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

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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

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102 1974, and (*phenology, n. : Oxford English Dictionary*, 2005). In contrast with broad

103 contemporary definitions of phenology, studies of phenology often reflect the origin and history

104 of the term by focusing on readily apparent biological events. These are generally aboveground

105 and accompanied by changes that are readily and reproducibly distinguished with human senses

106 such as visible changes in color, position, mass and volume. In plants, these include phenomena

107 such as germination in annual plants, synchronized leaf production (leaf flush) and abscission in

108 deciduous forests (Murali & Sukumar, 1993; Richardson & O'Keefe, 2009), and the onset of

109 anthesis (flower opening) (Schwartz, 2013). Some phenological patterns, such as deciduous

110 forest leaf onset, are also apparent at canopy and larger spatial scales with remote sensing tools

111 ranging from phenocams to satellites (Badeck et al., 2004; Buitenwerf, Rose, & Higgins, 2015).

112 Studying the timing and controls of such apparent biological events has contributed to

113 understanding the evolution of plant traits and strategies in response to cycles in temperature,

114 precipitation, photoperiod, and other physical variables (Chuine, 2010; Z. Huang, Liu, Bradford,

115 Huxman, & Venable, 2016; Pau et al., 2011; van Schaik, Terborgh, & Wright, 1993).

116 Phenological studies have also advanced our understanding of ecology, as many phenological

117 patterns are coupled to biotic interactions such as intra-annual dynamics of predator or mutualist

118 populations (Pau et al., 2011; Schwartz, 2013). More recently, some phenological events, such as

119 date of anthesis or first leaf emergence, have proven useful indicators of biological responses to

120 climate change (e.g. Parmesan & Yohe, 2003), and the relative ease of observing such events has

121 enabled citizen science at regional and continental scales (Schwartz, Betancourt, & Weltzin,

122 2012).

123   However, many processes in plants are *not* readily apparent, but are no less cyclic or

124 seasonal than the more easily observed phenomena that humans have historically monitored.

125   These phenologies are what might be called 'cryptic.' Some phenological patterns are difficult to

126   detect because they are hidden, including below-ground activities such as allocation to roots, and

127   internal processes such as allocation to carbohydrate reserves or cell differentiation. Other

128   phenological patterns are missed or misinterpreted based on common measurements at typical

129   scales of examination (e.g. changes in mass, area or volume of plant organs or of biomass pools).

130   Cryptic phenologies are not as well understood as apparent phenologies, and they have not been

131   used as indicators of climate change. Yet phenologies, including cryptic phenologies, play

132   critical roles in ecosystems, and mediate large-scale fluxes of carbon, nutrients, water, and

133   energy that are essential to consider as Earth's climate changes (Abramoff & Finzi, 2015;

134   McCormack, Adams, Smithwick, & Eissenstat, 2014; Noormets, 2009; Richardson, Keenan, et

135   al., 2013b).

136   To address the disparity between the narrow scope of apparent phenology and the much

137   broader scope of cyclic and seasonal plant activities, we first offer a framework with terminology

138   that identifies the underlying challenges to observing, interpreting, and modeling cryptic

139   phenologies. Then, focusing on trees, we review specific case studies in which missing cryptic

140   phenology leads to problems for understanding and modeling seasonal ecosystem processes:

141   wood allocation in a temperate mixed forest, and leaf phenology in tropical evergreen Amazon

142   forests. We emphasize that attention to cryptic phenology is timely because many terrestrial

143   biosphere models (TBMs, the models used to represent vegetation of the land surface in Earth

144   system models and needed for climate change predictions; Fisher, Huntzinger, Schwalm, &

145   Sitch, 2014), assume that cryptic phenologies are strongly correlated with apparent phenologies,

146   and that such assumptions can lead to misattribution of the causes behind observed fluxes of

147   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
Apparent				
Phases and events easily observed by humans.	• Bud burst[1] • Leaf abscission[2] • Anthesis[3] • Fruit maturation[4]	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).[5]	• Defining the duration of the growing season in seasonally dormant systems.[6,7] • Testing capacity of hydrothermal models to predict events such as germination.[8,9] • Using changes in timing of phenological events as indicators of climate change.[10,11,12]
Cryptic: hidden				
Phases and events that are internal or obstructed by some barrier and thus difficult to detect.	• Below-ground processes such as root production.[13,14] • Structural changes within cells or tissues such as xylem formation.[15] • Remote sensing in cloudy regions such as wet tropical forests.[16]	No, but these blind spots are generally acknowledged.	Often assumed to be linked to or dependent on apparent phenology.[17,18] This assumption is generally explicit.	• Modeling of whole plant carbon and water dynamics.[19,20] • Estimating intra-annual cycles of biomass gain.[15] • Identifying temporal variation in below-ground interactions and associations.[21,22]
Cryptic: ambiguous				
Phases and events that are missed or misinterpreted due to summed variables or compensatory processes in the same variable.	• Leaf quantity appears constant despite leaf turnover because new leaf production compensates for simultaneous old leaf abscission.[23] • Bole diameter can be affected by both wood formation and water status.[24]	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.	• Decomposing measurements into components that reveal phenological strategies.[25,26] • Attributing cycles of ecosystem flux to endogenous versus exogenous drivers.[27,28] • Resolving lagged responses from instantaneous responses and their relationship to periods of stress.[29,30]

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[1] 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

[2] (Escudero & Del Arco, 1987)

[3] (Smith-Ramirez, Armesto, & Figueroa, 1998)

[4] (Spellman & Mulder, 2016)

[5] (Huntzinger et al., 2012)

[6] (Churkina, Schimel, Braswell, & Xiao, 2005)}

[7] (Schwartz, 2013)

[8] (Bauer, Meyer, & Allen, 1998)

[9] (Hardegree, 2006)

[10] (Badeck et al., 2004)

[11] (Schwartz, AHAS, & AASA, 2006)

[12] (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007)

[13] (Steinaker & Wilson, 2008)

[14] (Radville, McCormack, Post, & Eissenstat, 2016)

[15] (Cuny et al., 2015)

[16] (Asner, 2001)

[17] (Delpierre, Berveiller, Granda, & Dufrene, 2015)

[18] (Abramoff & Finzi)

[19] (Hu, Moore, Riveros-Iregui, Burns, & Monson, 2010)

[20] (Michelot et al., 2012)

[21] (Mullen & Schmidt, 1993)

[22] (S. W. Simard et al., 2012)

[23] (Albert et al., 2018)

[24] (Chitra-Tarak et al., 2015)

[25] (Tang & Dubayah, 2017)

[26] (Smith et al. 2019)

[27] (Wu *et al.*, 2016)

[28] (Migliavacca *et al.*, 2015)

[29] (Ogle *et al.*, 2015)

[30] (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;

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175 Chavana-Bryant et al., 2017; Lopes et al., 2016; Richardson et al., 2018; Wu et al., 2017).

176 Hidden phenological patterns are challenging and/or time-consuming to measure, but the

177 scientific community frequently acknowledges the scarcity of these measurements, and models

178 including hidden phenology explicitly define their representation within allocation schemes (e.g.

