Commentary

Back to the future for plant phenology research

Blockbuster film serials – of the type often released around this time of year – sometimes recharge a popular, but somewhat dragging, franchise by a time-travel trip to the past. Such trips can invigorate by providing important background on characters and storylines, making the return to the current plot more compelling and rich. In this issue of *New Phytologist*, Panchen *et al.* in their article 'Leaf out times in temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy' (pp. 1208–1219) attempt a similar – and welcome – recharge to the current field of plant phenology research.

> '*The field has grown tremendously over the last 30 years . . . making plant phenology the most reported biological indicator of anthropogenic climate change.*'

The field has grown tremendously over the last 30 years as researchers have excelled at documenting shifts in leaf out and flowering times in step with rising temperatures, making plant phenology the most reported biological indicator of anthropogenic climate change. Yet, as studies and datasets have piled up, researchers have struggled to explain the tremendous variation in phenological responses across space, time, and species. Understanding such variation is critical to global carbon models, accurate predictions of future climate change and estimates of shifts in major ecosystem services. Progress towards understanding this variation is buoyed by the rich history of plant phenology research. As one of the oldest areas of scientific inquiry, the field is blessed with a long, diverse literature that, unfortunately, has not been fully exploited during phenology's recent rise in popularity. Panchen *et al.*, however, represent a shifting tide in this regard and a major basis to build towards understanding the documented variation in phenology. Drawing on past literature that considers how phenology correlates with several common plant traits (most prominently Lechowicz, 1984) the authors offer a tacit reminder that plant phenology is also a common – and likely critical – plant trait.

What drives variation in plant phenology: competing hypotheses

Variation in plant phenology offers the raw material to test whether phenology is an important functional trait. As a functional trait, phenology should strongly influence performance, with selection favoring events timed to increase fitness. Two major alternative hypotheses exist, however. First, that phenology is instead a null trait and phenological variation represents merely a random walk of a characteristic under minimal selection (Ollerton & Lack, 1992). A second hypothesis posits that phenology may be phylogenetically conserved (*sensu* Wiens *et al.*, 2010), such that species are constrained in their phenologies based on their clades (Kochmer & Handel, 1986). We note that these hypotheses are distinct but not mutually exclusive; instead, they together may explain current variation in plant phenology.

Recent studies tied to understanding climate change impacts on phenology can be leveraged to provide initial basic tests of these two hypotheses. Several recent studies provide evidence against the 'null trait hypothesis'. For example, warming-induced advances in phenology have been tied to increased performance compared to species that delay or do not shift with warming (Cleland *et al.*, 2012). Furthermore, the expansion of ranges of invasive plants, often rapidly, may be due in part to flexibility in phenology (Colautti *et al.*, 2010). This suggests that phenology may be a critical functional trait, rather than a null trait. With regards to the 'phylogenetic constraint hypothesis', recent studies, including Panchen *et al.*, have examined the importance of evolutionary history in explaining phenological variation with varied results (Willis *et al.*, 2008; Davies *et al.*, 2013). Studies generally find overall phylogenetic patterning in phenology. However, the strength of phylogenetic signal often varies widely across the phylogenies in these studies, with some clades displaying phenologies consistent with their taxonomy and others diverging. Furthermore, as Panchen *et al.* assert, the phylogenetic patterning of phenology may be due in 'part to its correlation with other phylogenetically conserved traits'. Taken together, these studies suggest that research examining drivers of variation in plant phenology should consider phylogeny as a possible, but often only partial, driver.

Plant phenology as a functional plant trait

If phenology is an important functional trait, successful research into what drives its variation must consider how it covaries with other plant traits. Decades of increasing research in plant traits should lay the ground work for such studies, but plant traits research has largely ignored the role of phenology as a trait (Fig. 1). This may be because phenological traits are often assumed to be environmentally determined, with a high degree of plasticity within species and ecotypes (Menzel *et al.*, 2006; Schwartz *et al.*, 2006). Alternatively, phenology may receive little attention in trait studies due to logistical challenges associated with its measurement: budburst, leaf out, and other phenological events require intensive, repeated sampling over time, whereas many other traits (i.e. leaf mass area, vessel diameter) can be precisely (though not necessarily accurately, see Messier *et al.*, 2010) measured with one sample. Regardless of the cause, the conspicuous absence of phenology within the recent explosion of trait literature (Fig. 1) has led to a dearth of contemporary research aimed at understanding how phenology is related to other traits.

