing effect of asynchronies, suggesting that it mainly operates at lower alpha-diversity levels (Qin et al., 2003; Stevens & Carson, 2001; Zhao et al., 2007). Furthermore, phenological synchrony can be also beneficial for survival, particularly for pollinator-dependent species (e.g. Dante et al., 2013; Fantinato et al., 2016; Olliff-Yang et al., 2020). Relatedly, remote sensing-based indicators of phenological stability, such as longer growing seasons, should not be automatically interpreted as evidence of ecological equilibria, as they may result from phenological mismatches among species cycles (Kharouba & Wolkovich, 2020; Samplonius et al., 2021), invasions (Bolch et al., 2020; Dronova et al., 2017), or other disruptions. More generally, remote sensing-based studies of complementarity have been remarkably scarce and require rigorous collaborations with field-based investigations.

### 3.2.2 | Indicators of recovery

Understanding resilience often involves the assessments of recovery from disturbance or perturbations. Multi-year remote sensing observations allow comparing phenological characteristics of a given season to 'regimes' of long-term variability, as shown by studies in various regions, including North American forests (Melaas et al., 2013), Brazilian savannas (Alvarado et al., 2017), the Okavango Delta (Neuenschwander & Crews, 2008), and European alpine grasslands (Di Mauro et al., 2014). Van Rooijen et al. (2015) found that taxonomic diversity can improve stability and resistance to droughts in dune ecosystems based on the magnitude of loss in NDVI relative to its time series. Swetnam

et al. (2021) developed an Ecosystem Moisture Stress Index based on the ratio of date-specific NDVI differences from their mean to their long-term standard deviation to assess phenological responses to different disturbances and detect changes in resilience (Swetnam et al., 2021). Similarly, Pilaš et al. (2014) developed several indices of resilience based on varying climatic responses in satellite-derived fraction of absorbed photosynthetically active radiation (FAPAR).

Remote sensing-based strategies to assess disturbance and recovery have increasingly used temporal segmentation, i.e., identification of shorter-term change patterns (such as temporary increases, declines or rapid shifts) within the spectral time series. This approach helps detect characteristic change typologies within complex, long-term series even when their onsets, durations and end dates vary in space. For example, LandTrendr algorithm (Kennedy et al., 2010) detects disturbance and recovery based on losses and gains within long-term time series of annual greenness that significantly exceed 'typical variability', and estimates their timing, duration, and magnitude for individual mapping units (e.g. pixels). LandTrendr has been applied in various types of forests (Fragal et al., 2016; Greig et al., 2018; Liang et al., 2016; Senf et al., 2015), woodlands (Filippelli et al., 2020; Viana-Soto et al., 2020) and grasslands (Dara et al., 2020). Another approach, Breaks For Additive Seasonal and Trend (BFAST; Verbesselt et al., 2010) detects phenological transitions in long-term time series while accounting for abrupt changes and noise. However, the applications of temporal segmentation methods still tend to focus on inter-annual SVI dynamics, and it remains less clear how their performance may be impacted by seasonal variability in both vegetation cycles and quality of remote sensing data.

### 3.3 | Phenology-based indicators of vegetation structure

Seasonal changes in three-dimensional (3-D) structure of plant canopies modify reflection, absorption, transmission and scattering of solar radiation, affecting temporal variation in ecosystem functions, as well as competition and co-existence among species. Field studies provide numerous examples of resulting phenological adaptations that are likely to affect remote sensing signatures. These include different seasonalities of forest overstory trees versus understory shrubs (Williams-Linera, 2003), contrasts in photosynthetic acclimation among understory species with different ecological strategies (Rothstein & Zak, 2001) or enhancement of productivity during successional transitions due to co-existence of species with different tolerances to shade (Dronova et al., 2011; Pastor & Bockheim, 1984). The effects of such interplays on temporal trajectories of canopy-level spectral signals provide a chance to infer certain aspects of canopy structure from remotely sensed phenological patterns (Dronova et al., 2021; Huesca et al., 2015).

This potential is especially appealing with active remote sensing tools directly responsive to canopy volume and structure. For example, monthly terrestrial lidar surveys in Amazonian forests

(Smith et al., 2019) detected different phenological strategies and drought responses among trees stratified by canopy height and light environments. Satellite-based lidar tools such as GEDI are highly promising for the repeated monitoring of 3-D structures over broad regions, and their importance is likely to grow in the future. Even temporally sparse lidar monitoring can support assessments of vegetation structure and its seasonality when combined with contiguous and frequent observations from passive sensors (Di Tommaso et al., 2021).