179 Abramoff & Finzi, 2015).

180   Phenological patterns in plants are *ambiguous* if phases and events are missed or

181 misinterpreted due to summed variables or compensatory processes in the same variable (Table

182 1). A measured variable (e.g. plant mass, canopy leaf area, or bole volume) may be a function of

183 multiple variables that are not synchronized with each other (Fig. 1a), making it difficult to

184 interpret the temporal changes in the measured variable. For example, determining whether

185 changes in tree stem diameter are caused by long-term carbon gain (such as xylem wall

186 thickening), or reversible changes in plant water status (such as stem expansion or shrinkage), is

187 difficult solely on the basis of stem diameter measurements (Chitra-Tarak et al., 2015; Cuny et

188 al., 2015; Sheil, 1997). Additional examples of ambiguous phenological patterns arise when, for

189 a given system, there are inputs and outputs of the same variable that are compensatory,

190 maintaining the appearance of constancy despite change. For example, compensatory leaf

191 production and abscission could maintain a constant total quantity of leaves in the canopy,

192 belying underlying cycles in leaf production and abscission (Albert et al., 2018; Doughty &

193 Goulden, 2008; Wu et al., 2016). In this example, at least two of the three terms (inputs, outputs,

194 and total) need to be sufficiently constrained by measurements to determine whether the steady

195 state of the total is achieved due to *constant* inputs and outputs (Fig. 1b) versus cyclic, but

196 *compensatory* inputs and outputs (Fig. 1c). Whatever the scale of study, measuring multiple

197 terms over time requires more effort and/or instrumentation, and this difficulty contributes to the

198 challenge of recognizing and resolving ambiguous phenology.

199   Whereas hidden phenological patterns are often acknowledged to exist, but rarely

200 measured, ambiguous phenological patterns are not frequently acknowledged because

201 measurements *are* being made—the challenge lies in interpreting those measurements. For

202 example, we understand that root phenology is hidden, and difficult to measure, because roots

203 are underground. By contrast, we may not even realize that leaf production and loss show

204 seasonal rhythms if the quantity of leaves in a canopy is largely constant (a compensatory

205 scenario). The distinction between hidden and ambiguous categories is not absolute because

206 phenology could be both hidden and ambiguous. For example, the mechanism of biomass gain

207 (xylogenesis) is hidden within stems, and stem diameter represents an integration of cells at

208 different stages in the sequence of xylogenesis: cell expansion, secondary cell wall thickening,

209 lignification and dead cells (Cuny et al., 2015; Plomion et al., 2001). Thus changes in stem

210 diameter emerge from expansion as well as biomass gain (Cuny et al., 2015), resulting in some

211 ambiguity.

212   Cryptic phenologies do not follow fundamentally different rules than their more apparent

213 counterparts. Plant phenologies, in general, are consequences of biology, climatic seasonality,

214 and their interactions. Yet a focus on cryptic phenology challenges us to explicitly consider our

215 current observational blind spots. These blind spots may prevent us from gaining a

216 comprehensive understanding of organismal strategies and limitations in relation to their biology

217 and physical environment, with consequences for our understanding of population, community,

218 and ecosystem ecology. Ultimately, our ability to document, understand, and model the

219 component processes that contribute to large-scale biosphere/atmosphere exchange of CO_2 and
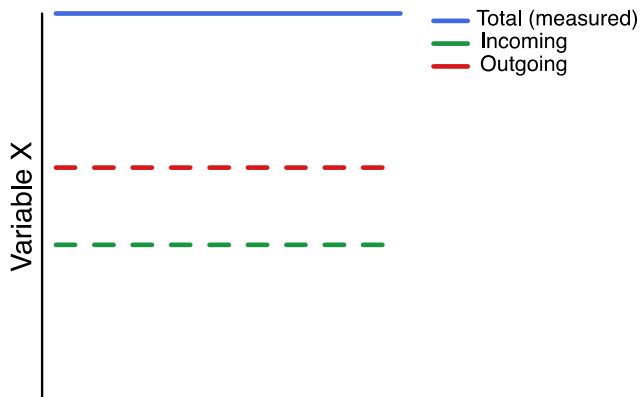
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220   water vapor, impacts our ability to predict responses of natural systems to global change (Getz et

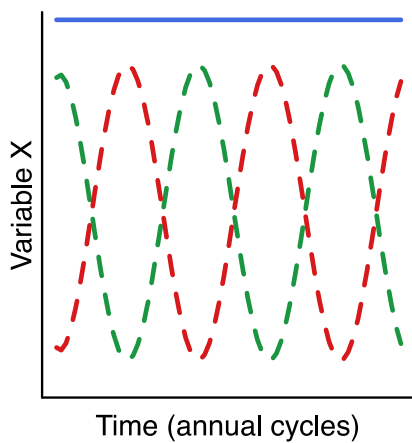221   al., 2017; Noormets, 2009; Richardson et al., 2012).

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(a) Example 1: Measured variable is the sum of multiple other variables with different temporal patterns

Legend: Total (measured), Variable Y, Variable Z

y-axis: Variable Y, Z, and Total
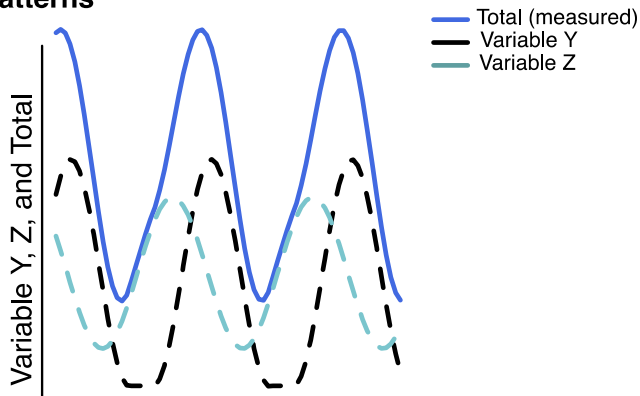
(b) Example 2: Measured variable is the sum of constant incoming and outgoing pools

Legend: Total (measured), Incoming, Outgoing

y-axis: Variable X

(c) Example 3: Measured variable is the sum of compensatory incoming and outgoing pools

y-axis: Variable X

x-axis: Time (annual cycles)

Figure 1: Examples of ambiguous phenological patterns. In example 1, multiple variables (Y and Z) contribute to some total that is measured. Variables Y and Z may have different peak timing, different rates of change, and/or different amplitudes, that become summed for the measured total. Thus the phenological patterns of individual variables Y and Z are ambiguous. In examples 2 and 3, the total for some biological variable X is the sum of an incoming (new) pool and outgoing (old) 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: gross primary productivity in tropical evergreen forests, and allocation to wood in

temperate deciduous 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

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251 processes can be necessary for correct attribution of cause and effect—and ultimately modeling

252 ecosystem processes—in many systems.

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254 **3.1 Cryptic phenology of bole growth in temperate forests: implications for the timing of**

255 **carbon allocation to wood**

256 A TBM model-data comparison of bole growth at Harvard Forest, a temperate mixed forest site,

257 reveals the challenge of estimating and modeling the hidden phenology of wood allocation.

