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REVIEW

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Macrophenology: insights into the broad-scale patterns, drivers, and consequences of phenology

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Abstract

Plant phenology research has surged in recent decades, in part due to interest in phenological sensitivity to climate change and the vital role phenology plays in ecology. Many local-scale studies have generated important findings regarding the physiology, responses, and risks associated with shifts in plant phenology. By comparison, our understanding of regional- and global-scale phenology has been largely limited to remote sensing of green-up without the ability to differentiate among plant species. However, a new generation of analytical tools and data sources—including enhanced remote sensing products, digitized herbarium specimen data, and public participation in science—now permits investigating patterns and drivers of phenology across extensive taxonomic, temporal, and spatial scales, in an emerging field that we call macrophenology. Recent studies have highlighted how phenology affects dynamics at broad scales, including species interactions and ranges, carbon fluxes, and climate. At the cusp of this developing field of study, we review the theoretical and practical advances in four primary areas of plant macrophenology: (1) global patterns and shifts in plant phenology, (2) within-species changes in phenology as they mediate species' range limits and invasions at the regional scale, (3) broad-scale variation in phenology among species leading to ecological mismatches, and (4) interactions between phenology and global ecosystem processes. To stimulate future research, we describe opportunities for macrophenology to address grand challenges in each of these research areas, as well as recently available data sources that enhance and enable macrophenology research.

KEYWORDS

biogeography, ecological mismatch, ecosystem processes, herbarium specimens, macroecology, plant phenology, range limits, remote sensing

Climate change is shifting phenology, the timing of seasonal biological events, around the world (Walther et al., 2002; Walther, 2010; Piao et al., 2019). At local scales, changes in plant phenology can alter biotic interactions, including herbivory, pollination, seed dispersal, and competition (Elzinga et al., 2007; Wolkovich and Cleland, 2011). At regional and global scales, phenology influences species ranges, invasiveness, climate, water and carbon cycling, and other phenomena (Chuine, 2010; Pau et al., 2011; Piao et al., 2019). Understanding these dynamics at different scales enhances our ability to forecast ecological responses to climate change that will have impacts on conservation, human well-being, and climate change mitigation. However, our ability to detect and investigate the role of phenology at broad scales has been limited by the availability of global phenological tools and data, and especially species-specific data, across regions and environmental gradients (Tang et al., 2016). Recent development of such tools has opened up exciting new opportunities to investigate regional- to global-scale plant phenology and the role of plant phenology in ecological processes, resulting in a new and growing subdiscipline we refer to as macrophenology (see Doi et al., 2017). More broadly, macroecology formally emerged decades ago (Brown and Mauer, 1989; Brown, 1995) as an area of study that distinctly takes large-scale and emergent perspectives to explain general ecological patterns (McGill, 2019). With the benefit of new perspectives and data sources, we suggest now is the time to similarly formalize and embrace macrophenology as a distinctly expansive study of phenology.

Field observations of phenology within and across taxa have traditionally covered relatively fine spatial units and a limited number of species due to research scope and limitations on time, funding, staffing, and broad-scale coordination and standardization efforts (McDonough MacKenzie et al., 2020). Local-scale research has generated important findings about the physiology, responses, and risks associated with plant and animal phenology. However, these local-scale studies have proven challenging to synthesize across methodologies and study systems (e.g., Gill et al., 2015). Researchers have been limited in the ability to move from seemingly idiosyncratic site- or species-level conclusions to broad-scale patterns (Doi et al., 2017). Instead, our knowledge of broad-scale phenology has relied on regional or global patterns of green-up and green-down detected by satellite-based remote sensing. However, the coarse spatial resolution (capturing canopy- and ecosystem-level phenology) of remote sensing data makes it difficult to disentangle species-specific mechanisms and consequences of phenological changes (Tang et al., 2016). This challenge of linking phenological metrics within and across scales has resulted in a conspicuous gap in our holistic, broader-scale understanding of phenology, including how phenological patterns and drivers vary across species, biomes, and regions, and how interactions between phenology and other ecological dynamics (e.g., competition, range limits, and ecosystem processes) vary across broad scales. It has also limited our ability to scale up local findings from particular ecosystems to regions for application in conservation and natural resource management.

A new generation of tools are emerging that support research into the patterns, predictors, and consequences of phenology at regional to global scales (Table 1). Community science (sometimes called citizen science, crowd science, volunteer monitoring, public participation in science) networks, high-resolution remote sensing tools, and digitization of herbarium specimens are expanding the density and breadth of species-level observations. Ecological observatory networks such as the U.S.-based National Ecological Observatory Network (NEON; Schimel et al., 2007) and national and regional Biodiversity Observation Networks (BONs; Scholes et al., 2008) are connecting phenology observations with species inventories, ecosystem flux data, and trait measurements, to place phenology in the context and at the cutting edge of regional community and ecosystem dynamics.

These tools have enabled a new wave of groundbreaking research in macrophenology, which we define as the study of broad-scale patterns and emergent properties of phenology across regions, environmental gradients, taxa, and evolutionary history. Just as the study of macroecology far predates the use of the term or formalization of the discipline, the conceptual basis of macrophenology is also not new. The term macrophenology itself was introduced as early as 2017 and was applied to specific biological problems, such as phenological mismatches, genetic variation, and clines in body sizes (Doi et al., 2017). Building upon the past decade of active phenological research, we expand and formalize macrophenology to emphasize phenological patterns and responses to a variety of drivers across biomes, land-use types, and species' ranges and historical biogeographies. While macrophenological approaches can and are being applied across taxonomic groups, we focus on plant phenology and exciting opportunities for macroscale studies within and across plant species.

In this paper, we review theoretical and applied advances, emerging tools, and opportunities in four key areas of macrophenology: (1) global drivers of phenology, (2) species range limits (3) interactions and mismatches among species, and (4) ecosystem processes (Figure 1). These areas describe major elements of macrophenology (and macroecology more broadly) and are interlinked; for example, global drivers of phenology can constrain species range limits, and ecosystem processes (climate, carbon, and water systems) are in constant feedback loops with global drivers of phenology (arrows in Figure 1). We also discuss three cross-cutting topics that should be considered throughout: first, historical biogeography and phylogenetic patterns; second, macrophenology of other taxonomic groups; and third, geographic gaps in phenology research. While we focus here on plant phenology, we recognize that macrophenology is a taxonomically diverse field, and we address some areas of further work beyond plants.