Future efforts to understand how phenology relates to other functional traits can build upon a relatively small but valuable body of past work. Past efforts to examine correlations between phenology and other traits (reviewed in Wolkovich & Cleland, 2014) have highlighted important correlations between phenology and other major plant traits, including a possible trade-off between earlier flowering or leafing and a suite of plant traits tied to greater return on investments (greater heights, deeper roots, larger seeds, etc.). This suggests that early species appear to grow fast and 'cheap' tissues while later species grow more slowly, producing more robust tissues that may draw down resources to lower levels and, in many ways, make mid-season species better competitors. As most habitats have few species active early but

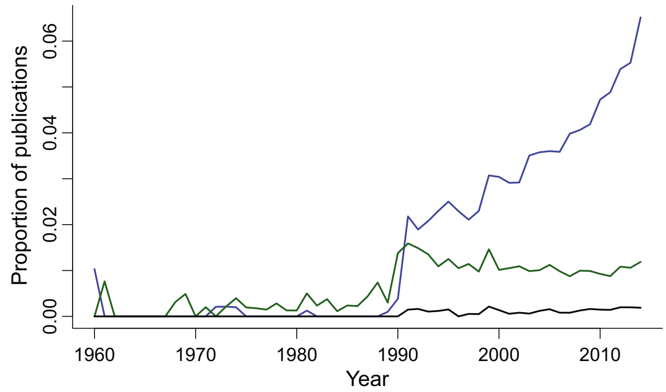

Fig. 1 Proportion of biological and ecological articles published annually on phenology (green line, TOPIC = 'phenolog*'), on traits (blue line, TOPIC = 'trait*'), and those that include both terms (black line). Ecological publications on traits and, separately, phenology have increased since 1990. Publications on traits have increased most notably, but these articles rarely include leaf out, budburst, or other phenological traits. The absence of phenology within the recent explosion of trait literature means we do not generally understand how phenology is related to other traits.

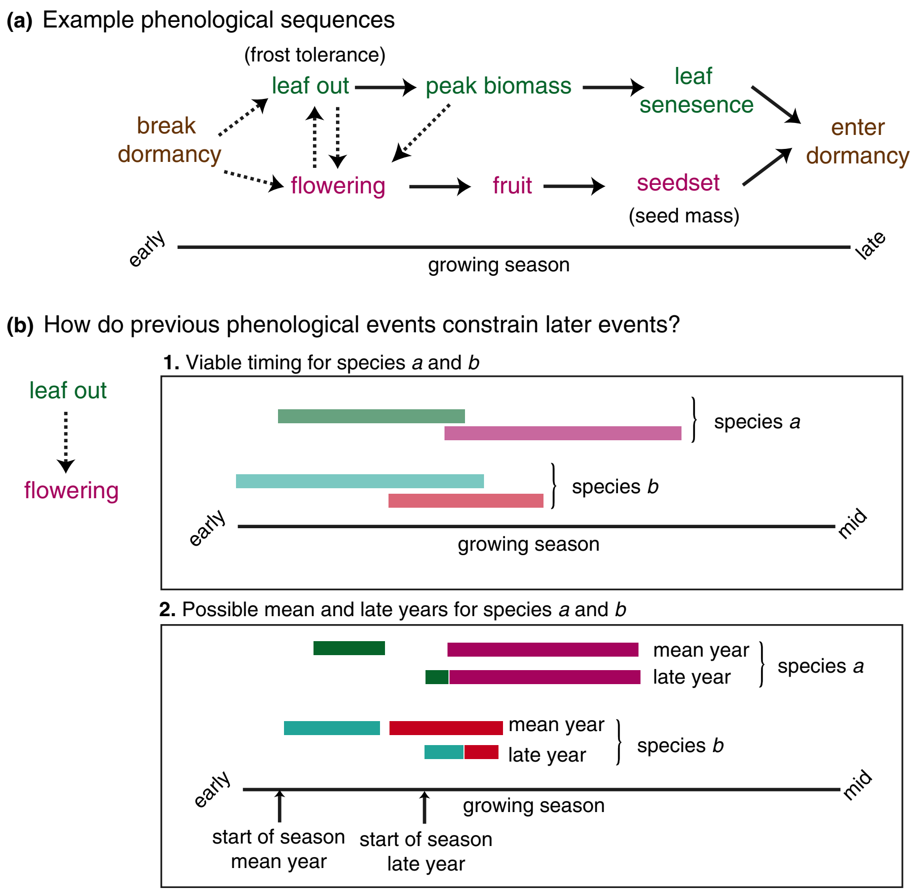

Fig. 2 Phenological events are sequential, with one example general sequence shown in (a) and dashed lines representing several possible variations (e.g. flowering may come before leafing). This ordering likely constrains phenological events and creates correlations among traits that must be carefully teased apart (e.g. frost tolerance may critically control leaf-out date, which in turn affects flower, fruiting and seed set dates, and thus could create a correlation between frost tolerance and seed mass). The extent of constraints between phenological events, however, is poorly understood, because few studies have integrated across events. In particular vegetative events, shown in (a) in green, and reproductive events, in magenta, are often considered separately. Constraints between events may be very important in some species, however. For example consider two hypothetical species where leaf out occurs before flowering (b). If constraints between events are not important, then flowering date should be largely unaffected by leaf-out date (species *a*). Alternatively, leaf-out date may highly constrain flowering date (species *b*), such that these two events may be highly correlated across years (or across space or experimental treatments that cause variation in phenology). In (b) colored bars in (1) represent viable periods for each species, while in (2) bars represent start and end dates of each event for each species in one mean and one late year.

many active mid-season (Wolkovich & Cleland, 2014) this trade-off could be considered effectively a competition–colonization trade-off. Such a trade-off may offer a starting model for future efforts to examine how phenology may be constrained by other traits and to bring phenology into the general research world of functional plant traits.

