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RESEARCH ARTICLE

Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants

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Abstract

1. The relative timing of growth and reproduction is an important driver of plant fitness. For deciduous woody species in temperate regions, leaves and flowers both appear in the early spring, but the order and duration of these phenological events vary among species, populations and individuals. Researchers have long hypothesized that this variation in flower–leaf sequences (FLSs) may be important—affecting the reproduction, recruitment and survival of individuals. Furthermore, FLSs appear to be shifting with climate change; thus, anticipating the extent of these shifts may influence projections of how climate change impacts species' performance and reshapes forest communities.
2. Predicting FLS shifts requires an improved understanding of how environmental variation dictates FLS patterns. To address this, we compared the phenological responses of flowers and developing leaves for 10 temperate woody species to varying levels of temperature and photoperiod in a lab experiment. Our experimental design allowed us to test competing hypotheses for how environmental cues determine FLS variation—specifically whether forcing (warm temperatures) alone drives variation or differential sensitivity to chilling (cool temperatures generally in the fall/winter) and/or photoperiod matter.
3. Within species, we found that flower and leaf phenology responded with differential sensitivity to environmental cues, with differences in their response to chilling being the dominant driver of FLS variation. These differences between flowering and leaf responses were consistent across species, but because species differ in the order of phenological events in their FLSs (flowering-first versus leafing-first), differences between flower and leaf phenology will have contrasting impacts on FLS variation across species. Simple projections of FLS shifts with climate change showed large shifts in species that flower before leafing, with flower–leaf interphases substantially shortened. For wind-pollinated species, this shorter interphase would reduce the time period for efficient pollen transfer, and thus raises the possibility that wind-pollinated taxa may experience reproductive declines due to FLS shifts.
4. *Synthesis*. Our study provides strong evidence that flower and leaf phenology responds with differential sensitivity to environmental variation. Because climate

change will amplify variability in temperature across time and space, our findings suggest that FLS shifts may be large, but are likely to vary substantially among populations and species. Our analyses indicate that climate change will likely decrease flower–leaf interphases, especially in flowering-first species. FLS shifts are likely to affect fitness for some species more strongly than others, thereby impacting community structure and function as climate continues to change.

KEYWORDS
chilling, climate change, deciduous forests, flower–leaf sequences, forcing, hysteranthy, phenology, wind pollination

1 | INTRODUCTION

Among the most widely documented biological effects of anthropogenic climate change are shifts in plant phenology, the timing of life cycle events (Cleland et al., 2007; Menzel et al., 2006; Parmesan & Yohe, 2003). While phenology is generally advancing with climate change, the strength of these phenological shifts can vary substantially among specific phenological phases (Augspurger & Zaya, 2020). These differences alter the timing of phases relative to each other, changing the duration between events that make up phenological sequences (Ettinger et al., 2018). Phenological sequences are a major driver of plant fitness that impact plant life history, resource allocation, demography and ecosystem processes (Post et al., 2008). Thus, shifting sequences with climate change will likely impact many of these processes. The effects of these shifts, however, depend both on their direction—whether distinct phases are shifting closer together or farther apart—and magnitude—how much they are shifting relative to each other.

For deciduous woody plants, the relative timing of flower and leaf phenology, or flower–leaf sequences (FLSs), may be particularly consequential to fitness in temperate regions where flowering prior to leaf development is common (Rathcke & Lacey, 1985). There are several hypotheses regarding the function of FLS variation (see Gougherty & Gougherty, 2018), and it is likely that the adaptive significance of FLSs varies among species, and may co-vary with other plant traits.

The flowering-first FLS is strongly correlated with wind pollination (Buonaiuto et al., 2021; Friedman & Barrett, 2009) and models of pollen movement show that for wind-pollinated species, flowering-first increases pollen dispersal distances and significantly reduces the amount of pollen intercepted by non-reproductive structures (Di-Giovanni et al., 1989; Tauber, 1967; Whitehead, 1969). Flowering-first is also prevalent in some biotically pollinated taxa, but its function is less clear. Some authors suggest that flowering-first impacts floral visibility to pollinators (Bukovac et al., 2017; Forrest & Thomson, 2009; Janzen, 1967) or modifies hydraulic demand (Franklin, 2016; Gougherty & Gougherty, 2018), while others suggest that in biotically pollinated taxa, there is no unique function to the sequence and flowering-first is a by-product of selection for early flowering in general (Primack, 1987).

Phenological observations over the last several decades indicate that, like other phenological sequences, FLSs are shifting with climate change (Ma et al., 2021). For several species, the time between flowering and leafing appears to be increasing, but the strength of this trend varies among species and the direction of FLS shifts is not consistent across populations (Buonaiuto et al., 2021; Ma et al., 2021). These changes could affect the important functions of FLSs, potentially putting some species at greater risk for fitness declines, while benefiting others.

The impact on FLS shifts with climate change on the fitness of woody plants depends on (a) the function of FLSs for that species and (b) the direction and magnitude of the shift. For example, in wind-pollinated species that rely on a substantial flower–leaf interphase for effective pollen transport, decreasing FLS interphases with climate change may drive a reduction in pollination success as more pollen is intercepted by vegetation. Conversely, pollination efficiency could improve for species with lengthening FLS interphases. However, a proportionate FLS shift in biotically pollinated taxa may have different fitness implications because of the contrasting function of FLS variation in these species.

While several recent analyses have examined the function of FLS variation (e.g. Buonaiuto et al., 2021; Gougherty & Gougherty, 2018), the factors that influence the magnitude and direction of FLS shifts are less well studied (but see Ma et al., 2021). Predicting FLS shifts requires identifying the proximate mechanisms that drive and constrain FLS variation, and how these mechanisms differ among species.

Decades of research suggest that cool winter temperatures (chilling), warm spring temperatures (forcing) and day-length (photoperiod) are the primary drivers of both reproductive and vegetative phenology for woody plants in temperate regions (Flynn & Wolkovich, 2018; Körner & Basler, 2010). However, observed FLS shifts indicate that there must be differences in how these cues influence the phenology of flowers and leaves (Buonaiuto et al., 2021).

