



A Mechanistic Framework for Understanding the Effects of Climate Change on the Link Between Flowering and Fruiting Phenology

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Phenological shifts are a widely studied consequence of climate change. Little is known, however, about certain critical phenological events, nor about mechanistic links between shifts in different life-history stages of the same organism. Among angiosperms, flowering times have been observed to advance with climate change, but, whether fruiting times shift as a direct consequence of shifting flowering times, or respond differently or not at all to climate change, is poorly understood. Yet, shifts in fruiting could alter species interactions, including by disrupting seed dispersal mutualisms. In the absence of long-term data on fruiting phenology, but given extensive data on flowering, we argue that an understanding of whether flowering and fruiting are tightly linked or respond independently to environmental change can significantly advance our understanding of how fruiting phenologies will respond to warming climates. Through a case study of biotically and abiotically dispersed plants, we present evidence for a potential functional link between the timing of flowering and fruiting. We then propose general mechanisms for how flowering and fruiting life history stages could be functionally linked or independently driven by external factors, and we use our case study species and phenological responses to distinguish among proposed mechanisms in a real-world framework. Finally, we identify research directions that could elucidate which of these mechanisms drive the timing between subsequent life stages. Understanding how fruiting phenology is altered by climate change is essential for all plant species but is particularly critical to sustaining the large numbers of plant species that rely on animal-mediated dispersal, as well as the animals that rely on fruit for sustenance.

Keywords: global change, flowering, fruiting, life history stages, phenological shifts, seed dispersal

INTRODUCTION

Phenological shifts are among the most visible ecological effects of global climate change. Research on individual species (e.g., CaraDonna et al., 2014), meta-analyses (Root et al., 2003; Munguía-Rosas et al., 2011), and community-wide taxonomic surveys (Ovaskainen et al., 2013) demonstrate that phenological, or the timing of life history, events in most species and stages are advancing in response to warmer temperatures. Well-studied life history stages include migration (Mayor et al., 2017) and breeding (Burger et al., 2012) in birds, hibernation in mammals (Sheriff et al., 2011), adult emergence in insects (Bartomeus et al., 2011; Renner and Zohner, 2018), and green-up and flowering in plants (Calinger et al., 2013; Rafferty and Nabity, 2017; Ettinger et al., 2018). In contrast, other life history stages, such as fruiting, have received relatively little attention (Chuine and Régnière, 2017; Mendoza et al., 2017; Ettinger et al., 2018). An important gap in our understanding concerns whether the latter of successive events in the life histories of an organism (e.g., fruiting which follows flowering) are shifting independently of, or are functionally constrained by, earlier stages.

It is reasonable to predict that climate-induced shifts in the timing of early life history stages result in parallel shifts in subsequent life-history stages of the same organism. The timing of life history stages is driven by a combination of external (climate) and internal (physiological or endogenous) factors. It is largely unknown, however, to what extent each factor drives the timing of one life history stage relative to earlier ones (McDermott and DeGroote, 2017; Ettinger et al., 2018; Gougherty and Gougherty, 2018; Augspurger and Zaya, 2020; Buonaiuto et al., 2021). With the exception of a few pioneering studies (e.g., Menzel et al., 2001; Post et al., 2008a,b; Haggerty and Galloway, 2011; Jiang et al., 2016; Segrestin et al., 2018), little research has yet explored whether successive life history stages predictably shift in concert with each other in response to climate change, nor, when they do, what drivers underlie this relationship (Chuine and Régnière, 2017; Ettinger et al., 2018). Parallel shifts might occur either if the interval between successive life-history events is constant or nearly so (likely a product of internal factors such as physiology or development), or if the external, proximate climatic cues for the two events are the same or tightly associated. Parallel shifts in successive life history stages could be related to reproductive strategy and traits (Forrest and Miller-Rushing, 2010; Ettinger et al., 2018; reviewed in Gougherty and Gougherty, 2018; Buonaiuto et al., 2021), genetics and selective processes (Crozier et al., 2008; Wilczek et al., 2010), and temporal boundaries on the growing or breeding season (Morales et al., 2005). Alternatively, successive life history stages could respond to different climatic conditions (Kingsolver et al., 2011), resulting in a changing interval between them as the climate changes (Lany et al., 2016). Determining which internal or external mechanisms are acting on the timing of life history events should offer critical predictive insights into whether and how climate change will affect the persistence not only of individual taxa, but also of the interactions among them.

Perhaps the most thoroughly documented phenological shift in response to climate change involves flowering. Advances in flowering time (conventionally noted by opening of flowers on an earlier date) have been found both across communities and within them, and contrasting responses across regions and taxa have been explored in some depth (e.g., Fitter and Fitter, 2002; Root et al., 2003; Miller-Rushing and Primack, 2008; CaraDonna et al., 2014; Rafferty and Nabity, 2017). Here, we use this wealth of knowledge on flowering phenology to explore whether subsequent life stages are linked, and if so, how they are linked. Although several investigators have speculated about whether advances in flowering time are accompanied by parallel shifts in fruiting time (Primack, 1987; Eriksson and Ehrlén, 1991; Forrest and Miller-Rushing, 2010), there are as yet few tests of these ideas (Chmielewski et al., 2004; Sherry et al., 2007; Segrestin et al., 2018). As a consequence, the response of fruiting phenologies to a changing climate remains poorly understood (Chuine and Régnière, 2017).

Experimental warming studies have shown that with higher temperatures, most species fruit earlier in the season (Sherry et al., 2007; Post et al., 2008a,b). However, observational studies of fruiting phenology, particularly those using datasets that span decades, vastly lag behind the number published for flowering. One possible reason for the focus on flowering phenology over fruiting is that assigning a date to fruiting is less straightforward because fruit morphology is more diverse across taxa than flower morphology, and stages of fruit development are less easily identified through observation. We follow convention of previous studies and, unless otherwise noted, use “fruiting” or “fruiting time” to denote the first date on which the presence of mature fruits or seeds is observed (e.g., Gordo and Sanz, 2009; Haggerty and Galloway, 2011; Ettinger et al., 2018), and, in our discussions of published studies and within the case study we present, we compare across taxa with different fruiting structures (e.g., fleshy, dry, indehiscent, dehiscent, animal-dispersed, and wind-dispersed; Menzel et al., 2006, 2020; Ge et al., 2015).

Here, we explore promising pathways for advancing understanding of which and how fruiting times are linked to flowering times. In animal-dispersed plants, shifts in fruiting phenology have the potential to affect or even disrupt seed-dispersal interactions (Forrest, 2014; Rafferty et al., 2015). Thus, an understanding of shifting fruiting phenologies is important to our ability to predict the effects of global change on plant-animal communities (Rogers et al., 2021). We incorporate plants that are animal-dispersed as well as those that employ abiotic seed dispersal, but we focus on the interaction and community repercussions for animal-dispersed plants. First, we synthesize current understanding of the linkages between flowering and fruiting stages across angiosperms. Second, to ground our discussion of life history stage linkages in a real-world framework, we report on a case study designed to determine how the flowering and fruiting times of individuals tracked over multiple decades at the same location are linked. Third, we leverage our extensive knowledge of climate-mediated shifts in flowering phenology to develop a conceptual model for how successive life history stages are linked and how climate change could affect these linkages. We then return to our case

study results to demonstrate how to distinguish and eliminate proposed mechanisms for these linkages. Finally, we suggest directions for future research to test these mechanisms, and discuss the implications of climate change-driven shifts in fruiting phenology for ecological communities.

