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Authors
Rafferty, Nicole E
CaraDonna, Paul J
Bronstein, Judith L

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Nicole E. Rafferty, Paul J. CaraDonna and Judith L. Bronstein

N. E. Rafferty (orcid.org/0000-0002-6350-1705)(nrafferty@email.arizona.edu), P. J. CaraDonna and J. L. Bronstein, Dept of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721, USA. NER also at: Center for Insect Science, Univ. of Arizona, Tucson, AZ 85721, USA. PJC also at: The Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA.

Climate change is altering the timing of life history events in a wide array of species, many of which are involved in mutualistic interactions. Because many mutualisms can form only if partner species are able to locate each other in time, differential phenological shifts are likely to influence their strength, duration, and outcome. At the extreme, climate change-driven shifts in phenology may result in phenological mismatch: the partial or complete loss of temporal overlap of mutualistic species. We have a growing understanding of how, when, and why phenological change can alter one type of mutualism–pollination. However, as we show here, there has been a surprising lack of attention to other types of mutualism. We generate a set of predictions about the characteristics that may predispose mutualisms in general to phenological mismatches. We focus not on the consequences of such mismatches but rather on the likelihood that mismatches will develop. We explore the influence of three key characteristics of mutualism: 1) intimacy, 2) seasonality and duration, and 3) obligacy and specificity. We predict that the following characteristics of mutualism may increase the likelihood of phenological mismatch: 1) a non-symbiotic life history in which co-dispersal is absent; 2) brief, seasonal interactions; and 3) facultative, generalized, interactions. We then review the limited available data in light of our a priori predictions and point to mutualisms that are more and less likely to be at risk of becoming phenologically mismatched, emphasizing the need for research on mutualisms other than plant–pollinator interactions. Future studies should explicitly focus on mutualism characteristics to determine whether and how changing phenologies will affect mutualistic interactions.

Climate change-driven shifts in the timing of life history events, including migration, germination, growth, reproduction and senescence, are occurring in a wide array of organisms (Parmesan and Yohe 2003, Root et al. 2003, Cleland et al. 2007). These phenological shifts, which are commonly species-specific in magnitude and even direction (Bradley et al. 1999, Fitter and Fitter 2002, Stefanescu et al. 2003, CaraDonna et al. 2014), can alter not only the abiotic conditions but also the biotic environments organisms experience. In particular, changes in phenology can affect both antagonistic and mutualistic interactions (Memmott et al. 2007, Both et al. 2009, Singer and Parmesan 2010, Yang and Rudolf 2010). Such changes can result in disruption of interactions via phenological mismatch: the partial or complete loss of temporal overlap between interacting species relative to historical, pre-climate change conditions. Mutualistic interactions might be especially prone to disruption via differential phenological shifts, as they often require the life history events of partner species to be coordinated in time, with a reduction of benefits likely in cases where such coordination fails. Because mutualisms are ubiquitous in nature, involving almost all species across the globe (Bronstein 2009), understanding the likelihood of phenological disruption is an important goal.

Indeed, because many mutualistic interactions require partner species to locate each other in time, differential phenological shifts should affect their strength, duration, and outcome. Hence, potential consequences of phenological shifts in mutualisms encompass altered effectiveness of partners, which can change the costs and benefits of interactions, as well as demographic responses that can lead to changes in partner densities (Hegland et al. 2009). Ultimately, these effects could result in rapid population declines, potentially leading to local extinction of interacting species (Burkle et al. 2013). At the evolutionary time scale, one can envision transitions of the interaction from mutualism to antagonism, switching of partners, and/or abandonment of the interaction altogether (Kiers et al. 2010).

Although mutualisms are commonly grouped according to the types of resources and services exchanged (transportation, protection, or nutrition), there are other, equally informative ways to group mutualisms that cut across these categories of benefit. In particular, and of interest in this paper, mutualisms can be characterized by their intimacy (e.g. symbiotic or free-living), specificity, obligacy, as well as by the proportion of the year in which the partners are in association. A systematic literature survey, which we describe below, clearly shows that almost all work to date on this question focuses upon a single type of transportation mutualism: pollination. There is indeed growing empirical evidence for negative consequences of phenological change

for plant–pollinator interactions (McKinney et al. 2012, Burkle et al. 2013, Kudo and Ida 2013).

