Mismatch managed? Phenological phase extension as a strategy to manage phenological asynchrony in plant–animal mutualisms

Rachael L. Olliff-Yang1,2, Thomas Gardali3, David D. Ackerly1,4

Species-specific shifts in phenology (timing of periodic life cycle events) are occurring with climate change and are already disrupting interactions within and among trophic levels. Phenological phase duration (e.g. beginning to end of flowering) and complementarity (patterns of nonoverlap), and their responses to changing conditions, will be important determinants of species’ adaptive capacity to these shifts. Evidence indicates that extension of phenological duration of mutualistic partners could buffer negative impacts that occur with phenological shifts. Therefore, we suggest that techniques to extend the length of phenological duration will contribute to management of systems experiencing phenological asynchrony. Techniques of phenological phase extension discussed include the role of abiotic heterogeneity, genetic and species diversity, and alteration of population timing.

We explore these approaches with the goal of creating a framework to build adaptive capacity and address phenological asynchrony in plant–animal mutualisms under climate change.

Key words: adaptive capacity, climate change, management, phenological asynchrony, phenological mismatch, phenology, restoration

INTRODUCTION

Considering phenological shifts (italicized terms—see Box 1) in management decisions may be critical for conserving species interactions, mitigating invasions, and maintaining ecosystem functions and services (Elzinga et al. 2007). Species-specific shifts in phenology are occurring with climate change and are already disrupting interactions within and among trophic levels (e.g. Schmidt et al. 2016). Species vary in their responses to temperature and moisture changes, and one or more environmental cues may influence whether or not timing will shift with climate changes (Cleland et al. 2007). Phenological asynchrony between mutualistic species is expected to decrease fitness and yield population declines (van Asch et al. 2007; Rafferty et al. 2013). With predictions of climate-induced asynchrony, and no clear solutions or management principles available for practitioners, we were motivated to explore strategies that may build the capacity of a system to respond to phenological shifts. We propose extending phenological phase duration in mutualistic partners as a mechanism to build adaptive capacity, and discuss techniques to achieve this goal.

The likelihood and consequences of phenological asynchrony in mutualisms will depend on the level of specialization, seasonality and duration of interactions, and the intimacy of the relationship (i.e. symbiotic or free-living; Rafferty et al. 2015). Phenological asynchrony in mutualisms has been most studied in transportation mutualisms (e.g. seed dispersal [Warren et al. 2020]).

Conceptual Implications

- Predictions of phenological asynchrony due to climate change call for novel conservation strategies.
- We propose extending phenological phase duration as one approach for buffering impacts of asynchrony.
- Techniques to extend the duration of plant or animal activity timing include utilizing abiotic heterogeneity, genetic and species diversity, and alteration of population timing.
- Existing biodiversity conservation techniques may have the potential to address mismatch concerns if put into the context of phenological shifts.
- We call on restoration ecologists to propose and test effectiveness of strategies to address mismatch concerns.

1Integrative Biology, UC Berkeley, 3040 Valley Life Sciences Building #3140, Berkeley, CA 94720, U.S.A.
2Address correspondence to R. L. Olliff-Yang, email rllolliff@berkeley.edu; http://rachaelolliffyang.wordpress.com/
3Point Blue Conservation Science, 3820 Cypress Drive, Suite #11, Petaluma, CA 94954, U.S.A.
4Environmental Science, Policy, and Management, UC Berkeley, Berkeley, CA 94720, U.S.A.

© 2020 The Authors. Restoration Ecology published by Wiley Periodicals, Inc. on behalf of Society for Ecological Restoration. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

doi: 10.1111/rec.13130
Supporting information at: http://onlinelibrary.wiley.com/doi/10.1111/rec.13130/supinfo
Box 1  Glossary of important concepts and definitions.
Adaptive capacity: capability of organisms or systems to adjust to potential stress, take advantage of opportunities, or respond to and mitigate negative impacts of environmental change.
Phenology: the timing of periodic life cycle stages of organisms.
Phase duration: time from start to end of a particular phenological phase (e.g., flowering period).
Phenological complementarity: complementary timing in species growth and reproductive timing (e.g., complementary flowering species flower at different times of the year). Complementarity is used here to describe patterns of nonoverlap in species of the same functional group or guild.
Phenological overlap: overlap in species growth and reproductive timing. Extent of overlap depends on amount of time both species are active simultaneously. Overlap in a mutualism occurs when a species or ecological phase is concurrent in time with its interacting partner.
Phenological mismatch/asynchrony: when a species or ecological phase is not concurrent in time with its interacting partner. Extent of asynchrony depends on amount of time both species are present or active in the absence of the other. A complete mismatch occurs when the phenological phases of mutualistic partners are entirely out of sync with each other.
Phenological shift: a change in the timing of life cycle stages, resulting in timing that is earlier or later in the year.