258 Allocation to wood in trees is necessary for estimations of forest carbon stocks (Kellner and

259 Clark 2012), and important for characterizing fast versus slow growth strategies across species

260 (Chave et al., 2009; Reich, 2014). The intra-annual timing of wood allocation may show how

261 carbon gain responds to seasonal climate, and reveal periods of vulnerability or resilience to

262 stress (Babst et al., 2014; Battipaglia et al., 2010). The process of woody biomass gain (from

263 xylogenesis) is hidden within boles (Cuny et al. 2015), and tree or plot scale biomass cannot be

264 directly measured without harvesting trees (Clark & Kellner, 2012). Because of this, the most

265 common approach of estimating woody biomass change is to measure bole diameter growth

266 increment for use with taxa-specific allometric equations (Chave et al., 2014; Chojnacky, Heath,

267 & Jenkins, 2014). This approach is used in both multi-year (e.g. McMahon, Parker, & Miller,

268 2010) and seasonal studies (e.g. Delpierre et al., 2016).

269 We asked whether TBMs captured the phenology of carbon allocation to wood, and the

270 phenology of carbon allocation to leaves, with equal success. We expected that TBMs would be

271 challenged to capture the phenology of carbon allocation to wood because it is hidden, whereas

272 carbon allocation to leaves is more apparent given that this forest contains many deciduous tree

273 species with spring leaf emergence and autumn senescence. To examine the phenological

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274   patterns of allocation to wood at Harvard Forest, we estimated the net primary productivity

275   (NPP) allocated to wood (NPP_{wood}) based on allometric regression equations applied to a bi-

276   weekly time series of high accuracy diameter at breast height (DBH) measurements from

277   dendrometer bands (McMahon & Parker, 2014) for three tree species (supporting information

278   appendix S1). We estimated NPP allocated to leaves (NPP_{leaf}, Fig. 2a) at Harvard Forest based

279   on leaf area index and litterfall time series (J. W. Munger, n.d.; W. Munger & Wofsy, 2018;

280   Urbanski et al., 2007; supporting information appendix S2). Resulting NPP_{leaf} and NPP_{wood}

281   reveal that carbon investment in leaves and wood is highest early in the growing season (Fig. 2).

282   The peaks in simulated NPP_{leaf} were within days of the estimated peak NPP_{leaf} (and close to leaf

283   budburst, which typically occurs around May 6 (Keenan and Richardson, 2015). By contrast,

284   simulated phenological patterns in wood-related output variables from three TBMs showed

285   greater variation (Fig. 2, appendix S3). While the Community Land Model version 4.5 (CLM4.5)

286   shows a peak close to that seen in the observations (around the time of budburst, at May 5), the

287   peak for $ORCHIDEE_{TRUNK}$ and CLASS are months later (August 1 and August 11 respectively).

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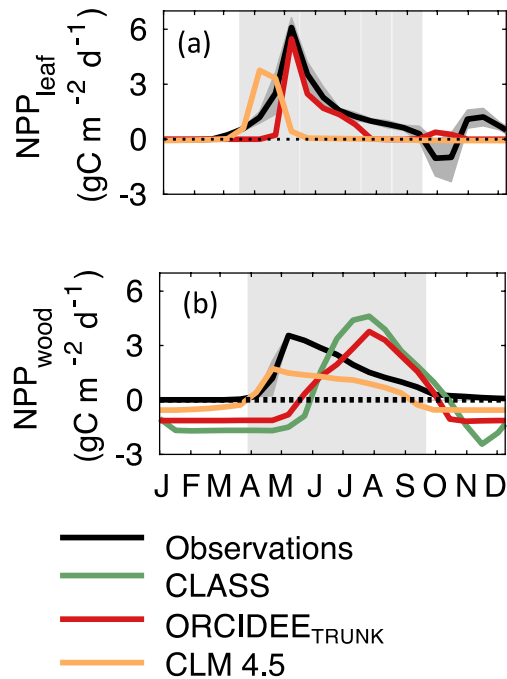
Figure 2: Seasonality of observed (black ± gray standard deviation) versus model-simulated (colors) Net Primary Productivity (NPP) allocated to a) leaf biomass (NPP$_{leaf}$), and b) woody biomass (NPP$_{wood}$) at a temperate deciduous forest. NPP$_{leaf}$ observations were calculated as $(d\text{LAI}/dt)$ • LMA + litterfall where LAI is leaf area index and LMA is leaf mass per area. For models, NPP$_{leaf}$ is calculated as the change in leaf biomass. NPP$_{wood}$ observations were from allometry using diameter-at-breast-height (DBH) increment measurements compared with outputs from three land surface models. For models, NPP$_{wood}$ was calculated as $(X_i - X_{i-1}) / (t_i - t_{i-1})$ where X is the model output variable most comparable to above-ground woody biomass (in gC m^{-2} day^{-1}) for each model (which was vegetation biomass for CLASS, aboveground heartwood plus sapwood for ORCIDEE$_{TRUNK}$, 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. NPP$_{leaf}$ simulations were not available for CLASS. Full NPP$_{wood}$ 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

woody biomass (Clark & Kellner, 2012), and to consider that TBMs differ in how the wood pool

is defined, which is not necessarily identical to above-ground 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

308   by changes in plant water status in addition to changes in biomass, and so seasonal changes in

309   water availability could affect biomass estimations derived from allometry unless a correction is

310   applied (Chitra-Tarak et al., 2015). The actual biomass gain (from xylogenesis) may also lag

311   increases in DBH by weeks (Cuny et al., 2015). Explicit recognition of the distinction between

312   measurable metrics (such as DBH) and the underlying variable we want to characterize or model

313   (such as carbon biomass gain) motivates investigators to quantify uncertainty, and test for

314   scenarios when proxies do not work well.

315   Despite the limitations of the observations and models, the comparison suggests that

316   some models (like CLM 4.5) align moderately well with DBH-derived NPP_{wood}, while others lag

317   DBH-derived NPP_{wood} by months. This divergence in model behaviors highlights the importance

318   of understanding the mechanisms driving both simulated and observed phenologies. The timing

319   of allocation to biomass and wood-related variables in these TBMs is primarily determined by

320   the pattern of NPP across seasons. In ORCHIDEE for example, a fraction of NPP is

321   instantaneously allocated to sapwood, then sapwood biomass is converted into heartwood

322   biomass based on a one-year time constant (Krinner et al., 2005). Ultimately, model NPP is

323   controlled by site-specific climate conditions and representations of forest physiology (e.g. plant

324   functional type), including leaf phenological patterns (e.g. leaf onset/abscission). Thus, in many

325   TBMs, leaf phenology represents wood phenology by proxy because wood allocation is

326   determined by a fraction of NPP, and the cycle of NPP is largely determined by leaf phenology

327   (Delpierre et al., 2016).