CLIMATE CHANGE AND POTENTIAL LINKAGES BETWEEN FRUITING AND FLOWERING

Few studies have determined the extent to which flowering and fruiting phenology are linked or physiologically constrained. We argue here that examining the flowering-to-fruiting interval can provide insight. We define the flowering-to-fruiting interval (hereafter, FTFI) as the period from flower opening to the first date on which the presence of mature fruits or seeds is observed. The FTFI is “constrained” if it remains fixed in length, including within warming experiments or in a changing climate. The FTFI is a trait defined at the level of the reproductive structure; i.e., it is the length of time from flowering to fruiting measured on a single flower developing into a fruit on an individual plant. In order to make use of historical datasets in which observations were not collected at this level, most previous studies have largely used population- or species-level measurements, with a few examples of individual-level measurements (Table 1). If flowering and fruiting are linked, internal drivers will dictate that fruiting times are related to flowering times as well as to the FTFI. If external factors are instead driving phenology, the FTFI could lengthen or shorten as flowering and fruiting respond to these external factors independently. If flowering and fruiting are responding independently to the same external factors, or if by chance these two life stages are responding in similar ways to different independent factors, the FTFI will stay the same.

The few previous studies of how flowering and fruiting are linked provide evidence for internal drivers, but also evidence for independent responses of flowering and fruiting to external factors (Post et al., 2008a,b; Ettinger et al., 2018; Segrestin et al., 2018; Table 1). Studies that present evidence for external factors independently driving fruiting and flowering times often show some evidence for internal drivers as well (Lechowicz, 1995; Menzel et al., 2006, 2020; Haggerty and Galloway, 2011; Jiang et al., 2016; Sethi et al., 2020; Table 1). Table 1 synthesizes the results of these previous studies and the mixed evidence for internal and external drivers of flowering and fruiting. An early study of the FTFI based on a nearly 30-year dataset found no evidence for a linear relationship between flowering and fruiting dates across many temperate species, even when grouped by time of season in which fruiting occurs (Lechowicz, 1995). In contrast, a more recent single-year study did find evidence for this linear relationship in 25 U.S. species (Ettinger et al., 2018), as did a 12-year study of 100 European species (Segrestin et al., 2018). Even concurrent studies on the same species have produced mixed evidence for internal and external drivers of the FTFI. A 1-year warming experiment revealed that higher temperatures shortened the entire reproductive cycle of *Betula nana* by 27 days on average, from flower bud set to fruit set (Post et al., 2008b),

TABLE 1 | Evidence from previous observational and experimental studies on the length of the flowering to fruiting interval (FTFI), the time between the flowering and ripe fruit phenophases, and for external and internal drivers of FTFI duration.

Authors	Year	Time	Level	Driver
Lechowicz (1995)	1995	30 years	Not reported	External
Post et al. (2008b)	2008b	1 year	Individuals	External
Jiang et al. (2016)	2016	3 years	Individuals	External
Sethi et al. (2020)	2020	5 years	Plots	External
Ettinger et al. (2018)	2018	1 year	Individuals	Internal
Segrestin et al. (2018)	2018	12 years	Population	Internal
Post et al. (2008a)	2008a	2 years	Plots	Both
Menzel et al. (2006)	2006	>15 years	Country	Both
Menzel et al. (2020)	2020	67 years	Country	Both
Haggerty and Galloway (2011)	2011	1 year	Individuals	Both

The citation for each study is listed in the first two columns. The third column lists the span of the dataset in number of years. The fourth column lists at what level phenology was tracked: individuals, plots, or population. “Individuals” denotes that phenological stages were tracked on marked individuals, and the mean across many individuals of the same species was analyzed. “Plots” denotes that phenological stages were recorded at the level of experimental or observational plots, across all individuals of the same species within a plot, and means were analyzed across multiple plots. “Population” denotes that phenological stages were recorded at the level of a site, which generally included multiple individuals of the same species, and means were analyzed across multiple sites. “Country” denotes that phenological stages were tracked by country, and means were analyzed across multiple countries. When it was unclear within the study whether individuals, plots, population, or country was tracked, we listed “not reported” within the column. The last column summarizes whether the study provides evidence for internal, external, or both internal and external drivers of FTFI duration.

thereby also shortening the FTFI. However, a concurrent 2-year warming experiment showed that higher temperatures did not decrease the FTFI in *B. nana* (Post et al., 2008a), even though flowering and fruiting were advanced.

Other experimental studies have yielded evidence for both internal and external drivers of the FTFI. Alpine plants transplanted to warmer and cooler altitudes for 3 years flowered earlier and later, respectively, but fruiting times remained the same (Jiang et al., 2016). These results support external drivers of the FTFI, but a different elevation transplant study (Haggerty and Galloway, 2011) showed evidence for both external and internal drivers: in a single-year common garden experiment, *Campanulastrum americanum* populations planted at lower elevations had a shortened FTFI relative to those planted at higher elevations. However, populations from low elevations planted at either elevation had a longer reproductive cycle overall than those from high elevations (Haggerty and Galloway, 2011).

Observational studies have similarly yielded mixed evidence. A recent observational study on 28 species of U.S. alpine plants showed mostly shortened FTFI with climate change, comparing observations taken in 2015 to those taken in 2011–2014 (Sethi et al., 2020). Shorter FTFI were shorter by 3–15 days, but two species showed an FTFI change of a day or less, and the FTFI of three species increased by 3–5 days (Sethi et al., 2020). Menzel et al. (2006) used phenological records to determine (1) how timing of life history stages was changing in 14 European countries over 30 years and (2) how

these phenological changes correlated with temperature across 9 European countries over 15 years. While flowering time was largely negatively correlated with temperature, fruiting time was more variable: the correlation with temperature was negative for most species, but positive for a few others. A recent update of this study incorporating data on the same European species from 1951 to 2018 showed the same pattern (Menzel et al., 2020). As temperature increases and flowering times advance, Menzel et al.'s (2006, 2020) findings imply that the FTFI will shorten for some species, remain the same for some, and lengthen for others, depending on how internal and external factors interact to determine fruiting times.

CASE STUDY: FRUITING PHENOLOGY SHIFTS AND LIFE STAGE LINKAGE IN EUROPEAN SPECIES

Nearly all of the few studies that directly analyze the FTFI do so on the scale of a year or a few years, and in the case of multi-year analyses, only for a single species (Table 1). Publicly available fruiting data at time scales longer than 20 years are particularly sparse (Chuine and Régnière, 2017; see **Supplementary Appendix 1** for descriptions of publicly available phenology databases). Yet, time series > 30 years are needed to estimate robust trends (Dose and Menzel, 2004; Menzel et al., 2020). Here, we use a three-and-a-half-decade dataset (from the PEP725 database; Templ et al., 2018) to assess how the FTFI is changing in individual plants. Our case study both illustrates the challenges of analyzing the phenology of certain life history stages on a decadal scale using publicly available data. At the same time, it provides compelling evidence that such data, when available, can be used to analyze changes to the length of time between phenophases with climate change. We do not present here a comprehensive treatment of FTFI across species. Although more long-term data are needed to assess changes in the FTFI across diverse taxa and regions (Mendoza et al., 2017; **Supplementary Appendix 1**), we use this case study to illustrate the potential power of analyzing relationships between the timing of different life history stages.

What Are the Relative Changes Between Flowering and Fruiting Life Stages?