Efforts to build on previous findings, however, should recognize some attributes of phenology and its research history that may uniquely affect how it fits as one important trait within an integrated set of other plant traits. Specifically, phenological events are inherently linked through their order (Fig. 2). For many trees, such linking may occur across successive growing seasons, as species set buds the year (or more) before. This ordering effectively constrains phenological events and may cause apparent correlations between one phenological event and other plant traits that are inherently due to constraints with a different phenological event (Fig. 2). Much more research, therefore, should integrate across phenological events. Basic work may begin with a study of the correlations among events, as to date the history of research in phenology has tended to bifurcate into two groups split across events. Studies have tended to either focus on (1) events related to leaf phenology, including leaf out, senescence and peak biomass, or (2) reproductive events especially flowering phenology and seedset. Researchers should also strongly consider how variation in the order of events across species may provide an opportunity to test the role of phenological sequences in driving phenology and its correlations with other plant traits.

Testing phenology as a functional trait: the unexploited value of living collections

Future research that includes phenology as an important plant functional trait can begin by drawing on existing resources – Panchen *et al.* highlight a major one of these in their use of botanic gardens from across the globe. Botanic gardens typically offer great taxonomic diversity, providing opportunities for comparative trait analysis across more species than generally possible in a natural area of equivalent size. For example, *c.* 1200 tree taxa of known wild origin are growing at the Arnold Arboretum in Boston, (MA, USA), while only 14–49 tree species occur in adjacent areas outside the arboretum (Welch, 1994; Urban Ecology Institute, 2008). In addition, botanic gardens often offer meticulous records of individual plants' histories, including phenological data, photographs, and herbarium specimens (Primack & Miller-Rushing, 2009), as well as exact provenance. Furthermore, using a network of botanic gardens around the world, as in Panchan *et al.*, allows for variation in phenology and other traits to be investigated in different climates.

Conclusions

Today the study of plant phenology is pressed to make predictions with future climate change; yet progress towards this goal has been stymied by high variation across species. Building from research of decades past, Panchen *et al.* offer a step in the right direction by bringing phenology into the general discussion of correlated plant traits. Fundamentally a more integrated view of phenology as a functional trait would push researchers to ask: what are the causes of, consequences for, and constraints on phenology and phenological shifts, at individual, physiological and functional levels? Answering such questions would return phenology to its role in basic physiology and development, with applications to forecasting of ecological effects of global change – not just for phenology but for the suite of plant traits that may shift in concert with phenology.

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References

Cleland EE, Allen JM, Crimmins TM, Dunne JA, Pau S, Travers SE, Zavaleta ES, Wolkovich EM. 2012. Phenological tracking enables positive species responses to climate change. *Ecology* **93**: 1765–1771.

Colautti RI, Eckert CG, Barrett SCH. 2010. Evolutionary constraints on adaptive evolution during range expansion in an invasive plant. *Proceedings of the Royal Society B-Biological Sciences* **277**: 1799–1806.

Davies TJ, Wolkovich EM, Kraft NJB, Salamin N, Allen JM, Ault TR, Betancourt JL, Bolmgren K, Cleland EE, Cook BI *et al.* 2013. Phylogenetic conservatism in plant phenology. *Journal of Ecology* **101**: 1520–1530.

Kochmer JP, Handel SN. 1986. Contraints and competition in the evolution of flowering phenology. *Ecological Monographs* **56**: 303–325.

Lechowicz MJ. 1984. Why do temperate deciduous trees leaf out at different times – adaptation and ecology of forest communities. *American Naturalist* **124**: 821–842.

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kubler K, Bissolli P, Braslavska O, Briede A *et al.* 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**: 1969–1976.

Messier J, McGill BJ, Lechowicz MJ. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**: 838–848.

Ollerton J, Lack AJ. 1992. Flowering phenology – an example of relaxation of natural-selection. *Trends in Ecology & Evolution* **7**: 274–276.

Panchen ZA, Primack RB, Nordt B, Ellwood ER, Stevens A-D, Renner SS, Willis CG, Fahey R, Whittemore A, Du Y *et al.* 2014. Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytologist* **203**: 1208–1219.

Primack RB, Miller-Rushing AJ. 2009. The role of botanical gardens in climate change research. *New Phytologist* **182**: 303–313.

Schwartz MD, Ahas R, Aasa A. 2006. Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology* **12**: 343–351.

Urban Ecology Institute. 2008. *State of the urban forest: a summary of the extent and condition of Boston's urban forest.* Cambridge, MA, USA: Tech. report, Urban Ecology Institute.

Welch J. 1994. Street and park trees of Boston – a comparison of urban forest structure. *Landscape and Urban Planning* **29**: 131–143.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes JA, Harrison SP *et al.* 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**: 1310–1324.

Willis CG, Ruhfel B, Primack RB, Miller-Rushing AJ, Davis CC. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences, USA* **105**: 17029–17033.

Wolkovich EM, Cleland EE. 2014. Phenological niches and the future of invaded ecosystems with climate change. *AoB Plants* **6**: plu013.

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