2011], but studies have also predicted the potential for asynchrony due to climate change in nutritional and protection mutualisms (Rafferty et al. 2015). Mutualistic species are under strong selection to remain in synchrony, and phenological asynchrony is therefore evolutionarily unstable (Renner & Zohner 2018). On ecological time scales, rapid anthropogenic climate change may increase asynchrony if species respond to different factors and not enough time is available for selection to offset these shifts. Where asymmetry in phenological shifts is occurring or expected to occur, reducing impacts of timing asynchrony may buy time for species to adapt.

Adaptive capacity is defined as the capability of organisms or systems to adjust to potential stress, take advantage of opportunities, or respond and mitigate negative impacts of environmental change (IPCC 2018). Improving and maintaining adaptive capacity provides an ecological buffer that protects the system from collapse when change occurs (Gunderson 2000). In this article we explore the potential for adaptive capacity of a community to phenological shifts to be improved by extending the phenological phase timing of mutualistic species to allow for adjustments and changes in species interactions, and community restructuring as necessary.

Lengthened duration of phenological activity may allow for adaptive capacity by supporting both animal and plant mutualists. Animal species require sufficient and abundant resources throughout their life cycles, and continual plant resources over the active season (e.g., flight, foraging, and nesting seasons) are needed for animal populations to maintain stability and function (Russo et al. 2013). If the timing of an animal species becomes out of sync with a plant mutualist resource, other plant species are essential to supplement its needs during the period of time when resources are unavailable (Waser & Real 1979). Plant species that bridge temporal gaps and extend resource timing may also allow for facilitation among plants by supporting mutualist animal populations (Moeller 2004). Recent evidence suggests that extended phenological timing can aid mutualisms (e.g., Frankie et al. 2013; Hindle et al. 2015; Mola & Williams 2018). Hence, increasing or maintaining availability of partner resources across time may support the survival of species in mutualistic interactions as the climate changes.

We propose that managing ecosystems in the face of mismatch will require implementing strategies to maintain and extend the duration of phenological activity. An extension in the duration of partner resources may allow for increased survival in species that are undergoing phenological shifts. This duration could be across a community for generalist mutualisms, with species at the beginning of the season starting earlier and those at the end of the season ending later to extend the total season-wide availability of the resource. Increased phenological phase duration may allow for adaptive capacity by maintaining natural patterns of overlap and buffering the impacts of timing shifts in the short term.

The focus here is on plant–animal mutualisms. However, building adaptive capacity to phenological shifts is not limited to mutualistic interactions. All interactions may experience mismatch with climate shifts, impacting species either positively or negatively depending on the type of interaction. For example, plant–herbivore relationships are dependent on the overlap between plant resources and herbivore timing (van Asch et al. 2007), and asynchrony may benefit plant species while negatively impacting herbivores, while overlap will benefit herbivores and other consumers. Longer phenological duration can benefit nonmutualistic partners (e.g., deer herbivory [Petrelli et al. 2005]), and therefore extending phenological phase duration may be a strategy to aid in short-term survival or balancing of ecosystem dynamics for any interactions.

