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**Title:** Cryptic phenology in plants: case studies, implications and recommendations

**Running title:** Cryptic phenology in plants

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litterfall data. For the temperate forest case study at Harvard Forest, SMM contributed DBH and  
allometry, and PC, AA, JM, WL, DMR, and XS contributed model runs and feedback on the  
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## ABSTRACT

Plant phenology – the timing of cyclic or recurrent biological events in plants – offers insight into the ecology, evolution, and seasonality of plant-mediated ecosystem processes. Traditionally studied phenologies are readily apparent, such as flowering events, germination timing, and season-initiating budbreak. However, a broad range of phenologies that are fundamental to the ecology and evolution of plants, and to global biogeochemical cycles and climate change predictions, have been neglected because they are “cryptic” – that is, hidden from view (e.g. root production) or difficult to distinguish and interpret based on common measurements at typical scales of examination (e.g. leaf turnover in evergreen forests). We illustrate how capturing cryptic phenology can advance scientific understanding with two case studies: wood phenology in a deciduous forest of the northeastern USA and leaf phenology in tropical evergreen forests of Amazonia. Drawing on these case studies and other literature, we argue that conceptualizing and characterizing cryptic plant phenology is needed for understanding and accurate prediction at many scales from organisms to ecosystems. We recommend avenues of empirical and modeling research to accelerate discovery of cryptic phenological patterns, to understand their causes and consequences, and to represent these processes in terrestrial biosphere models.

## 1. INTRODUCTION

All organisms have physical limits beyond which they function poorly or perish, and face trade-offs in the allocation of finite resources to different structures and functions (Araújo et al., 2013; Bennett & Lenski, 2007). Evolutionary strategies to establish, survive, grow, and reproduce are shaped by such fundamental constraints and trade-offs (Roff & Fairbairn, 2007; Stearns, 1989). When physical constraints or available resources vary regularly through time, organisms often evolve temporal patterns in their activities to match or complement these variations (Diamond, Frame, Martin, & Buckley, 2011). Temporal rhythms can also arise from time-dependent biological process such as ontogeny and demography (Niinemets, García-Plazaola, & Tosens, 2012; Thomas & Winner, 2002). The Earth surface experiences seasonal cycles in temperature, precipitation, and light that influence the availability of resources and the potential to carry out the chemistry underlying biological processes (Schwartz, 2013; A. H. Strahler & Strahler, 2006). Sessile organisms, such as most multicellular plants, are subjected to these seasonal cycles in-place. Plant phenology—the timing of cyclic or recurrent biological events in plants—represents functional strategies to persist within the bounds of natural climate seasonality and biological possibility (Forrest & Miller-Rushing, 2010; Rathcke & Lacey, 1985). The study of phenology has thus long been used as a means for gaining insight into the ecology and evolution of plants and other organisms (Lieth, 1974).

The term ‘phenology’ traces to the Greek root *phaino*, meaning ‘to show,’ or ‘to appear’ (Schwartz, 2013), and early influential works on phenology promoted observations of phenomena that were ‘sharp,’ ‘visible,’ and easy to detect (Leopold & Jones, 1947). In today’s lexicon, common definitions of phenology broadly encompass the timing of cyclic or recurrent biological events in plants, along with the causes and consequences of that timing (e.g. Lieth

1974, and (*phenology*, *n.* : *Oxford English Dictionary*, 2005). In contrast with broad contemporary definitions of phenology, studies of phenology often reflect the origin and history of the term by focusing on readily apparent biological events. These are generally aboveground and accompanied by changes that are readily and reproducibly distinguished with human senses such as visible changes in color, position, mass and volume. In plants, these include phenomena such as germination in annual plants, synchronized leaf production (leaf flush) and abscission in deciduous forests (Murali & Sukumar, 1993; Richardson & O’Keefe, 2009), and the onset of anthesis (flower opening) (Schwartz, 2013). Some phenological patterns, such as deciduous forest leaf onset, are also apparent at canopy and larger spatial scales with remote sensing tools ranging from phenocams to satellites (Badeck et al., 2004; Buitenwerf, Rose, & Higgins, 2015). Studying the timing and controls of such apparent biological events has contributed to understanding the evolution of plant traits and strategies in response to cycles in temperature, precipitation, photoperiod, and other physical variables (Chuine, 2010; Z. Huang, Liu, Bradford, Huxman, & Venable, 2016; Pau et al., 2011; van Schaik, Terborgh, & Wright, 1993). Phenological studies have also advanced our understanding of ecology, as many phenological patterns are coupled to biotic interactions such as intra-annual dynamics of predator or mutualist populations (Pau et al., 2011; Schwartz, 2013). More recently, some phenological events, such as date of anthesis or first leaf emergence, have proven useful indicators of biological responses to climate change (e.g. Parmesan & Yohe, 2003), and the relative ease of observing such events has enabled citizen science at regional and continental scales (Schwartz, Betancourt, & Weltzin, 2012).

However, many processes in plants are *not* readily apparent, but are no less cyclic or seasonal than the more easily observed phenomena that humans have historically monitored.

These phenologies are what might be called ‘cryptic.’ Some phenological patterns are difficult to detect because they are hidden, including below-ground activities such as allocation to roots, and internal processes such as allocation to carbohydrate reserves or cell differentiation. Other phenological patterns are missed or misinterpreted based on common measurements at typical scales of examination (e.g. changes in mass, area or volume of plant organs or of biomass pools). Cryptic phenologies are not as well understood as apparent phenologies, and they have not been used as indicators of climate change. Yet phenologies, including cryptic phenologies, play critical roles in ecosystems, and mediate large-scale fluxes of carbon, nutrients, water, and energy that are essential to consider as Earth’s climate changes (Abramoff & Finzi, 2015; McCormack, Adams, Smithwick, & Eissenstat, 2014; Noormets, 2009; Richardson, Keenan, et al., 2013b).

To address the disparity between the narrow scope of apparent phenology and the much broader scope of cyclic and seasonal plant activities, we first offer a framework with terminology that identifies the underlying challenges to observing, interpreting, and modeling cryptic phenologies. Then, focusing on trees, we review specific case studies in which missing cryptic phenology leads to problems for understanding and modeling seasonal ecosystem processes: wood allocation in a temperate mixed forest, and leaf phenology in tropical evergreen Amazon forests. We emphasize that attention to cryptic phenology is timely because many terrestrial biosphere models (TBMs, the models used to represent vegetation of the land surface in Earth system models and needed for climate change predictions; Fisher, Huntzinger, Schwalm, & Sitch, 2014), assume that cryptic phenologies are strongly correlated with apparent phenologies, and that such assumptions can lead to misattribution of the causes behind observed fluxes of carbon, water, nutrients, and energy. Although we focus on trees, we argue that cryptic



148 phenologies are ubiquitous, and their conceptualization, characterization, and interpretation are  
149 essential for accurate prediction at scales from organisms to ecosystems across the globe.

150 Table 1. Categorization of plant phenologies based on our current capacity for successful measurement, observation, and/or interpretation.

Plant phenology category	Specific examples	Frequently measured?	Model representation examples	Examples of current or possible use
<i>Apparent</i>				
Phases and events easily observed by humans.	<ul style="list-style-type: none"> <li>• Bud burst<sup>1</sup></li> <li>• Leaf abscission<sup>2</sup></li> <li>• Anthesis<sup>3</sup></li> <li>• Fruit maturation<sup>4</sup></li> </ul>	Yes, and some records extend for decades or longer.	May be prescribed by relying directly on observations to force the model (e.g. remote sensing indices), or may be simulated based on environmental controls (e.g. growing degree days). <sup>5</sup>	<ul style="list-style-type: none"> <li>• Defining the duration of the growing season in seasonally dormant systems.<sup>6,7</sup></li> <li>• Testing capacity of hydrothermal models to predict events such as germination.<sup>8,9</sup></li> <li>• Using changes in timing of phenological events as indicators of climate change.<sup>10,11,12</sup></li> </ul>
<i>Cryptic: hidden</i>				
Phases and events that are internal or obstructed by some barrier and thus difficult to detect.	<ul style="list-style-type: none"> <li>• Below-ground processes such as root production.<sup>13,14</sup></li> <li>• Structural changes within cells or tissues such as xylem formation.<sup>15</sup></li> <li>• Remote sensing in cloudy regions such as wet tropical forests.<sup>16</sup></li> </ul>	No, but these blind spots are generally acknowledged.	Often assumed to be linked to or dependent on apparent phenology. <sup>17,18</sup> This assumption is generally explicit.	<ul style="list-style-type: none"> <li>• Modeling of whole plant carbon and water dynamics.<sup>19,20</sup></li> <li>• Estimating intra-annual cycles of biomass gain.<sup>15</sup></li> <li>• Identifying temporal variation in below-ground interactions and associations.<sup>21,22</sup></li> </ul>
<i>Cryptic: ambiguous</i>				
Phases and events that are missed or misinterpreted due to summed variables or compensatory processes in the same variable.	<ul style="list-style-type: none"> <li>• Leaf quantity appears constant despite leaf turnover because new leaf production compensates for simultaneous old leaf abscission.<sup>23</sup></li> <li>• Bole diameter can be affected by both wood formation and water status.<sup>24</sup></li> </ul>	No, and these blind spots are not widely acknowledged. Measurements are needed at fine spatial or temporal scales, or with specialized tools, to capture and/or interpret the phenological pattern.	Often assumed to be represented by apparent phenology and/or assumed constant. These assumptions are generally implicit and often unrecognized.	<ul style="list-style-type: none"> <li>• Decomposing measurements into components that reveal phenological strategies.<sup>25,26</sup></li> <li>• Attributing cycles of ecosystem flux to endogenous versus exogenous drivers.<sup>27,28</sup></li> <li>• Resolving lagged responses from instantaneous responses and their relationship to periods of stress.<sup>29,30</sup></li> </ul>