SAR-based active remote sensing also shows substantial potential for monitoring of vegetation structure, particularly in systems where temporal and/or spatial heterogeneity of vegetation is likely to diversify the backscatter signals (Frison et al., 2018; Laurila et al., 2009; Rüetschi et al., 2017). Examples of this potential include sensitivity of satellite and UAV-based SAR signals to differential seasonality of deciduous and coniferous tree species and more general changes in foliar biomass in mixed temperate forests (Frison et al., 2018; Rüetschi et al., 2017), spatio-temporal variation in biomass, volume, and scattering of various crop canopies (Li et al., 2019; Liu et al., 2019), or hydrologically controlled structure and physical regimes of wetland vegetation (Chen et al., 2020; Niculescu et al., 2020).

Multi-temporal passive remote sensing data also offer insights into 3-D vegetation structure, especially in forest and shrubland settings (de Moura et al., 2017; Greig et al., 2018; Pisek et al., 2016). For example, seasonal amplitude of greenness (Box 1) is substantially lower for evergreen than deciduous vegetation and thus can help detect these structurally different types (Melaas et al., 2013). In an oak-hickory woodland in Maryland, USA (Reaves et al., 2018), Landsat-derived patterns of greendown, i.e., decline in near-infrared reflectance throughout the growing season, correlated with the abundance of an oak species showing a unique leaf angle orientation in late season. Similar effects may arise in herbaceous canopies; for example, accumulation of standing dead biomass in reed-dominated marshes results in limited light penetration, lower water temperatures and delayed start of greening in both field and remote sensing observations, affecting spatial variation in ecosystem productivity (Dronova et al., 2021). Multi-year shifts in phenometrics may represent changes in plant communities producing different seasonalities among vertical strata (Greig et al., 2018; Huesca et al., 2015), such as lower annual fluctuations in greenness of deciduous forests with the emergence of evergreen understory (Bergen & Dronova, 2007).

The potential to infer canopy structure based on phenology increases with multi-angular remote sensing observations and corrections for atmospheric effects dependent on view and illumination geometry (e.g. Lyapustin et al., 2018). By computing NDVI from a multi-angular satellite reflectance product, Pisek et al. (2016) characterized seasonal dynamics of understory vegetation in different forest types, which is not feasible with traditional reflectance datasets. After correcting satellite observations of an eastern Amazon tropical forest for multi-angular effects, de Moura et al. (2017) found that seasonality of EVI tracked leaf area index of mature leaves more closely—an important parameter for modelling canopy-level

ecosystem functions. A different spectral index in the latter study showed sensitivity to young leaf flushing as another important structural change (de Moura et al., 2017). Future advances in multi-angular reflectance products and correction algorithms thus could fill important gaps on the links between phenology and plant community diversity, ecological functioning, and responses to stressors (Hilker et al., 2009; Pacheco-Labrador et al., 2016; Sharma, 2021). These opportunities have already started to emerge in UAV applications using structure from motion to infer 3-D structure of landscapes from overlapping images (Dandois & Ellis, 2013); however, phenological analyses using this technique over full-season time frames are still few (Park et al., 2019).

## 4 | CAVEATS AND OPPORTUNITIES IN PHENOLOGICAL ESTIMATION

### 4.1 | Navigating phenological inputs, metrics, and paradigms

Despite the plethora of proposed phenological curve-fitting methods and metrics (Klosterman et al., 2014; Zeng et al., 2020), guidance on choosing among them remains somewhat limited. The selection of a curve-fitting model can significantly impact phenometrics and their correlation with field observations (Hird & McDermid, 2009; White et al., 2009). Furthermore, the analyses conducted by White et al. (2009) revealed that methods used to identify the start and end of the growing season (e.g. threshold-based, derivatives-based) could differ in their estimated timing by up to a month. Yet, studies vary in how exactly they define a meaningful phenological event. For example, phenometrics describing onsets and ends of green-up and senescence have included thresholds of a greenness index (e.g. White et al., 2009), different-order derivatives of the fitted functions (Zeng et al., 2020), or relative measures such as the dates of a certain percentage of increases or decreases in SVI (Bolton et al., 2020).

In addition, the performance of curve fitting approaches can vary significantly across biogeographic regions (Hird & McDermid, 2009) and ecosystem types. Most curve-fitting approaches have been developed for terrestrial deciduous ecosystems; yet, in a number of settings, it can be difficult to identify seasonal spectral peaks implied by such traditional phenological paradigms (Box 1). Besides data sparsity in cloudy regions, this can happen when vegetation changes are relatively subtle (e.g. in some evergreen systems), or when disturbance, background reflectance, and physical factors such as flooding obscure fluctuations in vegetation signals (Bolton et al., 2020; John et al., 2008; Kearney et al., 2009; Miller et al., 2021). Furthermore, certain phenological dynamics may not tightly conform to annual time frames, particularly in regions with long growing seasons; yet, such phenologies may still signal responses to climate change and stressors (e.g. Bush et al., 2017; de Moura et al., 2017; Park et al., 2019; Verbesselt et al., 2010; Williams-Linera, 2003). These issues indicate that traditional, peak-focused phenological estimation is not universally applicable across heterogeneous geographic

regions, and alternative, complementary approaches are needed to enable comparisons of phenology across landscapes or regions encompassing multiple ecosystem types.