Techniques to Extend Duration of Phenological Activity

We propose extending the duration of phenological activity as a management possibility where phenological mismatch is a concern. Phenological activity may be extended via plant resource timing extension, animal partner timing extension, or providing supplemental partners (Fig. 1). We propose three techniques that we predict could lead to an increase in phenological phase durations at local and landscape scales: (1) diversifying species and genotypes; (2) utilizing microclimate heterogeneity; and (3) alteration of population timing. These techniques are based on the idea that complementarity (patterns of nonoverlap) in the timing of mutualistic partner resources will yield overall longer resource availability (Fig. 2). In addition, techniques may work synergistically to yield additional extension in timing. The aim should be to maintain the ecosystem’s natural patterns of synchrony as much as possible in the face of climate change.
Technique 1: Diversifying Species and Genotypes. Introduction of species and genotypes, with complementary phenology, can supplement resources during periods of diminished availability that may be created by a phenological shift (Timberlake et al. 2019). Many restoration projects are designed with a diverse array of plant species with complementary traits and hence incorporating phenology into trait selection can extend the duration of resources across the year. In fact, at this time the only strategy that we know has been implemented to extend duration of fruiting and flowering resources is the selection of a palette of species with diverse timing (e.g. early and late flowering species; Fig. 2A) in restoration projects (Box 2). This practice may benefit a system in multiple ways, as it may serve to extend timing as well as increase functional redundancy and improve quality of resources (e.g. nutritional value) in a system. While this will be useful for generalist mutualisms, it may also support some specialized mutualisms if specialization occurs at the genus or family level, or on functionally similar species across clades (e.g. bats and Piper fruit (Marinho-Filho 1991); thrips and dipterocarps (Appanah 1993)).

A longer window of timing may also be achieved within species by diversifying genotypes. Genotypes with slightly different timing can complement each other, and yield an overall extended phenological duration (Smith et al. 2015). The extent of phenotypic plasticity can also vary by genotype (Pigliucci 2001). Therefore, managing for natural genotypic diversity in timing could extend phenological phases, via diversity in both fixed and plastic timing traits. Planting genotypes from diverse source locations in one place could yield an overall longer resource duration due to the complementarity of both early and late genotypes.

Genotypes with different phenologies may interbreed or adapt to have similar timing based on site conditions (Ware et al. 2019) potentially making the extension of timing short-lived. It may also be difficult to predict the exact timing of genotypes once moved to a new location due to phenotypic plasticity (Monty & Mahy 2009). However, this technique may still aid in increasing adaptive capacity, as the presence of different genotypes may allow for adaptive evolution, or may permit an interacting species to coexist long enough to adapt to new conditions (Millar et al. 2007). Evaluating risks will be important before implementing this technique, as swamping the population with nonadaptive genotypes may be a concern. However, in the case of an uncertain future, increasing the genetic diversity of local populations is likely to be beneficial (Millar et al. 2007).

Technique 2: Utilizing Microclimate Heterogeneity. Areas with different abiotic conditions within a patch and across a landscape may yield differences in phenological phase timing and duration (Fig. 2B). The nature of these areas, their spatial configuration, and scale at which they vary will determine phenological duration at the local and landscape levels. Heterogeneity in microclimates can yield lengthened duration by creating patterns of

---

Figure 1. Concept and strategy—extending phenological phase duration. (A) Example timing shift resulting in an asynchrony. If the timing of phenological activity (e.g. flight period, nesting) of a focal animal species (dark blue curves) undergoes a timing shift (from time 1 to time 2), this shift could reduce the overlap (green shading) with the phenological timing (e.g. flowering, fruiting) of its primary plant mutualist in this location (light blue curve). Extending the timing of the plant activity (e.g. flowering, fruiting) may reduce asynchrony with the mutualistic animal partner (pollinator, seed disperser, etc.). (C) Extending the timing of the mutualistic animal species may also reduce asynchrony. (D) Adding other complementary species (plants or animals) into the community as supplemental partners can also reduce asynchrony experienced by a focal species (here animal mutualist is represented as focal species).
complementarity in the timing in both plant and animal activity. Abiotic gradients and habitat heterogeneity can impact the timing of both animal and plant species distributed across a site (Hindle et al. 2015; Olliff-Yang & Mesler 2018). Management to conserve, maintain, and restore abiotic heterogeneity, and increasing connectivity across heterogeneous landscapes could extend phenology at both local and landscape scales.

