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MINI REVIEW

How Climate Change May Impact Plant Reproduction and Fitness by Altering the Temporal Separation of Male and Female Flowering

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ABSTRACT

The temporal separation of male and female flowering—known as dichogamy—is a widespread adaptation across the plant kingdom that increases reproductive success and enhances plant fitness. Differences in timing between male and female flowering can be highly sensitive to environmental variation—and with widespread evidence of shifts in seasonal timing of flowering (i.e., phenology) due to anthropogenic warming—climate change may alter the sequences of male and female flowering for a diversity of taxa around the globe. However, we currently lack a broad understanding of both the extent to which climate change may alter patterns of dichogamy and the potential implications of these shifts for plant reproduction. Here I present evidence that links variation in dichogamy to variation in temperature for a variety of plant taxa. I synthesize the limited number of studies that have investigated shifts in dichogamy specifically in the context of climate change, and detail the physiological, genetic, and developmental factors that control the relative timing of male and female flowering. The literature indicates that dichogamy is highly plastic and sensitive to temperature variation. Plasticity in dichogamy is observed across species with different sexual systems and growth habits, and in both female-first and male-first flowering taxa, but at present, no clear patterns of dichogamy shifts related to these associated traits are discernible. Together, these lines of evidence suggest that sequences of male and female flowering are likely to shift with climate change. However, more research is needed to better understand and predict the ecological consequences of shifting patterns of dichogamy in the context of global change.

1 | Introduction

The temporal separation of male and female reproductive events is a common feature across the tree of life (Barrett 2002; MØller 2004). In plants, the difference in the timing between male and female flowering—known as dichogamy—is a critical adaptation for reproductive success and is present in thousands of species (Bertin and Newman 1993; Routley, Bertin, and Husband 2004). Dichogamy comes in a diversity of forms. Species may be male- or female-flowering first (protandry vs. protogyny), have sex phases that are fully separated or partially overlapping (complete vs. incomplete dichogamy), or separated within flowers or among them (intra- vs. inter-floral dichogamy; Bertin and Newman 1993; Stout 1928). Species may also display more complex forms such as heterodichogamy—those with female-first and male-first genotypes in approximately a 1:1 ratio in a population.

Over the past several decades, climate change has driven substantial shifts in the seasonal timing of flowering (i.e., phenology) across a diversity of taxa (Menzel and Fabian 1999; Primack, Higuchi, and Miller-Rushing 2009), altering ecological processes from plant-pollinator mutualisms (Duchenne et al. 2020) to patterns of resource allocation (Nord, Shea, and Lynch 2011). While shifting phenology is one of the most prominent biological indicators of climate change to date, few studies directly compare shifts in timing between male and female flowers. Because of this, we currently lack the ability to assess the potential for shifts in dichogamy with climate change and their downstream consequences on plant fitness, population structure, and demography.

The impacts of shifts in dichogamy may be dependent on species' sexual systems. Species with bisexual and monoecious flowers can be self-compatible (able to be fertilized by their own pollen) or self-incompatible (unable to be fertilized by their own pollen). For self-compatible species, dichogamy is an important mechanism to reduce self-fertilization and prevent inbreeding depression (Cruden 1988; Darwin 1900). For self-incompatible species, dichogamy reduces interference between male and female reproductive function (Bertin 1993; Dai and Galloway 2011; Lloyd and Webb 1986). Dichogamy in dioecious species occurs at the population level, with male flowering typically occurring before female due to different resource constraints among the sex phases (Forrest 2014; Lloyd and Webb 1977). In all of these cases, individual variation in dichogamy is rarely measured, and little is known about how plasticity in dichogamy—and by extension sustained shifts—affects reproductive success (but see Jersakova and Johnson 2007).