A major contributor to these challenges is the variability in cloud-free remote sensing data (e.g. Ju & Roy, 2008; Kariyeva & Van Leeuwen, 2011; Schwieder et al., 2016), amplified by logistical and financial constraints on field surveys (Pereira et al., 2013). Denser datasets reduce the uncertainty in curve-fitting and accommodate more complex and nuanced functions. For example, daily phenocam images make it possible to fit multi-parameter non-linear functions that capture unique curvature rates not only between greening and senescence phases but also between their respective beginnings and endings (e.g. Klosterman et al., 2014). Frequent observations are also critical for detecting shorter-term reproductive events; for example, Chen et al. (2019) found that almond orchard bloom dynamics were best characterized by PlanetScope and Sentinel-2 imagery with  $\leq 5$ -day revisit.

Mismatches between field and remote observations can be a major challenge for attributing phenometrics to in situ plant diversity, stress or particular growth phase, especially in cloudy regions (e.g. John et al., 2008). Broad-scale studies must sometimes combine floristic surveys with satellite images varying by a few months (e.g. Taddeo et al., 2021; Taddeo, Dronova, & Harris, 2019), which can impact phenological interpretation (Gholizadeh et al., 2019, 2020). Timing of data, however, can be even more important than the number of images per se, which becomes especially relevant in applications of high-cost commercial imagery (Schuster et al., 2015). For example, a study in a European grassland (Schmidt et al., 2014) showed that increasing the number of seasonal satellite images beyond a certain level no longer improved differentiation of vegetation types, while the optimal quantity was SVI-dependent. To help coordinate remote sensing and field data collection, more research is needed on the most informative phenological assessment time frames and their sensitivity to ecosystem types, stress factors and management (Lopes et al., 2017).

## 4.2 | Solutions offered by improved remote sensing frequencies and archive length

Addressing challenges and needs in phenological estimation becomes increasingly feasible with gains in remote sensing observation frequencies, archive lengths and opportunities to strategically combine different products. For example, multi-decade open-access satellite datasets (e.g. AVHRR, MODIS, Landsat; Table 1) are already offering critical insights into phenological responses to climate, disturbance and shifting gradients of floristic composition and land use (Bolton et al., 2020; Brooks et al., 2020; Hufkens et al., 2012; Melaas et al., 2013; Zeng et al., 2020). Such long-term datasets facilitate assessments in complex systems by enabling comparison of individual years with long-term trends (Melaas et al., 2013; Miller et al., 2021). Advances in cloud-based data processing systems such as Google Earth Engine also help on data user's side, reducing the burden of

data download, pre-processing and storage (Gorelick et al., 2017; Zeng et al., 2020).

Progress in geostationary satellite systems offers critical advantages of monitoring specific locations over extended time frames and different times of the day, which becomes especially important for regions unreachable by frequent field surveys or ground-based phenological observation networks (Hashimoto et al., 2021; Wheeler & Dietze, 2021). For example, the application of GOES Advanced Baseline Imager over Amazon tropical forests (Hashimoto et al., 2021) revealed presence of seasonality in 85% of the region's evergreen forests, which would not be possible to detect with traditional sun-synchronous sensing. Geostationary systems can also substantially reduce the impact of clouds on estimation of phenological transition dates and improve the assessments of phenological trends and shifts over vast regions and multi-year periods. To better understand potential uncertainties due to still coarse spatial resolutions ( $\sim 1$  km) of such products, their time series can be cross-compared with high frequency in situ observations such as phenocam images (Wheeler & Dietze, 2021).

Increased temporal frequency and spatial resolution of recent satellite systems (e.g. Sentinel-1 and -2, Planet Labs; Table 1) further allows combining data from multiple instruments with complementary benefits. For example, fusion of multi-spectral products, such as the Harmonized Landsat-Sentinel-2 dataset (Claverie et al., 2018) and STARFM algorithm combining MODIS and Landsat data (Gao et al., 2006), increases representation of phenological stages at reasonably moderate spatial resolutions, especially in cloudy regions. Combining 3-m PlanetScope imagery with 10-m Sentinel-2 and 30-m Landsat phenological data successfully detected montane flowering phenology in Washington, USA (John et al., 2020). Fusion of passive and active sensing products can help capture the effects of plant canopy structure and morphology on spectral differences among vegetation types and their phenologies (Schuster et al., 2015). In particular, combining passive imagery and microwave radar products with low sensitivity to clouds and high sensitivity to canopy structure and flooding can characterize unique phenologies shaped by hydrological regimes (Silva et al., 2013; Wang et al., 2012) or seasonality of vegetation biomass parameters (Laurila et al., 2009; Tran et al., 2021).