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- <sup>1</sup> Budburst. (2019). Budburst: An online database of plant observations, a citizen-science project of the Chicago Botanic Garden. Glencoe, Illinois. <https://budburst.org/plant-groups>
  - <sup>2</sup> (Escudero & Del Arco, 1987)
  - <sup>3</sup> (Smith-Ramirez, Armesto, & Figueroa, 1998)
  - <sup>4</sup> (Spellman & Mulder, 2016)
  - <sup>5</sup> (Huntzinger et al., 2012)
  - <sup>6</sup> (Churkina, Schimel, Braswell, & Xiao, 2005)}
  - <sup>7</sup> (Schwartz, 2013)
  - <sup>8</sup> (Bauer, Meyer, & Allen, 1998)
  - <sup>9</sup> (Hardegree, 2006)
  - <sup>10</sup> (Badeck et al., 2004)
  - <sup>11</sup> (Schwartz, AHAS, & AASA, 2006)
  - <sup>12</sup> (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007)
  - <sup>13</sup> (Steinaker & Wilson, 2008)
  - <sup>14</sup> (Radville, McCormack, Post, & Eissenstat, 2016)
  - <sup>15</sup> (Cuny et al., 2015)
  - <sup>16</sup> (Asner, 2001)
  - <sup>17</sup> (Delpierre, Berveiller, Granda, & Dufrene, 2015)
  - <sup>18</sup> (Abramoff & Finzi)
  - <sup>19</sup> (Hu, Moore, Riveros-Iregui, Burns, & Monson, 2010)
  - <sup>20</sup> (Michelot et al., 2012)
  - <sup>21</sup> (Mullen & Schmidt, 1993)
  - <sup>22</sup> (S. W. Simard et al., 2012)
  - <sup>23</sup> (Albert et al., 2018)
  - <sup>24</sup> (Chitra-Tarak et al., 2015)
  - <sup>25</sup> (Tang & Dubayah, 2017)
  - <sup>26</sup> (Smith et al. 2019)
  - <sup>27</sup> (Wu *et al.*, 2016)
  - <sup>28</sup> (Migliavacca *et al.*, 2015)
  - <sup>29</sup> (Ogle *et al.*, 2015)
  - <sup>30</sup> (Guo & Ogle, 2018)

## 2. THE CHALLENGE OF CRYPTIC PHENOLOGY: A FRAMEWORK

As discussed above, we describe *apparent* phenologies as those that were selected for clear observation by humans, often with minimal technological support. By contrast, *cryptic* phenologies require extensive investigation or validation to capture, and as a consequence have rarely been measured at the temporal or spatial scale necessary to document and understand (Table 1). ‘Cryptic’ is a useful term because it implies concealment and ambiguity—two general challenges to capturing and understanding the full scope of cyclic/recurrent biological events in plants. To highlight these challenges, here we frame cryptic phenology as ‘hidden’ or ‘ambiguous.’

Plant phenological patterns are *hidden* when some physical or technological barrier obstructs observation (Table 1). Soil conceals below-ground processes such as cycles of root production and turn-over (Abramoff & Finzi, 2015; Delpierre et al., 2016). Internal plant structures are (by definition) hidden behind layers of cells, making the timing of recurrent processes such as secondary xylem (wood) formation difficult to observe *in vivo* (Chaffey, 1999; Plomion, Leprovost, & Stokes, 2001). Large-scale phenological processes can also be hidden, as cloud cover can consistently obstruct satellite observations of vegetation reflectance over humid regions such as tropical forests (Asner, 2001). In dense forests, the upper canopy leaves partly obstruct remote sensing observations of mid- and understory leaf area patterns (Tang & Dubayah, 2017) and vice versa for ground-based observations, (Smith et al., 2019). When phenological processes are hidden, describing them often requires time-consuming methods, such as minirhizotrons or soil cores (for roots; Abramoff & Finzi, 2015; Gaudinski et al., 2010), fixation of tissue samples from multiple time periods (for wood formation; Arend & Fromm, 2007), or ‘ground truth’ observations (for remotely-sensed vegetation greenness indices;

Chavana-Bryant et al., 2017; Lopes et al., 2016; Richardson et al., 2018; Wu et al., 2017). Hidden phenological patterns are challenging and/or time-consuming to measure, but the scientific community frequently acknowledges the scarcity of these measurements, and models including hidden phenology explicitly define their representation within allocation schemes (e.g. Abramoff & Finzi, 2015).

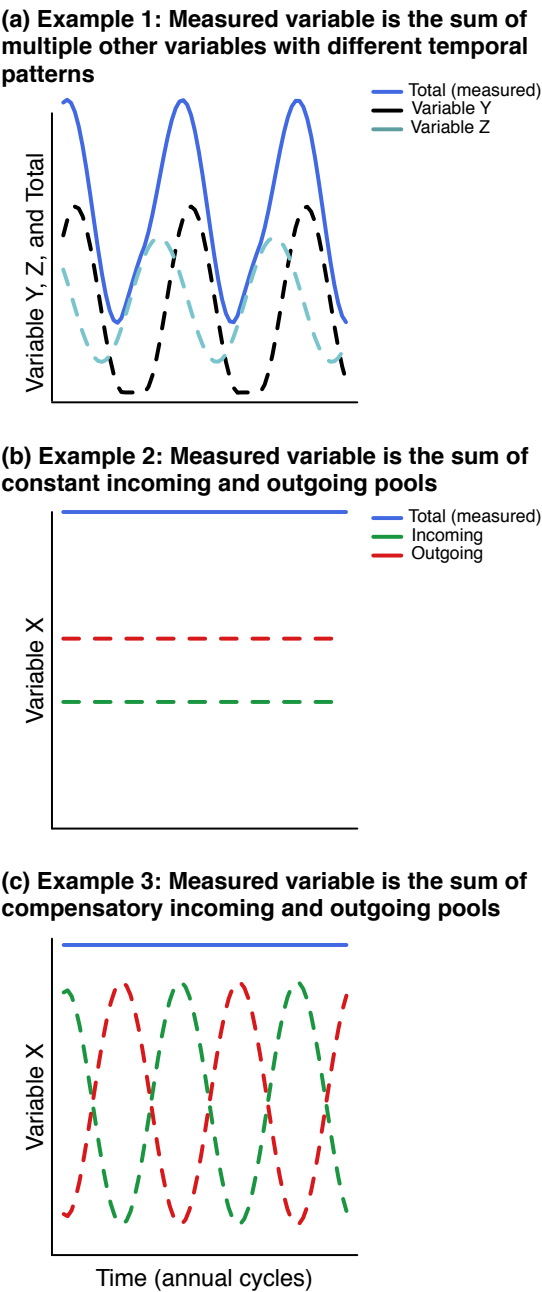
Phenological patterns in plants are *ambiguous* if phases and events are missed or misinterpreted due to summed variables or compensatory processes in the same variable (Table 1). A measured variable (e.g. plant mass, canopy leaf area, or bole volume) may be a function of multiple variables that are not synchronized with each other (Fig. 1a), making it difficult to interpret the temporal changes in the measured variable. For example, determining whether changes in tree stem diameter are caused by long-term carbon gain (such as xylem wall thickening), or reversible changes in plant water status (such as stem expansion or shrinkage), is difficult solely on the basis of stem diameter measurements (Chitra-Tarak et al., 2015; Cuny et al., 2015; Sheil, 1997). Additional examples of ambiguous phenological patterns arise when, for a given system, there are inputs and outputs of the same variable that are compensatory, maintaining the appearance of constancy despite change. For example, compensatory leaf production and abscission could maintain a constant total quantity of leaves in the canopy, belying underlying cycles in leaf production and abscission (Albert et al., 2018; Doughty & Goulden, 2008; Wu et al., 2016). In this example, at least two of the three terms (inputs, outputs, and total) need to be sufficiently constrained by measurements to determine whether the steady state of the total is achieved due to *constant* inputs and outputs (Fig. 1b) versus cyclic, but *compensatory* inputs and outputs (Fig. 1c). Whatever the scale of study, measuring multiple

terms over time requires more effort and/or instrumentation, and this difficulty contributes to the challenge of recognizing and resolving ambiguous phenology.