Here, I suggest that high individual variation in dichogamy is strongly linked to climatic variation. First, I present the evidence from the limited number of studies that have investigated shifts in dichogamy specifically in the context of climate change. I then detail what is known about the environmental cue system, and the genetic, developmental, and physiological factors that influence dichogamy. Together, these factors suggest that climate change is likely to shift patterns of dichogamy, though how significant these shifts will be, and how they will impact species fitness, demography, and ultimately their ability to adapt to climate change is a major uncertainty. My aim is to provide a first step forward for filling in these gaps and lay the foundation for continued research into this important phenological sequence.

2 | Individual Variation in Dichogamy

Some of the best evidence for high levels of plasticity in dichogamy comes from provenance trials of tree crops and their wild relatives. An early study with pecan (*Carya illinoinensis*) cultivars in Texas, USA reported that individuals switched between male-first and female-first flowering among years (Adriance 1931). Decades later, a 16-year study of eighty cultivars confirmed these high levels of variability (Worley et al. 1992). Shifts between female-first and male-first phenotypes have also been reported in hazelnuts (*Corylus avellana*; Capik and Molnar 2014; Piskornik, Wyzgolik, and Piskornik 2001; Taghavi et al. 2021), birches (*Betula pendula*; Rousi, Heinonen, and Neuvonen 2011), hickories (*Carya ovata* and *C. tomentosa*; McCarthy and Quinn 1990), and oaks (*Quercus rubra*; Alexander and Woeste 2016).

The temporal overlap of male and female flowering (i.e., the completeness of dichogamy) is also highly variable. A study of hazelnut cultivars across four sites in Portugal found that sexual overlap varied considerably across localities, reaching 80% overlap in some locations and having no overlap at others (Santos et al. 2005). Variation in temporal overlap has also been observed in sugar maple (*Acer saccharum*; Gabriel 1968), walnut (*Juglans regia*; Mariana and Niculina 2017; Solar, Štampar, and Smole 1997), and pine (*Pinus contorta*; Owens, Bennett, and L'Hirondelle 2005).

3 | Shifts in Dichogamy With Climate Change

Numerous studies not only report plasticity in dichogamy but also link this variation to climate (Table 1). For sugar maple, cooler springs (April–May) increased the overlap between male and female flowers while higher temperatures increased their separation (Gabriel 1968). A seven-year study of walnut cultivars in Romania indicated that warmer-than-average conditions prompted some female-first cultivars to simultaneously flower (Cosmulescu et al. 2010). In hazelnuts, several cultivars that were female-first in mild climates displayed male-first or simultaneous flowering in cold climates (Taghavi et al. 2021). Warmer conditions increased the time interval between the sexes of the female-first Cherimoya (*Annona cherimola*: Lora, Herrero, and Hormaza 2011). Investigations of dichogamy in ragweed (*Ambrosia artemisiifolia*) revealed a strong latitudinal cline in dichogamy. High-latitude populations demonstrated female-first flowering by up to 40 days and lower latitude population displayed male-first flowering with pollen shed preceding stigma receptivity by as much as 14 days (van Boheemen, Atwater, and Hodgins 2019), though this study cannot differentiate whether the observed variation is the product of plasticity or local adaptation. Changes in aridity, another result of climate change, can affect dichogamy. Aridity increased the time between sex phases of *Clarkia pulchella* (Gamble, Bontrager, and Angert 2018) but decreased the interval for *Dalechampia scandens* (Opedal et al. 2016).

Studies that explicitly investigate shifts in dichogamy due to climate change are rare and conflicting. A study of long-term observations of flowering in hazelnuts reported comparable advances for male and female phases over the past century (Črepinšek et al. 2012). By contrast, a study of the dioecious genus *Populus*, reported greater advances in male flowering than female flowering in herbarium records (Xie et al. 2023). In warming experiments with the female-first sedge *Carex bigelowii*, male flowers advanced more than female flowers, increasing their phenological overlap (Stenström and Jónsdóttir 2004). In an experiment with the male-first *Aquilegia coerulea*, a 5°C temperature increase reduced dichogamy (Van Etten and Brunet 2013).