Expanding in situ observation capacities also offers critical support to help interpret, calibrate, and validate observations from aerial and spaceborne platforms (Brown et al., 2016; White et al., 2009). In addition to long-term ecological research sites, examples of community-science datasets and data-sharing platforms include the Pan European Phenology Project (PEP 275), USA's National Phenology Network, Budburst, SeasonWatch and PlantWatch. The latter dataset showed consistency with independent satellite observations across Canada, highlighting the potential of community-science programs to support phenological monitoring at broad geographic scales (Delbart et al., 2015). Similarly, PhenoCam Dataset and Network promote sharing of in situ phenocam images from different ecosystems, providing opportunities to fill gaps in satellite-derived indicators (Hufkens et al., 2012), quantify local

attenuation factors to correct and select satellite images (O'Connell & Alber, 2016), monitor species-specific or understory phenology (Bater et al., 2011; Xie et al., 2018), or track phenological events that are difficult to detect with other datasets (de Moura et al., 2017; Vrieling et al., 2018). Similar efforts seek to develop long-term continuous phenological databases to improve monitoring of atmospheric and ground conditions for quality control in satellite time series, such as the Phenological Eyes Network (Nagai et al., 2018).

Finally, highly customizable UAVs can also provide cloud-free, fine-grain local-scale information on species-level phenological variations that cannot be captured by coarser satellite images (Anderson & Gaston, 2013; Assmann et al., 2020; D'Odorico et al., 2020; Park et al., 2019). For example, D'Odorico et al. (2020) used a UAV-derived index sensitive to carotenoid content to detect phenological variation in conifers that otherwise appeared stable from the perspective of a broadband sensor. Another UAV-based analysis of forest phenology (Klosterman et al., 2018) revealed the importance of plant diversity in shaping spatial variation of phenology and its sensitivity to pixel size. Although frequency of UAV surveys still depends on cost and logistical constraints, the overall flexibility of their use and ease of visual interpretation provide a great surrogate for field surveys for key phenological stages (Dixon et al., 2021).

Collectively, these improvements also offer a timely promise to help expand the portfolios of phenological indicators towards metrics that could be more universally compared across heterogeneous landscapes. Examples of such metrics can be found in time series analyses that seek to identify magnitudes and frequencies in characteristic cycles and their change over space and time in relation to environmental factors (Bush et al., 2017; Sturtevant et al., 2016). For instance, satellite-based phenological studies have used methods such as Fourier transforms and harmonic and wavelet analyses to characterize phenological cycles in complex time series and account for signal noise (Hermance, 2007; Moody & Johnson, 2001; Sakamoto et al., 2005). Yet, adoption of such approaches has been relatively slow compared to curve-based metrics and undoubtedly deserves further exploration.