Whereas hidden phenological patterns are often acknowledged to exist, but rarely measured, ambiguous phenological patterns are not frequently acknowledged because measurements *are* being made—the challenge lies in interpreting those measurements. For example, we understand that root phenology is hidden, and difficult to measure, because roots are underground. By contrast, we may not even realize that leaf production and loss show seasonal rhythms if the quantity of leaves in a canopy is largely constant (a compensatory scenario). The distinction between hidden and ambiguous categories is not absolute because phenology could be both hidden and ambiguous. For example, the mechanism of biomass gain (xylogenesis) is hidden within stems, and stem diameter represents an integration of cells at different stages in the sequence of xylogenesis: cell expansion, secondary cell wall thickening, lignification and dead cells (Cuny et al., 2015; Plomion et al., 2001). Thus changes in stem diameter emerge from expansion as well as biomass gain (Cuny et al., 2015), resulting in some ambiguity.

Cryptic phenologies do not follow fundamentally different rules than their more apparent counterparts. Plant phenologies, in general, are consequences of biology, climatic seasonality, and their interactions. Yet a focus on cryptic phenology challenges us to explicitly consider our current observational blind spots. These blind spots may prevent us from gaining a comprehensive understanding of organismal strategies and limitations in relation to their biology and physical environment, with consequences for our understanding of population, community, and ecosystem ecology. Ultimately, our ability to document, understand, and model the component processes that contribute to large-scale biosphere/atmosphere exchange of CO<sub>2</sub> and

220 water vapor, impacts our ability to predict responses of natural systems to global change (Getz et  
 221 al., 2017; Noormets, 2009; Richardson et al., 2012).



222  
 223 Figure 1: Examples of ambiguous phenological patterns. In example 1, multiple variables (Y and  
 224 Z) contribute to some total that is measured. Variables Y and Z may have different peak timing,  
 225 different rates of change, and/or different amplitudes, that become summed for the measured total.  
 226 Thus the phenological patterns of individual variables Y and Z are ambiguous. In examples 2 and  
 227 3, the total for some biological variable X is the sum of an incoming (new) pool and outgoing (old)  
 228 pool. In example 2, the total, the incoming, and the outgoing pools are constant. In example 3, the

total is also constant, but the incoming and outgoing pools are dynamic, with inputs compensating for losses. Distinguishing between the scenarios represented by examples 2 and 3 is difficult based solely on measurements of the variable X total, and so phenological patterns of the incoming and outgoing pools remain ambiguous.

### 3. CASE STUDIES IN CRYPTIC PHENOLOGY

In the two case studies below, we draw upon available studies, data, and models to examine the evidence for, and implications of, cryptic phenology in two different plant processes in distinct ecosystems: allocation to wood in temperate deciduous forests, and gross primary productivity in tropical evergreen forests. For each case study we compare observations with simulations from terrestrial biosphere models (TBMs; models that represent land surface vegetation in the Earth system models used to simulate current and future global energy, carbon and water budgets (Fisher et al., 2014; Le Quéré et al., 2015). These model-observation comparisons serve two purposes. First, comparisons of TBMs with observations offer a test of our current ability to reproduce the seasonality of biosphere-atmosphere mass exchanges and represent phenological processes (Richardson et al., 2012) with implications for improving models (Richardson, Keenan, et al., 2013b). Second, the model-observation comparisons, placed in the context of current literature examining multiple scales and using multiple tools, allows us to ask whether cryptic phenology presents obstacles to our ability to test hypotheses about the drivers, consequences, and even the presence of phenology. Together, these case studies represent different plant organs and ecosystems, demonstrating how capturing cryptic phenological processes can be necessary for correct attribution of cause and effect—and ultimately modeling ecosystem processes—in many systems.

#### 3.1 Cryptic phenology of bole growth in temperate forests: implications for the timing of



## **carbon allocation to wood**

A TBM model-data comparison of bole growth at Harvard Forest, a temperate mixed forest site, reveals the challenge of estimating and modeling the hidden phenology of biomass gain from wood allocation. Wood is a major component of aboveground biomass, and is important for characterizing fast versus slow growth strategies across species (Chave et al., 2009; Reich, 2014). The intra-annual timing of wood allocation may show how carbon gain responds to seasonal climate, and reveal periods of vulnerability or resilience to stress (Babst et al., 2014; Battipaglia et al., 2010). The process of woody biomass gain (from xylogenesis) is hidden within boles (Cuny et al. 2015), and tree or plot scale biomass cannot be directly measured without harvesting trees (Clark & Kellner, 2012). Because of this, woody biomass gain is rarely measured (Cuny et al. 2015). Aboveground biomass change, which includes non-wood components such as leaves, can be estimated by measuring bole diameter growth increment for use with taxa-specific allometric equations (Chave et al., 2014; Chojnacky, Heath, & Jenkins, 2014). This approach is used in both multi-year (e.g. McMahon, Parker, & Miller, 2010) and seasonal studies (McMahon & Parker, 2015; Delpierre et al., 2016).

We asked whether TBMs captured the phenology of carbon allocation to wood, and the phenology of carbon allocation to leaves, with equal success. We expected that TBMs would be challenged to capture the phenology of carbon allocation to wood because it is hidden and hence rarely measured at fine timescales, so there are few datasets available to improve, constrain, and test models (Delpierre et al., 2016). By contrast, carbon allocation to leaves is more apparent, particularly in forests with many deciduous tree species with spring leaf emergence and autumn senescence. We used fine scale changes in bole diameter growth as an estimation of the net primary productivity (NPP) allocated to wood ( $NPP_{wood}$ ). The allometric regression equations

were applied to a bi-weekly time series of high accuracy diameter at breast height (DBH) measurements from dendrometer bands (McMahon & Parker, 2015) for three tree species at Harvard Forest (supporting information appendix S1). We estimated NPP allocated to leaves ( $NPP_{\text{leaf}}$ , Fig. 2a) at Harvard Forest based on leaf area index and litterfall time series (J. W. Munger, n.d.; W. Munger & Wofsy, 2018; Urbanski et al., 2007; supporting information appendix S2). Resulting  $NPP_{\text{leaf}}$  and  $NPP_{\text{wood}}$  reveal that carbon investment in leaves and wood is highest early in the growing season (Fig. 2). The peaks in simulated  $NPP_{\text{leaf}}$  were within days of the estimated peak  $NPP_{\text{leaf}}$  (and close to leaf budburst, which typically occurs around May 6 (Keenan and Richardson, 2015). By contrast, simulated phenological patterns in wood-related output variables from three TBMs showed greater variation (Fig. 2, appendix S3). While the Community Land Model version 4.5 (CLM4.5) shows a peak close to that seen in the observations (around the time of budburst, at May 5), the peak for ORCHIDEE<sub>TRUNK</sub> and CLASS are months later (August 1 and August 11 respectively).