We examined whether a close temporal link exists between the flowering and fruiting life stages, and assessed the strength of this linkage. To determine how the FTFI has changed over time, we used phenology data from the PEP725 database (Templ et al., 2018) over 35 years (1980–2015). The FTFI is defined at the level of a single reproductive structure on an individual plant. Our data did not allow for this level of precision so instead we used the next most precise level, that of the individual. We used all six tree and shrub species with > 100 individuals per year for which both first flowering and first ripe fruits were recorded in the database: *Aesculus hippocastanum*, *Sorbus aucuparia*, *Vaccinium myrtillus*, *Sambucus nigra*, *Ribes grossularia*, and *Ribes rubrum*. These species represent both

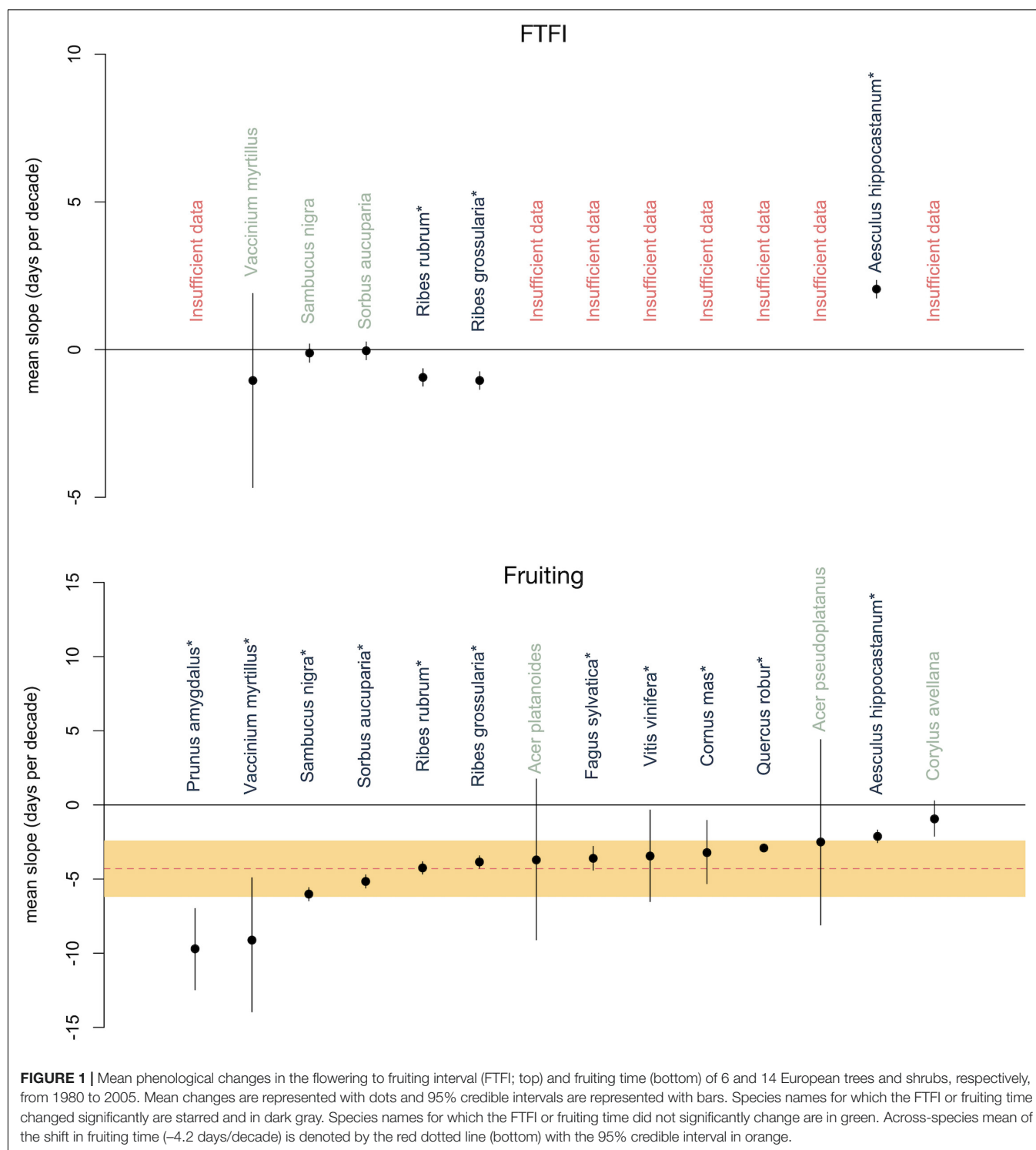
animal-dispersed (*Vaccinium myrtillus*, *Sambucus nigra*, *Ribes grossularia*, and *Ribes rubrum*) and wind-dispersed (*Aesculus hippocastanum* and *Sorbus aucuparia*) species; given that we had access to data on only a few species, we were unable to compare FTFI responses in biotically vs. abiotically dispersed species. We calculated the FTFI by subtracting the first flowering day from the first day at which ripe fruits were noted, for each individual within each species for each year. Number of days between flowering and fruiting became our response variable for a single multi-species analysis with a Bayesian regression framework (for analysis details see **Supplementary Appendix 2: Methods 2**).

The FTFI remained constant over time in three of the six species: *Sorbus aucuparia*, *Vaccinium myrtillus*, and *Sambucus nigra*. The other three species experienced either a significant increase (*Aesculus hippocastanum*) or significant decrease (*Ribes rubrum* and *Ribes grossularia*) in FTFI over time (Figure 1). If a close linkage exists, we would expect no change in FTFI. If, however, a close linkage does not exist because flowering and fruiting are responding to different external cues and a changing climate independently, the result could be a shortening or lengthening or lack of change in the interval between flowering and fruiting. The divergent results between species suggests that a range of mechanisms might be determining the role of climate change on the FTFI.

How Is Fruiting Phenology Shifting?

The magnitude of a shift in fruiting phenology for a species, and in which direction this shift occurs, can provide additional information about the mechanism driving the FTFI. To determine whether or not fruiting alone was advancing over the same time period as our FTFI analysis, we performed an additional analysis on fruiting for the same 6 plus an additional 8 European species. We analyzed fruiting at the level of the population, to be consistent with previous analyses of fruiting, which allowed us to include species that did not have enough individual observations spanning multiple years to be in the FTFI analysis. The incorporation of these additional 8 species allowed us to more broadly compare the results of our fruiting analysis to previous studies. We selected native, broad-leaved woody plant species that had records that occurred consistently from 1980 to 2015 in one location (for additional methods see **Supplementary Appendix 2: Methods 1**).

We found that fruiting had advanced by an average of 4.2 days per decade (days/decade; 95% CI: 2.4–6.2 days/decade, Figure 1), or 14.7 days from 1980 to 2015 (for additional results see **Supplementary Appendix 2: Results 1**). The 4.2 days/decade advancement in fruiting in our species is consistent with Ge et al.'s (2015) meta-analysis of 104 Chinese tree, shrub, and herb species, in which spring/summer phenophases, including fruiting, advanced by an average of approximately 2 days for trees and shrubs and 5.5 days/decade for herbs from 1960 to 2011. It is also consistent with Gordo and Sanz's (2009) findings of 3.2 days/decade for 29 perennial Spanish species from 1943 to 2003. It is likewise consistent with Menzel et al.'s (2006) findings of 2.4 days/decade for 542 European species from 1971 to 2000 and 1–2.5 days/decade, depending on the season of fruiting,



for the same species from 1951 to 2018 (Menzel et al., 2020). Collectively, these findings highlight the need to conduct similar, long-term, studies of how fruiting phenology is responding to climate change.