## 5 | IMPROVING MECHANISTIC UNDERSTANDING OF PHENOLOGY ACROSS SCALES

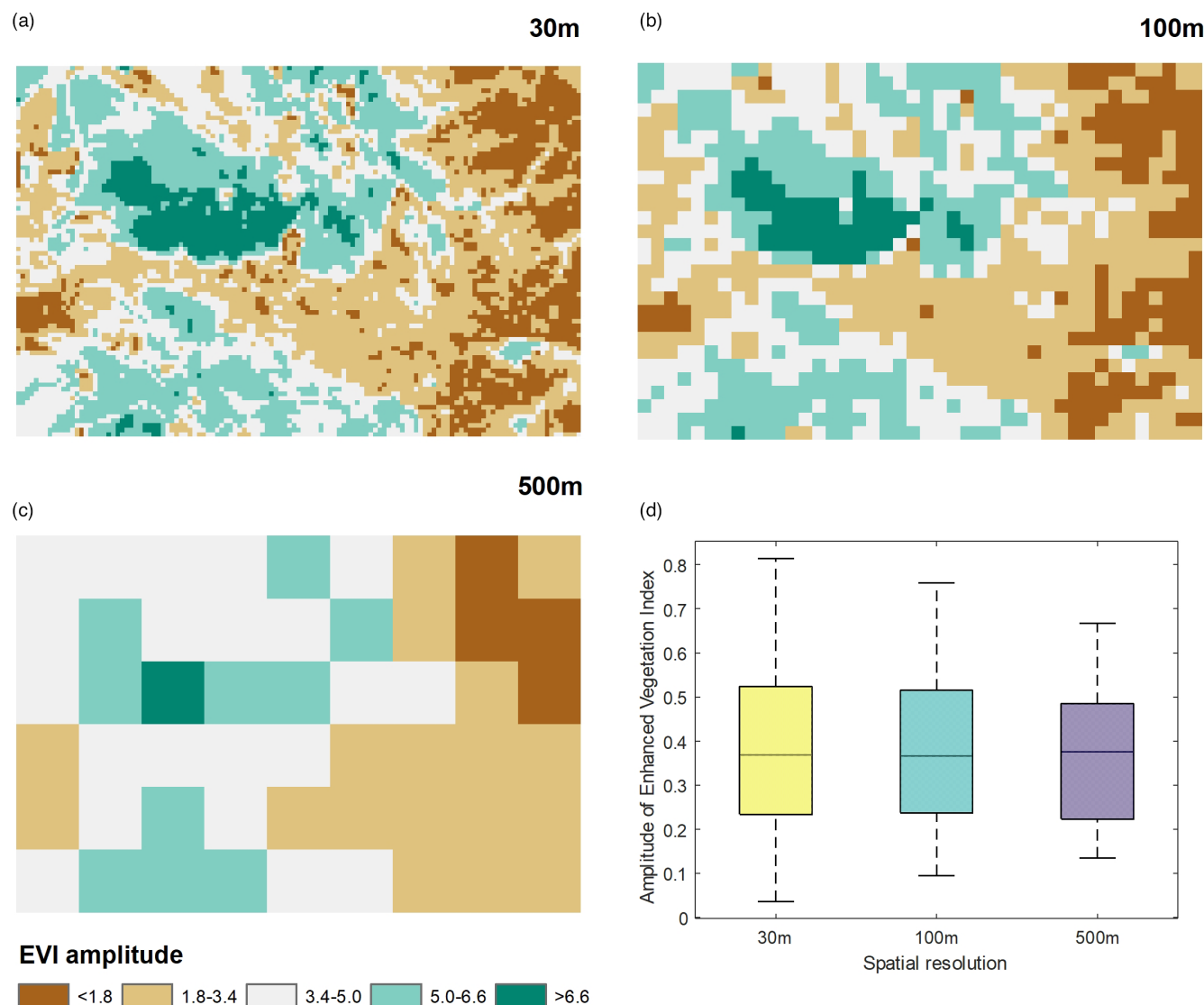
### 5.1 | Spectral vegetation indicators and their interpretation

Seasonal variation in community-level spectra results from various leaf-, plant- and canopy-level sources; however, disentangling their contributions remains difficult even with the most advanced remote sensing tools (Hashimoto et al., 2021; Klosterman et al., 2018; Schweiger et al., 2018). Such contributing drivers include changes in physiological traits and biochemistry of individual leaves over their lifespan (Chavana-Bryant et al., 2017; Niinemets, 2016; Serbin & Townsend, 2020; Ustin & Jacquemoud, 2020; Wilson

et al., 2001), shifts in leaf angle distributions and shadows (de Moura et al., 2017; Huemmrich, 2013; Wu et al., 2016), flowering and fruiting events (Chen et al., 2019; Shen et al., 2014; Verma et al., 2002; Zeng et al., 2020), environmental stressors, pests, and disturbance (Ainsworth et al., 2014; Cotrozzi et al., 2018; Fairbanks & McGwire, 2004), among others. Understanding relative importance of such factors is also challenged by species commonalities in metabolism, biochemistry and responses to stressors (Schrodt et al., 2020).

The choice of a spectral indicator may also strongly influence the outcome and takeaways of phenological interpretation (Helman, 2018). Both individual spectral bands and SVIs vary in sensitivity to drivers of phenological processes, such as maturation of leaves in forest trees (de Moura et al., 2017), seasonal contrasts in biomass of grasslands with varying cover of  $C_4$  species (Davidson & Csislag, 2001), changes in plant diversity (Wang et al., 2016), and reproductive events (Chen et al., 2019; Van Doninck et al., 2020). For example, in bamboo-dominated Amazon forests near-infrared reflectance in Landsat time series showed earlier responses to flowering and mortality than two shortwave infrared bands (Van Doninck et al., 2020). A study of temperate montane forests in China (Viña et al., 2012) found that an SVI most sensitive to seasonal changes in foliar anthocyanins showed the strongest association with floristic composition and unique relationship with elevation compared to other popular SVIs. Some bands and indices are also sensitive to context-specific spectral artefacts (Helman, 2018), such as attenuation of near- and shortwave-infrared signals in flooded setting (Kearney et al., 2009; Taddeo, Dronova, & Harris, 2019), which limits their potential to represent vegetation during certain seasons.