GLOBAL DRIVERS OF PHENOLOGY

The timing of plant phenological events like leaf-out, flowering, fruiting, fall bud set, and leaf senescence varies across regions and ecosystems (e.g., temperate vs. tropical regions, desert vs. forest ecosystems; Jolly et al., 2005; Gill et al., 2015; Garonna et al., 2018; Figure 2). These differences reflect the underlying drivers of global phenology: species identities, the relative importance of different environmental cues among species and populations, and variation in environmental cues over space and time. Describing patterns in plant phenology across biomes, environmental gradients, lineages, and functional groups is critical for predicting phenology in understudied regions and to forecasting phenology under future and no-analogue climate scenarios. It is often unclear whether patterns of phenology observed by coarse satellite-based remote sensing reflect variation in species composition, climate, or both (Helman, 2018). For example, earlier phenological events at the ecosystem level might be caused by a response to a warming climate or the arrival an early-leafing invasive plant (Polgar and Primack, 2011). Furthermore, widespread land-use changes, such as urbanization and forest succession, can impact species composition *and* climate conditions (McKinney, 2002; Bonan, 2008; Grimm et al., 2008), but the extent to which land-use interacts with climate change and produces predictable shifts in phenology across regions and biomes is poorly understood. Macrophenology can address these gaps by examining the patterns,

TABLE 1 Data sources for research in macrophenology, their scale of coverage, strengths, challenges, and examples of where to find them. Many of these sources were either created or grown significantly within the past decade

Data type	Strengths	Limitations	Examples
Traditional observation network	Long-term temporal coverage; species-specific observations; multiple phenophases (vegetative and reproductive) represented; phenological data collected using standardized protocols	Taxonomically limited; limited to regional spatial extent	Pan European Phenology network, PEP-725 (pep725.eu)
Community and citizen science	Spatially and taxonomically widespread; species-specific observations; multiple phenophases represented; large sample size; phenological often collected using standardized protocols	Short-term temporal coverage (>10 years); spatial biases; incidence of repeated observations over many years is low	USA National Phenology Network (www.usanpn.org) Plant Watch (Canada) (https://www.naturewatch.ca/plantwatch/) iNaturalist (www.inaturalist.org)
Ecological observatory network (ground observations)	Broad spatial coverage; species-specific observations; multiple phenophases represented; ecological variables collected (e.g., carbon flux, species inventories) and samples archived (e.g., leaf tissue, soils)	Short-term temporal coverage (<10 years); spatial density is low to maximize ecological domains represented	NEON (www.neonscience.org)
Museum specimens	Long-term temporal coverage (often hundreds of years); spatially and taxonomically widespread; multiple phenophases represented; identity of samples verifiable	Collection biases and inconsistencies; lack of "absence" data; phenological information must be extracted	iDigBio (www.idigbio.org) Global Biodiversity Information Facility (www.gbif.org) NEON Biorepository (https://biorepo.neonscience.org/portal/)
Satellite measurements	Medium-term (decades) temporal coverage; global coverage	Typically does not capture species-specific phenology, or reproductive phenology; large spatial gaps in coverage (e.g., in tropical and desert systems)	MODIS (https://modis.gsfc.nasa.gov/) LANDSAT
PhenoCams	Provides detailed local coverage; globally distributed; often paired with ecological observatory networks	Short-term temporal coverage (>10 years); North American bias	phenocam.us

drivers, and predictability of phenology in different regions around the world; how particular clades, species, and functional traits contribute to regional and global patterns; and the physiological limitations on future shifts in plant phenology with climate change.

Local-scale studies have identified three primary environmental cues that, broadly defined, trigger plant phenological events: temperature (e.g., as seasonal averages or accumulations), photoperiod, and available moisture (e.g., as precipitation, soil moisture, humidity) (Schwartz, 2003; Körner and Basler 2010; Polgar and Primack, 2011). Other local factors, including species interactions such as herbivory and pollination, can also influence plant phenology (Schwartz, 2003; Elzinga et al., 2007). Recent global satellite-based studies have shown how the relative importance of these cues varies around the world by latitude, biome, and plant functional group (Jolly et al., 2005; Dahlin et al., 2017; Garonna et al., 2018). For example, mid- and high-latitude systems in the northern hemisphere (e.g., temperate and boreal forests) leaf-out and senesce primarily in response to photoperiod and temperature (including chilling and spring forcing), while low-latitude systems with strongly seasonal or limited water availability (e.g., tropical forests, deserts, grasslands) respond more strongly to photoperiod and moisture (Figure 2).

Generalizing these findings across regions, however, is fraught with difficulty, highlighting the importance of biogeographic and evolutionary constraints. For instance, Buitenwerf et al. (2015) found that from 1981 to 2012 phenological change across savannahs around the world were markedly different from one another, despite similarities in vegetation and climate. Furthermore, recent