However, pollination mutualisms are not unique in their potential to be affected by climate change-driven shifts in phenology. Here, we move away from the pollination-centered perspective on mutualism disruption, to explore which characteristics are likely to predispose mutualistic species to phenological mismatches. We first develop a set of a priori predictions regarding these characteristics, then evaluate how well they match the characteristics of mutualistic interactions that have been shown in the literature to be at risk of phenological mismatch. We conclude by discussing future research that will be critical for reaching a deeper understanding of threats to mutualism as a whole.

Literature survey: phenological disruption in different forms of mutualism

To begin seeking patterns in the occurrence of phenological disruption across mutualisms, we first conducted a systematic survey of the literature. We used the search criterion of 'mutualis* AND phenolog*' spanning all years (through September 2013) in the ISI Web of Science database. This search provided an unbiased subset of the literature in which to seek patterns.

Our search returned 207 records. These were analyzed to determine if they contained information on a mutualistic species in the context of 1) phenological change (not necessarily due to climate change), 2) climatic variables and phenology, and/or 3) climate change and phenology. Of the initial records, 28 (13.5%) addressed one or more of these three topics, representing a mix of empirical studies, reviews/conceptual work, meta-analyses, and models. This literature is summarized in Table 1. Of these papers, 22 focused on transportation mutualisms, three protection, one nutrition, and two included conceptual or population dynamical models applicable to mutualisms more broadly. By far the most commonly studied transportation mutualism in these contexts was pollination, comprising 17 (77%) of the 22 studies. The remaining five studies explored seed dispersal mutualisms. The few studies of protection mutualisms involved ant–plant associations, and the one study on a nutrition mutualism (and on a symbiosis) focused on plant–mycorrhizal interactions. There was a particularly strong bias in which mutualisms have been studied in the context of either 1) phenological change or 3) climate change, rather than simply documenting relationships between 2) climatic variables and phenology. Of the studies that addressed either phenological change or climate change (15 and 18 of the 28, respectively), all but one focused on plant–pollinator interactions.

This literature survey clearly indicates that what we currently know about phenological disruption of mutualisms concerns the phenological disruption of one type of mutualism: pollination. Below, we step back to consider the characteristics of mutualisms that should be relatively more and less susceptible to phenological mismatches. Our primary objective in generating these predictions is to identify the key aspects of mutualisms that may determine risk of phenological disruption. Additionally, we hope that such information can improve our ability to predict how mutualisms in general will respond to future climate change and the associated phenological shifts.

Table 1. List of studies that contain information on a mutualistic species in the context of 1) phenological change, 2) climatic variables and phenology, and/or 3) climate change and phenology, organized by category of mutualism and type(s) of interaction.

First author	Year	Mutualism	Interaction 1	Interaction 2
Encinas-Viso	2012	all	–	
Yang	2010	all	–	
Sato	2012	nutrition	plant–mycorrhizae	
Frederickson	2006	protection	Ant–plant	
Muniz	2012	protection	ant–plant	
Rico-Gray	2012	protection	ant–plant	
Aldridge	2011	transportation	plant–pollinator	
Bartomeus	2011	transportation	plant–pollinator	
Berg	2010	transportation	plant–pollinator	
Burkle	2011	transportation	plant–pollinator	
Cleland	2012	transportation	plant–pollinator	
Cruz-Neto	2011	transportation	plant–pollinator	
Elzinga	2007	transportation	plant–pollinator	
Espindola	2011	transportation	plant–pollinator	
Gilman	2012	transportation	plant–pollinator	
Harrison	2001	transportation	plant–pollinator	
Hegland	2009	transportation	plant–pollinator	
Hoover	2012	transportation	plant–pollinator	
Memmott	2007	transportation	plant–pollinator	
Munguia-Rosas	2011	transportation	plant–pollinator	
Parsche	2011	transportation	plant–pollinator	
Rafferty	2011	transportation	plant–pollinator	
Wall	2003	transportation	plant–pollinator	
Aizen	2003	transportation	plant–pollinator	plant–seed disperser
Price	1998	transportation	plant–pollinator	plant–seed disperser
Yeo	2009	transportation	plant–pollinator	plant–seed disperser
Burns	2002	transportation	plant–seed disperser	
Warren	2011	transportation	plant–seed disperser	