Fruiting advanced for all of the six species in our FTFI analysis (Figure 1). The species in which fruiting advanced the most

were also the species for which the FTFI remained constant. *Vaccinium myrtillus*, *Sambucus nigra*, and *Sorbus aucuparia* advanced fruiting by an average of 9.0, 6.0, and 5.2 days/decade, respectively, while their FTFI did not significantly change. For *Ribes rubrum* and *R. grossularia*, fruiting advanced by an average of 4.3 and 3.8 days/decade while the FTFI shortened

by a mean of 1.0 and 0.9 days/decade, respectively. Fruiting in *Aesculus hippocastanum* advanced by 2.1 days/decade, while the FTFI lengthened by a mean of 2.0 days/decade. The similar responses of fruiting in these six species but differing responses of the FTFI suggest that separate mechanisms may be operating for each species.

WHAT MECHANISMS COULD EXPLAIN HOW SUCCESSIVE LIFE HISTORY STAGES ARE LINKED?

If the timing between flowering and fruiting is physiologically constrained, a shift in timing in flowering should have a direct effect on the timing of fruiting. This could result in flowering and fruiting times advancing in parallel, as in three of the six species in our case study. However, we cannot rule out the possibility that separate, possibly correlated external factors are acting on each of the life history stages. Furthermore, external factors could act on flowering and fruiting separately or jointly, such that the FTFI lengthens or shortens, as seen in the other three species in our case study. Below we propose four general mechanisms for how flowering and fruiting times may jointly or independently shift with climate change. While the specifics of these mechanisms can relate more strongly to one seed dispersal type than another, as noted below, all four mechanisms apply to plants with either biotic or abiotic seed dispersal. We additionally recognize that multiple mechanisms could be operating at once.

Mechanism 1: Physiological and Developmental Processes Constrain FTFI, Such That Fruiting Time Will Shift Only in Parallel With Flowering Time

The FTFI will always be somewhat variable across individuals and reproductive structures for any given species, but internal constraints such as developmental processes or seed and fruit size should impose limits on the variability possible for this interval and result in parallel shifts in flowering and fruiting, as shown in **Table 2** and **Figure 2**. Certain fruit or seed traits such as size could be correlated with, and could possibly dictate, the length of the fruit development and maturation periods (Primack, 1987; Segrestin et al., 2018). For example, animal-dispersed seeds, which are on average larger than wind-dispersed seeds, have a physiologically constrained lower limit on seed development time that is greater than that of smaller seeds (Primack, 1987), and a longer FTFI on average than wind-dispersed seeds (Segrestin et al., 2018). The minimum developmental time for fruits theoretically constrains the FTFI, regardless of external environmental effects like drought (Gordo and Sanz, 2010; Segrestin et al., 2018).

Similarly, seed mass and the amount of time that fruits need from flowering to ripening are phylogenetically constrained and positively correlated (Heydel and Tackenberg, 2016), suggesting that certain evolutionary histories dictate fruit development and maturation periods. Plants with life history stages such as leaf-out

and flowering that occur earlier in the spring display traits that are a product of rapid growth, which may translate to a shorter FTFI, resulting in smaller seeds or fruits due to the shorter development time (Wolkovich and Cleland, 2014). If phenology is phylogenetically constrained, we would expect the FTFI to be phylogenetically constrained. Studies have found phylogenetic signals in leaf-out, flowering, and fruiting phenology, but their strengths are highly variable, with some clades exhibiting a stronger pattern than others (Marco and Páez, 2002; Wolkovich and Ettinger, 2014; Gougherty and Gougherty, 2018). While this signal seems to indicate phylogenetic constraints, it may instead be that phenology is correlated with other plant traits that are themselves evolutionarily conserved (Marco and Páez, 2002; Davis et al., 2010; Wolkovich and Ettinger, 2014; Gougherty and Gougherty, 2018).

Mechanism 2: Stabilizing Selection on Fruiting Time Results in a Longer or Shorter FTFI

Stabilizing selection could be indirectly acting on fruiting times by promoting genotypes linked to a particular disperser-fruiting time relationship (e.g., Palacio et al., 2021) or climate-fruiting time (e.g., Inouye et al., 2019). If physiological and developmental constraints were keeping the FTFI the same length and stabilizing selection via an external driver were maintaining fruiting times, we would expect to see both unchanging fruiting times and unchanging flowering times in the face of climate change. However, we know that flowering time is largely advancing; therefore, we would expect stable fruiting times and thus lengthened FTFIs if fruiting time were driven by stabilizing selection (**Table 2** and **Figure 2**). When a fruit reaches maturity could be tightly associated with the historical activity of seed dispersers (e.g., bird-dispersed fruits, Noma and Yumoto, 1997) and could remain constant, even though the timing of disperser activity is itself shifting with climate change (e.g., in birds, Thomas and Lennon, 1999; Cotton, 2003; Marra et al., 2005; Tingley et al., 2009).

The second way in which stabilizing selection could be acting is if the fruiting time-climate relationship evolved in response to an abiotic driver that is unlikely to be affected in a direction predictable by climate change, such as solar irradiance and photoperiod (Hamann, 2004; Chapman et al., 2005; Zimmerman et al., 2007; Mendoza et al., 2017; Ettinger et al., 2021) or the onset of monsoon rains (Singh and Kushwaha, 2006). If fruit ripening times are synchronized by a biotic or abiotic event that does not significantly shift over time with climate change, whereas flowering phenology is responsive to shifting environmental cues, an increase or decrease in the length of the interval could result (**Table 2** and **Figure 2**).

Mechanism 3: Genotypic Variation Results in a Changing of the FTFI, Including Changes to Fruiting Time

The genetic underpinnings of flowering phenology, and less so fruiting phenology, in response to temperature have been

TABLE 2 | Proposed mechanisms for how the flowering to fruiting interval (FTFI), the time between the flowering and ripe fruit phenophases, will change or remain stable with climate change.