Figure 2. Techniques for extending phenological phase duration. Conceptual diagrams (Left panels) and empirical examples (Right panels). The overall duration (time between "start" and "end" dates) of phenological activity (e.g. flowering, fruiting) will be extended when the timings of these resources are staggered across the season. This can be achieved via: (A) Left—Technique 1: diversifying species and/or genotypes. Right—Flowering phenology of three different Clarkia species (from Moeller 2004); (B) Left—Technique 2: Utilizing microclimate heterogeneity. Right—Influence of topography on floral resources (SW facing 15° slope [open circles], flat [triangles], and N facing 11° slope [filled circles]; from Weiss et al. 1988); and (C) Left—Technique 3: Alteration of population timing. Right—Seasonal changes in the butterfly abundance, where the number of butterflies is the mean number per year at each study site. Treatments include fire breaks (circles), mowing (filled diamonds), road (open diamonds), abandoned grassland (grey squares), scrub (triangles), and forest (Xs) (from Kubo et al. 2009).
Box 2  Point Blue’s Climate Smart Planting design tool.
Point Blue Conservation Science in California was an early developer and adopter of “Climate Smart” restoration practices. A planting design tool created by Point Blue Conservation Science allows practitioners to (Fig. IA) select candidate plant species for restoration planting and then (Fig. IB) view how flowering and fruiting resources will likely be distributed through time once plants are established (Point Blue Conservation Science 2019). This allows project designers to select complementary flowering and fruiting species to provide resources across the full season. Areas restored using these metrics may reduce the impacts of phenological mismatch by supplementing plant resources for generalist animal species across the season.

| Grasses & Forbs (3 selected) | Flower and Seed Availability |
|-----------------------------|-----------------------------|
| Include? | Common Name | Scientific Name | Number of Species |
| y | narrow | Achillea millefolium | 3.5 |
| n | horsea mint | Agastache urticifolia | 3.0 |
| y | mugwort | Artemisia douglasiana | 2.5 |
| y | narrow leaved milkweed | Actaea racemosa | 2.0 |
| n | showy milkweed | Actaea speciosa | 1.5 |
| n | Pacific aster | Aster chilensis | 1.0 |
| y | sedge | Carex sp | 0.5 |
| N | red ribbons | Clerodendron trichotomum | 0.0 |
| y | farewell to spring | Clerodendron spp | 0.5 |

Figure I. (A) List of plant species available for restoration projects. Species are split by functional group, and listed with both common and scientific names. Species are selected using a “Y” in the “Include?” column. (B) Expected diversity and duration of species providing flower and fruit resources in a restoration is shown, based on species selected in list A.

[Forrest & Thomson 2011]). The scale of implementation of this technique will be dependent on the species, and microenvironments must be present within the average foraging range of the animal mutualist to be effective.

Increasing connectivity across microclimates may connect animal and plant mutualists with various timings, effectively increasing the duration of phenological activity on the landscape as a whole. Elevation gradients influence phenology for both plants and animals due to precipitation and temperature gradients (Forrest et al. 2010), and many montane animal species rely on moving to track differences in resource timing due to variation in snowmelt and spring vegetation onset across elevation (Pettorelli et al. 2005). Implementation of this technique would include providing linkages and corridors, enhancing habitat heterogeneity in closely adjacent locations, or otherwise facilitating the movement of organisms across abiotic gradients (Dunwiddie et al. 2009), with the goal of increasing the chances that suitable partners are within reach of one another at the right time.

Technique 3: Alteration of Population Timing.  Management that increases timing heterogeneity within populations may be used to extend the phenological phase timing of both plant and animal species, as complementarity in timing between individuals in a population will yield extended timing. Techniques to directly alter population timing may include direct manipulation of growth timing, as well as altering biotic and abiotic conditions that affect population timing (Fig. 2C).

Manipulating seasonal growth (e.g. via hormone or growth initiation treatments) can alter and extend phenological phase duration as individuals with different growth timing will experience different climactic conditions, which may lead to a variety of timing in one location. Planting on various dates could induce timing complementarity and yield extended duration of phenological activity in one growing season (Iannucci et al. 2008). Effectiveness of directly manipulating seasonal growth on lengthening phenological phase timing would require species that reproduce in the first growing season, and that are not strongly dependent on photoperiod cues. In addition, it is not likely that the effects of such treatments will last for multiple years without continued management.

Heterogeneity in both biotic and abiotic factors may foster a variety of phenological timing, leading to complementarity between patches, and an overall extended season at landscape scale. Grasslands with heterogeneous management practices can create a mosaic of timing, supporting successive flowering
Heterogeneity) of populations (see Technique 2 - Utilizing Microclimate (Tunes et al. 2017). Finally, directly planting or placing nesting habitat across heterogeneous microclimates can also extend timing of populations (see Technique 2 - Utilizing Microclimate Heterogeneity).