It is also likely that FLS variation is mediated by other internal mechanisms like developmental construction (Diggle, 1995; Diggle & Mulder, 2019), or other physical constraints like inflorescence architecture or bud type (Pope et al., 2013; Savage, 2019). For example, FLS variation in species with separate buds (buds containing either embryonic leaves or flowers) may be less constrained than species with mixed buds (buds containing both embryonic leaves and flowers together). Other factors like growth form (tree versus shrub) or colonization–competition trade-offs that have been shown to influence the phenological sensitivity of specific phenophases (Basler & Körner, 2012; Donnelly & Yu, 2021) may also influence the sensitivity of phenological sequences to climate.

While FLS variation in woody plants is no doubt the product of interactions between species-specific biology and complex environmental inputs, identifying the differences in how flower and leaf phenology responds to environmental change is a necessary step for predicting the direction, magnitude and—ultimately—fitness impacts of FLS shifts with climate change. Studies that have attempted to identify the differences between reproductive and vegetative phenology in woody plants (mostly focused on crop species) have yielded two common explanations, which we present below.

1.1 | Hypotheses for FLS variation

One hypothesis suggests that reproductive and vegetative buds utilize the same underlying environmental cues, but have different threshold responses to forcing, with whichever bud type bursts later—leaves or flowers—having a higher thermal requirement (i.e. they need a greater sum of warm temperature to trigger the phenological event, Cosmulescu & Calusaru, 2020; Cosmulescu & Ionescu, 2018; Guo et al., 2014). Under this hypothesis, which we call the forcing hierarchy hypothesis (FHH), leaf and flower buds share the same suite of cues and develop similarly to non-forcing cues (i.e. chilling and photoperiod), but differ in the thermal requirement for budburst.

In contrast, an alternative hypothesis suggests that flower and leaf buds differ in the strength of their phenological responses to multiple environmental cues (Aslamarz et al., 2009; Citadin et al., 2001; Gariglio et al., 2006; Mehlenbacher, 1991). Under this hypothesis, which we call the differential sensitivity hypothesis (DSH), each bud type relies more or less on certain cues, generating FLS variability.

While observational studies of phenology in the field are commonly used to evaluate the relationship between environmental conditions and phenology (Cleland et al., 2007), under current and recent climatic conditions, the FHH and DSH may produce similar phenological patterns, making it difficult to evaluate these hypotheses with such methods. However, experiments designed to isolate all three environmental cues have the potential to disentangle the two hypotheses. Studies aiming to differentiate these hypotheses can look for two different signatures. The key signature of the FHH is that the sensitivity to forcing (Δ day of phenological event/Δ°C) of the second phase in the phenological sequence is always greater than that of the first phase, with sensitivity differences being inversely proportional to the difference in thermal requirement among bud types (2× in our simulations; Figure 1a). By contrast, the signature of the DSH is that sensitivity estimates of flower and leaf buds to chilling and/or photoperiod will diverge (Figure 1b), but there is no characteristic pattern as to the strength or direction of this divergence (e.g. leaves may require longer or shorter photoperiods than flowers, or more or less chilling).

The clarity of these signatures from each hypothesis, however, may be obscured in certain situations. First, a species' buds could be both differentially sensitive to photoperiod or chilling (supporting the DSH) and also respond to forcing in a forcing hierarchy (i.e. both hypotheses can operate at once, see Figure 1c). Second, the differential sensitivity framework can generate the signature of the FHH when other cues are at high levels due to interactions between the chilling or photoperiod response and the thermal requirement, which make forcing the dominant phenological cue once other cue requirements have been met (see Figure 1b, force × chill interaction). When this happens, the FHH would effectively be a special case of the DSH.

While these two hypothesized mechanisms may produce similar phenology patterns under current conditions, differentiating them is important, as they have substantially different implications regarding the potential for FLS shifts with climate change. The FHH suggests that FLS variation is largely a product of climate variation during the interphase. If spring temperatures increase with climate change, the second phenophase of the FLS will be accelerated relative to the first and FLS interphases will decrease, but given the relative autocorrelation of spring temperatures (Di Cecco & Gouhier, 2018), these shifts should be muted. If FLSs are structured by a forcing hierarchy, the direction of FLS shifts is relatively straightforward to predict, and it is less likely that shifts will be large enough in magnitude to significantly affect woody plant fitness.

Climate change would also drive FLS shifts under the DSH, but the trajectory of these shifts is more complicated to predict. The DSH suggests that there could be strongly localized or regional effects of climate change on FLSs. Shifts in FLS variation will depend on the direction and rate of change in cues at given locations and the species-specific differential sensitivity of reproductive and vegetative phenology to cue combinations. This hypothesis allows for larger magnitude shifts in FLSs, on a scale that could impact pollen transport or the physiological functioning of woody plants. Furthermore, the DSH also suggests that the magnitude of shifts may be highly divergent both among species in a community and among populations of the same species, which could impact gene flow, population structure and demography.

In this study, we tested the FHH and DSH hypotheses in 10 temperate shrub and tree species. Using a full-factorial growth chamber experiment, we manipulated chilling, forcing and photoperiod cues for flower and leaf buds. We then leveraged these data to examine how FLSs may shift with climate change.