Given these complex responses of dichogamy to climate reported in just the handful of species that have been studied, it is clear we need a more mechanistic understanding of the factors that control dichogamy. Phenology is a complex interchange between exogenous factors such as climate and light and endogenous factors such as genetics, development and physical architecture (Forrest and Miller-Rushing 2010), and understanding the ways that these mechanisms interact is key to predicting shifts in dichogamy.

TABLE 1 | A summary of the taxa for which the effects of temperature and/or aridity on dichogamy have been evaluated.

Species	Dichogamy type	Sexual system	Response to climate variation/change
Acer saccharum	Heterodichogamous	Monoecious or dioecious	Warming **increased** dichogamy in protogynous morphs (Gabriel 1968)
Annona cherimola	Protogynous	Bisexual	Warming **increased** dichogamy (Lora, Herrero, and Hormaza 2011)
Ambrosia artemisiifolia	Usually protandrous	Monoecious	High-latitude populations flowered female-first and low-latitude populations male-first (van Boheemen, Atwater, and Hodgins 2019)
Aquilegia coerulea	Protandrous	Bisexual	Warming **reduced** dichogamy (Van Etten and Brunet 2013)
Carex bigelowii	Protogynous	Monoecious	Warming **reduced** dichogamy (Stenström and Jónsdóttir 2004)
Clarkia pulchella	Protogynous	Bisexual	Aridity **increased** dichogamy (Gamble, Bontrager, and Angert 2018)
Corylus avellana	Heterodichogamous	Monoecious	Cultivars in warm climates flowered female-first and in cool climates male-first (Taghavi et al. 2021); Comparable advances in male and female flowering times over time (Črepinšek et al. 2012)
Dalechampia scandens	Protogynous	Bisexual	Aridity **reduced** dichogamy (Opedal et al. 2016)
Epilobium (Chamerion) angustifolium	Protandrous	Bisexual	Warming **increased** dichogamy (Routley and Husband 2006)
Helleborus bocconei	Protogynous	Bisexual	Warming **reduced** dichogamy (Vesprini and Pacini 2005)
Helleborus foetidus	Protogynous	Bisexual	Warming **reduced** dichogamy (Vesprini and Pacini 2005)
Juglans regia	Heterodichogamous	Monoecious	Warming **reduced** dichogamy (Cosmulescu et al. 2010)
Persea americana	Protogynous	Bisexual	Warming **increased** dichogamy (Sedgley 1977)
Populus spp.	Protandrous	Dioecious	Warming **increased** dichogamy (Xie et al. 2023)
Pseudowintera colorata	Protogynous	Bisexual	Warming **increased** dichogamy (Wells and Lloyd 1991)

Note: Species varied in their dichogamy type, sexual system and whether increased temperature or aridity increased or reduced the time between flowering sex phases.

4 | Proximate Factors Controlling Variation in Dichogamy

The timing of flowering is primarily controlled by two temperature cues: forcing (exposure to warm temperatures in the spring, accelerating rates of cell activity; Diggle and Mulder 2019) and chilling (exposure to cool temperatures ~0°C–6°C, in the winter/spring, accelerating release from physiological dormancy; Rinne et al. 2011; Wolkovich et al. 2022). Plasticity in phenological sequences like dichogamy can be generated when phenological phases respond differently to the same environmental cues (Buonaiuto and Wolkovich 2021). Several studies of the Juglandaceae family report that variation in dichogamy is generally driven by higher plasticity in male-flowering times than in female-flowering times (Cosmulescu et al. 2010; Mariana and Niculina 2017; McCarthy and Quinn 1990), though an early study reported the opposite pattern (Adriance 1931). For hazelnuts, male flowers have a lower chilling requirement than female flowers (Germain 1994; Hlubik, Capik, and Molnar 2023; Mehlenbacher 1991), but have a higher forcing requirement (Taghavi et al. 2021).