Concluding Remarks and Future Perspectives

One of the most conspicuous responses of organisms to climate change has been shifts in timing of phenological events (Menzel et al. 2006). These shifts are already causing interacting species to become less synchronous in time than they have been. It will be important to keep the timing of interactions in mind while assessing climate risks and planning for the future, as this will help us envision and plan for instabilities (Russo et al. 2013). Considering novel ways to buffer the impact of climate change on ecosystems is critical for management success. Extending the phenological phase duration of mutualistic partners may be one way to buffer the impacts of timing shifts on asynchrony mutualisms.

It is important to keep potential trade-offs in mind. For example, techniques to extend phenological overlap may reduce the strength of selection that an asynchrony would cause. While increasing short-term survival may buy time for adaptive evolution, weaker selection pressures would slow the rate of adaptive response. On the other hand, selection cannot act if either partner in the mutualism is extirpated due to rapidly changing climatic conditions. Decreased overlap is only one of multiple factors that climate changes will impact, and short-term survival may depend on other conflicting factors, both biotic and abiotic, that have stronger impacts and undermine the effectiveness of techniques discussed here (Visser & Gienapp 2019). In addition, extending the duration of an activity may increase the overlap in time with undesirable interactions (e.g. Douglas fir trees and spruce budworm [Chen et al. 2003]).

It is also possible that invasive and weedy species may be facilitated or hindered with extended phenological phase timing, or in the implementation of techniques to extend timing. Any newly introduced species would yield an invasion risk, and introducing or changing disturbance may create opportunities for invasion (Hobbs 1989). Invasive species are typically more phenotypically plastic than noninvasives (Davidson et al. 2011), which may allow for the flexibility to capitalize on empty niches in time (Wolkovich & Cleland 2011). Our strategy to extend phenology may be an effective way to fill empty niches in time with native species rather than allowing invaders to take advantage of timing gaps. As always, focused study of individual systems may be needed to determine costs and benefits of phenological restoration and conservation strategies.

The selection of plant species and genotypes with complementary phenology lies at the heart of farm and garden design, where humans act as consumers seeking to enjoy a colorful display or fresh foods throughout the season. Not surprisingly, gardens can become important resources for animal pollinators and dispersers across the urban to rural gradient, and enhanced resource availability through the year has contributed to species range expansions (Greig et al. 2017). The line between habitat restoration and “artificial” gardens may become increasingly blurred in the face of climate change, as new species are selected that can manage novel conditions and hence contribute to biodiversity conservation (Dunwiddie & Rogers 2017).

Techniques to maintain and extend resource duration on the landscape are in line with many already used to support adaptive capacity to climate change. Increasing genetic and species diversity in restoration and forestry practices is a top recommendation for conservation of biodiversity under climate change (Heller & Zavaleta 2009). Expanding the number of seed source locations to boost genetic diversity is one strategy suggested for conserving plant populations in an uncertain future (Millar et al. 2007). Restoration projects alter population density and disturbance via seeding density, grazing, mowing, and prescribed burning (Stromberg et al. 2007). Utilizing diverse topography and microtopography on the landscape has also been implemented to support establishment of plant species and aid ecosystem function (Biederman & Whisenant 2011). Incorporating timing as a dimension of conservation and restoration planning can further achieve goals by aiming for adaptive capacity to climate-induced asynchrony. The strategies outlined here may also reduce asynchrony due to factors other than climate change, such as effects of landscape simplification and habitat loss.

The extent of phenological mismatch that will occur with climate change and the resulting impacts on population demography is unclear, as there is still a paucity of evidence for the effects of asynchrony on population fitness (Renner & Zohner 2018). It is likely that the extent and impact of phenological phase shifts and any need for management intervention will be context dependent. Continued research is needed on techniques to extend phenology, the risks and impacts of different techniques, and the relative increase in adaptive capacity with extended phenology in different systems. We consider extending phenological phase duration as a tool to add to the arsenal of strategies being developed with the aim of mitigating climate change impacts. We hope that the ideas proposed here will inspire continued discussion and research on creative strategies to mitigate the impacts of phenological mismatch with climate change.