328   In contrast with model representations, physiological and tree-ring studies suggest that

329   the mechanisms underlying wood phenology include environmental cues (e.g. temperature;

330   Delpierre *et al.* 2016), ontogeny of wood cells (Cuny et al., 2015; Plomion et al., 2001), and

331 priorities in allocation through time (e.g. allocation of carbon to wood growth versus storage as

332 nonstructural carbohydrates; Richardson, Carbone, et al., 2013a). These factors may play a role

333 in determining when trees are vulnerable or resilient to stress. For example, developing wood

334 cells expand before their cell walls thicken with carbon-rich polysaccharides and lignins, and late

335 wood is more dense than early wood in temperate species (Plomion et al., 2001), so trees at

336 different stages in the sequence of wood development could be more or less sensitive to drought

337 stress. Testing and developing model frameworks for such hypotheses is currently challenging

338 because the timing of carbon allocation to wood is hidden *in vivo*. More direct measurements of

339 wood formation (e.g. Cuny *et al.* 2016), and nonstructural carbohydrates (e.g. Newell, Mulkey,

340 & Wright, 2002), synchronized with frequent measurements of DBH and leaf phenological

341 patterns, would help us to understand and model controls over wood phenological patterns

342 (Delpierre et al., 2016; Guillemot et al., 2017), and how the timing of wood allocation relates to

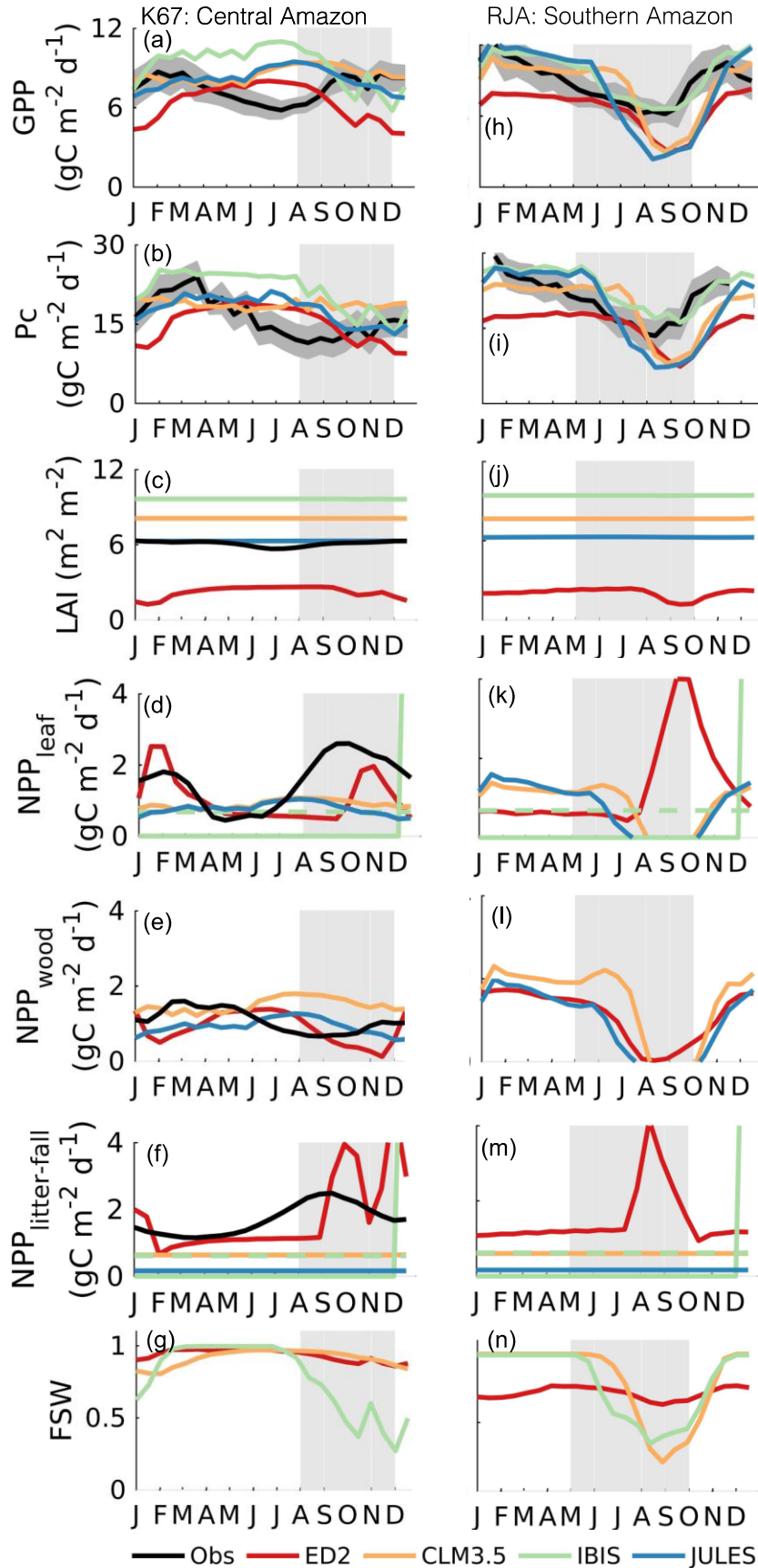343 growth strategy, environmental fluctuations, and other plant traits.

344

345 **3.2 Amazon evergreen forests: implications of cryptic phenology for seasonality of**

346 **ecosystem carbon fluxes**

347 The challenge of cryptic phenology is not confined to a particular plant organ. Amazon

348 evergreen forests near the equator offer a case study where leaf phenology is ambiguous. Much

349 of the Amazon basin experiences annual wet and dry seasons (Restrepo-Coupe et al., 2013), and

350 this regular seasonal variation in cloud cover and precipitation may select for phenological

351 strategies that match plant activities with resource availability (Doughty et al., 2014; Graham,

352 Mulkey, Kitajima, Phillips, & Wright, 2003; M. O. Jones, Kimball, & Nemani, 2014; van Schaik

353 et al., 1993). Most of the Amazon is remote, making ground-based observations of phenology

354 difficult, especially given the many observations needed to sample the high diversity of tree

355 species (Cardoso et al., 2017) and strategies (Reich, 1995). Observations of canopies from

356 satellites are often obstructed by clouds (Asner, 2001), difficult to interpret (Samanta et al.,

357 2012), and the subject of controversy surrounding technical artifacts and their correction (Huete

358 et al., 2006; Morton et al., 2014; Saleska et al., 2016). Yet many recent studies offer evidence

359 that leaf production, leaf abscission, wood production and root production exhibit annual

360 rhythms in Amazon forests (Doughty et al., 2014; Girardin, Malhi, & Doughty, 2016; Lopes et

361 al., 2016; Wagner et al., 2016).

362   Many TBMs seem to be missing these phenological processes (Restrepo-Coupe et al.,

363 2017). Evidence that TBMs are lacking adequate phenological representation comes from a

364 model inter-comparison for a network of ecosystem flux observations sites (eddy flux towers) in

365 Amazonia (Restrepo-Coupe, et al., 2017). For illustration, we discuss the contrasting cases of

366 equatorial versus southern evergreen forest sites in the Amazon basin of Brazil. At the equatorial

367 site (K67 in the Tapajós National Forest, Brazil), four TBMs showed significant divergence from

368 the estimated interannual pattern of whole-system photosynthetic fluxes (Fig. 3a, gross primary

369 productivity, (GPP; $gC\ m^{-2}\ d^{-1}$) and a metric of photosynthetic capacity, (Pc; $gC\ m^{-2}\ d^{-1}$) for K67;

370 (Restrepo-Coupe et al., 2017). The reason for the divergence is that modeled photosynthetic

371 patterns are driven by environmental variability -- measures of soil water stress in this case

372 (model calculated soil water stress index 'FSW' for K67, Fig. 3b-g) -- which suppresses GPP

373 during the long dry season. Yet the observed interannual pattern of photosynthesis in this

374 ecosystem appears to be driven by something beyond instantaneous responses to seasonal

375 climate fluctuations.