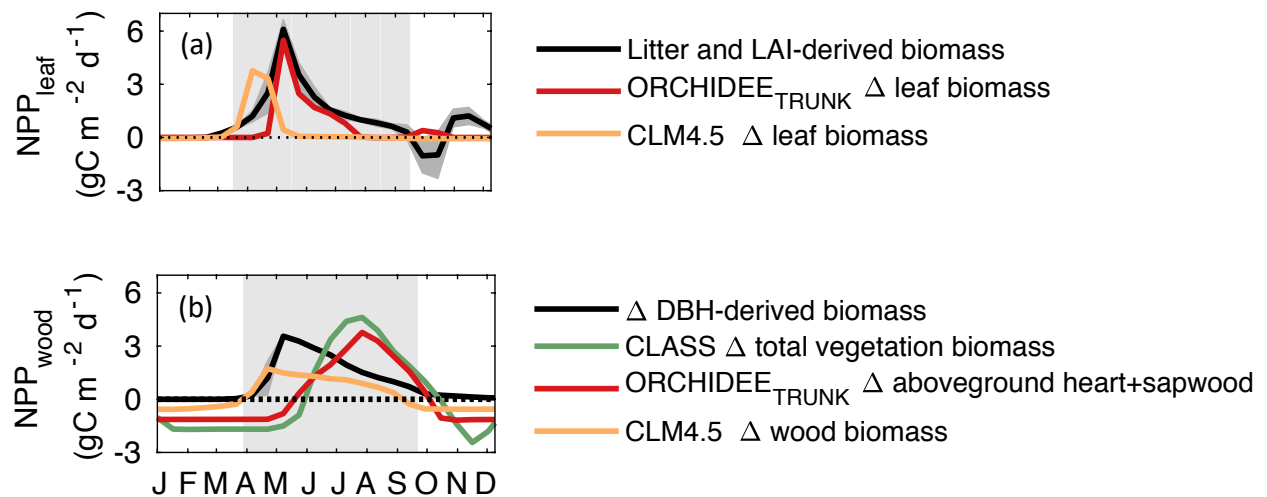


Figure 2: Seasonality of observed (black  $\pm$  gray standard deviation) versus model-simulated (colors) Net Primary Productivity (NPP) allocated to a) leaf biomass ( $NPP_{\text{leaf}}$ ), and b) woody biomass ( $NPP_{\text{wood}}$ ) metrics at a mixed deciduous evergreen temperate forest.  $NPP_{\text{leaf}}$  observations were calculated as  $(dLAI/dt) \cdot LMA + \text{litterfall}$  where LAI is leaf area index and LMA is leaf mass

per area. For models,  $\text{NPP}_{\text{leaf}}$  is calculated as the change in leaf biomass.  $\text{NPP}_{\text{wood}}$  observations were from allometry using diameter-at-breast-height (DBH) increment measurements compared with outputs from three land surface models. For models,  $\text{NPP}_{\text{wood}}$  was calculated as  $(X_i - X_{i-1}) / (t_i - t_{i-1})$  where  $X$  is the model output variable most comparable to aboveground woody biomass (in  $\text{gC m}^{-2} \text{ day}^{-1}$ ) for each model (which was vegetation biomass for CLASS, aboveground heartwood plus sapwood for ORCIDEETRUNK, and wood biomass for CLM4.5) and  $t$  is time in days. Temporal resolution is 16-day averages. The gray shaded area in all panels indicates the growing season, and the horizontal dotted line indicates zero.  $\text{NPP}_{\text{leaf}}$  simulations were not available for CLASS. Full  $\text{NPP}_{\text{wood}}$  estimation and model details are available in online supporting information.

In interpreting this model-observation comparison, it is important to remember that using DBH with allometric scaling equations produces estimates—not direct measurements—of biomass (Clark & Kellner, 2012), and to consider that TBMs differ in how the wood pool is defined, which is not necessarily identical to aboveground woody biomass (see Table S1 and S2 for model-specific definitions). In addition, there is some ambiguity in DBH-derived wood phenology because DBH represents multiple summed variables (Fig. 1a). DBH can be affected by changes in plant water status in addition to changes in biomass, and so seasonal changes in water availability could affect biomass estimations derived from allometry unless a correction is applied (Chitra-Tarak et al., 2015). The actual biomass gain (from xylogenesis) may also lag increases in DBH by weeks (Cuny et al., 2015). Explicit recognition of the distinction between measurable metrics (such as DBH) and the underlying variable we want to characterize or model (such as carbon biomass gain) motivates investigators to quantify uncertainty, and test for scenarios when proxies do not work well.

Despite the limitations of the observations and models, the comparison suggests that some models (like CLM 4.5) align moderately well with DBH-derived  $\text{NPP}_{\text{wood}}$ , while others lag DBH-derived  $\text{NPP}_{\text{wood}}$  by months. This divergence in model behaviors highlights the importance of understanding the mechanisms driving both simulated and observed phenologies. The timing of allocation to biomass and wood-related variables in these TBMs is primarily determined by the pattern of NPP across seasons. In ORCHIDEE for example, the allocation fractions to

different tissues primarily respond to environmental conditions: water, light, and nitrogen (Krinner et al., 2005). For the wood allocation in ORCHIDEE, a fraction of NPP is instantaneously allocated to sapwood, then sapwood biomass is converted into heartwood biomass based on a one-year time constant (Krinner et al., 2005). Ultimately, model NPP is controlled by site-specific climate conditions and representations of forest physiology (e.g. plant functional type), including leaf phenological patterns (e.g. leaf onset/abscission).

In contrast with model representations, physiological and tree-ring studies suggest that the mechanisms underlying wood phenology go beyond environmental controls to also include ontogeny of wood cells (Cuny et al., 2015; Plomion et al., 2001) and priorities in allocation through time (e.g. allocation of carbon to wood growth versus storage as nonstructural carbohydrates; Richardson, Carbone, et al., 2013a). Xylem production and differentiation follow a sequence, and shifts in one phase are associated with comparable shifts in successive phases (Rossi et al., 2013). This sequence offers a mechanism for wood phenology to respond to environmental conditions that are integrated over time—not just instantaneous drivers (Rossi et al., 2013). This sequence may also play a role in determining when trees are vulnerable or resilient to stress. For example, developing wood cells expand before their cell walls thicken with carbon-rich polysaccharides and lignins, and late wood is more dense than early wood in temperate species (Plomion et al., 2001), so trees at different stages in the sequence of wood development could be more or less sensitive to drought stress. Testing and developing model frameworks for such hypotheses is currently challenging because the timing of carbon allocation to wood is hidden *in vivo*. More direct measurements of wood formation (e.g. Cuny *et al.* 2016), and nonstructural carbohydrates (e.g. Newell, Mulkey, & Wright, 2002), synchronized with frequent measurements of DBH and leaf phenological patterns, would help us to understand and

model controls over wood phenological patterns (Delpierre et al., 2016; Guillemot et al., 2017), and how the timing of wood allocation relates to growth strategy, environmental fluctuations, and other plant traits.

### **3.2 Amazon evergreen forests: implications of cryptic phenology for seasonality of ecosystem carbon fluxes**

The challenge of cryptic phenology is not confined to a particular plant organ. Amazon evergreen forests near the equator offer a case study where leaf phenology is ambiguous. Much of the Amazon basin experiences annual wet and dry seasons (Restrepo-Coupe et al., 2013), and this regular seasonal variation in cloud cover and precipitation may select for phenological strategies that match plant activities with resource availability (Doughty et al., 2014; Graham, Mulkey, Kitajima, Phillips, & Wright, 2003; M. O. Jones, Kimball, & Nemani, 2014; van Schaik et al., 1993). Most of the Amazon is remote, making ground-based observations of phenology difficult, especially given the many observations needed to sample the high diversity of tree species (Cardoso et al., 2017) and strategies (Reich, 1995). Observations of canopies from satellites are often obstructed by clouds (Asner, 2001), difficult to interpret (Samanta et al., 2012), and the subject of controversy surrounding technical artifacts and their correction (Huete et al., 2006; Morton et al., 2014; Saleska et al., 2016). Yet many recent studies offer evidence that leaf production, leaf abscission, wood production and root production exhibit annual rhythms in Amazon forests (Doughty et al., 2014; Girardin, Malhi, & Doughty, 2016; Lopes et al., 2016; Wagner et al., 2016).