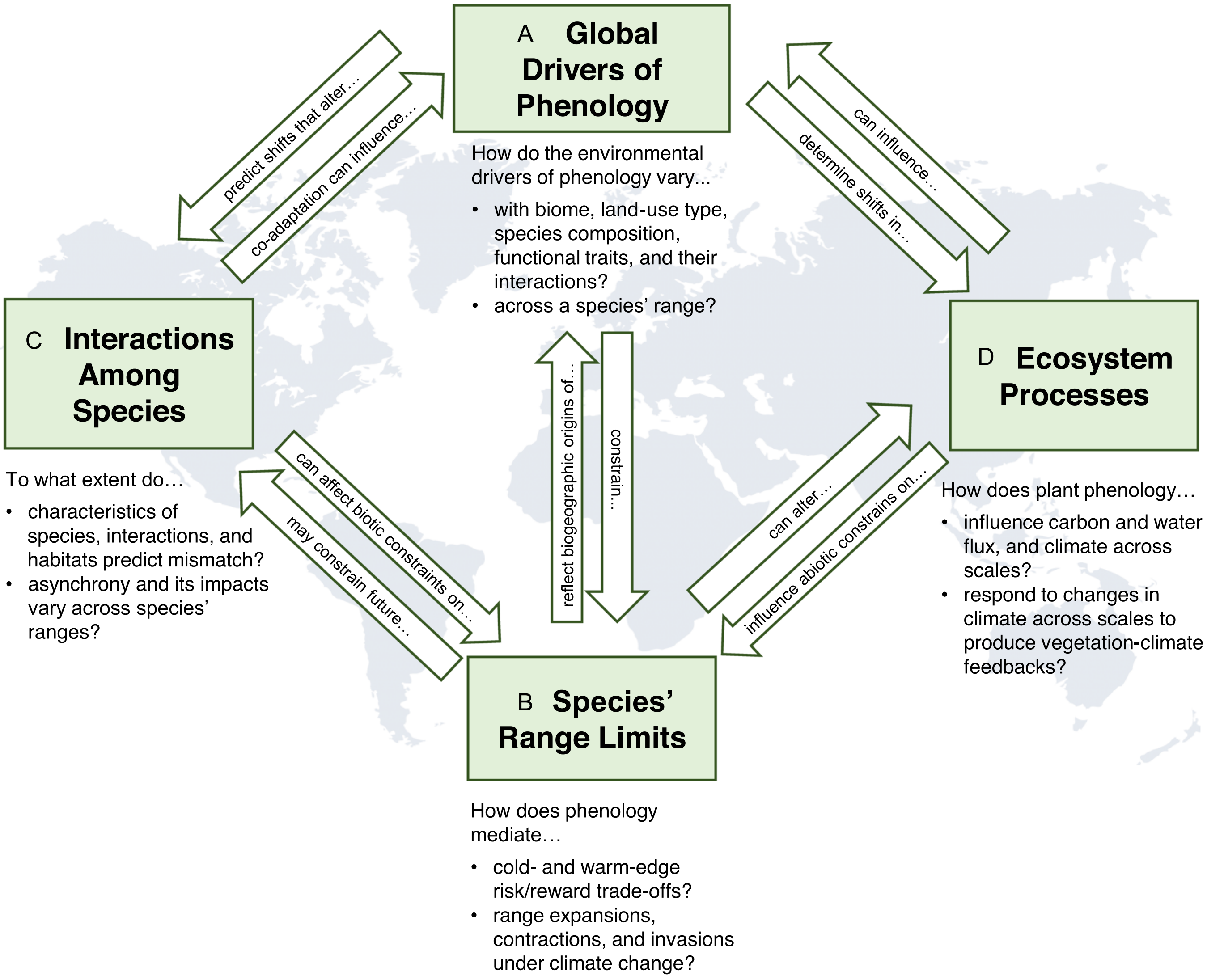

FIGURE 1 Core concepts of macrophenology, their interactions with one another, and open questions for future research. The (A) global drivers of phenology affect, and are affected by, (B) species' range limits, (C) interactions among species, (D) and ecosystem processes (including carbon, water, and climate systems). Each of these subject areas are also informed and enhanced by the exploration of species' evolutionary history and can draw from and offer insights into the macrophenology of other (non-plant) taxa. New data sources, technological advances, analytical techniques, and mechanistic models provide critical tools for future research to study these subject areas, their intersections, and the related roles of historical biogeography and phylogenetic patterns, macrophenology of other (non-plant) taxonomic groups, and geographic gaps in phenology research

research suggests that the relative influence of different drivers may be shifting under climate change. A study using observations from the regional Pan European Phenology network (PEP-725) found that as trees respond to continued warming with advancing leaf-out times, photoperiod controls can drive further variation in leaf-out date (Fu et al., 2015). Similarly, Zohner et al. (2017) found that woody species in biogeographic regions with more predictable spring temperature dynamics have lower chilling requirements. Macrophenological research is needed to further explain phenological differences among regional floras. The extent to which such shifts in phenological cues may be occurring in other regions and plant functional groups is important to the accuracy of even short-term projections of future growing season lengths. Land-use changes like urbanization and agriculture may be contributing to this complexity—they are known to influence phenology at local and regional scales, but little is known about the predictability of their impacts across regions. Li et al. (2019) found that the effects of urbanization on phenology depend on the underlying climate of the city—in cold regions, urbanization has advanced phenology, while in warmer regions it has had minimal impact—suggesting this is an important area for future study.

Macrophenology is poised to address many remaining gaps in our knowledge of the broad-scale patterns and drivers of plant phenology. Machine-made observations will continue to be important for global comparisons of drivers of leaf phenology, particularly for investigations at the grid-cell, or assemblage, level (i.e., typically hundreds of square

