Received: 31 October 2022 | Revised: 30 December 2022 | Accepted: 6 January 2023
DOI: 10.1002/ppp3.10359

Plants People Planet PPP Open Access

OPINION

Fruiting phenology matters

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Funding information
Portuguese Foundation for Science and Technology (FCT), Grant/Award Numbers: LIFE AFTER FIRE PTDC/BIA-ECO/1983/2020, SFRH/BD/144414/2019, UID/BIA/04004/2020, CEECIND/00135/2017.

Social Impact Statement
In the face of the unprecedented rate of climate change, understanding whether plant species can track favourable climatic conditions is an urgent challenge. Recent independent studies suggest that the timing of fruiting (fruiting phenology) can strongly affect future vegetation dynamics and composition via direct seed dispersal. With comprehensive datasets on fruiting phenology, researchers may predict the impact of climate on the future of forests. Nevertheless, long-term, broad-scale, and taxonomically comprehensive datasets of fruiting phenology are still lacking, leaving us unprepared to understand the consequences of climate change on entire floras. We urge stronger collaboration networks to assemble broader, longer, and more comprehensive fruiting phenology datasets.

Summary
Climate change is altering species phenology but still with underrated consequences to their ecology and conservation. For example, the production of ripe fruits and the dispersal of their seeds by frugivores are likely critical for their ability to track suitable growing conditions under global warming. Specifically, recent independent studies suggested that migrant birds and mammals are important to facilitate plant spread towards higher (i.e., cooler) latitudes and higher elevations. Interestingly, these studies coincide that spring-fruiting species will likely be particularly favoured, whereas autumn-fruiting species might be largely dispersed to undesirable (i.e., even hotter) areas. These studies show that the timing of fruit production can have a critical impact on future forest composition as plant communities adapt to warmer, more extreme, and unpredictable climates. Unfortunately, comprehensive datasets on fruiting times are very scarce and often temporary, spatially, and taxonomically restricted (particularly when compared with flowering datasets), strongly hampering our capacity to predict the real impact of climate change on long-term vegetation dynamics. Thus, we advocate for an urgent need for long-term, broad-scale, and taxonomically comprehensive datasets of fruiting phenology, and we point out some potential concrete steps towards this goal.

KEYWORDS
climate change, climatic envelope, frugivory, interaction disruption, migration, phenological mismatch, seed dispersal

1 | INTRODUCTION

Timing of the cyclic events that occur along the organisms' life cycles—that is, their phenology (Lieth, 1974)—has strong implications on fitness and consequently on their ecology and evolution (Bêty et al., 2004; Koenig et al., 2012). Unsurprisingly, the environmental triggers of massive biological events, such as animal migrations or plant blooming, have fascinated early naturalists (Primack & Miller-Rushing, 2012; Whitfield, 2001). However, the growing recognition that phenology is finely tuned to climate and that climate is rapidly changing has cascaded a renewed interest in the causes and consequences of changing phenologies (e.g., Cleland et al., 2007; Gallinat et al., 2021; Morellato et al., 2016; Peñuelas & Filella, 2001; United Nations Environment Programme, 2022). Species phenologies are the result of strong selective pressures as the timing of most of these events directly affects the way that organisms interact with their environment (e.g., will late cubs be able to survive the winter?; Stirling & Derocher, 2012) and also the way they interact with other organisms (e.g., will an early flowering plant find suitable pollinators?; Memmott et al., 2007). Accordingly, the escalating pace of anthropogenic climate change has raised concerns about whether many species will be able to survive and reproduce under the new climatic conditions that they are beginning to experience (Pecl et al., 2017; Peñuelas & Filella, 2001). These concerns are particularly serious for plants that not only form the basis of terrestrial food webs but also, as sessile organisms, might not be able to track favourable conditions as most animals can (Corlett & Westcott, 2013). Thus, it is not surprising that dispersal of seeds either by abiotic (e.g., wind) or biotic (e.g., frugivores) vectors will be critical for plants' ability to track more favourable climatic conditions, typically shifting towards higher latitudes (i.e., towards the poles) or higher elevations (i.e., towards mountain tops) (González-Varo et al., 2017; Kling & Ackerly, 2020; Walther et al., 2002).

2 | THE INTERPLAY BETWEEN FRUITING TIME AND SEED DISPERSAL IN A CHANGING CLIMATE

Although this issue has still received relatively little attention, a few recent studies in northern temperate regions have provided new and independent insights into which plants are most likely to obtain a safe ride with frugivorous animals towards cooler grounds. By collating plant–frugivore interaction data from 13 European forests, González-Varo et al. (2021) showed that common migratory birds will likely be pivotal in facilitating plants' colonization of northern latitudes fast enough to keep up with the pace of warming temperatures in Europe. On another front, the studies by Naoe et al. (2016, 2019) and Tsunamoto et al. (2020) showed how large terrestrial frugivores can help plants to escape warmer temperatures in Japanese mountains by dispersing them to uphill grounds. These movements exist because, in spring and summer, many European birds take advantage of milder temperatures in northern latitudes to reproduce (dispersing seeds along the way) and Japanese mammals explore trophic resources on the mountain tops (González-Varo et al., 2021; Naoe et al., 2016, 2019; Tsunamoto et al., 2020). Before the arrival of winter, European birds and Japanese mammals do the inverse movement to escape the cold. Importantly, these studies revealed the same intriguing pattern: That spring-fruiting species and species with long fruiting periods seem to be better equipped to disperse to desirable grounds in the north and on mountaintops (González-Varo et al., 2021; Naoe et al., 2016); whereas autumn-fruiting plant species with short fruiting periods tend to be dispersed in the opposite direction and thus will have to face ramping temperatures (González-Varo et al., 2021; Naoe et al., 2019).