376   Since TBMs already include climatic seasonality, their failure to capture GPP seasonality

377   suggests that phenological processes operate at the equatorial site that are separate from the

378   instantaneous physiological responses already represented. Canopy phenological activity could

379   drive the observed GPP via two mechanisms: 1) dry season increases in quantity of canopy

380   leaves (quantified as leaf area index, or LAI) and/or 2) dry season increases in canopy

381   photosynthetic capacity on a per unit area basis (Lopes et al., 2016; Restrepo-Coupe et al., 2017;

382   Wu et al., 2016). Observations of leaf quantity (LAI) from equatorial Amazon sites show that

383   LAI varies little across seasons (e.g. Fig. 3c 'LAI' shows low seasonality at K67). Leaf turnover,

384   however, exhibits a dry season pulse (Fig. 3e,f: 'NPP$_{leaf}$' and 'NPP$_{litter-fall}$'), suggesting that LAI

385   is maintained because leaf production compensates for near-simultaneous leaf fall during the dry

386   season. As a result, LAI exhibits modest seasonal variation relative to seasonal variation in leaf

387   litterfall and leaf flush (Fig. 4). The seasonality of total LAI also fails to represent within-canopy

388   dynamics, as compensatory leaf area patterns have been identified between the upper and lower

389   canopy levels at K67 (Smith et al., 2019). Since new (recently expanded) leaves have high rates

390   of photosynthesis, replacing old leaves with new leaves can increase photosynthetic capacity of

391   the canopy on a per unit area basis (Albert et al., 2018; Doughty & Goulden, 2008; Niinemets et

392   al., 2012; Pantin, Simonneau, & Muller, 2012; Wu et al., 2016).

23

K67: Central Amazon

RJA: Southern Amazon

(a) GPP (gC m^{-2} d^{-1})
(h)
(b) Pc (gC m^{-2} d^{-1})
(i)
(c) LAI (m^2 m^{-2})
(j)
(d) NPP$_{leaf}$ (gC m^{-2} d^{-1})
(k)
(e) NPP$_{wood}$ (gC m^{-2} d^{-1})
(l)
(f) NPP$_{litter-fall}$ (gC m^{-2} d^{-1})
(m)
(g) FSW
(n)

Obs — ED2 — CLM3.5 — IBIS — JULES

393

19

Figure 3: Annual cycles of observed (black ± 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 (725-875umol m^{-2} s^{-1}), vapor pressure deficit, air temperature and light quality measured as cloudiness index (all time mean ± 1 standard deviation)); leaf area index (LAI); net primary productivity (NPP) allocated to leaves (leaf production; NPP$_{leaf}$); NPP going to litterfall (NPP$_{litterfall}$), and NPP allocated to wood (NPP$_{wood}$); 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 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 increases early in the dry season and

decreases late in 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

424 plant water status.
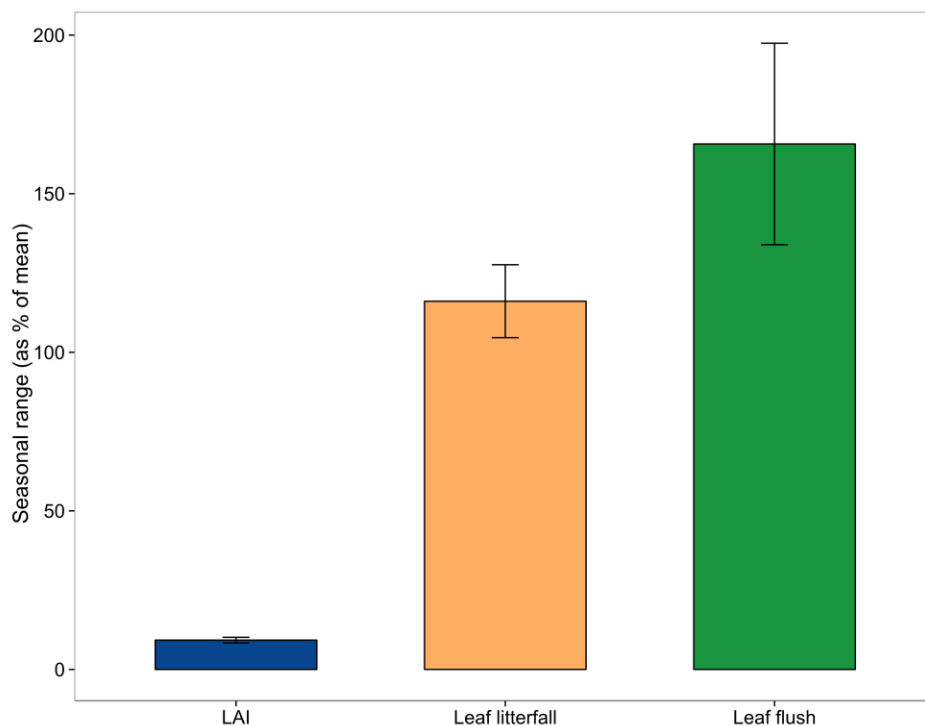
425

426 Figure 4: Seasonal canopy dynamics of Leaf Area Index (LAI), leaf litterfall, and leaf production
427 averaged across five Amazonian sites, showing that large leaf turnover is concealed by near-
428 constant LAI. The pulses of litterfall and leaf production support compensatory leaf phenology
429 (Fig 1c) rather than constant leaf phenology (Fig 1b). Bars show mean values of annual amplitude
430 scaled for studies (n=5 sites) of lowland evergreen tropical forests where both LAI and litterfall
431 have been measured. Seasonal range is the annual amplitude scaled by mean value and is calculated
432 as the difference between the maximum dry season value and the minimum wet season value,
433 divided by the mean annual value (%). Error bars show standard deviation of the mean. Studies
434 included in this figure: Tambopata-Candamo Reserve, south-eastern Peru (Girardin et al. 2016);
435 Caxiuana, Floresta Nacional de Caxiuana, Pará, Brazil (Girardin et al. 2015); K83 (Doughty &
436 Goulden 2008) and K67 (Brando et al. 2010 and Malhado et al. 2009) are located in the Tapajós
437 National Forest, Pará, Brazil. Sites experience a range of mean annual precipitation values (1900
438 – 2572 mm).

439 This interpretation is consistent with studies asserting that tropical evergreen forests produce new

440 leaves during periods of high light if they are not strongly water-limited (Doughty & Goulden,

441 2008; Graham et al., 2003; Guan et al., 2015; M. O. Jones et al., 2014; Reich & Borchert, 1984;

442 Restrepo-Coupe et al., 2013; van Schaik et al., 1993; Wu et al., 2016). This continuum between

443 precipitation-driven and light-driven tropical evergreen forest phenological strategies is not

444 included in most TBMs, and therefore might account for some of the divergence in their GPP

445 projections (Restrepo-Coupe et al., 2017).