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Characteristics of mutualism that may influence the likelihood of phenological mismatch

In this section, we offer three predictions for which characteristics of mutualisms should be associated with phenological disruptions in response to climate change. We focus on predicting the 'likelihood' of phenological disruption, rather than on evaluating the likely 'impact' of such disruption should it occur. While this is a central issue, it lies beyond the scope of the present paper. In the following section, we evaluate evidence for each prediction.

Prediction 1. Free-living, non-symbiotic mutualisms are more likely to become phenologically mismatched than are symbiotic, co-dispersing mutualisms

Of prime importance in determining the likelihood that phenological change will disrupt a mutualism is whether it is symbiotic, and, if so, whether partners have adaptations to prevent dissolution of the interaction during dispersal (Table 2). Though rather obvious, this prediction has not, to the best of our knowledge, been stated previously. In many mutualistic symbioses, i.e. mutualisms that are tightly integrated physically and physiologically and in which at least one partner cannot exist without its partner (Bronstein 2009, Douglas 2010), symbionts are transmitted vertically (from parent directly to offspring); in others, partners disperse as a unit (e.g. the soredium, an asexual propagule of lichens composed of a loose ball of fungal hyphae enclosing a group of algal cells). These adaptations reduce or eliminate the chance that symbiotic mutualists will fail to coincide in time and space. In effect, the partners may not even have individually identifiable phenologies. Instead, the symbiosis itself has a single, completely synchronized phenology.

In contrast, when partners reproduce and disperse independently, there is a critical need to locate and establish an association with a partner at the appropriate life history stage, or phenophase. Put more precisely, success and failure are functions of the ability to find partners in time. In these cases, which include the vast majority of non-symbiotic mutualisms, partners are potentially exposed to different abiotic cues and selective forces that shape how they respond to cues. Such differences might be expected to scale with geographic distance among partners so that migratory species are especially prone to mismatches (McKinney et al. 2012). Thus, free-living partners may be more likely to display differential phenological responses to changing climatic conditions, even when the cues they rely on are in fact the same (Iler et al. 2013). As a result, we expect non-symbiotic mutualisms to be more susceptible to phenological disruption. However, mutualistic symbioses lacking co-dispersal or vertical transmission are also likely to be vulnerable.

Prediction 2. Seasonal, short-term mutualisms are more likely to become phenologically mismatched than are aseasonal mutualisms

Both the seasonality and duration of mutualistic interactions are also likely to influence vulnerability to phenological change (Table 2). If the interaction is aseasonal, such that each partner is present at an appropriate phenophase year-round rather than sporadically or during a particular climatic season, temporal overlap of partners through-

Table 2. Mutualism attributes predicted to be related to risk of partner species becoming phenologically mismatched as a result of climate change.

Characteristics	Risk of phenological mismatch	
	Low	High
1) Intimacy	Symbiotic, co-dispersing	Free-living, disperse independently
2) Seasonality, duration	Aseasonal/continuous, long-term	Seasonal/episodic, short-term
3) Obligacy, specificity	Obligate, symmetrically specialized	Facultative, symmetrically generalized

out the interaction is guaranteed. Similarly, if partners are long-lived, there is likely to be repeated opportunity for interaction over multiple seasons. As a result, phenological shifts of one or both partners are likely to be less consequential. However, even when the interaction can occur at any time, the costs and benefits may change along with shifts in partner phenologies. For example, reward quality and quantity may vary across the year, making the interaction more and less beneficial to the reward-consuming mutualist at different times. Such aseasonal systems generally occur in tropical areas, where climate-driven phenological shifts are less apparent (Pau et al. 2011).