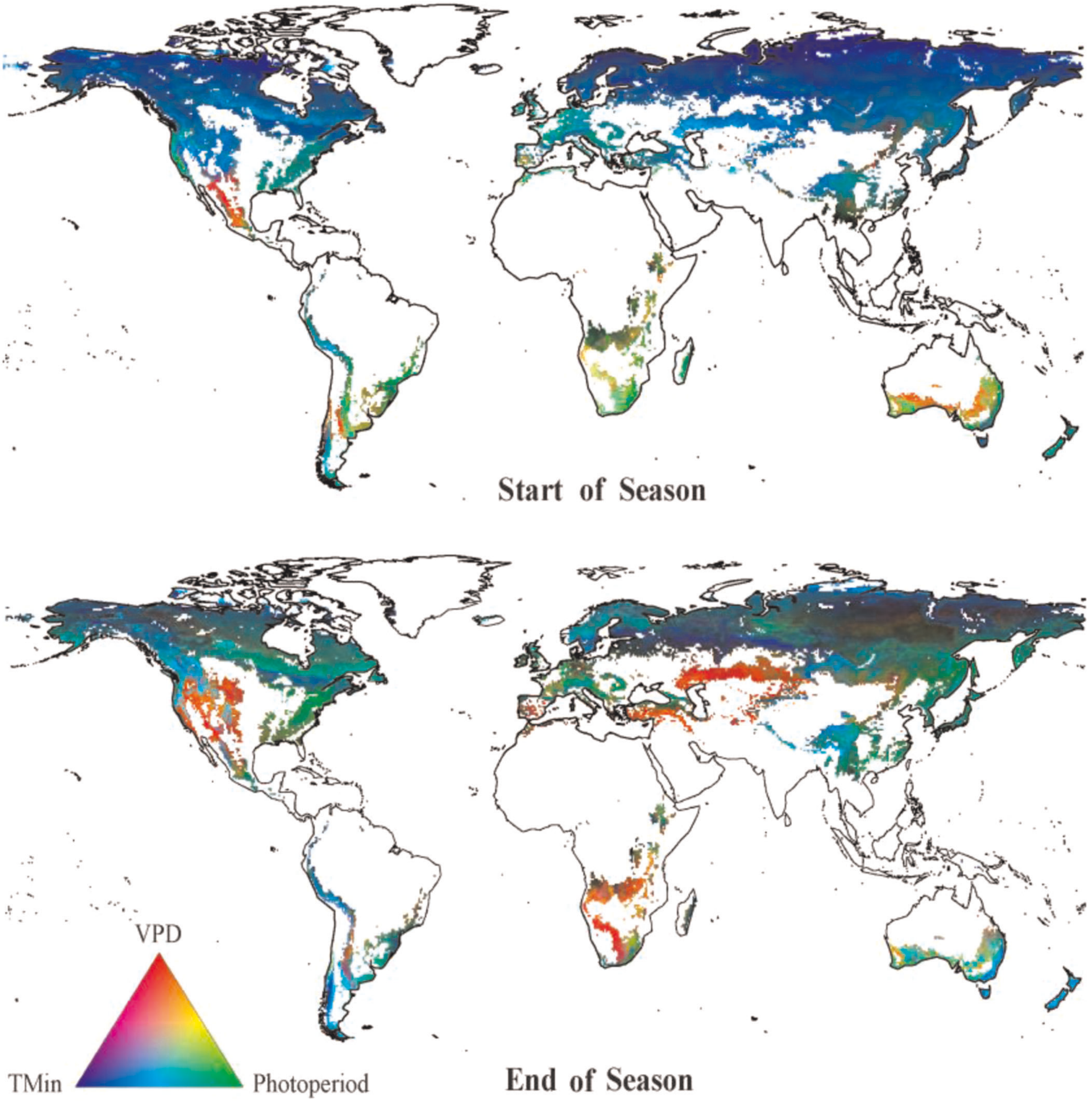

FIGURE 2 The relative influence of minimum temperature (TMin), photoperiod, and water vapor pressure deficit (VPD) on satellite-derived onset and end of growing season (averaged 1982–2011). Originally published in Garonna et al. (2018). High-latitude northern hemisphere systems are most strongly driven by temperature in spring and the combination of temperature and photoperiod affect bud set and leaf senescence in autumn, while mid-latitude and southern hemisphere regions show stronger photoperiod and vapor pressure deficit controls in both spring and autumn. White space on these maps represents environmental zones for which remotely sensed and modeled leaf area index were difficult to reconcile, including tropical and arctic regions. Geographically, taxonomically, and temporally diverse records from herbaria and public phenology records from iNaturalist represent two potential data sources that can be used to fill remaining gaps in our global understanding of phenological drivers, and to connect these broad trends to plant species and functional traits

meters or larger). Such observations typically come from satellites, aerial imagery (Klosterman and Richardson, 2017; Atkins et al., 2020), or fixed cameras such as PhenoCams (Richardson et al., 2018). Just as in traditional macroecology, the spatial scales (in particular, the resolution) of these different observations will affect phenological observations. Researchers can use this variation in resolution as a conceptual tool in macrophenology studies (see, for example, Swenson et al., 2006). For example, researchers can use global-to-regional comparisons to investigate key phenological drivers and sensitivities that differentiate ecoregions and influence species' ranges. Such investigations may include studies on phenological niche diversity (or similarity) or filling of phenological potential (i.e., taking full advantage of the available growing season), which is tightly linked to differences in phenological drivers and sensitivities across species. As an example of what this type of work can yield, researchers used a network of tree observations on a tropical island in China to show that the complementarity (i.e., diversity of timing) of leaf phenology reflected a diversity of other functional traits and was associated with increased aboveground biomass compared to ecosystems with greater overlap in leaf phenology (Ali et al., 2019). Expanding such studies to the macroscale can elucidate how phenological overlap among co-occurring species varies with global environmental drivers and how it impacts other dynamics such as species range limits, interactions, and ecosystem processes.

Understanding global drivers and patterns in phenology will also require deeper investigation into species-specific mechanisms of phenological change. Brown (1999) identified a similar need for mechanistic understanding for the broader field of macroecology. Satellite-based phenology data, however, are typically limited to broad patterns of plant vegetative phenology and rarely allow for differentiation among species (though methods for delineating individuals are improving; e.g., Hastings et al., 2020). To explore the mechanisms underlying regional and global patterns of vegetative *and* reproductive phenology, findings from remote sensing should be supported by species-specific observations. Herbarium specimens, collected around the world and increasingly accessible online, can add information about the timing of many plant phenological events, including leaf-out, flowering, fruiting, and leaf senescence, across time and phylogeny (Willis et al., 2017a; Meineke et al., 2019). Information from this geographical perspective, combined with physiological and growth chamber studies, can be used to develop mechanistic models to better understand the processes underlying these patterns (Chuine, 2000; Gauzere et al., 2017; Asse et al., 2020). For instance, Ettinger et al. (2020) used a global meta-analysis to parse the relative influence of three mechanistic cues—chilling, warming, and photoperiod—on leaf phenology. By comparing experimental results from around the world, they were able to model the relative importance of these drivers and create mechanistic phenology forecasts for different environmental conditions. Such mechanistic models will continue to be important for estimating phenology within and among species at regional and global scales, allowing researchers to test specific hypotheses about species' phenology in new locations and even no-analog environmental conditions.

Programs engaging the public in phenology research (e.g., contributing observations to iNaturalist and phenology networks in many countries, or adding phenology data to herbarium records) provide occurrence records spanning across habitat types (e.g., from urban to rural habitats) that can be used to further parse the impacts of species composition, functional traits, climate change, and land-use on phenology. For instance, Li et al. (2021) used over 270,000 flowering records from iNaturalist to analyze the roles of climate and urbanization (as mediated by plant traits) on flowering duration. Protocols for efficiently and accurately extracting phenological data from field and herbarium specimen images have been developed to facilitate such studies (Yost et al., 2018; Barve et al., 2020). Observation networks (e.g., PEP-725, NEON, and BONs; Table 1) offer opportunities to investigate functional traits and environmental features that help to explain regional differences in phenology, and to identify in which species and locations the relative influence of different phenological cues may be changing. In situ observations can be used to validate and add context to satellite observations. At the same time, new conceptual, methodological, and statistical frameworks such as the plant phenology ontology (Stucky et al., 2018), standardized observation, and collection protocols (e.g., Denny et al., 2014; Elmendorf et al., 2016; Yost et al., 2018), and data fusion models can help to enable the synthesis of data sources across scales.

SPECIES RANGE LIMITS

Many plant species naturally occupy large geographic ranges, some extending across entire continents. Such broad ranges often cover diverse environmental gradients, reflecting individual flexibility and intraspecific differences in phenology. For instance, Ellwood et al. (2019) used herbarium specimens to show that red maples (*Acer rubrum*) flower and leaf-out earlier at warmer locations and lower elevations across the species' range (Figure 3). Also, flowering occurs weeks in advance of leaf-out at warm locations, but flowering and leafing occur almost simultaneously at cold locations. Understanding these intraspecific differences is critical to predicting phenology in novel sites, as well as future responses to climate change. In addition, the variety of environments within a species' range represents different risks to plant fitness including risk of frost, drought stress, herbivore pressure, pollination success, seed dispersal, and competition. The extent to which phenology mediates the exposure to such pressures suggests it is an important factor in limiting species ranges (Chuine, 2010; Savage and Cavender-Bares, 2013). At broad scales, the mediating role of phenology is important for understanding the factors that define range limits, the processes underlying patterns of plant biodiversity and invasions, and for predicting future range shifts under climate change.