2 | MATERIALS AND METHODS

2.1 | Growth chamber study

We sampled plant material from Harvard Forest in Petersham, MA, USA (42.5314°N, 72.1900°W), on 25 October 2017, just as most

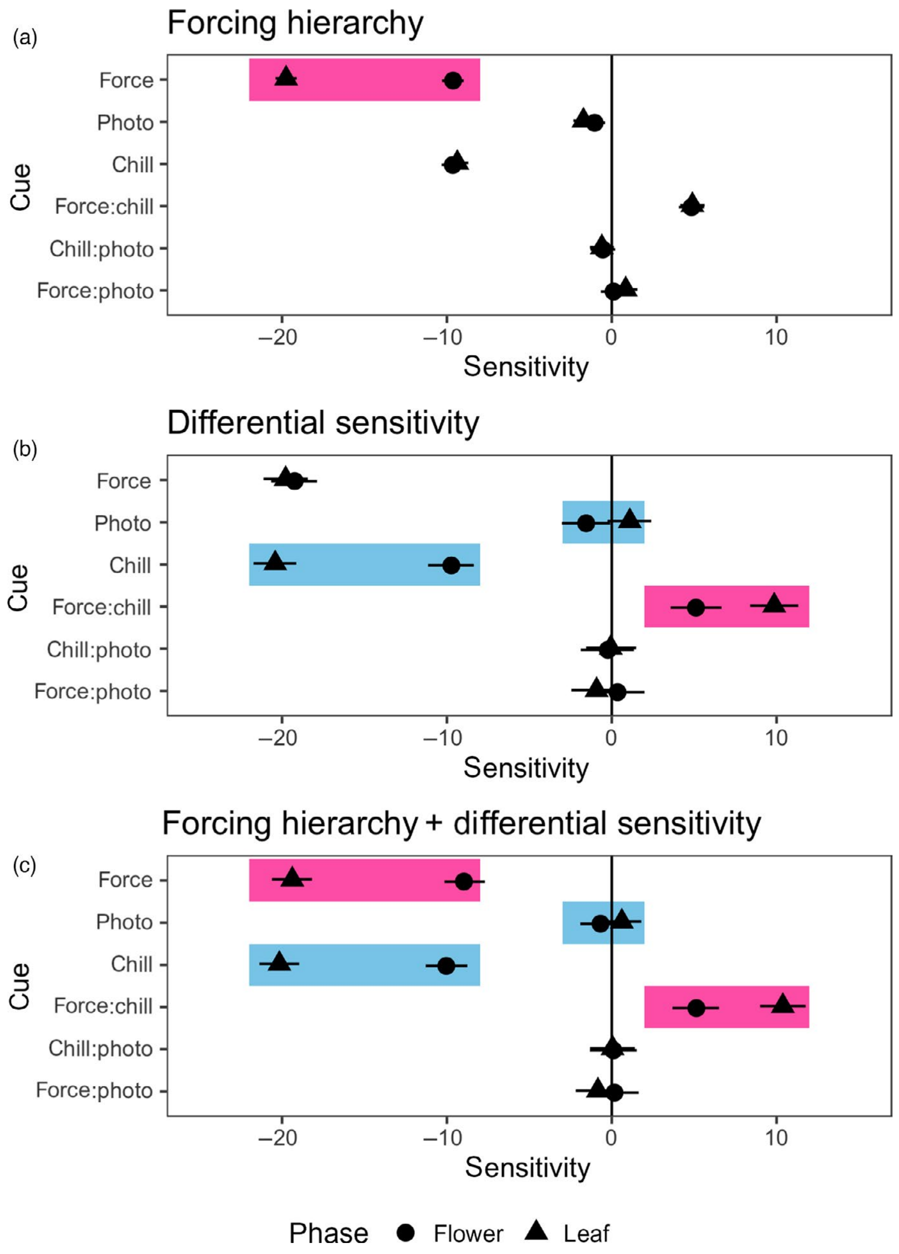

FIGURE 1 Characteristic sensitivity (Δ day of phenological event/Δ environmental cue) patterns of the phenological response to changing cue levels for the two major flower–leaf sequence hypotheses. (a) A signature pattern of the forcing hierarchy hypothesis (FHH, pink boxes)—with the second phenophase in the sequence (in this case leafing) having a higher sensitivity to forcing than the first. (b) A typical sensitivity pattern produced by the differential sensitivity hypothesis (DSH). (c) A scenario where both the FHH and the DSH contribute to flower–leaf sequence variation. Here, the characteristic forcing sensitivity of the FHH is still apparent but the differential sensitivity to chilling and photoperiod is seen as well (blue boxes). All plots above are based on simulations (see Supporting Information: Methods). Shapes indicate mean estimates and lines depict 95% credible intervals from Bayesian hierarchical models with advances in phenology shown as negative numbers, and delays in phenology as positive numbers

individuals dropped their leaves, to capture the period immediately after most plants in the area entered endo-dormancy, but before they could accumulate significant chilling in the field. We collected branch cuttings from 7 to 13 individuals of 12 woody plant species (4–12 cuttings per individual for a total of 48–56 per species), consisting of a mix of deciduous shrubs, understorey and canopy trees commonly found in mesic hardwood forests of the eastern United States. The use of branch cuttings to study woody plant phenology in artificial environments is common (Ettinger et al., 2020), and these methods have been shown to match whole-plant phenological patterns (Primack et al., 2015; Vitasse & Basler, 2014). We selected species displaying variation of the three major FLS patterns; species for which flowers appear before leaves (flowering-first; *Acer rubrum*, *Betula alleghaniensis*, *Comptonia peregrina* and *Corylus cornuta*), species for which flowers appear with their leaves (concurrent; *Acer pensylvanicum*, *Acer saccharum*, *Ilex mucronata*, *Prunus pensylvanica*, *Vaccinium corymbosum*) and species for which flowers appear after leaf development (leafing-first; *Ilex verticillata*, *Prunus virginiana*, *Viburnum acerifolium*). Because we expected that other characteristics such as pollination syndrome, bud type and growth habit were likely to impact FLS sensitivity, we made sure that the species we chose exhibited variation in these traits as well (see Table S1 for details and full species list). We included several congenerics in our study, explicitly choosing species with different FLS patterns to mitigate phylogenetic non-independence in our trait of interest (FLS; Revell, 2010).

We transported all cuttings to the Arnold Arboretum in Boston, MA (USA) where they were re-cut in water to prevent callousing and minimize embolism and placed in 500 ml Erlenmeyer flasks with distilled water.