Many mutualistic interactions, however, occur during circumscribed times of the year. Furthermore, as the window of opportunity for interaction within a season narrows, the greater the chance that phenophases will fail to overlap, leading to an increasing likelihood of mismatch. The combination of strong seasonality and ephemeral opportunity for interaction could make mutualisms at higher latitude regions particularly susceptible to disruption if phenologies shift. In fact, mutualisms in these regions are expected to be more likely to display climate-driven phenological change (Høye et al. 2007, Pau et al. 2011, McKinney et al. 2012). We therefore expect that the occurrence of phenological mismatches will be more likely for seasonal interactions that occur for brief periods of time.

Prediction 3. Facultative and generalized mutualisms are more likely to become phenologically mismatched than are obligate and specialized mutualisms

A third determinant of the likelihood that climate change will lead to phenological disruption is whether the mutualism is obligate or facultative, specialized or generalized (Table 2). Our prediction concerning these characteristics, which are continua rather than discrete categories, has as its basis the probability that interacting species have been shaped by selection to respond to the same abiotic cues in the same ways. Species participating in reciprocally obligate, symmetrically specialized mutualisms might be expected to have been under very strong selection to respond similarly to climatic cues and thereby to maintain phenological synchrony: in these cases, a miss in time is tantamount to zero fitness. Based on this assumption, we expect mutualisms that are obligate, specialized, or both to be less likely to become phenologically disrupted. However, because anthropogenic climate change is likely distinct from past climatic change in its rapidity, it is unclear whether past selection for synchrony among

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partner will determine robustness to future changes in phenological cues.

Because reciprocally facultative and symmetrically generalized interactions exhibit a reduced degree of mutual dependence, loss of interactions is much less likely to result in fitness costs. Species involved in these mutualisms are therefore expected to be under weaker selection to be coordinated in their responses to abiotic cues and to be buffered by other interactions should some interactions be disrupted. A feature of some mutualistic networks, though, is asymmetrical specialization: specialists tend to interact with generalists, whereas generalists tend to interact with a variety of both specialists *and* generalists (Bascompte and Jordano 2013). Hence, symmetrically specialized interactions can be rare (Waser et al. 1996), and symmetrically generalized, facultative interactions that predominate may be at a greater risk of phenological disruption.

Applying and evaluating predictions

We now consider how well our predictions align with the characteristics of mutualisms that have been deemed potentially vulnerable to disruption in the context of phenological change. At present, rigorous tests of these hypotheses across mutualisms as a whole are not possible; as we have shown, most of what we know about phenological disruption comes from a single form of non-symbiotic mutualism (pollination). However, some intriguing patterns emerge by combining data from seasonal versus aseasonal, obligate versus facultative, and generalized versus specialized pollination mutualisms.

Evaluation of prediction 1. Intimacy
Our first prediction was that mutualisms between free-living, non-symbiotic partners should be more vulnerable to phenological disruption than symbiotic ones in which partners disperse together or in which symbionts are vertically transmitted. Among mutualisms with free-living partners, if the likelihood of phenological disruption increases with the distance over which partners interact, we would expect mutualisms involving migratory species to be especially imperiled. For example, flowering/fruiting of temperate angiosperms and migration of pollinating/seed dispersing animals from the tropics are likely to be triggered by different cues, and/or climate change might proceed at different rates in different areas. Both of these phenomena would likely increase the risk of temporal mismatches. Consistent with this idea, McKinney et al. (2012) showed that hummingbirds migrating from southern Mexico are becoming increasingly mismatched with early season floral resources near the northern limit of their breeding range in the Rocky Mountains of the United States.

We are not aware of existing data that either support or refute our prediction regarding the relative likelihood of phenological mismatches in symbioses that do and do not involve co-dispersal or vertical transmission. Though some mutualistic symbioses, such as corals, have been well-documented to be highly sensitive to climate change (reviewed by Kiers et al. 2010), the focus has been on traits other than phenology (e.g. for corals, thermal tolerance). Although it may not frequently be a concern in light of the extensive adaptations these interactions exhibit to remain integrated through time, this is a topic that deserves attention in the future, especially in light of the centrality of symbioses to the structure of natural and agricultural communities (Rillig 2004).