These observed differences are well aligned with evolutionary theories of sexual dimorphism in plants more generally. Male reproductive investment occurs only in flowering, while female investment includes flowering and fruit development. It follows that there is a more substantial cost to mis-timed flowering in females than in males, selecting for a more consistent and conservative phenological strategy (Forrest 2014; Xie et al. 2023). If these patterns (higher phenological sensitivity for male flowers) hold broadly, it is important to recognize that the impacts on dichogamy would differ between typically male-first and female-first taxa. In the former, warming would increase the temporal separation between the sex phases and in the latter, it would decrease temporal separation (Figure 1a).

Importantly, patterns of dichogamy are not only determined by the start of the male and female reproductive stages but also by their duration. In birches, hazelnuts and walnuts, warmer air temperatures reduced the duration of both male flowering and female flowering (Bastias and Grau 2005; Črepinšek et al. 2012; Mariana and Niculina 2017; Piskornik, Wyzgolik, and Piskornik 2001; Rousi, Heinonen, and Neuvonen 2011). In contrast, the increased dichogamy reported for Cherimoya with warming was attributed to prolonged stigma receptivity (Lora, Herrero, and Hormaza 2011). In female-first *Pseudowintera colorata*, warming decreased the duration of the female phase, but did not affect the male phase (Wells and Lloyd 1991). In contrast, for male-first *Epilobium (Chamerion) angustifolium* warming decreased the duration of the male phase but did not affect the female phase (Sargent and Roitberg 2000).

The fact that these two aspects of flower phenology that determine dichogamy (the start and duration of flowering) can respond differently to temperature variation suggests additional complexity for anticipating how climate change may affect dichogamy. For example, increases in spring warming could drive the start of male and female phases closer together but shorten their duration, ultimately decreasing phase overlap despite their more similar start times (Figure 1b). This complex relationship highlights that it is important that both aspects of phenology be reported when assessing dichogamy.

Additionally, the timing of initial investment in flowers (i.e., floral induction) may affect the expression of dichogamy. In bisexual flowers, the relative timing of male and female phases may be influenced by their position within the flower, as flower