446
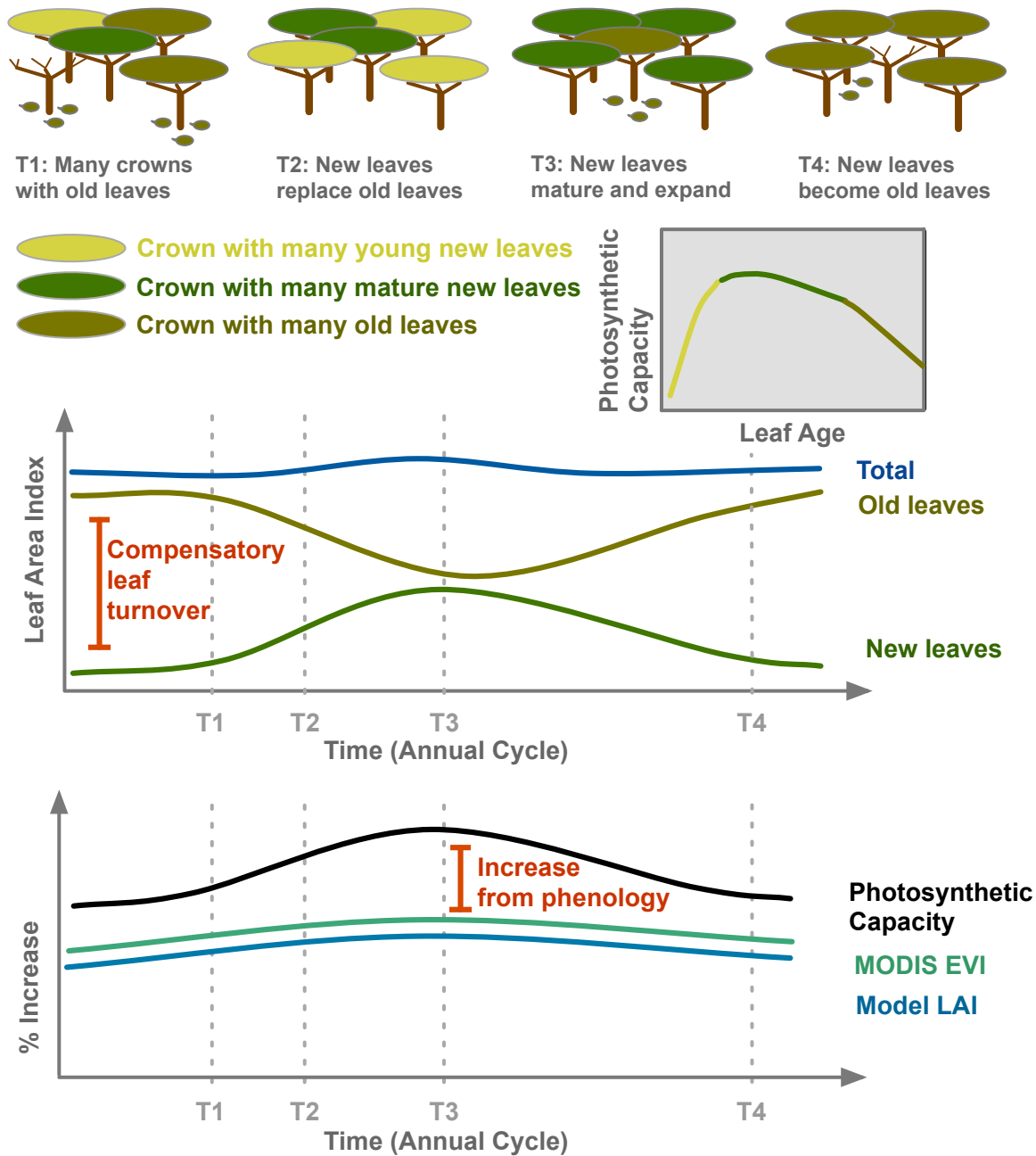
Figure 5: Illustration of how cryptic leaf turnover creates a phenological pattern in canopy
photosynthetic capacity. Top: Individual crowns drop old leaves and produce new leaves with
some degree of synchronization. Middle: the proportion of leaf area index belonging to previous

450 year's growth (old leaves) and new leaf growth (new leaves) changes through the dry season. Here
451 leaf phenology is difficult to detect because of compensatory inputs and outputs (see Fig 1c). Inset:
452 leaf photosynthetic capacity depends upon leaf age. Lower panel: the combination of leaf turnover
453 and leaf ontogeny increase the canopy photosynthetic capacity, but neither total LAI nor satellite-
454 based proxies for LAI and greenness show this same increase.

455   Equatorial Amazon sites such as K67 provide an example where resolving ambiguous

456 phenology by testing whether leaf phenology is compensatory versus constant, and

457 acknowledging the age-dependent physiology of leaves, is important for understanding and

458 modeling a process, such as forest photosynthesis, at a large scale. Some plant functional types

459 (PFTs) within TBMs allow for photosynthesis to vary with leaf age, but with a focus on

460 temperate deciduous plants. For example, the Joint UK Land Environment Simulator (JULES)

461 accounts for damage and senescence accumulation by reducing photosynthesis during the

462 growing season (Clark et al., 2011), and the Ecosystem Demography model (ED2) decreases the

463 maximum carboxylation rate of Rubisco (V_{cmax}) in the autumn as a function of Julian day

464 utilizing historical MODIS data (Medvigy, Wofsy, Munger, Hollinger, & Moorcroft, 2009). In

465 these cases, time of year or 'season' serves as a proxy for leaf age, which may work well for

466 some PFTs, but not for tropical evergreen broadleaf forests where the 'evergreen' canopy belies

467 cyclic leaf turnover that the PFT ruleset does not include. This case study suggests that

468 accounting for cryptic phenology is necessary for correctly detecting, attributing, and modeling

469 the carbon exchange dynamics of tropical forests (De Weirdt et al., 2012; Y. Kim et al., 2012;

470 Manoli, Ivanov, & Fatichi, 2018; Restrepo-Coupe et al., 2017).

471

472 **4. IMPLICATIONS OF CRYPTIC PHENOLOGY FOR PREDICTION ACROSS**

473 **SCALES**

474 Fine-scale processes, integrated over space and time, create large-scale exchanges of mass and

475 energy between the biosphere and the atmosphere (Monson & Baldocchi, 2014). Here we

476 consider some of the fine scale processes associated with cryptic phenology that, scaled up, have

477 implications for our ability to understand, model, and predict biosphere-atmosphere interactions

478 under climate change.

479

480 *Organ scale*

481   Plant traits can show very high within-species variation due to phenology (Chavana-

482 Bryant et al., 2017), and this variation can surpass interspecific variation for some traits (Fajardo

483 & Siefert, 2016). Specifically, leaf development and aging is associated with changes in internal

484 leaf structure (Lim, Kim, & Gil Nam, 2007; Niinemets et al., 2012), concentrations of secondary

485 metabolites (Z. Liu et al., 1998; Virjamo & Julkunen-Tiitto, 2014), emissions of volatile organic

486 compounds (Alves, Harley, Goncalves, da Silva Moura, & Jardine, 2014; Niinemets et al., 2010),

487 and metabolic rates (Albert et al., 2018; Niinemets et al., 2012; Pantin et al., 2012). For the goal

488 of scaling fluxes from leaves to canopies, these many physiological changes associated with leaf

489 age suggest that distinguishing between constant leaf phenology and compensatory leaf

490 phenology is important not only for tropical forests (as we describe in the first case study above),

491 but for evergreen forests in general.