Many TBMs seem to be missing these phenological processes (Restrepo-Coupe et al., 2017). Evidence that TBMs are lacking adequate phenological representation comes from a

model inter-comparison for a network of ecosystem flux observations sites (eddy flux towers) in Amazonia (Restrepo-Coupe, et al., 2017). For illustration, we discuss the contrasting cases of equatorial versus southern evergreen forest sites in the Amazon basin of Brazil. At the equatorial site (K67 in the Tapajós National Forest, Brazil), four TBMs showed significant divergence from the estimated interannual pattern of whole-system photosynthetic fluxes (Fig. 3a, gross primary productivity, (GPP;  $\text{gC m}^{-2} \text{d}^{-1}$ ) and a metric of photosynthetic capacity, (Pc;  $\text{gC m}^{-2} \text{d}^{-1}$ ) for K67; (Restrepo-Coupe et al., 2017). The reason for the divergence is that modeled photosynthetic patterns are driven by environmental variability -- measures of soil water stress in this case (model calculated soil water stress index 'FSW' for K67, Fig. 3b-g) -- which suppresses GPP during the long dry season. Yet the observed interannual pattern of photosynthesis in this ecosystem appears to be driven by something beyond instantaneous responses to seasonal climate fluctuations.

Since TBMs already include climatic seasonality, their failure to capture GPP seasonality suggests that phenological processes operate at the equatorial site that are separate from the instantaneous physiological responses already represented. Canopy phenological activity could drive the observed GPP via two mechanisms: 1) dry season increases in quantity of canopy leaves (quantified as leaf area index, or LAI) and/or 2) dry season increases in canopy photosynthetic capacity on a per unit area basis (Lopes et al., 2016; Restrepo-Coupe et al., 2017; Wu et al., 2016). Observations of leaf quantity (LAI) from equatorial Amazon sites show that LAI varies little across seasons (e.g. Fig. 3c 'LAI' shows low seasonality at K67). Leaf turnover, however, exhibits a dry season pulse (Fig. 3e,f: 'NPP<sub>leaf</sub>' and 'NPP<sub>litter-fall</sub>'), suggesting that LAI is maintained because leaf production compensates for near-simultaneous leaf fall during the dry season. As a result, LAI exhibits modest seasonal variation relative to seasonal variation in leaf

392 litterfall and leaf flush (Fig. 4). The seasonality of total LAI also fails to represent within-canopy  
393 dynamics, as compensatory leaf area patterns have been identified between the upper and lower  
394 canopy levels at K67 (Smith et al., 2019). Since new (recently expanded) leaves have high rates  
395 of photosynthesis, replacing old leaves with new leaves can increase photosynthetic capacity of  
396 the canopy on a per unit area basis (Albert et al., 2018; Doughty & Goulden, 2008; Niinemets et  
397 al., 2012; Pantin, Simonneau, & Muller, 2012; Wu et al., 2016).

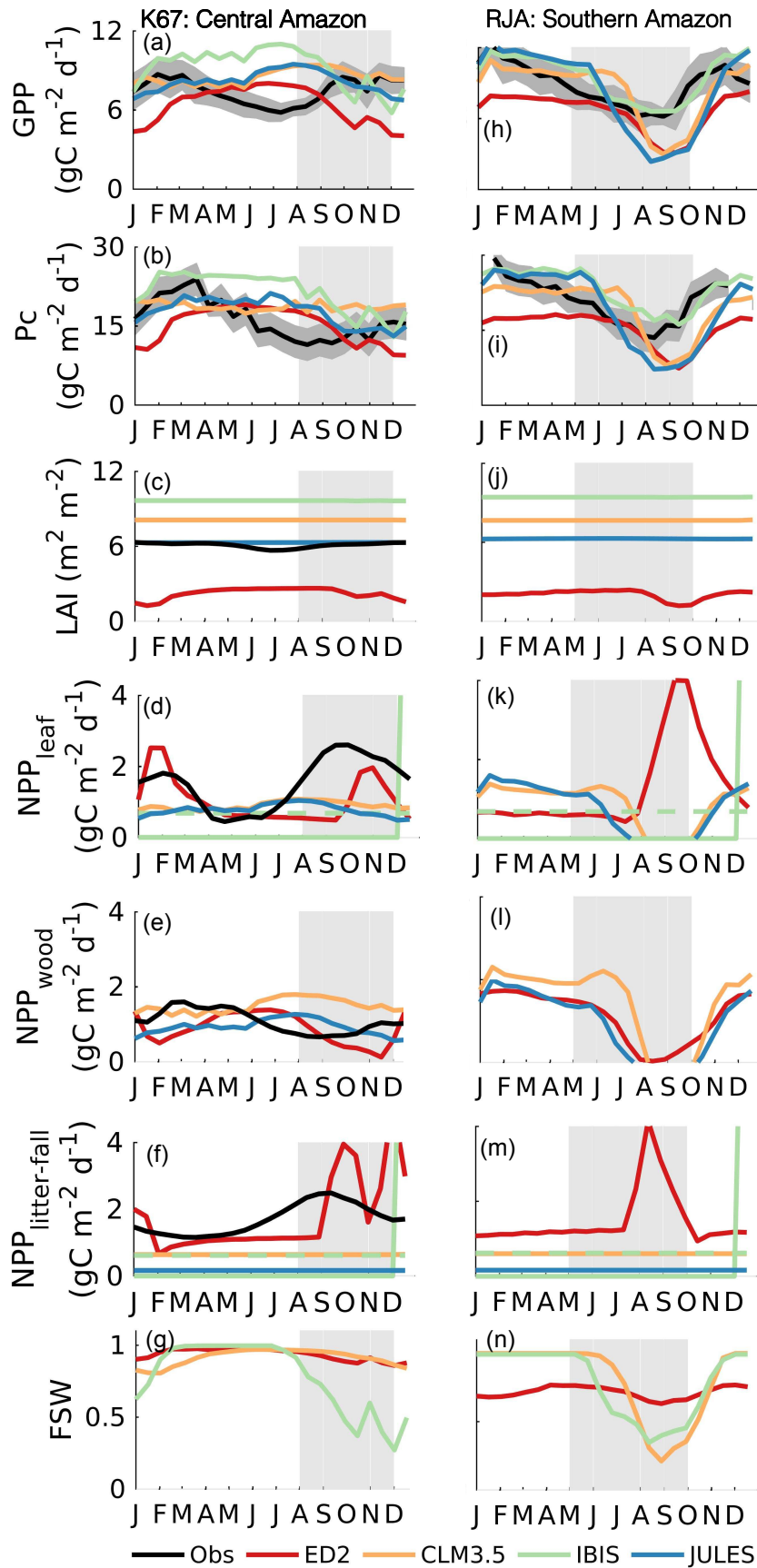




Figure 3: Annual cycles of observed (black  $\pm$  gray standard deviation) versus model-simulated (colors) forest metrics in two Amazon forests (an equatorial Amazon forest, K67, and a southern Amazon forest, RJA), including (panels from top to bottom): daily average ecosystem-scale photosynthesis (GPP); daily average ecosystem-scale photosynthetic capacity (Pc, GPP at a fixed PAR range (725-875  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), vapor pressure deficit, air temperature and light quality measured as cloudiness index (all time mean  $\pm$  1 standard deviation)); leaf area index (LAI); net primary productivity (NPP) allocated to leaves (leaf production;  $\text{NPP}_{\text{leaf}}$ ); NPP going to litterfall ( $\text{NPP}_{\text{litterfall}}$ ), and NPP allocated to wood ( $\text{NPP}_{\text{wood}}$ ); soil water stress metric (FSW), where 1=no stress (Ju et al., 2006). The light gray shaded box all panels represents the dry season. For K67 LAI data, we use data from the control plot of a close-by drought experiment (Juárez et al. 2007; Brando et al. 2010). LAI and NPP observations were not available for the RJA site. Lines are dashed for IBIS NPP to indicate that NPP is allocated only at the end of the year. For further details on model intercomparison, see Restrepo-Coupe et al. (2017).

The combination of leaf turnover and leaf age-dependent  $\text{CO}_2$  assimilation capacity creates a scenario at K67 in which ecosystem photosynthetic capacity varies more than LAI (Fig. 3b,c). Therefore, the observable canopy total LAI time series does not fully capture phenological patterns of leaf turnover or the resulting shifts in canopy photosynthetic capacity at this site (Fig. 5) because leaf phenology is compensatory (Fig. 1c).

In contrast to the equatorial Amazon site, at a southern Amazon forest (Reserva Jarú, RJA), observations and models coincide, with GPP and Pc declining during the dry season, consistent with increasing water limitation as the dry season progresses (Fig. 3h,i,n). We lack an observational time series of LAI and litterfall for the southern site, but remote sensing (GLAS satellite lidar) suggests that in the southern Amazon, LAI decreases during the dry season (Tang & Dubayah, 2017). Thus the equatorial (K67) and southern (RJA) Amazon sites appear to include trees with different phenological strategies (Restrepo-Coupe et al., 2013). We hypothesize that many trees in high water availability equatorial sites may be adapted to optimize light use over time, synchronizing leaf production with the sunny dry season as a strategy for increasing annual carbon gain (Restrepo-Coupe et al., 2017). The tree communities at southern sites like RJA may experience a weaker peak in dry season sunlight (Restrepo-Coupe et al., 2013), and may shed leaves during dry seasons to protect plant water status.