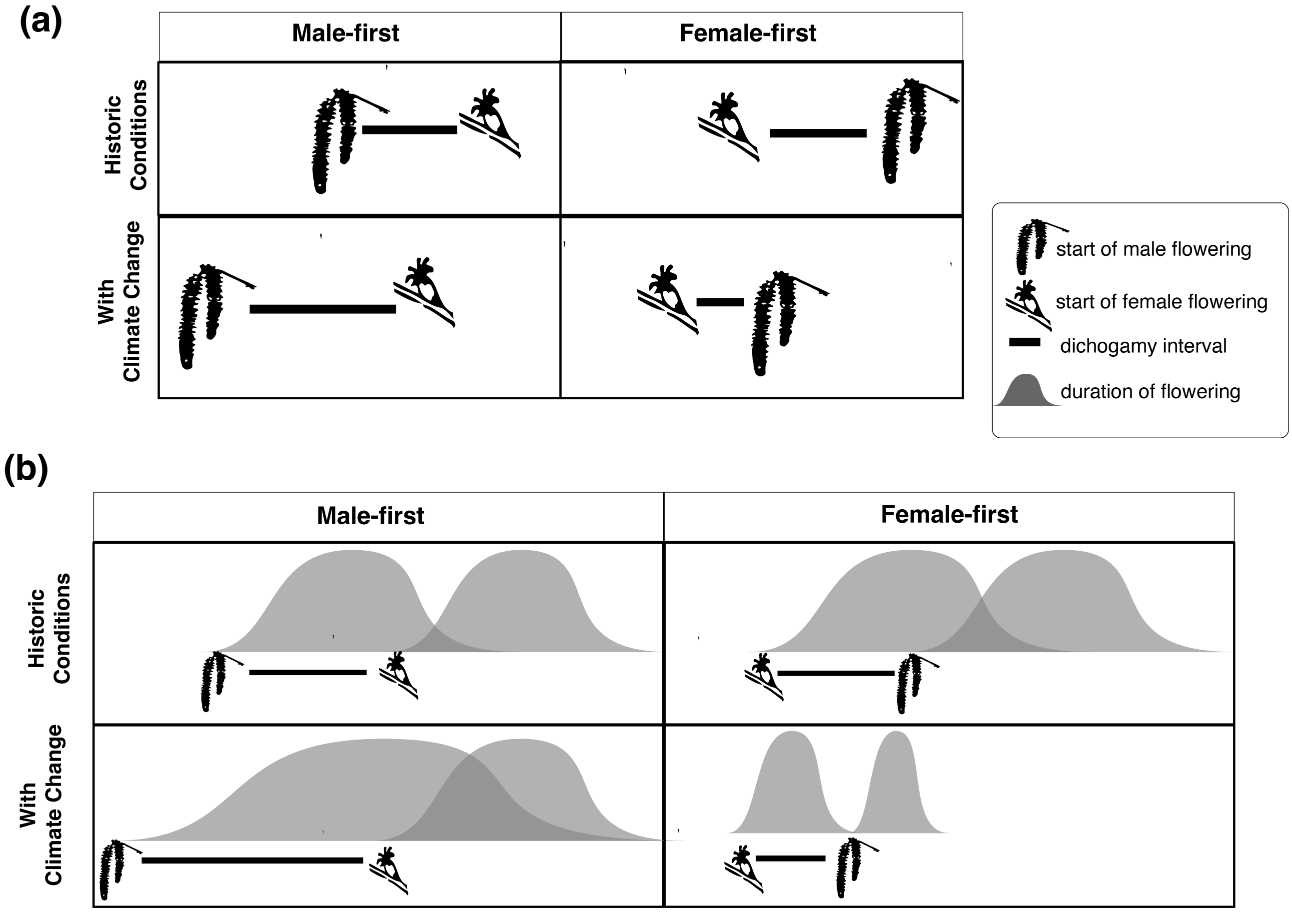

FIGURE 1 | Differences in phenological sensitivity to climate among male and female flowers can result in complex dichogamy shifts. While several studies report male flowering phenology is more sensitive to warming than female flowering (Cosmulescu et al. 2010; Mariana and Niculina 2017; McCarthy and Quinn 1990) this conceptual diagram highlights that the implications of these sensitivity differences can result in contrasting shifts in dichogamy depending on whether a species is male-first or female-first flowering (a). Additionally, warming not only alters the start of male flowering and female flowering, it also can affect the duration of each phase, which can result in complex patterns of phase overlap. Depicted in (b) is a scenario in which warming changes the duration of each sex phase, thereby either increasing the overlap between male flowering and female flowering despite extending the phenological interval between the start of each phase or reducing the overlap between female and male flowering despite reducing the phenological interval between the start of each sexual phase.

primordia are usually initiated from the axis base to the tip (Harder and Prusinkiewicz 2013). Often, identities of male and female organs only differentiate during the later stages of development (Sobral and Costa 2017), and their shared developmental program may constrain differences in their response to changing climate. However, their short intervals of dichogamy (hours to days) suggest that even small differences in responses between the sex organs can have proportionately large effects on dichogamy.

For other species—especially woody perennials—floral induction can occur one or more years prior to flowering (Diggle and Mulder 2019), and male and female flowers can develop completely separately (Sobral and Costa 2017). This multi-season developmental process could make it difficult to isolate whether the effects of temperature on dichogamy relate primarily to the pre-season conditions leading up to flowering, as is often assumed in phenological studies, or are more strongly influenced by conditions during development in previous years (Diggle and Mulder 2019).

In walnuts, female flowers of female-first phenotypes were more developed than in male-first phenotypes (Polito and Pinney 1997), and the anthers of male-first phenotypes were more developed than in female-first phenotypes at the time they entered winter dormancy (Luza and Polito 1988). Similarly, in hazelnuts, male flower induction usually precedes female flower induction by more than a month (Germain 1994). In male-first Cork Oak (*Quercus suber*), male flowering preceded female by 4–8 weeks, and male flower induction occurred in the summer of the previous season while female flowers were induced during the current spring's vegetative flush (Sobral et al. 2020). These temporal patterns of development suggest that climate change could alter patterns of dichogamy at multiple stages across the development cycle.