The mechanisms underlying species range limits remain poorly understood (Sexton et al., 2009), but recent macrophenology research reveals a role for phenology. Phenology can mediate species' range limits through direct climate effects at the cold and warm edges of ranges. Early leaf-out extends the growing season for plants, which can confer a competitive advantage through biomass accumulation and

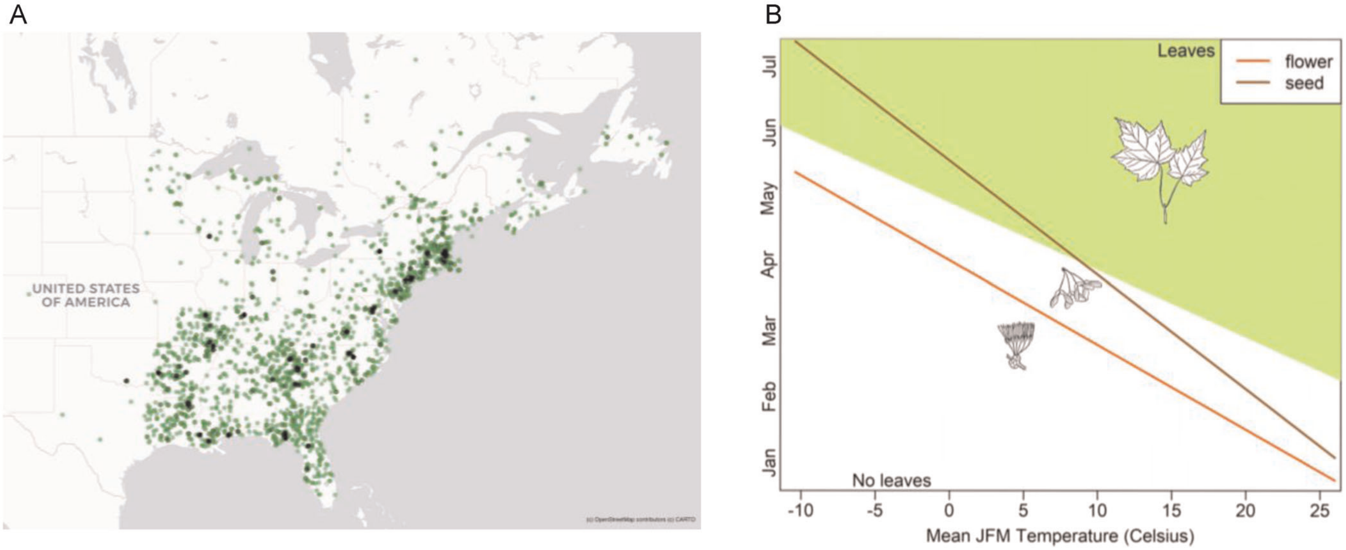

FIGURE 3 Comparisons of the effect of temperature on spring phenology—including flowering, seed set, and leaf-out—estimated from herbarium specimens of red maple (*Acer rubrum*). Adapted from Ellwood et al. (2019). (A) Red maple specimens ($N = 2945$) were used to estimate phenology and were collected across eastern North America between the years 1832 and 2016. Darker green areas represent those with greater sampling intensity. (B) Linear models represent the effect of temperature (average of January, February, and March [JFM]) on the date of collection for specimens with flowers and seeds, while the green shading shows the timing of leafing out relative to temperature. All events occur earlier at warmer sites. The cooler the site, the closer together leaf-out and flowering are likely to occur, and the more likely it is that seed set will occur *after* leaf-out (whereas flowering and seed set both occur before leaf-out at warmer sites). The inset illustrations depict red maple leaves, flowers, and fruits and were adapted from Britton and Brown (1913)

earlier access to resources. However, early leaf-out also increases risk of damage from frost or drought (Wolkovich and Cleland, 2011), and tends to be associated with other physiological features (e.g., small-diameter xylem vessels and diffuse-porous stem anatomy) that make plants less vulnerable to damage (e.g., cavitation) during winter (Lechowicz 1984; Panchen et al., 2014). Recent research leveraged herbarium specimens to show that this trade-off between limiting frost risk and maximizing the growing season constrains the northern (cold-edge) range limits of three temperate, northern hemisphere deciduous species (Zohner et al., 2020). Phenology can also mediate warm-edge limits if the range of plant species extends into climates at which they no longer meet physiological requirements. For instance, plants experiencing warm winters may not meet environmental chilling requirements for leaf-out, leading to delays or disruptions in leaf-out times (Campoy et al., 2019). Similarly, at the warm edge of the range, drought stress and high temperatures might cause premature cessation of growth and leaf senescence toward the end of the growing season. For evergreen species, high temperatures and drought stress might shorten leaf longevity.

The effects of climate on phenology can also indirectly affect species ranges through biotic associations. Herbivory, which is frequently implicated as a range limit for plants, is highly dependent on leaf phenology. Meineke et al. (2021) analyzed over a century of herbarium specimens to show that herbivory is higher in plant species with greater temperature sensitivity in warmer years. Plants with the ability to take advantage of a long growing season may therefore be exposed to increased herbivory. Further, many pest species are extending their range to higher latitudes as the climate warms (Parmesan, 2006), providing further potential for high levels of herbivory-based pressure on species ranges in spring.

Competition on the basis of phenology may also vary by latitude and contribute to range limits. These contributions could include increasing phenological overlap during shorter seasons at cold-edge limits or increasing competition with higher biodiversity at warm-edge limits. The potential for phenological overlap among species across latitudinal gradients requires more investigation because such overlap and the resulting availability of early- and late-season resources has been identified as a potential mechanism of range expansion (Wolkovich and Cleland, 2014). Research on invasive plants in temperate North America suggests phenology is an important mediator of how these species expand their ranges (Wolkovich and Cleland, 2011); invasive plants tend to have greater phenological flexibility (e.g., lower chilling requirements, greater sensitivity to warming) and longer growing periods due to the climates in which they evolved, which provides a competitive edge (Zohner and Renner, 2017). The influence of phenology on invasion success into non-deciduous and non-temperate systems remain far less studied.

The dynamics of invasive species and shifting species ranges brings to light another gap in our current understanding of macrophenology: How do species' phenological sensitivities vary across geographic and environmental gradients? The phenology of some widely distributed species has been shown to vary dramatically across locations (Ellwood et al., 2019; Park et al., 2019). Furthermore, a growing number of studies indicate that different populations within species can exhibit different, or even contrasting, phenological sensitivities, suggesting the existence of phenological ecotypic variation. For example, these may be responses to local microsite differences, such as wetter versus drier sites or warmer versus colder sites. Prior studies have shown mixed results, including stronger responses to warming at lower-latitude sites (Park et al., 2019), higher-latitude sites (Morin et al., 2009), and similar responses across latitudes (Phillimore et al., 2013). In many cases, it is unclear if intraspecific differences in phenological sensitives are evolved or plastic responses to other factors. Aggregated range-level patterns may be obscured or misleading if regional scale drivers causing those patterns are overlooked. How much of this variation is driven by genetic differences and local adaptation versus phenotypic plasticity? The genetic basis of geographic differences in phenology is only known in detail for a few model systems, such as *Arabidopsis thaliana* (Wilczek et al., 2010) and economically important tree species (Jensen and Hansen, 2008; Allard et al., 2016; Bükücü et al., 2020). The cause of geographic variation in phenology, though, has important implications for anticipating shifts in species ranges (including the spread of invasive species). Understanding phenological responses to microclimate might also inform climate change-motivated conservation actions, such as managed relocation of species within and outside of their ranges.