The uncertainty around selecting and comparing SVIs is amplified by their sensitivity to image spatial resolution (Figure 2), which is sometimes referred to as the modifiable areal unit problem (i.e. when data aggregation at broader scale reduces variance and captures the combined spectral signature of different vegetated and non-vegetated surfaces; Jelinski & Wu, 1996). Seasonal trajectories of very small pixels may reflect nuanced spectral variability and noise within similar vegetation types (Dronova et al., 2021; John et al., 2020; Klosterman et al., 2018). However, vegetation signatures of large pixels are often impacted by background reflectance from non-vegetated surfaces (John et al., 2008; Taddeo, Dronova, & Depsky, 2019), obstruction of lower canopy levels by taller plants (Huesca et al., 2015; MacFadyen et al., 2016; Taddeo, Dronova, & Harris, 2019), and similar factors making it difficult to distinguish vegetation seasonality from 'land surface' phenology at such data scales (Helman, 2018). Such effects may further vary with seasonal changes in plant cover, sun angles and abiotic conditions (de Moura et al., 2017; Feilhauer & Schmidtlein, 2011; Kalacska et al., 2007). As a result, local phenological variability may become muted at coarser image spatial resolutions (Figure 2), while distinct data products may differently estimate seasonal transitions for the same region and time frames (Dronova et al., 2021; Klosterman et al., 2018). These issues call for in-depth analyses of phenological scale-sensitivity and product cross-comparisons, which are still uncommon (Mazzochini et al., 2019).



**FIGURE 2** Effects of image spatial aggregation or grain size at (a) 30m, (b) 100m, and (c) 500m on (d) the variation in seasonal amplitude of the enhanced vegetation index (EVI) within the extent of the area of interest (see Jelinski & Wu, 1996, Klosterman et al., 2018, and Assmann et al., 2020 for more discussions on the effect of aggregation on SVIs) this example uses 2018 EVI amplitude for a portion of point Reyes National Seashore in California, USA from NASA's multi-source land imaging (MuSLI) land surface phenology (LSP) yearly North America 30-m version 1 product (MSLSP), (DOI: [10.5067/Community/MuSLI/MSLSP30NA.001](https://doi.org/10.5067/Community/MuSLI/MSLSP30NA.001), Bolton et al., 2020). Aggregation of the product for demonstration purposes was performed using aggregate tool with the mean value aggregation option in ArcGIS desktop software v. 10.8 (ESRI Inc.)

## 5.2 | Towards more holistic phenology assessments

Meaningful interpretations of phenology must consider the biophysical basis of different SVIs and their sensitivities to properties of vegetation and other landscape components (Davidson & Csillag, 2001; Schweiger et al., 2021; Taddeo, Dronova, & Harris, 2019; Wang & Gamon, 2019). Progress in high-frequency narrowband sensors, such as recently (2018–2019) launched moderate-resolution (20–30m) hyperspectral satellites PRISMA (Italy), HISUI (Japan) and DESIS (Germany) will support this capacity via increased spatial detail, temporal frequency and spectral richness, thus providing more sensitivity to vegetation properties. At local scales, similar opportunities

are offered by new hyperspectral imaging sensors compatible with UAVs (e.g. Wang et al., 2021). There are also notable increases in both spatial detail and temporal frequency among broadband instruments, which create possibilities for cross-comparisons of phenometrics across different scales and image products. Complementary use of UAVs and satellite instruments is particularly promising in this regard both to understand scaling of phenology and to help validate and interpret satellite-based analyses at broader scales (Dixon et al., 2021; Klosterman et al., 2018).

It is also important to consider progress in other sensors offering complementary information at high temporal frequencies that might help distinguish phenological contributions of plant functional performance from those of species diversity and inter-specific



interactions. For example, new opportunities to sense solar-induced chlorophyll fluorescence (SIF) provide an enhanced ability to track photosynthetic capacity of vegetation across different temporal scales and link it to the underlying plant and ecosystem drivers (Magney et al., 2019). New thermal remote sensing products from ECOSTRESS satellite mission (Fisher et al., 2020) include indicators of evapotranspiration and vegetation stress which could aid in attribution of seasonal changes to environmental conditions and drought stress.