492   Similarly, root production is accompanied by physiological changes. There are species-

493 specific relationships between root age and root physiology such as respiration rates and nutrient

494 uptake capacity (Bouma et al., 2001; Fukuzawa, Dannoura, & Shibata, 2011). Existing studies

495 that have characterized the hidden phenology of roots have shown evidence of interspecific

496 differences in cycles of fine root production—single flushes, multiple flushes, or constant

497 growth—that could represent strategies for responding to seasonal changes in climate or resource

498 availability (Fukuzawa et al., 2011; McCormack et al., 2014).

24

499

500 *Organismal scale*

501 Natural selection would be expected to favor coordination in the timing of resource acquisition

502 with resource storage and allocation (Sala, Woodruff, & Meinzer, 2012). Since selection acts at

503 the level of individuals, if we want to understand the adaptive value of phenological changes, we

504 need to understand how all plant organs function together, as a unit, through time. It is very

505 difficult to study 'whole' plants in the wild, especially woody plants. Few (if any) studies have

506 quantified the phenologies of all plant organs in wild woody plants to gain an integrated

507 organism-level perspective on phenology (but see Hu et al., (2010) for whole-tree carbon

508 assimilation during the growing season; see Würth, Peláez-Riedl, Wright, & Korner (2005) for

509 seasonal variation in non-structural carbohydrate pools by plant organ; and see Doughty et al.,

510 (2014) for an example plot-scale study of wood, fine root, and canopy phenology). Studies

511 examining phenologies of two organs suggest that phenology is often asynchronous across

512 organs (Abramoff & Finzi, 2015; Wagner, Rossi, Stahl, Bonal, & Hérault, 2013). Comparing

513 phenological patterns of roots and shoots frequently reveals offsets between maximum root

514 growth and shoot growth, and these offsets vary across biomes (Abramoff & Finzi, 2015). In

515 tropical forests, leaf and wood production is often asynchronous (Wagner et al., 2013). The onset

516 and/or termination of growth may also vary; roots in temperate deciduous white oak, for

517 example, continue to elongate in winter after senescence of leaves (Teskey & Hinckley, 1981).

518 Nonstructural carbohydrate reserves also show phenological patterns that are species-dependent

519 (Würth et al., 2005) and affected by phenological patterns of leaves (Palacio, Maestro, &

520 Montserratmarti, 2007). Rates of carbon use regulate carbon uptake in plants (sink-driven

521 photosynthesis; (Fatichi, Leuzinger, & Korner, 2014), so phenological changes in carbon

522   demand should impact the timing of photosynthetic activity.

523   These findings show that capturing the patterns and drivers of hidden and ambiguous

524   phenologies will be needed for a comprehensive understanding of how plants prioritize amongst

525   competing uses of resources and maintain carbon balance, with implications for modeling plant

526   resource use. In most TBMs, the temporal patterns of leaf activity (the size of the leaf pool and

527   the rate of photosynthesis) drive temporal patterns of carbon allocation because carbon allocation

528   to other plant organs is often modeled as a constant proportion of carbon uptake (Abramoff &

529   Finzi, 2015; Delpierre et al., 2016; Guillemot et al., 2017). However, if different plant organs

530   respond to different environmental drivers (Wagner et al., 2016), then models that use leaf

531   activity to generate interannual patterns of activity in hidden organs may fail to simulate

532   observed patterns of root or bole activity at seasonal timescales.

533   How plants prioritize their allocation, through time, to various plant organs or to storage

534   may have consequences for plant resilience or vulnerability to extreme events, and several

535   studies already show that plant vulnerability and/or resilience to extreme events varies due to

536   phenological status and/or season (Craine et al., 2012; M. Huang, Wang, Keenan, & Piao, 2018).

537   We suggest that the timing of extreme events in relation to plant phenological status may be

538   necessary for predicting plant community responses to future climate. For example, plant

539   tolerance to drought or cold could depend on nonstructural carbohydrates (Dietze et al., 2014;

540   Sala et al., 2012), and nonstructural carbohydrates follow seasonal cycles that could indicate

541   internal phenology (Richardson, Carbone, et al., 2013a). Tests of such hypotheses are timely,

542   given that the frequency of extreme climate events is increasing under global climate change

543   (Bellprat & Doblas-Reyes, 2016; Ummenhofer & Meehl, 2017).

544

Community scale

545

546   As climate changes, many studies have demonstrated that phenological patterns shift,

547   impacting species interactions (CaraDonna, Iler, & Inouye, 2014; Memmott, Craze, Waser, &

548   Price, 2007; Miller-Rushing, Hoye, Inouye, & Post, 2010; Polgar & Primack, 2011; Rafferty,

549   CaraDonna, & Bronstein, 2014; Yang & Rudolf, 2010). Fewer studies have probed how hidden

550   phenologies shape species interactions, or how those interactions may be changing. To do so

551   could reveal that phenology mediates impacts of species interactions on plant mortality,

552   reproduction, and metabolism. For example, the timing of insect outbreaks in relation to

553   nonstructural carbohydrate reserves (which are affected by the timing of leaf renewal) may

554   explain interspecific differences in tolerance to defoliation (Chen, Wang, Dai, Wan, & Liu,

555   2017). Further investigation into how species interactions affect hidden phenologies would help

556   gain a more complete understanding of the interplay between climate change, whole plant

557   physiology, and species interactions.

558

Ecosystem to global scale

559

560   Projections of Earth's future climate are particularly sensitive to uncertainties in the land

561   carbon cycle (Friedlingstein et al., 2014). Improving representation of the land carbon cycle in

562   TBMs requires understanding the drivers of phenology, and the role of phenology in mediating

563   biosphere-atmosphere exchanges (Richardson, Keenan, et al., 2013b). Recognizing phenological

564   rhythms at scales from plant organs to communities is prerequisite to identifying their role in

565   large scale (ecosystem to global) cycling of carbon. For example, investigating the distribution of

566   root ages at different times of the year could elucidate larger scale autotrophic respiration or soil

567   resource acquisition processes (because root age affects root respiration and nutrient uptake

27

568 capacity; Bouma et al., 2001). TBMs which are calibrated to match current observations, but that

569 include inaccurate relationships between drivers and vegetation responses, risk making biased

570 predictions of forest response to future climate changes because they do not incorporate

571 underlying biological mechanisms (De Weirdt et al., 2012; Restrepo-Coupe et al., 2017).

572

5. RECOMMENDATIONS FOR MEASURING AND MODELING CRYPTIC

573 PHENOLOGY

5.1 Recommendations for empirical research

576 To reveal cryptic phenological patterns empirically, we need to consider the target, frequency,

577 and methods of measurements. We recommend complementing existing studies and

578 measurements of above-ground, clearly visible phenological changes with measurements of

579 hidden phenological changes (Table 1). Specifically, we need more time series of development

580 and growth of roots (e.g. Abramoff and Finzi 2015, McCormack et al 2014), and internal

581 structures (e.g. Cuny et al. 2015), to learn when leaf phenology directly fuels the phenological

582 patterns of other plant organs (and thus can represent them by proxy), and when it does not.