As tools and data expand to examine species' phenology across their ranges, there are new opportunities to investigate intraspecific variation in plant phenology and how phenology mediates species ranges. Future macrophenology research should leverage herbarium specimens and community science to examine differences in phenology, the drivers of phenology, and shifts in phenology across species ranges. For instance, Nature's Notebook, a project of the USA National Phenology Network (USA NPN), has amassed over 20 million phenology observations (most of which are of plants) collected by scientists and the public across the United States (Crimmins, 2021). Such broad-scale, species-specific data can be used to ask: Are chilling requirements and other cues the same in the northern and southern portion of species' ranges? How does phenology influence range limits for species other than model species, such as *A. thaliana* and relatively well-studied northern hemisphere temperate tree species? Can phenology help us anticipate which groups of plants (e.g., invasive species) are most likely to shift their ranges as climate conditions change? And how can we use this information to facilitate conservation practice with climate change, using such methods as managed relocation and maintaining ex situ living plants and seed collections (Primack et al., 2021)?

INTERACTIONS AND MISMATCHES AMONG SPECIES

Different sensitivities to environmental change can result in the phenologies of species shifting in different directions or magnitudes, disrupting species interactions. The resulting asynchronies, known as phenological mismatches (Renner and Zohner, 2018) can have consequences for the fitness of the organisms and populations involved. Examples of mismatches in the literature typically occur between trophic levels, but for plants they can also include interactions with pollinators, seed dispersers, and heterospecific neighboring plants (e.g., asynchrony between spring wildflowers and trees which can shade them). The potential for mismatch has been a primary motivation for much recent phenology research, but there is still a great deal that is unknown about how common mismatches are, which traits, species, or ecosystems are associated with the greatest risk of mismatch, and how the severity and impacts of mismatch vary across species' ranges. While there is some (mostly site-specific) evidence supporting the presence and impacts of mismatches (Kharouba et al., 2018), most support for mismatches is difficult to generalize even to nearby sites and communities, let alone regions (Renner and Zohner, 2018). Macrophenology research should aim to place mismatches in context, by estimating the transferability of mismatch results between sites, by quantifying and comparing fitness costs (or benefits) across species' ranges, and by identifying vulnerable populations to motivate conservation action.

Among the earliest and most oft-cited examples of phenological mismatch is that of pied flycatchers (*Ficedula hypoleuca*) and their primary spring food source of caterpillars (Both et al., 2006). As the insects advance their peak abundance with warming local temperatures, researchers found that many flycatchers did not advance their migratory arrival enough to match the caterpillar peak. These birds were unable to adequately feed their nestlings, leading to declines of around 90% in mismatched bird populations. However, even in this highly publicized example, asynchrony did not occur at all locations included in the study. In habitats with later insect peaks, flycatchers had mild, if any, population declines (Both et al., 2006). As the pursuit to rigorously investigate phenological mismatch has progressed, most studies have neglected spatial variation, leading to difficulty understanding or applying findings beyond immediate local surroundings; indeed, there is a major gap in understanding how mismatches occur across species ranges (Samplonius et al., 2021).

Insights from reviews and meta-analyses offer some generalizations for vulnerabilities to mismatch and associated potential fitness costs. In temperate regions, species with phenologies that track changes in climate seem to be more successful than those that do not track changes in climate (Willis et al., 2008; Cleland et al., 2012). Mutualists may be less likely to experience mismatch (due to co-adapted environmental responses) compared to predator–prey relationships (Renner and Zohner, 2018), and specialists may face harsher consequences from individual asynchronies than generalists. Others have found few patterns among mismatches that can be used to predict which species and interactions are most vulnerable (Kharouba et al., 2018). Recent work suggests this lack of pattern may be due to the challenge of obtaining the rigorous data needed for critically testing for mismatch (Kharouba and Wolkovich, 2020; Samplonius et al., 2021).

Evidence also suggests that the phenology of co-occurring plant species (even large groups of co-occurring species) relative to one another may affect plant fitness and species composition. Plants that can take advantage of a particularly early spring or late autumn window to extend their growing season receive a competitive advantage through increased resources and carbon allocation to growth, which can in turn result in changes to species composition. Extended phenology appears to be a major factor driving the success of many invasive shrubs in eastern North America (Fridley, 2012; Polgar et al., 2014; Wolkovich and Cleland, 2014). In another North American example, Heberling et al. (2019) found that trees are shifting their leaf phenology more rapidly than herbaceous species, resulting in significant losses to wildflower carbon budgets due to shading. Mismatches in forest structure like these could lead to major changes in plant communities across large regions. Therefore, understanding the capacity for plants' relative phenological positions to shift across environments is an important goal for macrophenology. Recent research on hundreds of woody plant species at botanical gardens in North America, Asia, and Europe found that the order of leaf-out across plant species is highly consistent across years and locations, while the order of fruiting is moderately consistent, and that of leaf senescence is inconsistent over space and time (Panchen et al., 2014, 2015; Gallinat et al., 2018). Such research from networks of botanical gardens should be expanded and replicated in wild populations.

The study of phenological mismatch between plants and other organisms is still at an early stage, with no consensus on the best methods and systems to investigate. The roles of scale, context, and transferability will likely be key areas for future research. Does ecological mismatch (among plants, and between plants and animals) scale up from the local to regional scale? Are there features common to mismatches that help us predict vulnerable species and interactions across regions? Emerging tools will help researchers address these questions. One promising route is to pair new (and growing) broad-scale data from community science programs focused on animal taxa (such as eBird; Sullivan et al., 2009) with comparable broad-scale plant phenology data (such as satellite-derived data or plant community science data) to determine the potential for broad-scale mismatches. Using this technique, Mayor et al. (2017) found that in North America, eastern-breeding birds increasingly arrive after green-up, whereas the opposite trend is true for western-breeding birds. Similarly combining herbarium data with other museum data also provides great promise to include historical baselines (Kharouba et al., 2019) especially as more insect natural history collections become digitized.

Investigations into shifts in the relative position of plant species compared to their heterospecific neighbors across regions and with climate change, will benefit from the growing availability of community-level phenology data from observation networks like NEON, as well as from herbarium specimens, and further aided by tools for detecting phenology from specimens, such as machine learning techniques (Pearson et al., 2020) and crowdsourcing tools like CrowdCurio (Willis et al., 2017b) and Notes from Nature (Yost et al., 2020). While herbarium specimens generally do not represent strictly co-occurring plants, they do offer unique opportunities to investigate phenology of co-occurring species over periods of decades or more and across a broad geographic range. By incorporating the phenological responses of species across environments with network analyses of the species' interactions, macrophenology should be able to help predict the potential geographic extents of mismatches and their impacts on species and ecosystems.