We randomly assigned cuttings to a fully crossed set of eight experimental treatments; two levels of chilling (30 versus 60 days at 4°C), two levels of temperature (24°C:18°C (day/night) warm versus

18°C:12°C (day/night) cool) and two levels of photoperiod (12 versus 8 hr). We alternated day/night temperature periodicity on a 12-hr schedule to reduce co-variation with photo-periodicity. We re-cut all twigs and changed the water every 7–10 days and rotated all treatments between growth chambers every 2 weeks to minimize chamber effects. We made phenological observations every 2–3 days using a modified BBCH scale for woody plants (Finn et al., 2007) for 3 months following release from chilling conditions. In this period, we assessed three phenological phases: leaf budburst (BBCH phase 07), leafout (BBCH phase 15) and first flower open (BBCH 60). While leaf budburst is the first stage of vegetative expansion and therefore most directly comparable to first flowering, we also included leafout in our observations because several of the functional hypotheses for FLS variation are predicated on developing leaves be sufficiently large enough to impact canopy structure, which would only happen at later stages of leaf development.

At the conclusion of this period, we assessed all individuals that did not undergo budburst and excluded 56 dead twigs from our analyses.

2.2 | Data analysis

To assess the phenological sensitivity of each phase, we fit mixed-effects hierarchical models with chilling, forcing, photoperiod and all two-way interactions as the fixed effects and species as a grouping factor on both the slopes and the intercepts. We chose a Bayesian hierarchical approach in order to identify systematic trends across species' responses while accounting for sample size, variance and the unique effect of each species. We modelled the effects of environmental parameters on flower opening, leaf budburst and leafout separately. We also fit a model with FLS interphase (day of budburst–day of flowering) as a response variable to compare these estimates with field observations. Two species, *Betula alleghaniensis* and *Acer saccharum*, produced no flowers in our trial, likely because flowering branches were out of reach during our field sampling, so we excluded them from our analysis. In total, our analyses included 464 twigs from 10 species.

The models we fit appear below:

$$y_{[i]} : N\left(\alpha_{\mathrm{sp}_{[i]}} + \beta_{\mathrm{forcing}_{\mathrm{sp}[i]}} + \beta_{\mathrm{chilling}_{\mathrm{sp}[i]}} + \beta_{\mathrm{photoperiod}_{\mathrm{sp}[i]}} + \beta_{\mathrm{forcingxchilling}_{\mathrm{sp}[i]}} + \beta_{\mathrm{forcingxphotoperiod}_{\mathrm{sp}[i]}} + \beta_{\mathrm{chillingxphotoperiod}_{\mathrm{sp}[i]}}, \sigma_y^2, \right)$$

where $y_{[i]}$ is either the day of the experiment of leaf budburst, day of first flower opening, day of leafout or FLS interphase length, and σ_y^2 the error. We modelled the intercept (α) and each slope (β) parameter at the species level using the formula:

$$\alpha_{x_{sp}} \text{ or } \beta_{x_{sp}} : N\left(\mu_x, \sigma_x^2\right).$$

To test the hypothesis that the FHH is a special case of the DSH that occurs when other cue (i.e. chilling and photoperiod) requirements are met, we re-ran our leaf budburst and flowering models on a subset of our data which included both levels of the forcing treatment but only the high photoperiod and chilling treatment levels. This model included forcing as the only main effect but, like our main models written above, included species as a grouping factor on the slopes and intercept.

We fit all models using the R package 'BRMS' (Bürkner, 2018). We ran each model on four chains with 4,000 iterations and a 3,000-iteration warm up for a total of 4,000 posterior draws for each parameter. In all models, we used weakly informative priors and increasing the priors fivefold did not affect the model results. We assessed model performance through ensuring $\hat{R}$s were between 1 and 1.01 and bulk and tail effective sample sizes were high (1,800–2,800 for most parameters, but as low as 800–900 for some). We present 50% credible intervals in figures because they are the most computationally stable (Gelman et al., 2013), but provide other intervals in the Supporting Information (Tables S3–S5). All of our estimates of phenological sensitivity (Δ day of phenological event/Δ environmental cue) are scaled by treatment level (chilling: Δ 30 days, forcing: Δ 6°C, photoperiod: Δ 4 hr; for example, when we report a forcing effect of −19 days it means an advance of 19 days given a 6°C temperature difference).

2.3 | Climate change scenarios

To apply our model results to general climate change scenarios, we chose environmental treatments in the experiment to broadly reflect historic and future conditions at our sampling site. Our low forcing treatment approximated average spring temperature (March/April) at the site while our high temperature treatment reflects a 6°C increase. Average field chilling (calculated from 15 October to 15 April, measured in Chill Hours, Weinberger, 1950) at Harvard Forest is 1,170.7, approximately 63% of the difference between our low and high chilling treatment (Table S2). Thus, our low chilling treatment represents a feasible estimate for a decrease in chilling with climate change and our high chilling treatment approximates a reasonable increase (Luedeling, 2012). Our low photoperiod treatment (8 hr of daylight) is well below the photoperiod experienced at Harvard Forest, but given that the photoperiod effects are expected to be small (Laube et al., 2014), we chose more extreme values in order to robustly estimate an effect (i.e. increasing statistical power). For this reason, our climate change scenarios for FLS variation are based on our high photoperiod treatment alone.

We used our flower, leafout and leaf budburst models to project for each species in our study:

1. FLSs under average environmental conditions (low forcing, 45 days of chilling)
2. FLS shifts with spring warming only (high forcing, 45 days of chilling)
3. FLS shifts with warming and increased chilling (high forcing, 60 days of chilling)
4. FLS shifts with warming and decreased chilling (high forcing, 30 days of chilling)

To validate our predictions, we compared our FLS interphase model estimates of ‘average’ condition FLS interphases to long-term phenological records from Harvard Forest (O'Keefe, 2015) for five species in our dataset (Figure S1), and found them comparable.

Given the variable dynamics of shifts in environmental forcing and chilling with climate change over time and space (Luedeling et al., 2011), these scenarios should not be treated as absolute predictions of the magnitude of FLS shifts with climate change. Instead, we provide these scenarios to identify general trends in how FLSs could shift with warming and demonstrate that the range of possibilities varies based on characteristics of plant species and the specific climate dynamics.