Importantly, the genetic mechanisms that control and coordinate induction, development, and flowering states in dichogamous species have not been widely explored (Çetİnbaş and Ünal 2014; Harder and Prusinkiewicz 2013), and therefore, the molecular biology of dichogamy is poorly understood. However, recent studies in hazelnuts and cork oaks have identified separate genes associated with male and female flowers during development, and numerous candidate genes for the expression of dichogamy, which could help begin to explain the genetic basis for dichogamy in monoecious woody plant species more generally (Sobral et al. 2020; Valentini et al. 2021).

5 | Toward Predicting Shifts in Dichogamy and Their Implications

The summary provided here deals only with a small handful of the more than 4200 species (Bertin and Newman 1993) in which dichogamy has been described. Shifts in dichogamy and their fitness consequences likely depend on correlated traits (e.g., sexual systems, dichogamy types), but the number of taxa that have been studied in this context is too small to be able to make any useful inferences about how these associated traits may correlate with the magnitude and direction of dichogamy shifts with climate change (Figure 2).

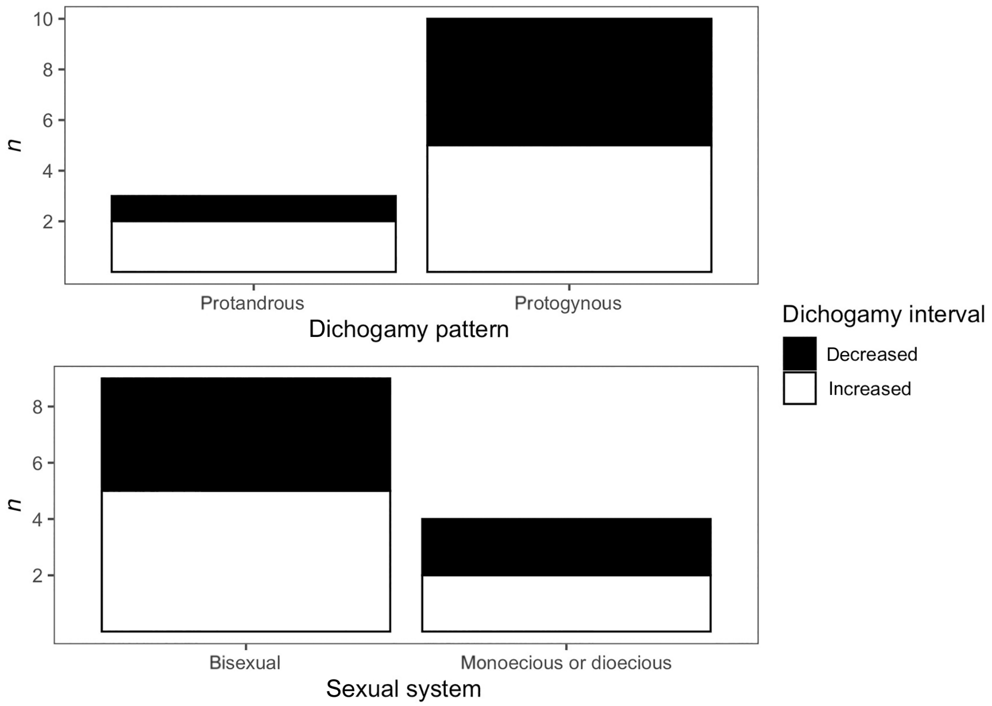

FIGURE 2 | Shifts in dichogamy due to warmer/drier climate conditions are common, but there are no clear trends as to whether dichogamy intervals will increase (i.e., more separation between sex phases) or decrease (i.e., less separation between sex phases) with climate change based on protandrous (male-first) or protogynous (female-first) phenotypes or, based on species' sexual systems. The summary here is based on data from 13 studies for which the relationships between temperature/aridity and dichogamy were explicitly evaluated.