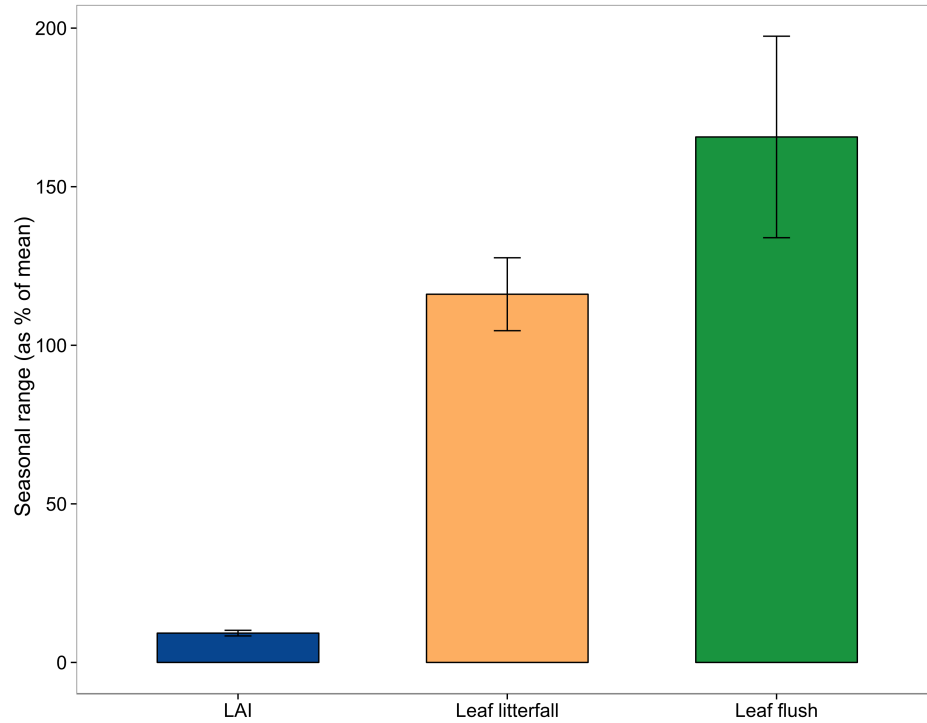


Figure 4: Seasonal canopy dynamics of Leaf Area Index (LAI), leaf litterfall, and leaf production averaged across five Amazonian sites, showing that large leaf turnover is concealed by near-constant LAI. The pulses of litterfall and leaf production support compensatory leaf phenology (Fig 1c) rather than constant leaf phenology (Fig 1b). Bars show mean values of annual amplitude scaled for studies (n=5 sites) of lowland evergreen tropical forests where both LAI and litterfall have been measured. Seasonal range is the annual amplitude scaled by mean value and is calculated as the difference between the maximum dry season value and the minimum wet season value, divided by the mean annual value (%). Error bars show standard deviation of the mean. Studies included in this figure: Tambopata-Candamo Reserve, south-eastern Peru (Girardin et al. 2016); Caxiutana, Floresta Nacional de Caxiutana, Pará, Brazil (Girardin et al. 2016); K83 (Doughty & Goulden 2008) and K67 (Brando et al. 2010 and Malhado et al. 2009) are located in the Tapajós National Forest, Pará, Brazil. Sites experience a range of mean annual precipitation values (1900 – 2572 mm).

This interpretation is consistent with studies asserting that tropical evergreen forests produce new leaves during periods of high light if they are not strongly water-limited (Doughty & Goulden, 2008; Graham et al., 2003; Guan et al., 2015; M. O. Jones et al., 2014; Reich & Borchert, 1984; Restrepo-Coupe et al., 2013; van Schaik et al., 1993; Wu et al., 2016). This continuum between precipitation-driven and light-driven tropical evergreen forest phenological strategies is not

included in most TBMs, and therefore might account for some of the divergence in their GPP projections (Restrepo-Coupe et al., 2017).

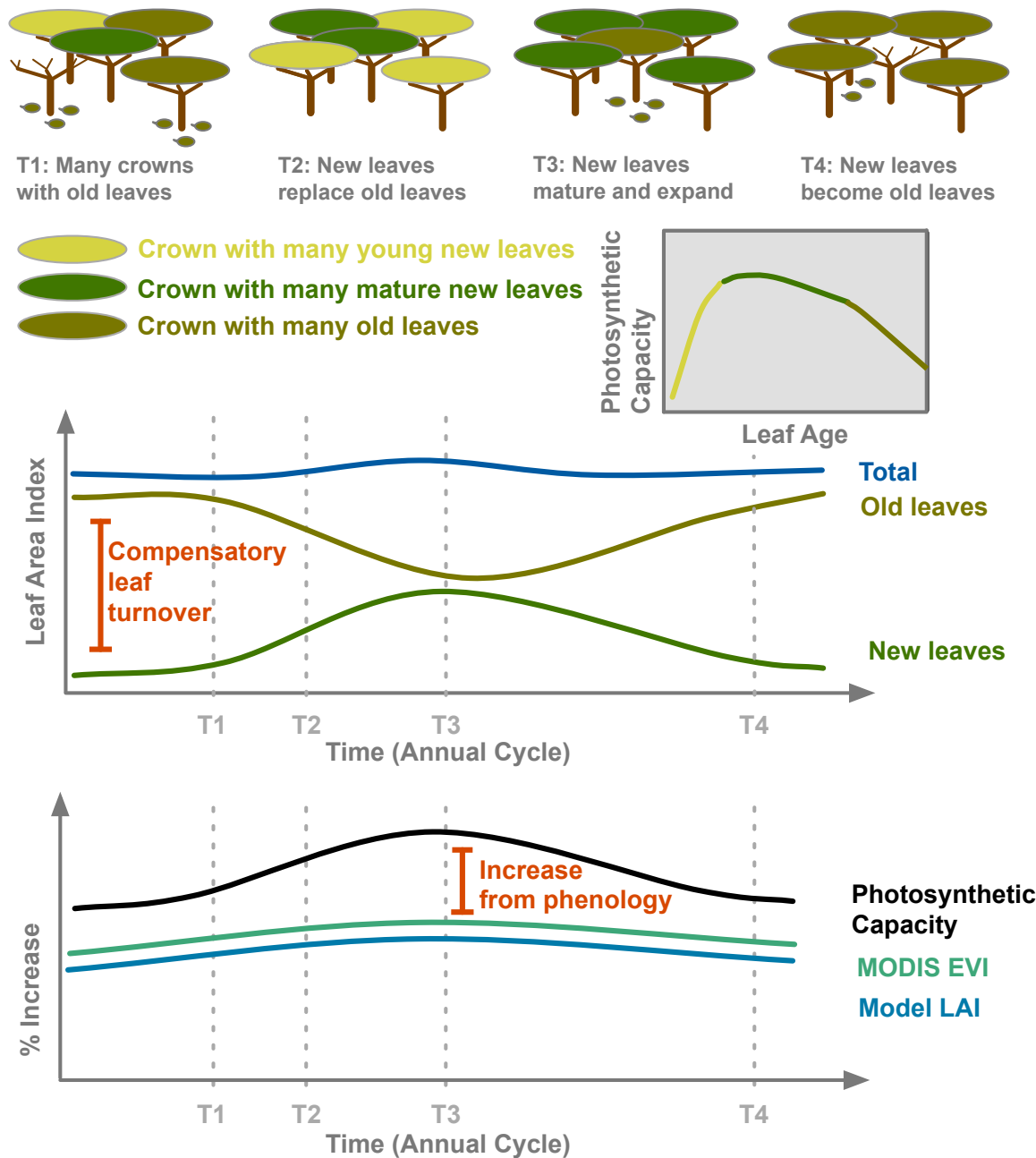


Figure 5: Illustration of how cryptic leaf turnover creates a phenological pattern in canopy photosynthetic capacity. Top: Individual crowns drop old leaves and produce new leaves with some degree of synchronization. Middle: the proportion of leaf area index belonging to previous year's growth (old leaves) and new leaf growth (new leaves) changes through the dry season. Here leaf phenology is difficult to detect because of compensatory inputs and outputs (see Fig 1c). Inset:

leaf photosynthetic capacity depends upon leaf age. Lower panel: the combination of leaf turnover and leaf ontogeny increase the canopy photosynthetic capacity, but neither total LAI nor satellite-based proxies for LAI and greenness show this same increase.