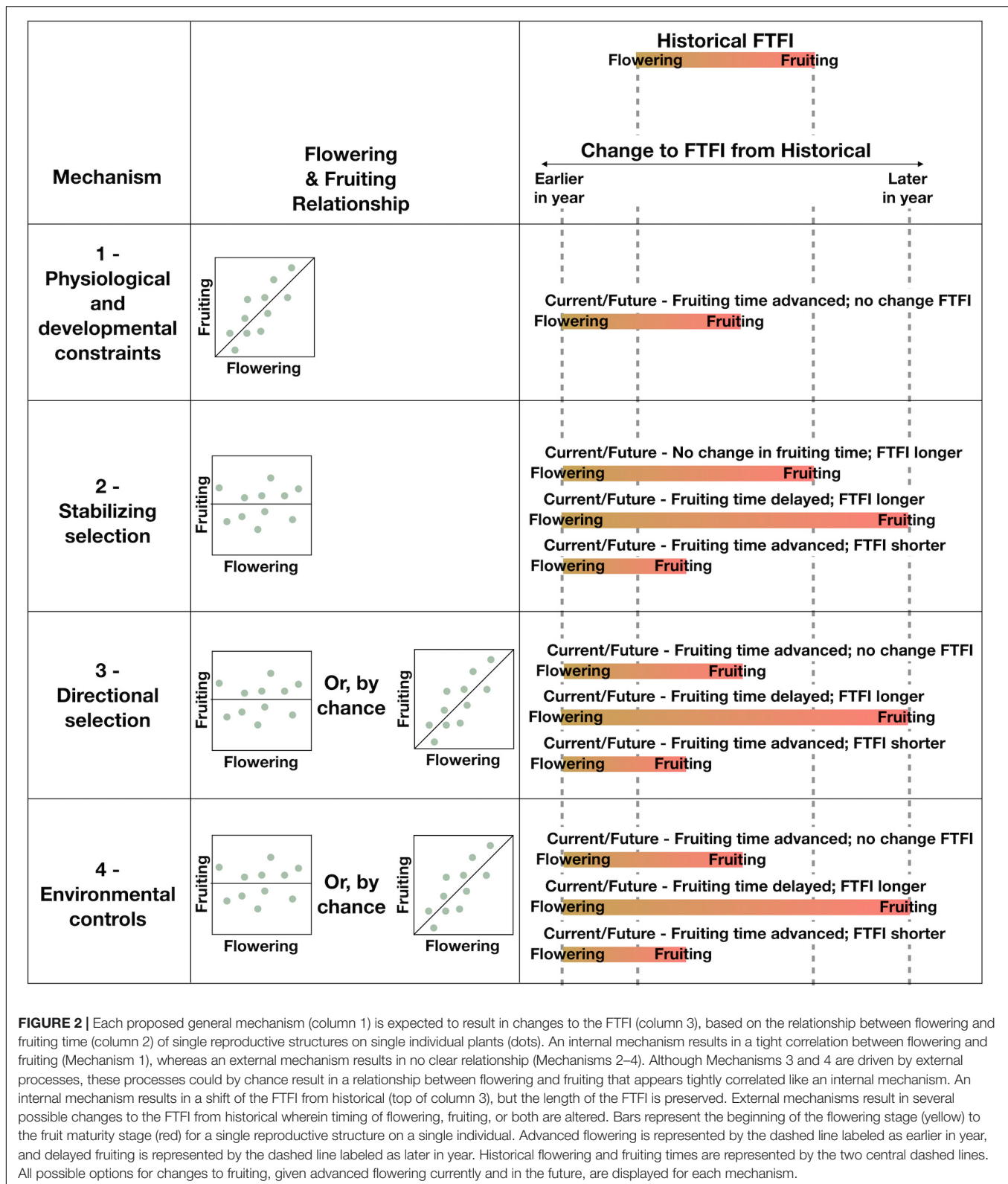
Mechanism	Internal vs. External	Change to FTFI	Pathway(s) and evidence for mechanism
1—Physiological and developmental constraints	Internal	Shortened	None
		No change	Physiological and developmental constraints on the FTFI (Primack, 1987; Gordo and Sanz, 2010; Segrestin et al., 2018)
2—Stabilizing selection	External	Lengthened	None
		Shortened	Fruit timing does not change from current with respect to other climatic or phenological event (but flowering is delayed) (Hamann, 2004; Chapman et al., 2005; Singh and Kushwaha, 2006; Zimmerman et al., 2007)
		No change	None
		Lengthened	Fruit timing does not change from current or with respect to other climatic or phenological event (Noma and Yumoto, 1997; Hamann, 2004; Chapman et al., 2005; Singh and Kushwaha, 2006; Zimmerman et al., 2007)
3—Directional selection	External	Shortened	Higher temperatures advance fruiting (Chuine et al., 1999; Sherry et al., 2007; Misson et al., 2010; Haggerty and Galloway, 2011; Darbyshire et al., 2014; Gallinat et al., 2015)
		No change	Changes in precipitation do not alter fruiting times (Sherry et al., 2007)
		Lengthened	Higher temperatures delay fruiting (Sherry et al., 2007; Gordo and Sanz, 2009)
			Changes in precipitation delay fruiting (Peñuelas et al., 2004; Mazer et al., 2015; Dunham et al., 2018)
4—Environmental controls	External	Shortened	Phenotypic plasticity (response to temperature and precipitation) Phenotypic plasticity (flower longevity shortened) (Nagahama et al., 2018) Resource acquisition takes less time, advancing fruiting (Chuine and Beaubien, 2001; Klapwijk et al., 2013; Tripathi et al., 2016; Guillaume et al., 2018)
		No change	Phenotypic plasticity (response to temperature and precipitation)
		Lengthened	Phenotypic plasticity (response to temperature and precipitation) Phenotypic plasticity (flower longevity lengthened) (Arroyo et al., 1981; Moore and Lauenroth, 2017)
			Resource acquisition takes more time, delaying fruiting (Klapwijk et al., 2013; Guillaume et al., 2018)

Numbers beside each of the mechanisms correspond to the numbers of the proposed mechanisms within the text. For each mechanism, the evidence for the expected change(s) to the FTFI are summarized in bold in the rows corresponding to the expected change(s): shortened, no change, and lengthened. Supporting evidence and references are listed under the bold summaries.

well-studied in certain species, most of which are commercially grown (e.g., Usenik and Štampar, 2011; Satake et al., 2013; Marrano et al., 2019; Bernard et al., 2020; Chen et al., 2020). These studies show diverse responses of life history stages to climate change between closely related species and even individuals of the same species, and suggest that the underlying genetic differences influencing these life history stages dictate whether or not the FTFI is altered by climate change. In contrast, there is poor understanding of the genetics of fruiting phenology in wild species, and experiments on intraspecific genetic variation interacting with climate change-induced environmental conditions are rare (e.g., Faticov et al., 2020). Most of our understanding is based on observational and experimental studies of plant responses to temperature and precipitation without knowledge of the underlying genetic architecture, which suggest either selection favoring genotypes that are able to fruit earlier in the growing season, or plastic phenological responses to temperature and precipitation. In conjunction with flowering responses to climate change, we can make inferences about how selection on or plasticity of fruiting times will affect the

flowering to fruiting interval (Table 2 and Figure 2). In multiple studies, higher temperatures generally advanced flowering and advanced fruiting by a greater magnitude than flowering, which shortened the FTFI (Sherry et al., 2007; Misson et al., 2010; Haggerty and Galloway, 2011; Gallinat et al., 2015; Carbognani et al., 2018), but in some U.S. and European species, fruiting advanced less than flowering, resulting in a longer FTFI (Sherry et al., 2007; Gordo and Sanz, 2009). A temperature-based modeling framework for flowering phenology (e.g., Chuine et al., 1999) extended to the FTFI largely predicts a shorter FTFI (Darbyshire et al., 2014).

Both increased and decreased precipitation have led to variable effects on FTFI in observational and experimental studies (Peñuelas et al., 2004; Sherry et al., 2007; Mazer et al., 2015; Dunham et al., 2018; Table 2 and Figure 2). Doubling precipitation had no effect on fruiting times and FTFI in a controlled experiment (Sherry et al., 2007). In three studies that did not track the FTFI, increased precipitation resulted in delayed fruiting (Peñuelas et al., 2004; Mazer et al., 2015) as did decreased precipitation during the dry season (Dunham et al., 2018). If we



assume that most species in these studies experienced advanced flowering, we can then assume that FTFI has lengthened as a consequence. However, more studies on the effects of

precipitation generally are needed, especially because studies on the effects of decreased precipitation on fruiting specifically are lacking (but see Sethi et al., 2020).