583 Building upon studies examining synchrony in phenology of multiple plant organs (Bazié et al.,

584 2017; Delpierre et al., 2016; Michelot, Simard, Rathgeber, Dufrene, & Damesin, 2012; Omondi,

585 Odee, Ongamo, Kanya, & Khasa, 2016; Perrin, Rossi, & Isabel, 2017; Wagner et al., 2013),

586 whole-plant phenology studies in which all plant organs and their associated processes

587 (acquisition and allocation of carbon, water, and nutrients) are continuously monitored in the

588 same individual plants across seasons could elucidate the relationship between the phenology of

589 plant organs with each other, and with climate, and test the representation of phenology for

590 various PFTs.

28

591   Revealing cryptic phenological patterns will require more studies explicitly testing

592   whether compensatory processes (Fig. 1c) mistaken for constancy (Fig. 1b) mislead our

593   interpretation of mass, area, or volume time series. To this end, sampling schemes need to go

594   beyond measuring mass, area or volume of plant organs or "pools" (in aggregate) to also

595   measure rates of inputs and outputs to and from organs/pools across time. (Since mass-balance

596   equations have three terms—inputs, outputs, and the accumulated pool—at least two must be

597   measured to obtain a single solution). For example, litterfall time series should be collected to

598   correspond with total leaf area time series. To examine the metabolic consequences of constant

599   versus compensating phenology, we need more (1) measurements of plant organ activity as

600   organs develop and age, and (2) experiments manipulating phenological status to test the

601   interaction betwee phenology and physiology (including photosynthesis and respiration) under

602   various treatments (e.g. drought, temperature, and herbivory). When a measured variable (e.g.

603   mass or volume) is the sum of multiple component variables (Fig 1a) then those components

604   should be characterized (if possible) in tests for scenarios when the time series of the measured

605   variable is not aligned with that of the component variable of interest. Fourier analysis is a

606   promising tool for decomposing phenological cycles (Bush et al., 2016), and should be explored

607   for revealing phenology that is otherwise ambiguous.

608   Phenological events can happen quickly and vary across landscapes. Fine temporal and

609   spatial resolution will capture patterns that might otherwise be missed (e.g. Smith et al. 2019).

610   How we measure phenological patterns has moved beyond plant-level measurements to

611   landscape measurements as technology has evolved, and we need to continue expanding our

612   capacity for detecting plant phenological activity at multiple spatial scales (e.g. leaves to

613   canopies to landscapes). Remote sensing technologies offer valuable tools for gathering

614   phenological data on large spatial scales. Chlorophyll fluorescence remote sensing products

615   promise to test the physiological interpretation of 'greenness' from the more traditional MODIS

616   products (Guan et al., 2015; Lee et al., 2013; Porcar-Castell et al., 2014). Continuous or frequent

617   high resolution near-surface remote sensing instrumentation such as phenocams (Klosterman et

618   al., 2014; Lopes et al., 2016; Wu et al., 2016) and lidar (Calders et al., 2015) offer finer spatial

619   resolution data to complement and potentially validate satellite-based phenology-related

620   products.

621   Although satellite-derived products are valuable tool for phenology (e.g. Guan et al

622   2015), some phenological patterns remain cryptic when relying on remote sensing tools.

623   Reflectance-based indices from satellites reveal more about the phenological status of upper

624   canopy leaves and shoots than about the hidden phenological activity of roots, boles, and internal

625   plant processes. Further development of remote sensing tools may help reveal hidden

626   phenologies; for example, lidar can be used to estimate the LAI of understory plants, helping

627   infer leaf phenological patterns for canopy layers that are hidden from other sensors (Tang &

628   Dubayah, 2017). The development of high-throughput methods for evaluating gene expression

629   (Kris et al., 2007), together with the growing databases of annotated genomes, offer the

630   opportunity to complement above-ground measurements with information about regulation of

631   internal or below-ground activities. We urge more tests to evaluate when remote sensing signals

632   do, and do not, link to phenology, including time series of comparisons between remote sensing

633   signals and plant-level measurements (e.g. changes in leaf production or woody biomass).

634

635   **5.2 Recommendations for model development**

636   In TBMs, plant structures (e.g. leaves) are produced or shed, and processes are switched 'on' or

637   'off', based on rule sets about temperature, moisture, and photoperiod, or (in about a third of

638   TBMs), are prescribed based on remotely sensed indices and other derived products instead of

639   being simulated internally (Fisher et al., 2014; Huntzinger et al., 2012). In either case, the TBM

640   representation of phenological processes relies heavily on observations that are readily collected

641   at large scales, such as climate data and satellite-based remote sensing products. We need to

642   determine when this reliance on apparent phenology limits our ability to make robust long-term

643   predictions of terrestrial carbon, water, and energy budgets or future boundary shifts of biomes.

644   A process or parameter in a model is important, in terms of our predictive ability, if it

645   causes large changes in a response that we want to predict (high sensitivity), and/or if it is highly

646   uncertain (Dietze, 2017). For TBMs, we need more sensitivity analyses that evaluate the impact

647   of including or excluding potential phenological schemes, and uncertainty assessments that

648   quantify sources of uncertainty (e.g. Migliavacca et al., 2012). Specific phenological dynamics

649   ripe for possible implementation in TBMs include asynchronous allocation to various plant

650   organs (e.g. through prioritization schemes or time lags), environmental controls over carbon

651   allocation (Guillemot et al., 2017), and plant organ age-dependency of metabolic capacity (e.g.

652   photosynthetic capacity as a function of leaf age and root respiration as a function of root age;

653   (Albert et al., 2018; De Weirdt et al., 2012; Fukuzawa et al., 2011). By examining the sensitivity

654   of modelled ecosystem-scale fluxes to such processes, modelers can strike a balance between

655   over-parametrizing versus excluding important processes in TBM models. Knowledge of which

656   phenological states, processes, and parameters within models show high sensitivity or

657   uncertainty can also help guide empirical research priorities.

31

658   Evaluations of uncertainty and sensitivity require first having model formulations of

659   phenology. As we have argued, study efforts are not uniform, and phenological patterns may be

660   cryptic such that they can only be resolved with multiple measurements (e.g. inputs and outputs

661   or multiple variables). In these cases, it may be difficult to find enough information to develop

662   phenology schemes. Model-data comparisons, with observational data coming from multiple

663   independent sources (and multiple organs) at multiple scales (e.g. eddy covariance time series,

664   and measurements of allocation in individuals) should help determine if an important

665   phenological process could be wholly missing from models. Joint model and empirical efforts

666   can then identify, characterize, model, and evaluate the importance of the excluded phenological

667   processes.

668   Finally, we emphasize the value of drawing upon empirical and theoretical ecology,

669   evolution, and physiology for the development and refinement of phenological models. In

670   systems where the temporal dynamics of plant acquisition and allocation have been shown to be

671   under selection to increase fitness within climatic and biological constraints, optimization models

672   may be useful (e.g. Caldararu, Purves, & Palmer, 2014; Kikuzawa, 1991; 1996), but they should

673   be expanded to include multiple resources (e.g. moisture and nutrient optimization in addition to

674   carbon), and trade-offs between multiple purposes, such as growth and reproduction (Iwasa,

675   2000). However, it is also important to recognize that life history imposes temporal structure

676   relevant to modelling at the seasonal time scale, such as timelines for recruitment, maturation,

677   and mortality in annual plants, or timelines for development of the photosynthetic apparatus in

678   new leaves with different lifespans. Thus, a valuable challenge will be to formalize demographic

679   and physiological timelines in models and test their impact on model sensitivity and uncertainty.

680

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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