Equatorial Amazon sites such as K67 provide an example where resolving ambiguous phenology by testing whether leaf phenology is compensatory versus constant, and acknowledging the age-dependent physiology of leaves, is important for understanding and modeling a process, such as forest photosynthesis, at a large scale. Some plant functional types (PFTs) within TBMs allow for photosynthesis to vary with leaf age, but with a focus on temperate deciduous plants. For example, the Joint UK Land Environment Simulator (JULES) accounts for damage and senescence accumulation by reducing photosynthesis during the growing season (Clark et al., 2011), and the Ecosystem Demography model (ED2) decreases the maximum carboxylation rate of Rubisco ( $V_{\text{cmax}}$ ) in the autumn as a function of Julian day utilizing historical MODIS data (Medvigy, Wofsy, Munger, Hollinger, & Moorcroft, 2009). In these cases, time of year or ‘season’ serves as a proxy for leaf age, which may work well for some PFTs, but not for tropical evergreen broadleaf forests where the ‘evergreen’ canopy belies cyclic leaf turnover that the PFT ruleset does not include. This case study suggests that accounting for cryptic phenology is necessary for correctly detecting, attributing, and modeling the carbon exchange dynamics of tropical forests (De Weirdt et al., 2012; Y. Kim et al., 2012; Manoli, Ivanov, & Fatichi, 2018; Restrepo-Coupe et al., 2017).

#### **4. IMPLICATIONS OF CRYPTIC PHENOLOGY FOR PREDICTION ACROSS SCALES**

Fine-scale processes, integrated over space and time, create large-scale exchanges of mass and energy between the biosphere and the atmosphere (Monson & Baldocchi, 2014). Here we consider some of the fine-scale processes associated with cryptic phenology that, scaled up, have

implications for our ability to understand, model, and predict biosphere-atmosphere interactions under climate change.

#### *Organ scale*

Plant traits can show very high within-species variation due to phenology (Chavana-Bryant et al., 2017), and this variation can surpass interspecific variation for some traits (Fajardo & Siefert, 2016). Specifically, leaf development and aging is associated with changes in internal leaf structure (Lim, Kim, & Gil Nam, 2007; Niinemets et al., 2012), concentrations of secondary metabolites (Z. Liu et al., 1998; Virjamo & Julkunen-Tiitto, 2014), emissions of volatile organic compounds (Alves, Harley, Goncalves, da Silva Moura, & Jardine, 2014; Niinemets et al., 2010), and metabolic rates (Albert et al., 2018; Niinemets et al., 2012; Pantin et al., 2012). For the goal of scaling fluxes from leaves to canopies, these many physiological changes associated with leaf age suggest that distinguishing between constant leaf phenology and compensatory leaf phenology is important not only for tropical forests (as we describe in the first case study above), but for evergreen forests in general.

Similarly, root production is accompanied by physiological changes. There are species-specific relationships between root age and root physiology such as respiration rates and nutrient uptake capacity (Bouma et al., 2001; Fukuzawa, Dannoura, & Shibata, 2011). Existing studies that have characterized the hidden phenology of roots have shown evidence of interspecific differences in cycles of fine root production—single flushes, multiple flushes, or constant growth—that could represent strategies for responding to seasonal changes in climate or resource availability (Fukuzawa et al., 2011; McCormack et al., 2014).

*Organismal scale*

Natural selection would be expected to favor coordination in the timing of resource acquisition with resource storage and allocation (Sala, Woodruff, & Meinzer, 2012). Since selection acts at the level of individuals, if we want to understand the adaptive value of phenological changes, we need to understand how all plant organs function together, as a unit, through time. It is very difficult to study ‘whole’ plants in the wild, especially woody plants. Few (if any) studies have quantified the phenologies of all plant organs in wild woody plants to gain an integrated organism-level perspective on phenology (but see Hu et al., (2010) for whole-tree carbon assimilation during the growing season; see Würth, Peláez-Riedl, Wright, & Korner (2005) for seasonal variation in non-structural carbohydrate pools by plant organ; and see Doughty et al., (2014) for an example plot-scale study of wood, fine root, and canopy phenology). Studies examining phenologies of two organs suggest that phenology is often asynchronous across organs (Abramoff & Finzi, 2015; Wagner, Rossi, Stahl, Bonal, & Hérault, 2013). Comparing phenological patterns of roots and shoots frequently reveals offsets between maximum root growth and shoot growth, and these offsets vary across biomes (Abramoff & Finzi, 2015). In tropical forests, leaf and wood production is often asynchronous (Wagner et al., 2013). The onset and/or termination of growth may also vary; roots in temperate deciduous white oak, for example, continue to elongate in winter after senescence of leaves (Teskey & Hinckley, 1981). Nonstructural carbohydrate reserves also show phenological patterns that are species-dependent (Würth et al., 2005) and affected by phenological patterns of leaves (Palacio, Maestro, & Montserratmarti, 2007). Rates of carbon use regulate carbon uptake in plants (sink-driven photosynthesis; Fatichi, Leuzinger, & Korner, 2014), so phenological changes in carbon demand should impact the timing of photosynthetic activity.

These findings show that capturing the patterns and drivers of hidden and ambiguous phenologies will be needed for a comprehensive understanding of how plants prioritize amongst competing uses of resources and maintain carbon balance, with implications for modeling plant resource use. In most TBMs, the temporal patterns of leaf activity (the size of the leaf pool and the rate of photosynthesis) drive temporal patterns of carbon allocation because carbon allocation to other plant organs is often modeled as a constant proportion of carbon uptake (Abramoff & Finzi, 2015; Delpierre et al., 2016; Guillemot et al., 2017). However, if different plant organs respond to different environmental drivers (Wagner et al., 2016), then models that use leaf activity to generate interannual patterns of activity in hidden organs may fail to simulate observed patterns of root or bole activity at seasonal timescales.

How plants prioritize their allocation, through time, to various plant organs or to storage may have consequences for plant resilience or vulnerability to extreme events, and several studies already show that plant vulnerability and/or resilience to extreme events varies due to phenological status and/or season (Craine et al., 2012; M. Huang, Wang, Keenan, & Piao, 2018). We suggest that the timing of extreme events in relation to plant phenological status may be necessary for predicting plant community responses to future climate. For example, plant tolerance to drought or cold could depend on nonstructural carbohydrates (Dietze et al., 2014; Sala et al., 2012), and nonstructural carbohydrates follow seasonal cycles that could indicate internal phenology (Richardson et al., 2013a). Tests of such hypotheses are timely, given that the frequency of extreme climate events is increasing under global climate change (Bellprat & Doblas-Reyes, 2016; Ummenhofer & Meehl, 2017).

*Community scale*

As climate changes, many studies have demonstrated that phenological patterns shift, impacting species interactions (CaraDonna, Iler, & Inouye, 2014; Memmott, Craze, Waser, & Price, 2007; Miller-Rushing, Hoyer, Inouye, & Post, 2010; Polgar & Primack, 2011; Rafferty, CaraDonna, & Bronstein, 2014; Yang & Rudolf, 2010). Fewer studies have probed how hidden phenologies shape species interactions, or how those interactions may be changing. To do so could reveal that phenology mediates impacts of species interactions on plant mortality, reproduction, and metabolism. For example, the timing of insect outbreaks in relation to nonstructural carbohydrate reserves (which are affected by the timing of leaf renewal) may explain interspecific differences in tolerance to defoliation (Chen, Wang, Dai, Wan, & Liu, 2017). Further investigation into how species interactions affect hidden phenologies would help gain a more complete understanding of the interplay between climate change, whole plant physiology, and species interactions.

### *Ecosystem to global scale*

Projections of Earth's future climate are particularly sensitive to uncertainties in the land carbon cycle (Friedlingstein et al., 2014). Improving representation of the land carbon cycle in TBMs requires understanding the drivers of phenology, and the role of phenology in mediating biosphere-atmosphere exchanges (Richardson, Keenan, et al., 2013b). Recognizing phenological rhythms at scales from plant organs to communities is prerequisite to identifying their role in large scale (ecosystem to global) cycling of carbon. For example, investigating the distribution of root ages at different times of the year could elucidate larger scale autotrophic respiration or soil resource acquisition processes (because root age affects root respiration and nutrient uptake capacity; Bouma et al., 2001). TBMs which are calibrated to match current observations, but that



include inaccurate relationships between drivers and vegetation responses, risk making biased predictions of forest response to future climate changes because they do not incorporate underlying biological mechanisms (De Weirdt et al., 2012; Restrepo-Coupe et al., 2017).