ECOSYSTEM PROCESSES

While plant phenology can be highly sensitive to climate, phenology also exerts control over climate by seasonally altering environmental structure and fluxes and partitioning of carbon, water, and energy (Peñuelas and Filella, 2009). The timing of leaf-out, bud set, and leaf senescence in deciduous plants and the length of the growing season across ecosystems impact ecosystem productivity, respiration, evapotranspiration, and vegetation-associated shifts in temperature and precipitation. These climatic changes can potentially lead to shifts in plant phenology (Piao et al., 2020). For instance, a longer growing season in a warm year can increase rates of evapotranspiration and reduce streamflow (Kim et al., 2018), in turn altering soil moisture and phenology in subsequent seasons or years. Warmer springs can also increase fire risk in some regions (e.g., Westerling et al., 2006), leading to huge fluxes of carbon and water and changes in local microclimate conditions and phenology in the following years (Harris et al., 2016; Wang and Zhang, 2020). Climate–vegetation feedbacks result from the combined phenological cues and functional properties of individual plants (Richardson et al., 2013), which makes understanding how particular plants interact with ecosystem processes—and scaling up to global predictions on the basis of environmental and functional trait patterns—important for the accurate inclusion of such feedbacks in global ecosystem models (Richardson et al., 2012). Therefore, an important step for macroecology is to investigate not only how variation in climate, land-use, biogeographic history, and species composition alter spring and autumn plant phenology (section 1), but also to identify spatial, taxonomic, and physiological patterns in the relationship between plant phenology and carbon, water, and climate systems.

Local-scale observations have shown that the onset of the growing season is accompanied by increases in carbon and water exchange between ecosystems and the atmosphere (Schwartz and Crawford, 2001). The upsurge in evapotranspiration triggered by early-season leaf-out and opening of stomata alters surface temperature, cloud cover, precipitation, soil moisture, and stream discharge

(Ziter et al., 2019; Piao et al., 2020); for these reasons, hydrological models improve when they incorporate phenology. At the same time, the combination of the timing of seasonal leaf-out and leaf senescence together adjust annual carbon balance and the accumulation of above- and belowground plant biomass in many ecosystems around the world (Cleland et al., 2007). In the case of temperate systems with distinct seasons, climate change is generally extending the growing season at both ends, resulting in greater annual carbon uptake (Keenan et al., 2014). However, the sensitivity of carbon uptake to growing season length varies widely both across and within biomes (Richardson et al., 2013). Eddy covariance measurements reflect that a longer growing season results in a greater increase in net carbon uptake in broadleaf compared to evergreen forests, while results vary drastically among grasslands (Churkina et al., 2005; Baldocchi, 2008).

Even in well-studied temperate forests, recent work highlights how considerable uncertainty about end-of-season leaf phenology limits predictions of future carbon flux. By pairing broad-scale, species-level observations with experiments, Zani et al. (2020) found that some plants have limitations on annual carbon uptake that could result in earlier senescence under continued warming. And in some high latitude forests, continued warming is expected to cause late-season ecosystem respiration to outweigh carbon uptake, turning these forests from carbon sinks into carbon sources (Piao et al., 2008). Similarly, newly arriving invasive species, often with different phenologies and more sensitive phenological responses to warming, will likely affect regional productivity and associated biogeochemical cycling (Ehrenfeld, 2010; Fridley, 2012). These results suggest the major difficulty in scaling up from local- to macroscale carbon, water, and climate feedbacks is the need to link species- and community-level mechanisms of change to broad-scale patterns throughout the year.

Macrophenological studies are needed to fill these gaps in the scaling of phenological impacts and feedbacks with climate. Fundamentally, predicting these feedbacks requires improved models of phenology; in a call for stronger representation of phenology in terrestrial biosphere models, Richardson et al. (2012) showed that most such models are particularly limited in predicting spring and autumn phenology for deciduous species. In addition to honing the global drivers of phenology, researchers should investigate how phenology currently influences carbon, water, and nutrient cycling across spatial scales and biomes and how ecosystems will change with future shifts in phenology. Addressing these questions should include testing the impacts of phenology on carbon uptake and climate for species and communities. Eddy flux data can inform local-scale carbon flux for monocultures—which provide species-specific data but are an ecological oversimplification—and, more often, for plant communities—which are ecologically more realistic but mask species-level dynamics. Integrating these types of data with measurements of species' abundance and traits, community biodiversity, and environmental characteristics offers the opportunity to investigate the physiological mechanisms underlying patterns in phenology–climate relationships and to identify generalizations that enable scaling up to global models (Gauzere et al., 2017; Chuine, 2000; Asse et al., 2020; Ettinger et al., 2020).

The NEON program provides data that can quantify the relationships among carbon flux, plant phenology, and other traits and species inventories at many sites in a range of biomes. Previous work on temperate forests (using satellite-derived productivity estimates and species inventories from the U.S. Forest Inventory & Analysis program) suggests that temperate forests with greater biodiversity have had larger increases in growing season length under climate change (Oehri et al., 2017). Local-scale data like those from NEON can be used to investigate potential links between mechanisms among phenology, biodiversity, and carbon sequestration. Future macrophenology research should also further investigate how plant phenology feeds back to climate models. How will changes in species ranges and community composition affect the phenology of global ecosystem models? What and where are the limitations on future changes and feedbacks? It will be particularly important to know whether early-season increases in evapotranspiration and earlier phenology with warming could lead to mid-season drought, the loss of vulnerable species, and changes in community composition in some sites and regions. These types of limitations are poorly understood, particularly across regions, but could drastically alter forecasts of phenology, carbon uptake, energy exchange, albedo, and climate change at the global scale.

FUTURE RESEARCH OPPORTUNITIES

The four main topics we focus on in this review—global drivers of phenology, species' range limits, interactions among species, and ecosystem processes—provide an abundance of future research opportunities in the field of macrophenology. Many novel research opportunities can be found within and at the intersections of these topic areas (Figure 1). For instance, to understand the trade-offs that constrain species' ranges, researchers must examine how the environmental drivers of phenology vary across the species' ranges, and with other factors such as land use type and plant functional traits (Figure 1, intersection between A and B). And as environmental drivers of phenology constrain shifts in species' ranges with climate change, researchers should model and test how such constraints will influence interactions among species, including competitive and mutualist dynamics (Figure 1, intersection between B and C).

Future research in plant macrophenology can also benefit from and enhance several other research areas. In particular, there are key opportunities to expand plant macrophenology temporally—to include historical biogeography and evolutionary patterns, to apply the principles of macrophenology to other taxonomic groups like birds and insects, and to identify and address geographical gaps in phenological information. Individually, each of these areas has the potential to inform phenological research at new scales. Further discoveries will be enabled by research capable of expanding across temporal, taxonomic, and geographic scales simultaneously.