These advances create new opportunities to assess plant phenology more holistically and expand the inference beyond indicators of greenness and photosynthetic functions. For example, they can help characterize reproductive events as indicators of plant functioning, resource utilization, and mechanisms of competition and co-existence (Wolf et al., 2017; Wolkovich et al., 2014). Most relevant applications to date have been limited to classification-based mapping of flowering events (Duan et al., 2021; Landmann et al., 2015), while direct spectral indicators of blooms (Chen et al., 2019; Mahmud et al., 2020) and fruiting phases are rare. Under-studied aspects of foliar seasonality, such as senescence and late-season coloration, may also hold important clues on plant community diversity and adaptations to environmental changes (Gallinat et al., 2015; Xie et al., 2018; Zhou et al., 2020) and, similarly, require unique approaches for their detection that may be enabled by novel instruments and datasets.

Increased information content of novel time series with greater spatial, temporal and spectral resolution would allow looking at all these phenological phenomena together and more rigorously cross-compare greenness SVIs with indicators of reproductive phenophases, dynamics of specific pigments, and seasonal variation in contributions of species and functional groups. This could ultimately enable new models of multi-scale and multi-temporal analyses capturing different levels of 'ecological resolution' and interactions promoting species co-existence (Cavender-Bares et al., 2016; Huesca et al., 2015; MacFadyen et al., 2016; Parviainen et al., 2009; Schweiger et al., 2021; Taddeo et al., 2021). Holistic approaches to phenology can also help elucidate the synergies among taxonomic, functional and phylogenetic aspects of diversity (Schweiger et al., 2018; Wang & Gamon, 2019; Wolkovich et al., 2014) and connections between seasonal changes in spectra and evolutionary history of plant structure, chemistry and their effects on ecosystem functions (Cavender-Bares et al., 2016; Meireles, O'Meara, & Cavender-Bares, 2020).

### 5.3 | Enhancing causal inference of phenological patterns

It is increasingly recognized that mechanistic understanding of phenological variation cannot be achieved based on remote sensing observations alone (Cavender-Bares et al., 2016; Hashimoto et al., 2021; Taddeo, Dronova, & Depsky, 2019; Wu et al., 2016). For example, using phenocams and ecological surveys, Wu et al. (2016)

demonstrated that seasonality of Amazon tropical forest CO<sub>2</sub> fluxes was more strongly driven by age-dependent variation among leaves and crowns than the earlier emphasized seasonality of climate drivers. In another notable example, higher quality satellite products did not detect the green-up of Amazon forests during droughts identified by earlier dataset versions and initially interpreted as evidence of their resilience to climatic anomalies (Saleska et al., 2007). Instead, the latter pattern was attributed to atmospheric correction issues in the earlier version of the spectral products (Samanta et al., 2010). Such uncertainties underscore urgent needs to better understand the causal drivers of phenology, such as relative importance of genetic adaptations versus plasticity (Wolkovich et al., 2014), or plant diversity versus abiotic factors in shaping community-level seasonality (Rheault et al., 2020; van Rooijen et al., 2015; Viña et al., 2016).

These gaps also indicate that, in order to fully utilize the potential of remote sensing in phenological studies, researchers need to more strategically select and apply ancillary data, ideally guided by hypotheses grounded in field observations. For example, a comprehensive analysis of satellite-based greenness declines in the Mongolian Steppe found a greater impact of overgrazing than climatic trends on these patterns (Hilker, Natsagdorj, et al., 2014). This connection was established by using the official annual estimates of livestock animal populations (Hilker, Natsagdorj, et al., 2014) in addition to remote sensing and climatic information. This and other broad-scale studies (e.g. García-Palacios et al., 2018; Oehri et al., 2017; Rheault et al., 2020) remind us that in real-world landscapes outside of controlled experiments, phenological dynamics observed by remote sensors often respond to multiple factors simultaneously. Uncovering their roles and relative importance requires robust strategies to differentiate among potential causal mechanisms of phenological change and account for artefacts in remote sensing data contributing to spectral variability (Helman, 2018).

Navigating these tasks is increasingly feasible thanks to advances in mathematical and statistical approaches, as well as efficient data processing platforms and computing packages, some of which are especially well suited for phenological questions. For instance, panel multi-variate regression models use multi-date observations of the same locations or spatial units to help understand which candidate predictors are most likely responsible for explaining 'change' while controlling for time-invariant factors (e.g. Gaughan et al., 2013; Muir et al., 2021). Among other methods, structural equation models (SEMs) developed from earlier applications of path analysis (Fan et al., 2016; Wright, 1921) have been increasingly used to test hypotheses about direct and indirect relationships among ecological variables. Such applications include analyses of remote sensing-based indicators of greenness and its phenological variability (e.g. García-Palacios et al., 2018; Oehri et al., 2017). Although SEMs cannot establish causality per se (Fan et al., 2016), they can support and guide phenological interpretations by bridging hypothesis- and data-driven modelling strategies (Fan et al., 2016; García-Palacios et al., 2018).