Evaluation of prediction 2. Seasonality and duration
Our second prediction was that seasonal, short-term mutualisms should be more susceptible to disruption than should aseasonal ones in which partners interact for prolonged periods. There is some evidence consistent with this prediction for pollination and seed dispersal. For example, spring ephemeral wildflowers and overwintering bumble bees that pollinate them often have a relatively narrow window of time in which they are simultaneously present; differential shifts in partner phenologies can result in temporal mismatches (Kudo et al. 2004, Thomson 2010, Burkle et al. 2013, Kudo and Ida 2013). Phenological mismatches in plant-seed disperser mutualisms involving a spring-fruiting plant and the emergence and foraging activity of its ant dispersers have been detected as well (Warren et al. 2011). Pertaining to mutualisms more broadly and at the community level, a population dynamical model showed that season length is an important determinant of network resilience, with communities with shorter interaction seasons potentially more vulnerable to disruption (Encinas-Viso et al. 2012). However, evidence from aseasonal systems is lacking, limiting our ability to evaluate the accuracy of this prediction.

Evaluation of prediction 3. Obligacy and specificity
Our third prediction, that facultative, generalized mutualisms are more likely to be disrupted than obligate, specialized mutualisms, is more difficult to evaluate given available evidence, in part because the true spectrum of partner species is often unknown. However, some supporting evidence comes from work on one bee guild in the southwestern United States. Minckley et al. (2000) found that specialist bees occur more commonly in regions where host plant (creosote, *Larrea tridentata*) flowering is least predictable. As Minckley et al. (2000) and Minckley and Roulston (2006) hypothesize, it is under such conditions that selection for phenological matching of bee emergence and flowering may be strongest. Following this logic, if creosote phenology were to shift with climate, bees that specialize on creosote should be expected to track the phenology of their host plants more closely than generalist bees. Also in support of this prediction, among six plant species in the midwestern United States showing climate change-driven advances in flowering, it was only the species that was most generalized in taxonomic richness of visitors that experienced reduced visitation rates when forced to flower earlier (Rafferty and Ives 2011). More-specialized interactions are generally thought to be most at risk from global change (Memmott et al. 2007, Miller-Rushing et al. 2010, Burkle et al. 2013). However, as we pointed out above, the prediction that generalized, facultative mutualisms will more commonly experience phenological mismatches rests on the assumption that they are under weaker selection to respond in parallel to cues. It does not preclude the fact that more-generalized species will be better able to compensate for the loss of some interactions; nor does it dispute the idea that, when

specialists do become phenologically mismatched, the fitness consequences will likely be more severe (e.g. local extirpation: Harrison 2000, Burkle et al. 2013).

Despite the expectation that obligate, specialized mutualisms may be under stronger selection to remain synchronized, Bronstein (unpubl.) found that *Yucca elata* flowering was strongly delayed following a cold winter, while their obligate yucca moth pollinators were not. Hence, the very earliest flowers were pollinated by the very latest moths, which overwinter as larvae at the base of plants. Long-term observations among botanists in this region suggest that this was not an isolated occurrence (Mark Dimmitt pers. comm.). These patterns suggest the possibility that the cues that trigger flowering in yuccas and emergence in yucca moths are decoupled enough that mismatches could occur regularly, even in this obligate, symmetrically specialized mutualism. Similarly, Kudo and Ida (2013) found that a spring ephemeral (*Corydalis ambigua*) specialized on queen bumblebee pollinators experienced phenological mismatch, leading to reduced seed set.

Discussion

We have suggested here that mutualism intimacy, seasonality and duration, and obligacy and specificity – regardless of the nature of benefits exchanged – are key characteristics that determine the likelihood of phenological disruption of interactions. In particular, non-symbiotic, seasonal, facultative, symmetrically generalized mutualistic interactions may be the most likely to be disrupted if the phenologies of partners differentially shift. Although many mutualisms possess that these characteristics, most have not been studied in this context.