Finally, we characterized FLS shifts for three broad FLS groups (flowering-first, concurrent, leafing-first) by extracting all sampling posterior estimates from our main models using the R package TIDYBAYES (Kay, 2020), and grouping them by FLS pattern. We also include the species-specific estimates on which these grouped estimates are based in Figure S3.

3 | RESULTS

3.1 | Growth chamber study

Flowering, leaf budburst and leafout advanced with higher forcing and longer chilling duration (flowering: chilling effect: −21.2 days, forcing effect: −19.0 days, leaf budburst: chilling effect: −30.4 days, forcing effect: −17.8 days, leafout: chilling effect: −39.7 days, forcing effect: −32.6 days; Figure 2, Figure S2, Tables S3 and S4—all sensitivity estimates are scaled by treatments; see Section 2.2 above), but increases in both of these cues together offset these advances (flowering: chill × force effect: 7.0 days, leaf budburst: chill × force effect: 12.4 days, leafout: chill × force effect: 21.4 days; Figure 2, Figure S2, Tables S3 and S4). Leaf and flower phenologies diverged in their responses to photoperiod, with flower phenology advancing at longer photoperiod and leaf phenology remaining unaffected (leafout) with photoperiod changes, or delaying (budburst) at longer photoperiods when the other two cues were at low levels (Figure 2, Figure S2, Tables S3 and S4). As seen in the interactions between photoperiod and chilling and photoperiod and forcing, increasing chilling or forcing with longer photoperiod advanced the phenology of all three phases. For flowering, leaf budburst and leafout, chilling and forcing were the dominant cues, while photoperiod produced a more muted phenological response (Figure 2, Figure S2, Tables S3 and S4).

While leaf and flower phenological responses to environmental cues were qualitatively similar, the strength of their responses to each cue differed substantially. Leaf budburst and leafout responded more strongly to chilling than flowering (budburst: 1.4X, leafout: 1.9X), and had stronger responses to all cue interactions (leaf budburst: chilling × forcing: 1.8X, chilling × photoperiod: 5.8X, photoperiod × forcing: 2.2X, leafout: chilling × forcing: 3.1X,

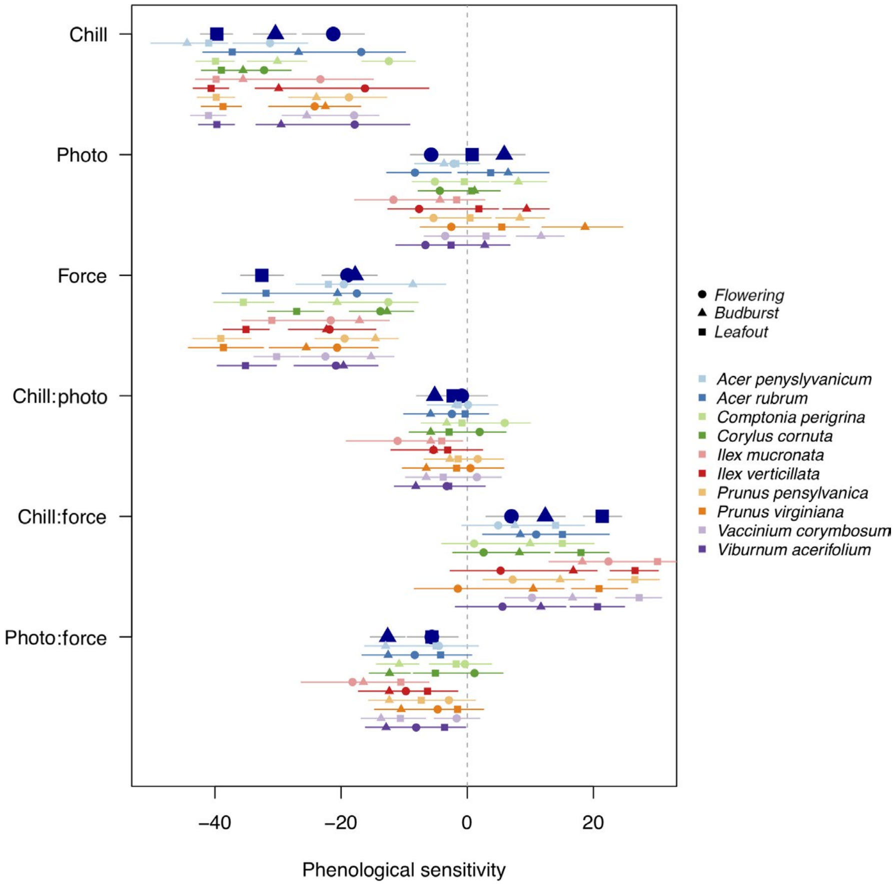

FIGURE 2 Effects of forcing temperature, chilling duration and photoperiod on the leaf budburst (triangles), leafout (squares) and flowering (circles) phenology of 10 temperate woody plant species collected from Harvard Forest (Petersham, MA, USA). Shapes indicate mean estimates and lines depict 50% credible intervals (see Tables S3 and S4 for other intervals) from Bayesian hierarchical models with advances in phenology shown as negative numbers, and delays in phenology as positive numbers. Flower and leaf phenology differs in sensitivity (Δ day of phenological event/Δ environmental cue; 30 days chilling/6°C forcing/4 hr photoperiod) to these environmental cues. See Figure S2 for an alternative presentation of these results that depicts the difference between the mean estimates of each phase (shapes)