Historical biogeography and phylogenetic patterns

Plant phenology and phenological sensitivity are shaped by evolutionary history (Davies et al., 2013). Investigating the evolutionary (phylogenetic) patterns of plant phenology can help researchers understand how evolution constrains phenology in the present and how phenology may have affected species interactions in the evolutionary past (e.g., competition on the basis of phenological overlap). Phylogenetic signal in plant phenology, or the tendency for closely related species to have more similar timings and sensitivities than would be expected by chance, can reflect the impacts of species' shared historical biogeography (e.g., a lineage with early flowering and leaf-out may have diversified under milder winters). At the broadest scale, flowering, fruiting, and leaf-out times tend to be evolutionarily conserved (Davis et al., 2010; Panchen et al., 2014; Gallinat et al., 2018), as do plants' phenological sensitivity to the environment (Willis et al., 2008; Davies et al., 2013). The non-independence of species' phenology suggests that patterns among clades can provide insights into broader rules about what drives phenology across space, and so each of the above topic areas above benefit from phylogenetic insight. Phylogenetic patterns of phenology, sensitivity to environmental cues, and ecosystem impacts (e.g., annual carbon uptake) can inform estimates of phenology for rare species and other species that have not been directly observed. Historical biogeography of species and their close relatives can better inform present-day range limits and plant invasions. And phylogeny can add depth to studies of mismatch by testing whether phenological sensitivities reflect that interacting groups (such as plants and pollinators) have co-evolved or represent more recent interactions (Gallinat and Pearse, 2021). Moreover, ignoring historical biogeography and phylogeny can lead to misleading conclusions (Davies et al., 2013), particularly when scaling up observations or translating them from one location to another as is essential for macrophenology.

It is noteworthy that leaf senescence times appear to have a weaker phylogenetic component than other phenological characteristics (Panchen et al., 2014, 2015; Gallinat et al., 2018) and appear to respond to a wider variation of environmental cues than flowering, leaf-out, and fruiting times (Gallinat et al., 2015; Gill et al., 2015). In general, leaf senescence is also less studied and more difficult to define and observe with discrete phenophases (Gallinat et al., 2015). As a consequence, future studies of the macrophenology of leaf senescence may be both more challenging and potentially more rewarding than other phenological changes.

Macrophenology of other taxonomic groups

In this paper, we have focused on plant phenology, but similar principles of macrophenology apply across other taxonomic groups. There are strong linkages between plant and animal phenology that influence drivers of plant phenology, species ranges, interactions, and sometimes even ecosystem processes (e.g., large-scale herbivory by mammals or insects). The sensitivity of animal emergence, migration, breeding, and (to a lesser extent) dormancy to climate change have been investigated at local and regional scales (Parmesan, 2006; Thackeray et al., 2016; Cohen et al., 2018), but there remain large gaps in our knowledge of the global-scale predictors of phenology, their sensitivity, and their consequences. A major difference between animal macrophenology and plant macrophenology is that many animal species are able to rapidly disperse and shift their ranges in response to temperature and precipitation (as in Lenoir and Svenning, 2015). As a result, rapid changes in animal community composition are important to consider in predictions of future climate impacts on phenology and species interactions (including mismatch) between plants and animals. In addition, animal migration is often an inherently macroscale process, as many species, especially birds, mammals, and certain insects, annually cross regional and continental scales. As such, animal macrophenology may provide examples from which plant macrophenology can draw. For instance, researchers have demonstrated the value of broad-scale public observations of phenology for informing geographic variation in climate sensitivities. Using the eBird database from the Cornell Lab of Ornithology, Hurlbert and Liang (2012) showed that a species' migration speed, distance, breeding latitude, and niche breadth were important to determining the relative sensitivity of its spring arrival time to climate. Other promising data sources for regional and global animal phenology records include museum specimens (see McLean and Guralnick, 2020), iNaturalist records, bird banding records, agricultural pest records, and historical journals from naturalists and others.

The phenology of bacterial and fungal communities, particularly relative to plant communities (above and belowground), is another important and growing research area (Andrew et al., 2018; Buscardo et al., 2018; Sorensen et al., 2020) that presents many opportunities for future study in macrophenology. Studying the macrophenology of these organisms in the context of their global drivers, mismatch with plants, and ecosystem processes, can help predict the phenology of ecosystem processes that follow seasonal patterns—such as ecosystem respiration or gross primary production—that reflect the cumulative activities of the whole ecosystem. Seasonal shifts in ecosystem processes related to water, carbon, and nutrients (e.g., snowmelt and air and soil warming) in relation to the activity of microbes and plants can have important consequences for year-round ecosystem processes. For instance, larger advances in the timing of snowmelt compared to leaf-out can increase the amount of early-season root and microbial respiration, increasing annual carbon losses (Contosta et al., 2017). By pairing data identifying microbial community taxa and functional groups (e.g., NEON; the International Long-term Ecological Research Network, ILTER) with information on ecosystem respiration (e.g., eddy flux sites), researchers can explore the potential for current and future mismatch among plants and microbes.

Geographical gaps in phenology research

As macrophenology looks ahead toward global syntheses of phenological drivers and consequences, it is critical that we identify and fill the geographic gaps in our knowledge of even basic patterns of phenology. These gaps can stem from a lack of funding to monitor phenology, the difficulty of monitoring complex seasonality, and technological challenges (e.g., heavy cloud cover masking satellite images). Therefore, phenology research tends to be concentrated in northern hemisphere temperate regions, while the southern hemisphere, and particularly tropical, desert, and grassland systems have been comparatively neglected. Funds, research efforts, and the expansion of existing networks should aim to fill these geographical gaps. At the same time, digitized herbarium specimens from around the world are increasingly allowing researchers to expand global coverage of species-specific phenology observations, especially in the tropics (Willis et al., 2017a).

CONCLUSIONS

In this review, we have argued that the field of macrophenology allows researchers to address grand challenges that depend on understanding phenology—and the emergent properties of taxa, communities, and ecosystems—at broad scales (Table 1). We have framed macrophenology within the overlapping themes of global drivers of phenology, species' range limits, interactions and mismatches among species, and ecosystem processes (Figure 1). As the study and techniques develop, so too might the range of macrophenology concepts and approaches presented here.

Like the broader field of macroecology, macrophenology emphasizes the fundamental principle that we must examine local process and circumstances to understand larger regional patterns, and vice versa. This approach does not lessen the importance or need for continued local-scale studies but instead increases their value by both providing a broader view and considering what emergent patterns and processes emerge from synthesizing across studies. To understand what determines local-scale phenological responses, phenology-associated risks for individual plants, and interactions between plants and their ecosystems, we need a sufficiently broad lens to capture both the evolutionary and ecological contexts. With this synthetic approach, macrophenology can contribute to conservation and natural resource management by testing the transferability of phenological timing, sensitivities, and mismatches to novel environments and rare species.

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