Mechanism 4: Environmental Controls Result in a Changing of the FTFI, Including Changes to Fruiting Time

As previously stated, many of the responses of the FTFI to climate listed under Mechanism 3 could have been due to phenotypic plasticity in response to environmental conditions, since genetic responses were not tracked. Segrestin et al. (2018) found that across plant species, the onset of fruiting was more variable than the onset of flowering, perhaps indicating that the timing of fruiting is more plastic. Warmer air temperatures and earlier snow melt were found to be correlated with reductions in the FTFI of alpine plants (Sethi et al., 2020), indicating a plastic response to these environmental changes. Phenotypic plasticity could allow the FTFI to lengthen, shorten, or remain the same in response to biotic interactions or a variety of environmental conditions, including flowering and fruiting phenologies responding independently to these drivers (Table 2 and Figure 2).

Plasticity in flower longevity, i.e., how long an individual flower is open, is another way in which plants could respond to environmental conditions and might result in a change to the FTFI. Some species can show variable flower longevity in response to pollen receipt, wherein the flower closes anywhere from a few hours to a few days after successful pollination (Primack, 1985; Proctor and Harder, 1995; van Doorn, 1997; Niu et al., 2011; Trunschke and Stöcklin, 2017). The time from pollination to fruiting could thus be fixed by physiological and developmental constraints on fruit development, as discussed above, but the FTFI may instead reflect the time from flower opening to pollination (Segrestin et al., 2018). If a species' flowering time becomes partially mismatched from pollinator availability, time to pollination could lengthen, resulting in a longer FTFI (Table 2 and Figure 2).

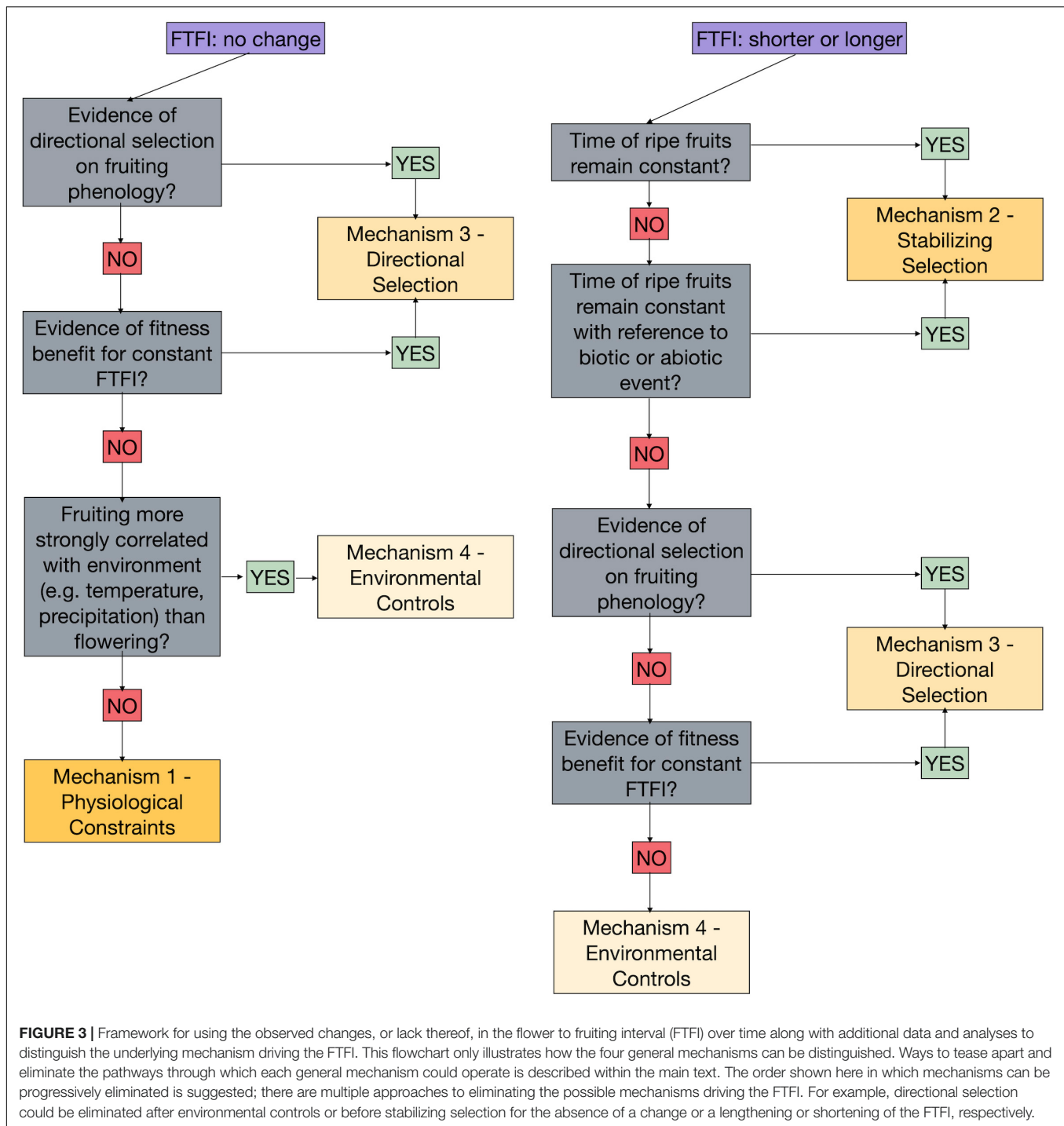
Flower longevity, and thus the FTFI, could also be influenced by environmental factors such as warmer or cooler temperatures (Arroyo et al., 1981; Molau, 1997; Steinacher and Wagner, 2010; Nagahama et al., 2018) or increased precipitation (Moore and Lauenroth, 2017), resulting in a shortened or lengthened FTFI (Table 2 and Figure 2). For example, Nagahama et al. (2018) found that climate warming causes flowers to senesce earlier, which could result in a shorter FTFI. Flower longevity increases due to lower temperatures (Arroyo et al., 1981), meaning that advanced flowering could result in flowers periodically experiencing lower than normal temperatures, which could result in longer flower longevity and thus a lengthened FTFI. Increased precipitation resulted in increased flower longevity for late-season species (Moore and Lauenroth, 2017), indicating that changes to precipitation in either direction could also alter flower longevity, and in turn, the FTFI.

A third way in which environmental conditions could influence the FTFI is through resource acquisition pathways. When a fruit matures may depend on how quickly a plant is able to acquire resources from photosynthesis, resulting in a shorter or longer FTFI. Resource acquisition via photosynthesis, in turn, can be impacted by an array of factors (Table 2 and Figure 2). Warmer temperatures could result in fewer

leaves damaged by frost, allowing plants to acquire resources more quickly, thus advancing fruiting times and shortening the FTFI (Chuine and Beaubien, 2001; Guillaume et al., 2018). Alternately, warmer temperatures could result in earlier leaf-out times, which could lead to greater frost damage of leaves, leading to a slower acquisition of resources, thus delaying fruiting times and lengthening the FTFI (Guillaume et al., 2018). Changing climate and the timing of insect emergence or population booms could either result in decreased or increased herbivore damage, leading to faster or slower acquisition of resources, respectively (Klapwijk et al., 2013). Lastly, with warmer temperatures, plants could produce more leaf mass or area, or thicker leaves, increasing photosynthetic capacity and leading to a faster acquisition of resources and advanced fruiting times (Tripathi et al., 2016).