This fact highlights a critical research need—to increase the number of quantitative observations of dichogamy for a diversity of taxa. This starts with developing new frameworks to observe and report the phenology of male and female flowers separately. Some of the most common approaches to measuring phenology (e.g., the BBCH scale: Finn et al. 2007) and phenological data repositories (e.g., PEP 725; Templ et al. 2018, National Phenology Network; Denny et al. 2014) that have contributed so much to our understanding of global change phenology do not include a reliable way to report female and male flower phenology separately. However, these existing protocols can be readily adapted to do this (e.g., Taghavi, Rahemi, and Suarez 2022), and researchers and volunteers alike can be trained to identify and report these phases.

Second, this review highlights several major gaps in our understanding of the proximate factors that control individual variation in dichogamy. Continued research about how environmental cues affect the differentiation, development, dormancy, and phenological expression of male and female flowers, and the molecular mechanics underlying these processes, will be essential for forecasting shifts in dichogamy with climate change. Experiments that systematically manipulate temperature and measure the effects on dichogamy can address critical questions about the relative importance of temperature across floral development stages, as well as differences in plasticity between bisexual, monoecious and dioecious taxa, and between self-incompatible and self-compatible species. Common garden studies that transplant populations to shared environments can assess the relative importance of local adaptation vs. plasticity in dichogamy, offering insights as to whether dichogamy can evolve with climate change.

Finally, we must further our understanding of the consequences of dichogamy shifts for fitness and demography. Decades of research linking pollination biology and population genetics provides concrete hypotheses about how shifting dichogamy is likely to affect fitness. Decreased dichogamy (more overlap between sex phases) should result in increased self-pollination rates for self-compatible species (e.g., Koski et al. 2018) which could result in inbreeding depression, reduced fertility, lower fecundity and less fit offspring (Charlesworth and Charlesworth 1987). Selfing also reduces the genetic diversity of populations, which can lower their potential to adapt to novel environmental conditions brought about by climate change (Etterson and Mazer 2016). Decreased dichogamy in self-incompatible species should result in more interference between inviable self-pollen and receptive female flowers, reducing total fecundity (e.g., Kawagoe and Suzuki 2005). Shifts that result in increased dichogamy may have the opposite effect, improving fitness. Understanding these nuances across a diversity of taxa would help researchers identify vulnerable populations and increase the effectiveness of conservation actions such as assisted migration or genetic augmentation that rely on phenological synchrony to succeed.

These predictions for dichogamy with climate change can be directly tested. Because dichogamy is highly responsive to temperature, experiments could leverage both natural and manipulated climate treatments to alter patterns of dichogamy and measure differences in reproductive success and offspring fitness using techniques from pollination biology and molecular ecology. These studies could be combined with models of population structure and inbreeding depression (e.g., Cheptou and Mathias 2001; Sargent, Mandegar, and Otto 2006) to better anticipate the long-term consequences of sustained shifts in dichogamy.

6 | Conclusion

Individual patterns of dichogamy can be highly plastic, and this variability is strongly linked to climate variability—indicating potential for dichogamy to shift with climate change. There is evidence that these shifts have already begun to occur, but observations have been restricted to a small number of taxa, and the mechanisms that control variability in dichogamy are still poorly understood. Studies that quantitatively assess the potential for shifts in dichogamy due to climate change, elucidate the mechanisms that influence these shifting patterns, and consider their implications for plant reproduction and fitness are critical research needs.

Author Contributions

D. M. Buonaiuto: conceptualization, data curation, investigation, methodology, project administration, visualization, writing – original draft, writing – review and editing.

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Conflicts of Interest

The author declares no conflicts of interest.

Data Availability Statement

The data presented in this paper are available at KNB: Knowledge Network for Biocomplexity at https://knb.ecoinformatics.org/view/doi:10.5063/F1833QG2.

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