For instance, many seed dispersal mutualisms occur seasonally, and are both facultative and generalized; all are non-symbiotic. Although the possibility of phenological mismatches between plants and seed dispersers has been noted, it has rarely been studied directly; climate change-driven range shifts and other drivers of global change have received considerably more attention (McConkey et al. 2012, but see Warren et al. 2011, Warren and Bradford 2014). We would, however, expect seed dispersal mutualisms involving animals with exceptional abilities to seek out plant resources over long distances to be relatively robust to local shifts in flowering and fruiting times. Additionally, when both partners are long-lived, as is the case in some vertebrate–tree seed dispersal mutualisms, individuals may be able to wait out occasional partner absences (Bronstein et al. 2004). Ant–plant protection mutualisms, particularly those in the temperate zone, also tend as a rule to be seasonal, facultative and generalized. These too might therefore be susceptible to phenological disruption. Indeed, phenological coordination of ant reproduction and nest site availability, likely via temperature cues, has been shown to be important in the interactions between an Amazonian ant species and its plant host (Frederickson 2006). Visitation to extrafloral nectaries by ants can vary with plant phenology (Muniz et al. 2012), and climate-driven variation in plant phenology can shape the structure of ant–plant networks (Rico-Gray et al. 2012).

Ideally, to assess the relative importance of each characteristic that we suggest puts mutualisms at risk of phenological disruption, future research should contrast mutualisms that differ in only one attribute. For example, comparing phenological matching in non-symbiotic, facultative, generalized ant–plant mutualisms in seasonal versus aseasonal habitats could isolate the importance of seasonality. Similarly, seed dispersal mutualisms that are similar in seasonality but vary in generalization could be compared to gain an understanding of the relationship between generalization/specialization and phenological synchrony, akin to geographic tests of synchrony in the peak abundances of avian seed dispersers and fruits (Burns 2002).

It is important to recognize that some of the same characteristics that may make mutualisms vulnerable to disruption also translate into less severe consequences if interactions are in fact lost. In particular, the loss of individual facultative mutualists, or even entire facultative mutualistic interactions, should have less dire short-term implications for their partners than should the loss of obligate interactions. For example, a plant that flowers for a short period and thus interacts with pollinators only briefly may be capable of autonomous self-pollination as a form of reproductive assurance (Bond 1994). Similarly, generalized mutualisms often involve a degree of ecological redundancy, potentially buffering organisms from the loss of a subset of their partner species (Morris 2003). For example, both Memmot et al. (2007) and Burkle et al. (2013) found that loss of interactions was less severe for generalist pollinators, which are able to switch to new floral resources in the absence of their usual partners. Disruption might therefore occur at one level but not at another, in that a generalized mutualist can lose links with particular partners while retaining others in the network, resulting in persistence of the mutualistic interactions. Furthermore, species engaged in generalized interactions commonly interact with specialists (Bascompte and Jordano 2013); those specialists would be expected to be under selection to maintain synchrony with their generalist partners and could thereby further buffer focal species from the loss of some interactions. More generally, network-level studies indicate that the nested structure commonly observed in mutualistic assemblages can contribute to their stability, as can highly connected super-generalists (Memmott et al. 2004, Okuyama and Holland 2008, Thébault and Fontaine 2010, Guimarães et al. 2011, Lever et al. 2014, but see James et al. 2012).

Some mutualisms at risk of disruption due to other aspects of climate change are probably not likely to become phenologically mismatched. Coral–algal nutritional symbioses, for example, are under threat from temperature stress (Hughes et al. 2003, Frieler et al. 2013), but this is unlikely to cause differential phenological shifts between partners. In part, this is because these symbioses are relatively aseasonal and obligate, in the sense that corals are unable to persist long-term without zooxanthellae. Plant mycorrhizal mutualisms, too, may fall into this category: the intimate physical contact between plant roots and fungal hyphae suggest that they may be phenologically coordinated throughout the year, although this needs to be tested explicitly. When host plants have higher net photosynthesis rates or are allocating more photosynthate to roots, mycorrhizal fungi are more likely to produce fruiting bodies, or larger fruiting bodies (Sato et al. 2012). However, intimate, year-round

mutualistic interactions such as this could become decoupled if, for example, one partner is dormant for part of the year while the other is not.