Summarizing, these studies suggest that future forests might be dominated by spring-fruiting species, as these will tend to be favoured while trying to escape drier and hotter climates. Although these findings still need to be corroborated on other systems (particularly in the southern hemisphere and in the tropics) before they can be regarded as a global pattern, the migrations patterns are very similar on both hemispheres (Dingle, 2008; Terry Chesser & Levey, 1998), and altitudinal migration is also a fairly consistent behaviour across the globe (Barçante et al., 2017; Luccarini et al., 2006). However, more importantly than confirming any specific pattern, these studies highlight a more general, key message: Understanding fruiting phenology patterns (i.e., the timing of fruit production) seems critical to predict the future of forests and consequently our own future.

3 | AN URGENT NEED FOR COMPREHENSIVE FRUITING PHENOLOGY RESEARCH

Relevant efforts have already been made to document and explore the functional implications of fruiting phenology, particularly in the tropics (e.g., Chapman et al., 2005; Mendoza et al., 2017, 2018; Morellato et al., 2013; Polansky & Boesch, 2013). Recently, Mendoza et al. (2017) reviewed fruiting phenology datasets in the neotropics and found that 70% of the studies lasted less than 2 years and only a small minority lasted for more than 10 years, a shortcoming shared by most temperate studies (mostly restricted to 5 years or less; e.g., Herrera, 1986; Noma & Yumoto, 1997; Tébar et al., 2004). Furthermore, most of these studies do not follow the phenology of a sizeable fraction of the local flora, usually including only a few species and very rarely more than 100 species (e.g., Chuine et al., 2004; Gordo & Sanz, 2010; Lechowicz, 1995; Mendoza et al., 2017, 2018; Miller et al., 2021; Rosbakh et al., 2021). The conclusion is that despite relevant seminal work, current knowledge of fruiting phenology is still embarrassingly poor, if compared, for example, with that of flowering phenology (to which it might or might not be directly correlated; Sandor et al., 2021). A clear sign of the historical primacy given to flowering phenology is that most published Floras contain information on the main flowering months for the plant species in a particular area (e.g., Tutin et al., 1964). Similarly, long-term datasets of detailed flowering dates for particular species allowed ecologists to detect the anticipation of flowering as a result of climate change (e.g., Cleland et al., 2007; Menzel et al., 2006), which has in turn catalysed further research on the interlinks between climate change, flowering phenology, and pollination phenology (e.g., Bartomeus et al., 2013; Hegland et al., 2009). Unfortunately, neither taxonomically comprehensive nor long-term datasets of plants' fruiting times of entire floras are yet available for any region of the world, leaving us largely ignorant about the effects of climate change on fruiting phenology and about the impacts of fruiting phenology on the future of vegetation under warming climates. This information is critical due to at least four important reasons: First, the timing of seed production will largely affect multiple biotic and abiotic factors of a plant's life cycle, such as seed viability, its disperser assemblage, pre- and post-dispersal seed predation, and seedling emergence and survival (Espelta et al., 2009; González-Varo et al., 2019; Solbreck & Knape, 2017); second, it is important to identify potential mismatches between the availability of ripe fruit and the presence of frugivores (including migratory ones) (Gallinat et al., 2021; González-Varo et al., 2019; Rafferty et al., 2015); third, it is important to understand how the increase of extreme and unpredictable climatic events, such as droughts or wildfires, will affect plant recruitment as this will be largely determined by the capacity to produce and release viable diaspores in increasingly shorter temporal windows (Walck et al., 2011); and, finally, because there is increasing evidence that fruiting (a)synchrony between native and introduced plants is critical to determine the seed dispersal services available to facilitate the spread of invasive plants (Heleno et al., 2020).

4 | CONCLUSION

Given the importance of fruiting phenology for the future of forests in a rapidly changing climate, we advocate an urgent need for a strengthening of the existing collaboration networks to construct long-term, broad-scale, and taxonomically comprehensive datasets of fruiting phenology. These efforts might be particularly fruitful if they are openly embraced by well-established international networks such as networks of Botanic Gardens (e.g., BGCI, 2022) and Biological Field Stations (e.g., OBFS, 2022) or by broader sampling schemes such as the International Long term Ecological Research Network (e.g., ILTER, 2022) or specific phenological projects (e.g., IPG, 2022; PEP, 2022; USANPN, 2022).

ACKNOWLEDGEMENTS

We are thankful for the informal discussions with multiple colleagues and for the insightful contributions from the anonymous reviewers.

AUTHOR CONTRIBUTIONS

Ruben Heleno and Sara Beatriz Mendes conceived the initial ideas. Sara Beatriz Mendes lead the writing with contributions from Ruben Heleno, Jens M. Olesen, and Sérgio Timóteo.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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How to cite this article: Mendes, S. B., Olesen, J. M., Timóteo, S., & Heleno, R. (2023). Fruiting phenology matters. *Plants, People, Planet*, *5*(3), 324–328. https://doi.org/10.1002/ppp3.10359