Finally, increases in data availability and richness create opportunities to apply causality inference methods suited for

complex systems towards phenological questions. Approaches such as Granger causality and related frameworks (e.g. Granger, 1969; Sugihara et al., 2012) work with time series of independent, complementary observations of phenomena. Such approaches may help reveal meaningful relationships among the contributing factors while distinguishing them from spurious linkages. The growing variety of independent time series of environmental datasets and complementary remote sensors including optical (Claverie et al., 2018; Coops et al., 2019; Wulder et al., 2012), thermal (Fisher et al., 2020), and SAR (Frison et al., 2018; Niculescu et al., 2020), are becoming very promising for mechanistic assessments of phenological dynamics. For example, phenocam images are sometimes collected together with micrometeorological data and eddy covariance greenhouse gas fluxes (e.g. in AmeriFlux network sites operating across North, Central and South America), which creates a prime opportunity to examine their causal inter-relationships and feedbacks (e.g. Sturtevant et al., 2016). These opportunities also underscore the critical importance of collaboration between field and remote sensing studies which together can provide new perspectives on landscape-scale responses of ecosystem function to synergistic effects of climate change and biodiversity loss (Wolf et al., 2017).

## 6 | CONCLUSIONS

Remote sensing of phenology offers a significant promise to advance under-explored areas of plant ecology, beyond vegetation-climate relationships alone, by offering large spatial coverage and repeated observations over spatial extents unfeasible to field surveys. Such a capacity can greatly support monitoring of plant diversity by highlighting floristic gradients with variable seasonality, providing new empirical indicators of diversity, and enabling early warning indicators of ecosystem shifts due to species loss, invasions and other biodiversity changes. Evidence of biodiversity linkages with ecosystem-level phenological patterns, such as length of the growing seasons and inter-annual stability of phenological variation, makes remote sensing of phenology relevant to studies of resilience and recovery in response to disturbance and stressors. Increases in archive length, temporal frequency, spatial detail and spectral variety of products from both passive and active remote sensors provide a new phenological lens on under-studied aspects of vegetation structure and relationships with ecosystem function, which remain less well understood beyond the scales of experimental plots and long-term monitoring sites. However, taking full advantage of this potential requires more guidance on phenological estimation strategies and mechanistic interpretation of remote sensing-detected patterns. Historically non-uniform availability, frequency and spatial resolution of remote sensing datasets have been a major source of uncertainty in choosing the appropriate phenological metrics and methods of their extraction, such as seasonal curve functions. Recent advances in higher-frequency products, multi-source data fusion, and in situ observation networks can help fill gaps in sparse time series, improve the accuracy and agreement

among phenological estimation, and more explicitly measure the effects of spatial resolution on phenological metrics and their trends. Progress in hyperspectral sensing from both satellite and unoccupied platforms may help better distinguish among local drivers of phenological processes, from leaf-level processes to community-level dynamics, and include previously under-studied reproductive and senescence-related phenological events. However, it remains critical to recognize that remote sensing alone is not sufficient for mechanistic understanding of phenological patterns due to risks of misattribution, confounding artefacts in data products and still little understood scale-sensitivity of estimated metrics. Moving forward from documenting patterns to informed interpretations and predictions of phenology requires rigorous collaborations between field and remote sensing-based ecological studies, well-informed choices of ancillary data and stronger engagement of statistical and mathematical approaches for causal inference.

## ACKNOWLEDGEMENTS

This research is partially supported by the National Aeronautics and Space Administration Grant No. 80NSSC18K0755 issued to Dr. Iryna Dronova through the New (Early Career) Investigator Program (NNH17ZDA001N-NIP, proposal No.17-NIP17-0069). We also thank the editors and three anonymous reviewers for their time and valuable comments and suggestions. The icons used in Figure 1 were created by DinosoftLabs, Smashicons, Pixel Perfect, and Vectors Market, and imported from [www.flaticon.com](http://www.flaticon.com).

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

I.D. and S.T. conceived the ideas, designed the structure of this review and synthesized the literature; I.D. led the writing of the manuscript and prepared Box 1 and Figure 2; S.T. substantially contributed to writing, editing and revisions, and prepared Figure 1. All authors contributed critically to the drafts and gave final approval for publication.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13897>.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable for this article as no datasets were generated or analysed during the current study.

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**How to cite this article:** Dronova, I. & Taddeo, S. (2022).

Remote sensing of phenology: Towards the comprehensive indicators of plant community dynamics from species to regional scales. *Journal of Ecology*, 110, 1460–1484. <https://doi.org/10.1111/1365-2745.13897>