USING THE CASE STUDY TO DISTINGUISH POTENTIAL MECHANISMS FOR CLIMATE-DRIVEN SHIFTS IN FRUITING AND FLOWERING

Several of the mechanisms proposed above for how fruiting and flowering phenology respond jointly or independently to climate change could produce identical results in the FTFI over time (Table 2 and Figure 2). Here we return to our case study to demonstrate how we could use the FTFI in combination with additional research to tease apart the mechanisms behind changes, or lack thereof, to the FTFI (Figure 3). For example, an absence of change in the FTFI, such as we found in three of our six species (Figure 1), indicates that the mechanism driving the FTFI for these species could be internal. Stabilizing selection is expected to produce a change in the FTFI, so that mechanism can be discarded. Constancy in the FTFI is consistent with Mechanisms 3, directional selection, and 4, environmental controls. The mechanism of environmental controls is difficult to rule out because, for example, an incremental increase in temperature across many years could have an equally strong correlation with fruiting as flowering has with fruiting. If, over many years and across yearly temperature and/or precipitation fluctuations, fruiting time is more strongly correlated with flowering time than with environmental cues, we could rule out environmental controls. The other processes affecting environmental controls are either difficult to track or require vastly more data. If length of flowering time, specifically from flower opening to pollination, does not affect fruiting time and thus FTFI, environmental controls via flower longevity could be ruled out. If any of the processes related to the acquisition of resources, like frost or herbivore damage to leaves, are not correlated with FTFI, we can rule out environmental controls. However, collecting data to discriminate multiple processes related to environmental controls is a massive undertaking. This will make discerning the importance of environmental controls via resource acquisition difficult. If we find no genetic evidence for directional selection on fruiting times (e.g., see Giménez-Benavides et al., 2011;



Munguía-Rosas et al., 2011; Anderson et al., 2012; Yeoh et al., 2017, for studies on flowering), or if we find no fitness benefits for those individuals for which the FTFI remains constant, we can rule out directional selection.

Ruling out stabilizing selection, directional selection, and environmental controls leaves only physiological and developmental constraints as mechanisms producing a constant FTFI over time and in the face of climate change. Comparing

the FTFI among species within the same genus and to species of genera with similar fruit or seed sizes could point to whether phylogenetic or developmental constraints are operating. Accounting for phylogenetic signal in the analysis of changes in FTFI across multiple years, species, and continents (i.e., Davis et al., 2010 for flowering) could point to the relative influence of evolutionary history on phenological responses to changing climate. However, none of these approaches permits

elimination of either pathway through which the internal mechanism could be operating.

One of the six species in our case study, *Aesculus hippocastanum*, experienced an increase in FTFI over time (Figure 1). We expect physiological and developmental constraints to result in a constant FTFI over time, suggesting that the other three mechanisms we have proposed—stabilizing selection, directional selection, or environmental controls—could be responsible. Stabilizing selection could be acting if the time of first ripe fruits remains constant. However, for *A. hippocastanum* the timing of fruiting shifted earlier (Figure 1). Another indication of stabilizing selection might be fruit ripening that remains constant in reference to an abiotic or biotic event. If we found no correlation between fruiting times and abiotic or biotic events, or no genetic evidence for stabilizing selection on fruiting times, we could rule out this mechanism. Furthermore, if we found no genetic evidence of directional selection on fruiting times, or if we found no fitness benefits for those individuals for which the FTFI increases, we could rule out directional selection. If flower longevity was driving the lengthening of the FTFI by an increased amount of time between flower opening (the beginning of the FTFI, as defined above) and flower closing, we would expect to observe a lengthening of the first flowering to flower senescence interval over multiple years. We would also potentially expect to see a strong correlation between date of pollination and first ripe fruit dates. If neither this correlation nor a correlation between pollination and first ripe fruits were found, environmental controls via flower longevity could be rejected. If both flowering and fruiting were correlated with the same or independent environmental conditions, with no evidence for selection on either, environmental controls might be driving the increased FTFI. However, correlations with environmental conditions may be direct (e.g., temperature and/or precipitation acting directly on flowering and fruiting) or indirect, via resource acquisition. A number of pathways that affect photosynthesis could be involved in this indirect relationship, and teasing them apart would require extensive data collection in, for example, leaf damage and cloudless days.

Two of the six species represented in this case study experienced a decreased FTFI (Figure 1), again suggesting that stabilizing selection, directional selection, or environmental controls could be responsible. As with *A. hippocastanum*, in *Ribes rubrum*, and *R. grossularia* fruiting occurred earlier (Figure 1), indicating that stabilizing selection could only be acting if fruit ripening time remained constant in reference to an unknown abiotic or biotic event. The same process of eliminating mechanisms just described for *A. hippocastanum* could be applied to these *Ribes* species.

RECOMMENDATIONS FOR FURTHER RESEARCH ON THE PROPOSED MECHANISMS DRIVING THE FTFI

Throughout this paper, we have stressed that additional research is needed to further distinguish which mechanisms are driving the FTFI, and through what pathways. Here we discuss research

directions for internal drivers of the FTFI, how genetics and selection influence the FTFI and will determine future fruiting responses to climate change, and the interactions among different environmental controls and how these affect fruiting both now and with climate change. Although different species may be driven by different mechanisms, and all of the mechanisms discussed here may be operational in nature, simultaneous, standardized studies of multiple species could provide evidence for or eliminate possible mechanisms on a broad scale. We additionally emphasize that long-term studies of phenology are essential because short-term interannual variation could reflect phenological plasticity rather than evolutionary change.

Further research could elucidate how physiological mechanisms determine the FTFI, and to what extent different mechanisms co-occur and can interact. Taking a trait-based approach to determine differences in seed and fruit development time across the range of seed and fruit traits could advance our understanding of the extent to which the time of fruit development is constrained, or varies, along trait axes (e.g., Singh and Kushwaha, 2006). Determining which families or clades have long fruit or seed development times closely linked to the number of growing degree days within a season could shed light on the extent to which phylogenetic constraints work in concert with environmental controls to determine the length of the fruit development period. Similarly, studies that compare the relative influence of evolutionary history and environmental controls could tease apart the extent to which internal vs. external process are driving phenology (e.g., Staggemeier et al., 2015), particularly with the incorporation of phenological shifts due to climate change (Davis et al., 2010). We suggest incorporating standardized FTFI measures into existing phenological data collection protocols so as to more accurately compare across datasets, as Buonaiuto et al. (2021) have suggested for the interval between flowering and leaf-out.

If fruit or seed dispersal mode does not predict the strength of selection on fruit ripening times (e.g., Schluter, 1988; Kingsolver et al., 2001; Palacio et al., 2021), it is less likely that stabilizing selection is acting on fruit ripening times across many species. Additionally, if peak activity of seed dispersers and fruit ripening times are shifting and becoming out of phase with climate change, instead of shifting in parallel, biotic interactions driving stabilizing selection in animal-dispersed fruits can be discarded as a general pattern. To determine how peak activity of dispersers and fruit ripening times are responding to each other and climate change, more long-term studies that track disperser phenology along with fruiting phenology, particularly in the tropics where biotic interactions are assumed to play a greater role than climatic factors, are sorely needed (Mendoza et al., 2017).