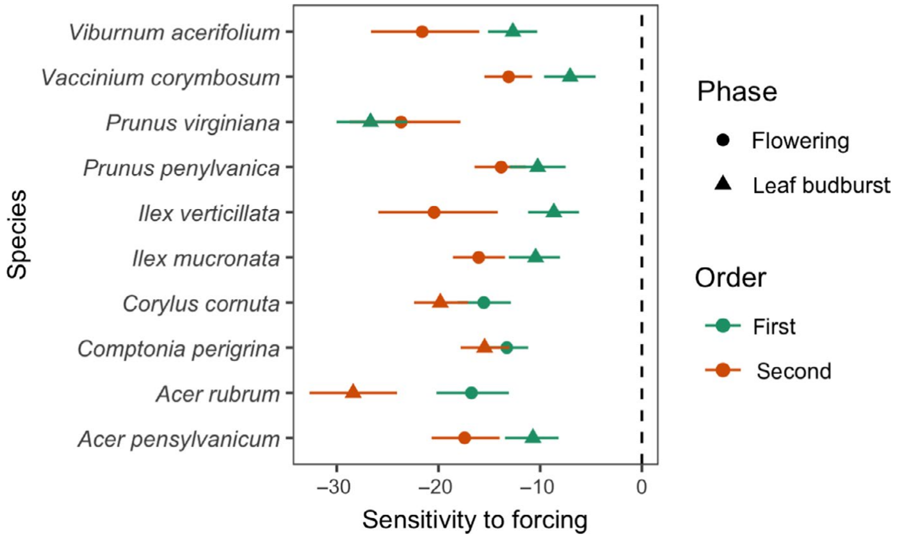

FIGURE 3 Phenological sensitivity (Δ days of phenological event/Δ 6°C) to forcing temperatures of leaf budburst (triangles) and flowering (circles) phenology from 10 temperate deciduous woody plants at long (12-hr) photoperiod and long chilling duration treatments (60 days at 4°C). Shapes indicate mean estimates and lines depict 50% credible intervals (see Table S5 for other intervals) from Bayesian hierarchical models with advances in phenology shown as negative numbers. When photoperiod and chilling are high, most species follow the predicted pattern of the forcing hierarchy hypothesis (FHH), with the second phenophase of the sequence consistently more sensitive to forcing than the first. This result suggests that the FHH should be considered a special case of the differential sensitivity hypothesis (DSH) that occurs when the chilling and photoperiod requirements are met for both tissue types

chilling × photoperiod: 2.4X, photoperiod × forcing: 1.0X; Figure 2, Figure S2, Tables S3 and S4). Across all species, both leaf budburst and flowering displayed a similar magnitude advance with increased forcing, while leafout responded comparatively much stronger (Figure 2, Figure S2, Tables S3 and S4).

Our results did not show the characteristic sensitivity pattern of the FHH across most species in our experiment (Figure 2, Figure S2, see Figure 1a,b), though there was significant variation among species in the relative strength of their response to forcing between flowering and leaf budburst. However, when we re-ran our flowering and leaf budburst models on the subset of data which included phenological observations at only high levels of chilling and photoperiod, we found the sensitivity to forcing for nine of 10 species followed the predicted pattern of the FHH, with the second phases of the FLS showing stronger sensitivity to forcing than the first phases (Figure 3, Table S5).

3.2 | Climate change scenarios

Our models project that flowering, budburst and leafout will advance in our generalized future scenarios. FLS shifts depended strongly on how forcing levels change relative to chilling exposure (Figure 4). Given the significant differences in sensitivity to chilling between flowering and leafing phenology we found in our experiment, our scenarios showed that FLS interphases will be more strongly influenced by changes in chilling duration than increased forcing alone.

The direction and magnitude of shifts in FLS interphases varied among species, varying especially by whether or not they displayed a flowering-first FLS. Under some warming scenarios, flower–leafout interphases were strongly reduced in a number of taxa, and flower–budburst interphases for some species effectively disappeared or the order of phenophases in the FLS switched (Figure 4, Figure S3). Several species, *Acer rubrum*, *Ilex verticillata*, *Prunus pensylvanica*, *Prunus virginiana* and *Viburnum acerifolium*, had FLSs that were relatively robust to changing environments. For other species, *Acer pensylvanicum*, *Vaccinium corymbosum* and *Ilex mucronata*, which typically begin to produce leaves shortly before flowers open, the magnitudes of projected FLS shifts were moderate. The two species with the most significant FLS shifts in both direction and magnitude across treatment combinations and climate change scenarios were the flowering-first, wind-pollinated shrubs *Comptonia peregrina* and *Corylus cornuta* (Figure S3). In all of our climate change scenarios, the FLS interphase was dramatically reduced in these taxa.

4 | DISCUSSION

Our experiment supports the hypothesis that flower–leaf sequences are structured by differential sensitivity (DSH) to the environment between flower and leaf phenology. Specifically, differences in the chilling response among flowering and leaf phenology were the strongest driver of FLS variation. We also found that under high chilling and long photoperiods, the FLSs of most species followed the predicted sensitivity pattern of the FHH, supporting the hypothesis that the FHH is likely a special case of the DSH that occurs when other phenological cues are met for both vegetative and flowering phenology. Together, these results explain why the two FLS hypotheses have been difficult to distinguish, and suggest that climate change has the potential to significantly disrupt FLSs as global