Acknowledgments

Funding was provided by the S.D. Bechtel Jr. Foundation and the Marin Community Foundation. Additional support was provided by the National Science Foundation Graduate Research Fellowship Grant (#1049702) (to R.L.O.-Y.). Any opinion, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. We thank C. Willing, S. Pierre, E. Beller, M. King, and P. Papper for helpful comments on early drafts of this manuscript. This manuscript
was improved following critiques from L. Reid, A. Stephens, and five anonymous reviewers.

**LITERATURE CITED**

Appanah S (1993) Mass flowering of dipterocarp forests in the aseasonal tropics. Journal of Biosciences 18:457–474

van Asch M, van Tienderen P, HOLLERMAN L, Visser M (2007) Predicting adaptation of phenology to response to climate change, an insect herbivore example. Global Change Biology 13:1596–1604

Ávila B, Bonatto F, Priotto J, Steinmann AR (2016) Effects of high density on spacing behaviour and reproduction in Akodon azarae: a fencing experiment. Acta Oecologica 70:67–73

Biederman LA, Whisenant SG (2011) Using mounds to create microtopography alters plant community development early in restoration. Restoration Ecology 19:53–61

Chen Z, Clancy KM, Kolb TE (2003) Variation in budburst phenology of Douglas-fir related to western spruce budworm (Lepidoptera: Tortricidae) fitness. Journal of Economic Entomology 96:377–387

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22:357–365

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14:419–431

Dunwiddie PW, Rogers DL (2017) Rare species and aliens: reconsidering non-native plants in the management of natural areas. Restoration Ecology 25: S164–S169

Dunwiddie PW, Hall SA, Ingraham MW, Bakker JD, Nelson KS, Fuller R, Gray E (2009) Rethinking conservation practice in light of climate change. Ecological Restoration 27:320–329

Elzinga JA, Atlan A, Biree A, Gigord L, Weis AE, Bernasconi G (2007) Time after time: flowering phenology and biotic interactions. Trends in Ecology & Evolution 22:432–439

Forrest JK, Thomson JD (2011) An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. Ecological Monographs 81:469–491

Forrest J, Inouye DW, Thomson JD (2010) Flowering phenology in subalpine meadows: does climate variation influence community co-flowering patterns? Ecology 91:431–440

Frankie GW, Vinson SB, Rizzardi MA, Griswold TL, Coville RE, Grayum MH, Martinez LES, Foltz-Sweat J, Pawelek JC (2013) Relationships of bees to host ornamental and weedy flowers in urban northwest Guanacaste Province, Costa Rica. Journal of the Kansas Entomological Society 86:325–351

Fukuyo S, Kurihara M, Nakashinden I, Kimura K, Iijima Y, Kobayashi Y, et al. (1998) Short-term effects of wind shield on phenology and growth of alpine plants in Mount Kiso-Komagatake, Central Japan. Proceedings of the NIP Symposium on Polar Biology 11:147–158

Greig EI, Wood EM, Bonter DN (2017) Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. Proceedings of the Royal Society B: Biological Sciences 284:20170256

Gunderson LH (2000) Ecological resilience— In theory and application. Annual Review of Ecological Systems 31:425–439

Heinrich B (1976) Flowering phenologies: bog, woodland, and disturbed habitats. Ecology 57:890–899

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation 142:14–32

Hindle BJ, Kerr CL, Richards SA, Willis SG (2015) Topographical variation reduces phenological mismatch between a butterfly and its nectar source. Journal of Insect Conservation 19:227–236

Hobs R (1989) The nature and effects of disturbance relative to invasions. Pages 389–405. In: Biological invasions: a global perspective. John Wiley & Sons, New York

Iannucci A, Terribile MR, Martiniello P (2008) Effects of temperature and photoperiod on flowering time of forage legumes in a Mediterranean environment. Field Crops Research 106:156–162

IPCC (2018) Glossary. In: Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change. World Meteorological Organization, Geneva, Switzerland

Kubo M, Kobayashi T, Kitahara M, Hayashi A (2009) Seasonal fluctuations in butterflies and nectar resources in a semi-natural grassland near Mt. Fuji, central Japan. Biodiversity and Conservation 18:229–246

Marinho-Filho JS (1991) The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. Journal of Tropical Ecology 7:59–67

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahles R, et al. (2006) European phenological response to climate change matches the warming pattern. Global Change Biology 12:1969–1976