Mechanistic research that addresses the molecular and regulatory basis of fruit ripening in wild species would further disentangle selection for particular genes associated with ripening from changing environmental cues and altered physiological processes (Chen et al., 2020). Additionally, determining how selection is acting on the reaction norm for fruit ripening times (Inouye et al., 2019) as climate changes, and how genetic variation in wild species of genes associated with fruiting

responds to changes in temperature, precipitation, and other climatic factors, would help further our understanding of how a changing environment is interacting with selective pressures. Agricultural scientists are exploring the genetic underpinnings of plant phenology (e.g., Satake et al., 2013; Marrano et al., 2019; Chen et al., 2020) and phenological responses to climate change of cultivated species (e.g., Chmielewski et al., 2004; Darbyshire et al., 2014); future research that draws on this body of literature could inform our understanding of wild plants in natural systems. Additionally, studies that correlate climatic cues with gene expression in genes associated with fruiting in wild plants (e.g., see Kudoh, 2016; Yeoh et al., 2017 for this type of research with genes associated with flowering) would increase our ability to tease apart the pathways and extent to which different climatic variables impact the genetic component of fruiting. Lastly, in animal-dispersed species, disperser activity could directionally select for fruiting phenology, and further studies are needed to explore to what extent and in which species dispersers drive phenotypic selection, particularly with reference to the FTFI and population-level traits like crop size and fruiting duration (Palacio et al., 2021).

We have emphasized that different types of environmental controls can interact with each other. Further studies are needed to understand and differentiate among these effects. For example, in an analysis of the midpoint of listed fruiting dates of 11,605 Chinese species within a compiled flora, Du et al. (2020) found that mean annual precipitation, precipitation seasonality, temperature seasonality, and temperature of the coldest quarter were included in the best supported models of the variation in fruiting times across species. Reduced soil moisture was a climate-related variable that was correlated with shortened FTFI in some alpine plant species, as was increased temperature in most species, although the interaction between them was not specifically tested (Sethi et al., 2020). Further, interactions between temperature and precipitation (e.g., Misson et al., 2010; Butt et al., 2015; Mazer et al., 2015) with climate change could be additive and cause fruiting times to advance more than changes to temperature or precipitation alone. Further research is also needed on how precipitation affects fruiting phenology, including the effect of higher or lower precipitation on the FTFI and how timing of precipitation affects fruiting (e.g., Molau, 1997; Fitter and Fitter, 2002; Parmesan and Yohe, 2003; Du et al., 2020). Additionally, seasonality of precipitation and how it relates to fruiting phenology in tropical wet forests needs to be further investigated, as current studies show contradictory patterns (Mendoza et al., 2017). Finally, environmental controls could interact with other factors influencing a species' phenology and our other proposed mechanisms. For example, higher temperatures due to climate change could interact with biogeography (e.g., Loarie et al., 2009; Butt et al., 2015; Ge et al., 2015, reviewed in Du et al., 2020), phylogeny (Davis et al., 2010), and life form (Du et al., 2020; Ganjurjav et al., 2021) to produce patterns in the FTFI across many species.

Lastly, we recommend that future research precisely define the beginning and end of the FTFI and that these definitions are incorporated into study design. Because FTFI is defined at

the level of a single reproductive structure on an individual plant, the start and end of the FTFI can be defined in terms of flower opening, closing, or pollen deposition, and the end of the FTFI can be defined as when the individual fruit is ripe, with the recognition that "ripeness" will need to be precisely delineated for each species. While our case study was limited by available phenological data, future studies can tease apart flower longevity by defining the beginning of the FTFI at the time of pollen deposition or flower closing and can investigate intraspecific, and even intraindividual, variation in FTFI. Long-term studies using these definitions on the boundaries of the FTFI, which are currently lacking, can then be used to determine interannual variation.

IMPLICATIONS FOR ANIMAL-MEDIATED SEED DISPERSAL AND DISPERSAL COMMUNITIES

The mechanisms we propose that could drive the FTFI in the context of a changing climate are relevant to all plants with biotic and abiotic seed dispersal. However, FTFI and fruiting phenology changes in animal-dispersed plants are particularly important to study since they have larger repercussions for the communities of which these plants are a part. For example, changes in fruiting phenology and animal abundance or activity could result in a temporal mismatch between partners, especially if plants and animals are responding to different environmental cues or responding in different ways (Forrest, 2014; Rafferty et al., 2015; Palacio et al., 2021). If the timing of peak disperser activity is shifting in response to environmental changes in a similar direction to fruiting times, with fruiting times responding via either genotypic variation or environmental controls in plants, no phenological mismatch will result. However, if the FTFI is internally driven, fruiting times will shift earlier in the season in conjunction with earlier flower times. If the FTFI is externally driven, changing environmental conditions could result in fruiting times that are out of step with peak disperser activity, resulting in a similar phenological mismatch outcome as if FTFI were internally driven. The same is true if the FTFI is a result of stabilizing selection, unless other selective pressures act to re-align fruiting times with peak disperser activity. Phenological mismatch could result in dispersal failure via fruiting occurring before dispersers are active (Warren and Bradford, 2013), lower plant fitness via reduced disperser activity (McConkey and Drake, 2006; Traveset et al., 2012; Rogers et al., 2017), animal population declines via reduced fecundity or increased mortality (van Schaik et al., 1993; Wright et al., 1999; Saino et al., 2011), or changes in community composition (Moegenburg and Levey, 2003; Peralta et al., 2020).

Phenological mismatch is not the only way in which plant and animal populations, communities, and ecosystems could be affected by climate change impacts on the FTFI. Plant and seed-disperser populations could be affected by reduced fruit production resulting from higher than average temperatures, increases or decreases in precipitation, or a combination

(Young et al., 2004; Augspurger, 2009; CaraDonna and Bain, 2016; Babweteera et al., 2018; Benlloch-González et al., 2018; Chapman et al., 2018; Lee et al., 2018; Mendoza et al., 2018; Pardee et al., 2018; Nussbaumer et al., 2020; Rogers et al., 2021) if internal or external drivers of the FTFI pull fruiting times into less than ideal climatic conditions. Additionally, fruiting phenology could shift earlier at different magnitudes across elevation or space (e.g., Rafferty et al., 2020), leading to shifting spatial activity of seed dispersers in response to changed resource levels across the landscape (Curran and Leighton, 2000). Lastly, major shifts in frugivorous animal activity could lead to a cascade of effects that impact ecosystem function (Rogers et al., 2021), even if seed dispersal is not directly affected. For example, red elderberry fruiting early in Alaska caused bears to leave salmon runs to gorge on fruits, disrupting a strong predator-prey interaction (Deacy et al., 2017) and likely causing a reduction in nitrogen influx to the forest (Helfield and Naiman, 2006).

CONCLUSION

We have leveraged here the extensive data on flowering phenology to explore how flowering and fruiting phenologies are linked. We found strong evidence in some species but not in others for a link between flowering and fruiting times. These results suggest that we should rapidly expand our understanding of the FTFI and shifts in fruiting phenology to enable better predictions for future climate change-influenced conditions. For those plant species demonstrating climate-driven phenological shifts in either direction, we need to explore *when* and *to what extent* those shifts will affect the ecological functioning and conservation concerns of plant and/or animal populations and/or mutualisms (e.g., Saino et al., 2011; Rafferty et al., 2015; Renner and Zohner, 2018). A better understanding of the magnitude of the effects on plant and animal populations and communities, as well as the factors that produce those effects, could enable parameterization of fitness models, and increase our ability to predict population trajectories and community composition in a changing climate.

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DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. Data were provided by the members of the PEP725 project: <http://www.pep725.eu> (PEP725).

AUTHOR CONTRIBUTIONS

MES performed case study analyses. MES, CEA, LP, and JLB jointly wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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SUPPLEMENTARY MATERIAL

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