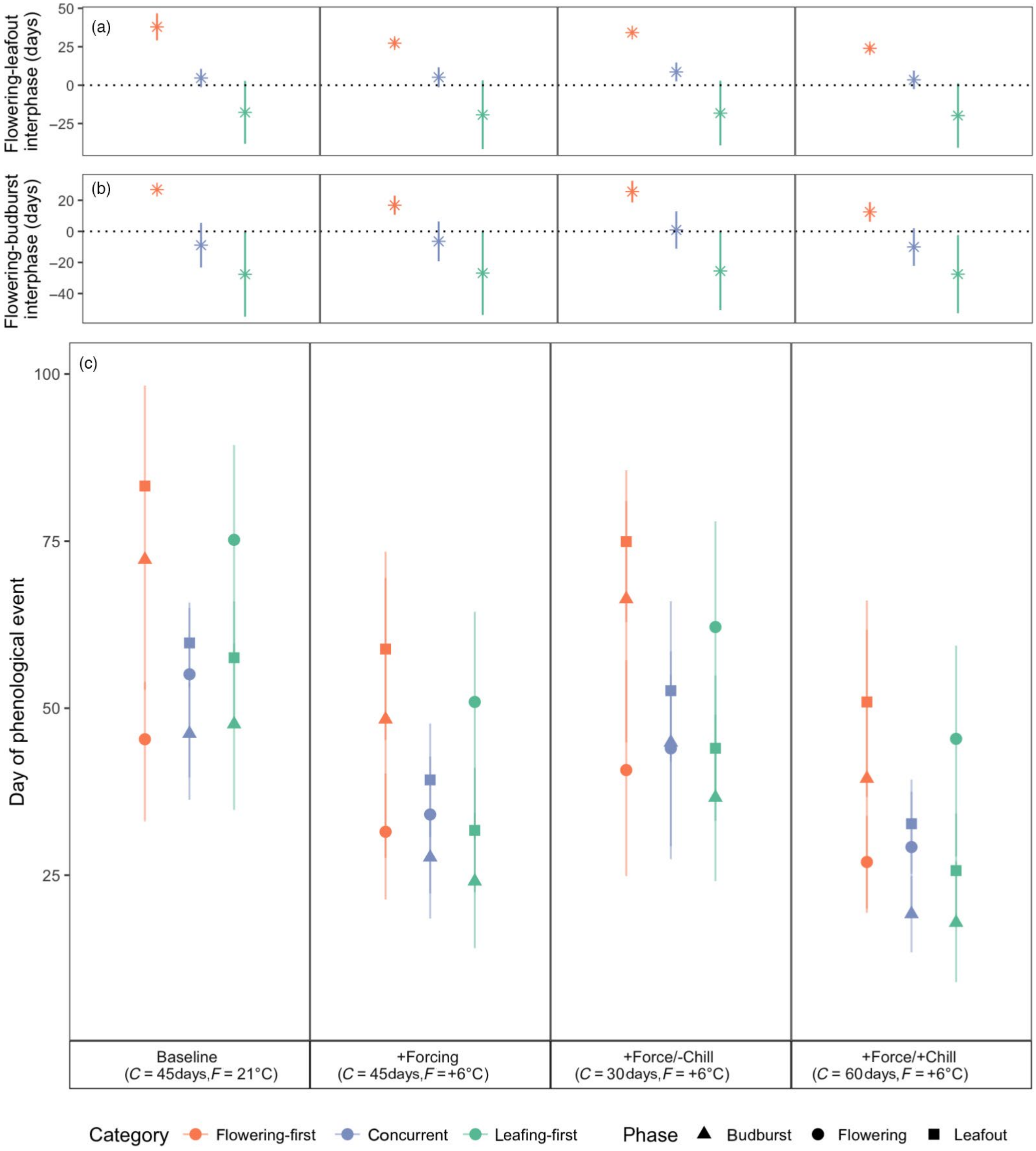

FIGURE 4 Projected shifts in flower–leaf sequences under current environmental conditions (Baseline) and three climate change scenarios (increase forcing, increase forcing/decrease chilling, increase forcing/increase chilling) predict that FLS shifts differ among the three major FLS types, and will be strongest in flowering-first species. (a, b) The mean time between flowering and vegetative phenological events (shapes) with 50% credible intervals (lines). (c) The predicted event day for each phase. Predictions are based on species-level posterior estimates grouped by FLS category (flowering-first, concurrent, leafing-first) from Bayesian hierarchical models comparing flowering (circles), leaf budburst (triangles) and leafout (squares) phenological responses to variable chilling duration and forcing temperatures. Shapes represent the mean estimates and lines represent the 50% credible intervals

warming alters historic chilling patterns across the temperate zone (Morin et al., 2009).

4.1 | Reconciling the differential sensitivity and the forcing hierarchy hypotheses

The relationship we found between the FHH and the DSH in our experiment offers a path forward for reconciling previous studies that have favoured one hypothesis over the other. Support for the FHH is most often associated with observational studies (e.g. Cosmulescu & Calusaru, 2020; Guo et al., 2014). By contrast, experimental studies which manipulate chilling levels beyond historically observed minima in the field tend to support the DSH (e.g. Aslamarz et al., 2009; Gariglio et al., 2006). This pattern can be explained by the FHH being a special case of the DSH, if historic climate regimes make detection of the DSH in the field difficult.

Under historic climate regimes, seasonal chilling requirements were usually met (Chuine et al., 2016; Gauzere et al., 2019), making it difficult to detect any effect of chilling in observational studies, let alone differences in flower versus leaf responses. It would take larger reductions in chilling to reveal the signature of the DSH, which at present, rarely occurs in the field, but can be induced in artificial environments, which explains the discrepancy between these two methods. These dynamics are consistent with findings in other phenological studies that suggest simple growing degree models (which underlie the FHH) accurately predict phenology under current climate, but underperform under climate change scenarios when shifts in chilling accumulation become more pronounced (Chuine et al., 2016; Linkosalo et al., 2008). Our findings suggest that as climate continues to change, differential sensitivity to the environment between flower and leaf phenology should become more apparent in field observations, and that the magnitude of interannual FLS variation is likely to extend beyond historically observed reaction norms.

4.2 | Population-level implications of the DSH with climate change

Predicted shifts in chilling are highly variable across both time and space—because chilling only accumulates at intermediately low temperatures, warming may increase chilling at some locations while decreasing it in others (Man et al., 2017; Zhang et al., 2007). Layered onto these variable shifts in chilling, spring warming from climate change also differs by location (Karmalkar & Bradley, 2017; Loarie et al., 2009), suggesting that forcing may increase more rapidly in some places than others. These shifts in both chilling and forcing suggest that the direction and magnitude of FLS shifts are likely to vary substantially among populations based on the specific cue combinations at a given locality (Chmielewski et al., 2012). Long-term phenology records show that there was already substantial intraspecific variation in FLSs at the population level (Buonaiuto et al., 2021) and our findings suggest that these population-level differences may be further amplified by climate change. In this way, all the three generic FLS climate change scenarios depicted in Figure 4 should not be considered alternatives to each other, but could occur contemporaneously across a species' range.