Miliar CL, Stephenson NL, Stephens SL (2007) Climate and forests of the future: managing in the face of uncertainty. Ecological Applications 17: 2145–2151

Moeller DA (2004) Facilitative interactions among plants via shared pollinators. Ecology 85:3289–3301

Mola JM, Williams NM (2018) Fire-induced change in floral abundance, density, and phenology benefits bumble bee foragers. Ecosphere 9:1–9

Monty A, Mahy G (2009) Climatic differentiation during invasion: Senecio inaequidens (Asteraceae) along altitudinal gradients in Europe. Oecologia 159:305–315

Olliff-Yang RL, Mesler MR (2018) The potential for phenological mismatch between a perennial herb and its ground-nesting bee pollinator. AoB PLANTS 10:1–11

Pettorelli N, Mysterud A, Yoccoz NG, Langvatn R, Stenseth NC (2005) Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proceedings of the Royal Society B: Biological Sciences 272:2357–2364

Pigliucci M (2001) Phenotypic Plasticity: beyond nature and nurture. The Johns Hopkins University Press, Baltimore, Maryland

Point Blue Conservation Science (2019) Climate-smart restoration toolkit. https://www.pointblue.org/climate-smart-restoration-toolkit/ (accessed 11 Feb 2020)

Rafferty NE, Caradonna PJ, Burke L, Iler AM, Bronstein JL (2013) Phenological overlap of interacting species in a changing climate: an assessment of available approaches. Ecology and Evolution 3:3183–3193

Rafferty NE, Caradonna PJ, Bronstein JL (2015) Phenological shifts and the fate of mutualisms. Oikos 124:14–21

Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16:179–214

Renner SS, Zohner CM (2018) Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annual Review of Ecology, Evolution, and Systematics 49:165–182

Russo L, DeBarros N, Yang S, Shea K, Mortensen D (2013) Supporting crop pollinators with floral resources: network-based phenological matching. Ecology and Evolution 3:3125–3140

Schmidt NM, Mosbacher JB, Nielsen PS, Rasmussen C, Høye TT, Roslin T (2016) An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. Ecology 97:1250–1255

Schmitt L (1983) Individual flowering phenology, plant size, and reproductive success in Linanthus androsaceus, a California annual. Oecologia 59:135–140

Smith DS, Lau MK, Jacobs R, Monroy JA, Shuster SM, Whitham TG (2015) Rapid plant evolution in the presence of an introduced species alters community composition. Oecologia 179:563–572

Stromberg M, D’Antonio C, Young T, Wirka J, Kephart P (2007) California grassland restoration. California grasslands: ecology and management. University of California Press, Berkeley, California

Timberlake TP, Vaughan IP, Memmott J (2019) Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. Journal of Applied Ecology 56:1365–2664, 13403

504

Restoration Ecology May 2020
Tunes P, Alves VN, Valentin-Silva A, Batalha MA, Guimarães E (2017) Does fire affect the temporal pattern of trophic resource supply to pollinators and seed-dispersing frugivores in a Brazilian savanna community? Plant Ecology 218:345–357
Visser ME, Gienapp P (2019) Evolutionary and demographic consequences of phenological mismatches. Nature Ecology & Evolution 3:879–885
Ware IM, van Nuland ME, Schweitzer JA, Yang Z, Schadt CW, Sidak-Loftis LC, Stone NE, Busch JD, Wagner DM, Bailey JK (2019) Climate-driven reduction of genetic variation in plant phenology alters soil communities and nutrient pools. Global Change Biology 25:1514–1528
Warren RJ, Bahn V, Bradford MA (2011) Temperature cues phenological synchrony in ant-mediated seed dispersal. Global Change Biology 17: 2444–2454
Waser NM, Real LA (1979) Effective mutualism between sequentially flowering plant species. Nature 281:670–672
Weiss SB, Murphy DD, White RR (1988) Sun, slope, and butterflies: topographic determinants of habitat quality for Euphydryas editha. Ecology 69: 1486–1496
Wolkovich EM, Cleland EE (2011) The phenology of plant invasions: a community ecology perspective. Frontiers in Ecology and the Environment 9: 287–294

A strategy to manage phenological asynchrony

Coordinating Editor: Leighton Reid

Received: 15 September, 2019; First decision: 14 October, 2019; Revised: 12 January, 2020; Accepted: 30 January, 2020; First published online: 3 March, 2020