## **5. RECOMMENDATIONS FOR MEASURING AND MODELING CRYPTIC PHENOLOGY**

### **5.1 Recommendations for empirical research**

To reveal cryptic phenological patterns empirically, we need to consider the target, frequency, and methods of measurements. We recommend complementing existing studies and measurements of aboveground, clearly visible phenological changes with measurements of hidden phenological changes (Table 1). Specifically, we need more time series of development and growth of roots (e.g. Abramoff and Finzi 2015, McCormack et al 2014), and internal structures (e.g. Cuny et al. 2015), to learn when leaf phenology directly fuels the phenological patterns of other plant organs (and thus can represent them by proxy), and when it does not. Building upon studies examining synchrony in phenology of multiple plant organs (Bazié et al., 2017; Delpierre et al., 2016; Michelot, Simard, Rathgeber, Dufrene, & Damesin, 2012; Omondi, Odee, Ongamo, Kanya, & Khasa, 2016; Perrin, Rossi, & Isabel, 2017; Wagner et al., 2013), whole-plant phenology studies in which all plant organs and their associated processes (acquisition and allocation of carbon, water, and nutrients) are continuously monitored in the same individual plants across seasons could elucidate the relationship between the phenology of plant organs with each other, and with climate, and test the representation of phenology for various PFTs.

Revealing cryptic phenological patterns will require more studies explicitly testing whether compensatory processes (Fig. 1c) mistaken for constancy (Fig. 1b) mislead our interpretation of mass, area, or volume time series. To this end, sampling schemes need to go beyond measuring mass, area or volume of plant organs or “pools” (in aggregate) to also measure rates of inputs and outputs to and from organs/pools across time. (Since mass-balance equations have three terms—inputs, outputs, and the accumulated pool—at least two must be measured to obtain a single solution). For example, litterfall time series should be collected to correspond with total leaf area time series. To examine the metabolic consequences of constant versus compensating phenology, we need more (1) measurements of plant organ activity as organs develop and age, and (2) experiments manipulating phenological status to test the interaction between phenology and physiology (including photosynthesis and respiration) under various treatments (e.g. drought, temperature, and herbivory). When a measured variable (e.g. mass or volume) is the sum of multiple component variables (Fig 1a) then those components should be characterized (if possible) in tests for scenarios when the time series of the measured variable is not aligned with that of the component variable of interest. Fourier analysis is a promising tool for decomposing phenological cycles (Bush et al., 2016), and should be explored for revealing phenology that is otherwise ambiguous.

Phenological events can happen quickly and vary across landscapes. Fine temporal and spatial resolution will capture patterns that might otherwise be missed (e.g. Smith et al. 2019). How we measure phenological patterns has moved beyond plant-level measurements to landscape measurements as technology has evolved, and we need to continue expanding our capacity for detecting plant phenological activity at multiple spatial scales (e.g. leaves to canopies to landscapes). Remote sensing technologies offer valuable tools for gathering

phenological data on large spatial scales. Chlorophyll fluorescence remote sensing products promise to test the physiological interpretation of ‘greenness’ from the more traditional MODIS products (Guan et al., 2015; Lee et al., 2013; Porcar-Castell et al., 2014). Continuous or frequent high resolution near-surface remote sensing instrumentation such as phenocams (Klosterman et al., 2014; Lopes et al., 2016; Wu et al., 2016) and lidar (Calders et al., 2015) offer finer spatial resolution data to complement and potentially validate satellite-based phenology-related products.

Although satellite-derived products are valuable tool for phenology (e.g. Guan et al 2015), some phenological patterns remain cryptic when relying on remote sensing tools. Reflectance-based indices from satellites reveal more about the phenological status of upper canopy leaves and shoots than about the hidden phenological activity of roots, boles, and internal plant processes. Further development of remote sensing tools may help reveal hidden phenologies; for example, lidar can be used to estimate LAI at all canopy heights, helping infer leaf phenological patterns for deeper canopy layers that are hidden from other sensors (Tang & Dubayah, 2017). We urge more tests to evaluate when remote sensing signals do, and do not, link to phenology, including time series of comparisons between remote sensing signals and plant-level measurements (e.g. changes in leaf production or woody biomass). In addition, the development of high-throughput methods for evaluating gene expression (Kris et al., 2007), together with the growing databases of annotated genomes, offer the opportunity to complement aboveground measurements with information about regulation of internal or below-ground activities.

## **5.2 Recommendations for model development**

In TBMs, plant structures (e.g. leaves) are produced or shed, and processes are switched ‘on’ or ‘off’, based on rule sets about temperature, moisture, and photoperiod, or (in about a third of TBMs), are prescribed based on remotely sensed indices and other derived products instead of being simulated internally (Fisher et al., 2014; Huntzinger et al., 2012). In either case, the TBM representation of phenological processes relies heavily on observations that are readily collected at large scales, such as climate data and satellite-based remote sensing products. We need to determine when this reliance on apparent phenology limits our ability to make robust long-term predictions of terrestrial carbon, water, and energy budgets or future boundary shifts of biomes.

A process or parameter in a model is important, in terms of our predictive ability, if it causes large changes in a response that we want to predict (high sensitivity), and/or if it is highly uncertain (Dietze, 2017). For TBMs, we need more sensitivity analyses that evaluate the impact of including or excluding potential phenological schemes, and uncertainty assessments that quantify sources of uncertainty (e.g. Migliavacca et al., 2012). Specific phenological dynamics ripe for possible implementation in TBMs include asynchronous allocation to various plant organs (e.g. through prioritization schemes or time lags), environmental controls over carbon allocation (Guillemot et al., 2017), and plant organ age-dependency of metabolic capacity (e.g. photosynthetic capacity as a function of leaf age and root respiration as a function of root age; (Albert et al., 2018; De Weirdt et al., 2012; Fukuzawa et al., 2011). By examining the sensitivity of modelled ecosystem-scale fluxes to such processes, modelers can strike a balance between over-parametrizing versus excluding important processes in TBM models. Knowledge of which phenological states, processes, and parameters within models show high sensitivity or uncertainty can also help guide empirical research priorities.

Evaluations of uncertainty and sensitivity require first having model formulations of phenology. As we have argued, study efforts are not uniform, and phenological patterns may be cryptic such that they can only be resolved with multiple measurements (e.g. inputs and outputs or multiple variables). In these cases, it may be difficult to find enough information to develop phenology schemes. Model-data comparisons, with observational data coming from multiple independent sources (and multiple organs) at multiple scales (e.g. eddy covariance time series, and measurements of allocation in individuals) should help determine if an important phenological process could be wholly missing from models. Joint model and empirical efforts can then identify, characterize, model, and evaluate the importance of the excluded phenological processes.

Finally, we emphasize the value of drawing upon empirical and theoretical ecology, evolution, and physiology for the development and refinement of phenological models. In systems where the temporal dynamics of plant acquisition and allocation have been shown to be under selection to increase fitness within climatic and biological constraints, optimization models may be useful (e.g. Caldararu, Purves, & Palmer, 2014; Kikuzawa, 1991; 1996), but they should be expanded to include multiple resources (e.g. moisture and nutrient optimization in addition to carbon), and trade-offs between multiple purposes, such as growth and reproduction (Iwasa, 2000). However, it is also important to recognize that life history imposes temporal structure relevant to modelling at the seasonal time scale, such as timelines for recruitment, maturation, and mortality in annual plants, or timelines for development of the photosynthetic apparatus in new leaves with different lifespans. Thus, a valuable challenge will be to formalize demographic and physiological timelines in models and test their impact on model sensitivity and uncertainty.

## 6. CONCLUSION

A growing body of research shows that capturing cryptic phenologies is required for a complete picture of seasonal resource allocation and acquisition strategies, constraints, and consequences across many scales. Understanding the full scope of cyclic and recurrent biological events in plants is critical for advancing our understanding of plant ecology and evolution, and for predicting responses and feedbacks to climate change. We call for further recognition and exploration of cryptic phenologies—including compensatory processes, non-structural carbohydrates dynamics, wood formation, and root production —through new technologies, TBM development, and time series of intensive plant-scale measurements.

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