This increased population-level heterogeneity in FLSs that our models project has the potential to influence patterns of pollen dispersal across the landscape (Borycka et al., 2017; Pace et al., 2018). For example, in wind-pollinated species advancing canopy closure relative to flowering can impede long-distance pollen transport (Milleron et al., 2012), which may in turn alter patterns of gene flow across a landscape. In biotically pollinated species, FLS shifts may interact with other drivers of global change such as phenological mismatches with pollinators (Burkle et al., 2013) or flowering asynchrony among populations (Cresti et al., 2013; Zohner et al., 2018) to impact gene flow, but more research is needed to determine if and how FLS variation affects the foraging behaviour of pollinators. Our findings regarding FLS shifts should be integrated with projections of pollinator movement or prevailing wind directions (Kling & Ackerly, 2020) to better understand how FLS variation may contribute to population structure in the long term.

While changes in chilling and forcing from climate change may increase FLS variation, the climate change implications of strong differential sensitivity to photoperiod among flower and leaf phenology are more difficult to predict. Climate change does not directly impact photoperiod, but may alter the photoperiods plants experience as they approach their temperature optima for phenological activity. However, in most temperate regions, temperature would have to drive phenological shifts by a minimum of several weeks before the experienced photoperiod of plants would change substantially. Because these dynamics are more extreme than most studies suggest (Thackeray et al., 2016) and the photoperiod effect we observed on our study was relatively weak, we modelled climate change scenarios with a constant photoperiod in our FLS scenarios. Such an approach may be useful at temperate and some boreal latitudes, but may not work at high latitudes, where photoperiod changes more rapidly over the season, and thus, temperature-driven phenological shifts may significantly alter the experienced photoperiod of plants. Our results suggest that such shifts could mute or amplify the FLS shifts, which may be particularly important as species shift their distribution poleward with climate change and begin to encounter novel photoperiod regimes (Way & Montgomery, 2015).

4.3 | Species-level implications of the DSH with climate change

The impact of FLS shifts with climate change relies on both the function of FLS variation and the magnitude of FLS shifts. Just as previous analyses suggest that the function of FLS variation may differ among species (Buonaiuto et al., 2021; Gougherty & Gougherty, 2018), our study highlights that the direction and magnitude of FLS shifts with climate change are also species-specific. We found that FLSs of some species were very sensitive to changing climate conditions, while others remain fairly resilient (Figure 4, Figure S3).

The different FLS response patterns we observed across species may correlate with a suite of interrelated anatomical, physiological and phenological traits. Just as pollination syndrome appears to be a major driver of differences in the function of FLSs in woody plants (Buonaiuto et al., 2021), we also found significant differences in the magnitude and direction of FLS shifts between biotically and wind-pollinated species.

The species that maintained FLS structure across our climate change scenarios were biotically pollinated. They also generally shared a strongly leafing-first FLS, with a fairly long FLS interphase (Figure 4). As expected, these species tended to have mixed buds so there may be strong physical constraints on their FLSs. Our models suggest that the FLSs of a subset of biotically pollinated taxa, those classified as 'concurrent', are expected to shift under some scenarios (see Figure 4), but it is unclear if these FLS shifts would be large enough in magnitude to impact plant performance.

By contrast, the species that were most sensitive to FLS shifts were monoecious, flowering-first, wind-pollinated shrubs (Figure 4, Figure S3). This result supports other evidence that the reproductive phenology of wind-pollinated species may be more sensitive to climate change compared to biotically pollinated taxa (Ziello et al., 2012). In all scenarios, our projections suggest that the flower–leaf interphase will decrease for these species. Given this period is considered critical for successful pollination in these taxa (Whitehead, 1969), this pattern suggests that these species, and flowering-first, wind-pollinated taxa in general, may face particular risk for reproductive performance reductions with climate change.

However, there are several caveats to this prediction. The function of FLS variation in wind-pollinated species suggests that leaves must create a substantial barrier to pollen movement. In our study, we observed both leaf budburst, a stage that is unlikely to contribute much to canopy structure, and leafout, a stage more likely to impact airflow though the canopy. It is unclear at what point in leaf development wind pollination becomes impaired, so the effective duration of the FLS interphase that impacts wind pollination may be somewhere in between the two interphases we measured (flower–leaf budburst and flower–leafout) or beyond the interphases used in our projections. Secondly, in growth chamber experiments such as ours, it is difficult to evaluate the full duration of phenological episodes (Primack et al., 2015). Shifts in the duration of flowering or period of leaf expansion could compensate for, or exacerbate, the shifts in FLSs we observed.

Finally, many wind-pollinated species are monoecious or dioecious (Ackerman, 2000) and in several families (e.g. *Betulaceae*, *Juglandaceae*), male flowers occur in separate buds, while female flowers occur in mixed buds (Pope et al., 2013). This suggests that the phenology of female flowers may be more tightly constrained by leaf phenology and, if this is the case, even increases in the FLS interphases for flowering-first wind-pollinated taxa such as those observed in the field (e.g. Ma et al., 2021) could adversely affect wind pollination by disrupting floral synchrony of male and female flowers (Alizoti et al., 2010; Elkassaby & Davidson, 1991; Mutke et al., 2005).

While much of the public interest around phenology and pollination in the context of global change has centred around trophic mismatches between pollinator and floral phenology (Memmott et al., 2007), our study identified the possibility that the effects of FLS shifts with climate change may be particularly important for wind-pollinated woody plants. The direction and magnitude of FLS shifts we observed in these taxa, coupled with the hypothesized function of a flowering-first FLS in wind-pollinated species, suggest that FLS variation in this functional group should be explored in greater detail in the future. More research is needed to identify species' traits that may correlate with the potential for FLS shifts, but flowering-first, wind-pollinated species may be particularly sensitive to FLS shifts. Our results suggest that species in this functional group should be considered a research priority for the study of spring phenological sequences in deciduous woody plants.

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AUTHORS' CONTRIBUTIONS

D.M.B. and E.M.W. conceived of the experiment; D.M.B. collected the data and performed the statistical analyses; D.M.B. and E.M.W. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and R code for this study are available online at Knowledge Network for Biocomplexity: https://doi.org/10.5063/PG1Q4B (Buonaiuto & Wolkovich, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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