We anticipate that the mutualism characteristics identified here are not independent of each other. Indeed, they may often occur in suites, rendering certain interactions much more likely than others to be disrupted. Non-symbiotic, free-living mutualisms as a rule are likely to be more seasonal and episodic than mutualistic symbioses, although, as noted, reproduction and dispersal in non-vertically transmitted symbioses may represent events in which even symbiotic interactions could be disrupted by mismatched timing. For example, to form lichens, the sexual spores of fungal partners must encounter compatible algae/cyanobacteria (Douglas 2010). In general, though, seasonality is expected to be more relevant for non-symbiotic mutualisms in which partner phenologies are always distinct. Likewise, symbiotic interactions have been suggested to be more likely to involve symmetrical specialization (Ollerton 2006), and reciprocally obligate mutualisms are expected to be more specialized, with mechanisms that promote phenological synchrony between partners. An exciting step for the future will be to conduct a comprehensive analysis of linkages among the mutualistic traits we focus upon, and to test whether certain sets of traits do indeed render mutualisms particularly resilient or vulnerable.

Consideration of factors beyond those we have based our predictions on will ultimately be important to achieve a full understanding of phenological disruption of mutualisms. We give four examples here. First, understanding the fitness consequences for each individual partner is critical to formulating predictions about how the interaction itself is likely to respond to mismatches when they occur. When interactions are neither reciprocally obligate nor symmetrically specialized, shifts may commonly have different consequences for each partner, so a mismatch that has negative effects for one partner need not necessarily have negative effects for the others. For example, a plant that begins flowering earlier may become mismatched with its pollinator and experience pollination failure. However, that pollinator may not be affected by the absence of that particular floral resource if it has access to other, ecologically equivalent floral resources. In this case, the plant may be under selection to maintain synchrony with the pollinator, but not vice versa.

Second, again assuming that a phenological mismatch has arisen, the duration of the mismatch relative to the total duration of the phenophase will influence whether a given mutualism is likely to be disrupted. For example, at the population level, the consequences of a mismatch that occurs only for the very earliest individuals in a phenophase versus a mismatch that spans an entire phenophase could differ greatly. However, determining what magnitude of temporal shift constitutes a mismatch that is likely to negatively affect the focal species can be a complicated task, as it depends in part on the historical, and often unknown, degree of prior synchrony (Singer and Parmesan 2010, Burkle et al. 2013, Rafferty et al. 2013).

Third, another, more indirect characteristic that influences whether a given mutualism will be disrupted by phenological change is whether its fate depends upon a preceding mutualism that has been disrupted by shifted phenology. For example, if a plant–pollinator mutualism becomes sufficiently disrupted phenologically that flowers produced at the start of the flowering season are not pollinated and consequently fail to set fruits and seeds, then there could also be a temporal gap in the availability of food resources early in the season for the local community of frugivores and seed dispersers. This kind of cascading mismatch, which has not to our knowledge been suggested or studied to date, could have similar consequences as direct disruption of mutualism via changed phenology.

Finally, there is the possibility that focal mutualists will be affected not by altered temporal overlap, but instead by changed interactions with antagonists or other mutualists that result from phenological shifts. If the phenologies of focal partner species change such that the synchrony between them is maintained, but that simultaneously brings them into novel community contexts and interaction dynamics, then the mutualism could still be disrupted. Thus, it is essential that we not consider mutualisms to take place in isolation from other interactions within a community.

Conclusions

We conclude that intimacy, seasonal duration, and degree of obligacy and specificity are characteristics of mutualisms that may determine the likelihood of phenological disruption. Our central point is the benefits that mutualists confer (transportation, protection or nutrition) are not the most useful predictors of how vulnerable any particular mutualism will be to phenological disruption. Rather, there is a set of characteristics that can help to predict vulnerability, and these cut across traditional ways of grouping mutualisms. Clear support for our predictions in many cases is equivocal, owing in part to the paucity of research in this area, especially outside of pollination. There is thus much room for research into whether species involved in mutualisms other than plant–pollinator interactions are likely to become temporally mismatched. In addition, as empirical evidence on the effects of rapidly and directionally changing climate cues on phenological matching of mutualists grows, predictions specific to anthropogenic climate change should be possible. Looking forward, studies that extend beyond system-specific details to consider general characteristics that can predispose mutualisms to phenological disruption should be especially valuable.

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