Humming along or buzzing off? The elusive consequences of plant-pollinator mismatches

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Abstract—Temporal mismatches among plants and pollinators, driven by climate change, are considered a potential cause of population declines of these mutualists. However, field studies demonstrating population declines as a result of climate-driven phenological mismatches are uncommon, and the extent to which mismatches will be a problem in the future remains unclear. We revisit predicted consequences of climate-driven phenological mismatch in plant-pollinator systems by identifying nine previously-applied assumptions that are violated or insufficiently understood in real systems. Briefly, the assumptions are: (1) Dates of first-flowering (DFF) or dates of first activity (DFA) correctly describe phenology, and disparities between DFF and DFA represent the magnitude of mismatch. (2) "Optimal" matches are measured correctly. (3) Advancement of DFF or DFA will be the primary phenological change in the future. (4) Future phenological shifts will be independent for each species. (5) All plant-pollinator interactions are equally effective. (6) Populations of plants and pollinators are limited by mutualistic interactions. Some previous models have also assumed that the effects of future mismatches will not be influenced by (7) emergence of novel interactions, (8) competition or facilitation from altered co-flowering and co-flight, and (9) phenotypic plasticity and rapid adaptive evolution of phenology. Those assumptions affect the direction, extent, and accuracy of predicted consequences of future phenological mismatch. In discussing them, we identify important topics for future research in pollination ecology.

Keywords: Phenology, plant-pollinator interactions, flowering time, mismatch, climate change, evolutionary ecology

Introduction

A "pollination crisis" is reducing diversity and abundance of plants and pollinators, and having important economic impacts on agriculture (e.g. Steffan-Dewenter et al. 2005; Berenbaum et al. 2007). Many drivers contribute to pollinator declines (e.g. Potts et al. 2010; Willmer 2011), one of which may be climate change. A concern is that rapid climate change will cause mismatches to arise in the timing of seasonal interactions (phenology) between pollinators and their host plants (Bazzaz 1990), and that those mismatches will have severe demographic consequences for both pollinators and plants (Inouye et al. 2000). Phenological synchrony is said to occur "when the peak timing of pollinator feeding coincides with the peak requirement by… plant[s] for pollinator visits" (Singer & Parmesan 2010). Recent reviews (e.g. Hegland et al. 2009; Miller-Rushing et al. 2010; Donnelly et al. 2011; Diez et al. 2012; Willmer 2012) summarize evidence for past and anticipated phenological mismatches. However, determining (1) the likelihood that mismatches will occur in the future as a result of climate change, and (2) the demographic impacts of mismatches, should they occur, is challenging (Rafferty et al. *in press*). Mismatch will affect plant-pollinator interactions if "a change in interaction strength or frequency [will occur], this change is the result of climate change and…the change [will alter] the vital rates of one or more of the species involved" (Forrest & Miller-Rushing 2010).

The purpose of this paper is to review and improve understanding of the consequences of climate-driven phenological mismatch between plants and pollinators, first by identifying and discussing previous assumptions about mismatch, and second by highlighting recent advances and future directions for research in this field. We identify nine key assumptions (Table 1) about mismatch that affect how studies are conceived, data collected, and results interpreted. Authors of papers on phenological mismatch frequently state and discuss assumptions of the models used, and test them in later studies (e.g. Memmott et al. 2007; Kaiser-Bunbury et al. 2010). However, the risks of population declines resulting from mismatch relative to potential for adaptation and resilience remain unclear. Here we show what assumptions have been used, how or if they have been examined empirically, and how they might benefit from further investigation. Three of the assumptions about mismatch relate to the nature of phenology, and how it is measured (Table 1, Assumptions 1-3). Two concern the identities (taxonomy and phylogeny) of plants and pollinators (Table 1, Assumptions 4-5). One examines the link between phenological synchrony and demographic consequences for plants and pollinators (Table 1, Assumption 6). Three involve the long-term flexibility or resilience of interactions between plants and pollinators (Table 1, Assumptions 7-9).

TABLE 1.   Key assumptions in studies of the consequences of climate-driven phenological mismatch for plant-pollinator interactions.

Assumption	Examples	Challenges/new concepts	Effect?	Methods to address
1) Dates of first flowering (plants) or activity (pollinators) provide useful estimates of phenology at the population level	Gordo & Sanz 2005, 2006; Memmott et al. 2007; Rafferty & Ives 2010; Bartomeus et al. 2011.	Phenology occurs over time rather than at one instant. It can be described as "area under the flowering/activity curve" or a population mean, constrained by first and last dates of flowering/activity (Forrest & Miller-Rushing 2010). Shapes and temporal shifts of phenological curves might differ between pollinators and flowers due to physiological differences, leading to altered overlap. Pollination can affect the duration of flowering (Doorn 1997; Fründ et al. 2011).	Underestimates risk of mismatch in cases of mid or late season deficits in floral resources or pollinators. Overestimates severity if flowering and activity are long and pollinators are abundant. Overestimates severity by ignoring cases where unvisited flowers stay open.	Monitor random plots and flowers, or track individuals through time. Assess multiple phenological stages as frequently as possible throughout the growing season. Work in degree-days instead of calendar days (Lindsey & Newman 1956; Schemske et al. 1978).
2) "Optimal" matches are measured correctly; perceived mismatches are not merely short-term measurement of longer-term adaptive strategies	Many papers: e.g. Wall et al. 2003; Bartomeus et al. 2011, 2013b	Precise synchrony may not be the baseline state in some systems, and may not be as widespread as we assume. Poor synchrony could be driven by other important tradeoffs relating to life-histories (Visser & Both 2005; Singer & Parmesan 2010). Phenology can be "patchy" (Kudo & Hirao 2006).	Overestimates severity of mismatch if precise synchrony is not the norm and other factors are more important, but disruption of systems with low baseline synchrony could have severe impacts if timing is still important.	Multi-year studies of plant-pollinator interactions, using repeated measures on long-lived plants; consideration of trade-offs and multiple, interacting aspects of life history, including *lifetime* fitness.
3) Advancement of flowering and activity will be the primary response of plants and pollinators to climate change	Gordo & Sanz 2005, 2006; Memmott et al. 2007; Bartomeus et al. 2011	Early flowers may advance; late-season flowers may be delayed (e.g. Cook et al. 2012). Multiple flowering peaks can emerge (Aldridge et al. 2011). Voltinism may change (Altermatt 2010a).	Underestimates severity of mismatch in case of mid-season or late-season deficits in floral resources or pollinator availability. Overestimates severity if flowering activity times are lengthened.	Link physiology with cues and develop phenological models for particular species using field studies and manipulation of cues. Assess nature of long-term phenological shifts in multiple interacting species.
4) Phenological responses of species (plants and pollinators) to climate change will be independent	Memmott et al. 2004, 2007; Kaiser-Bunbury et al. 2010	Responses to cues are correlated among taxa (Willis et al. 2008; Davis et al. 2010), and vary according to evolutionary history or life history (Altermatt 2010b; Bartomeus et al. 2013a). Some species appear to respond adaptively while others do not (Rafferty & Ives 2011; Bartomeus et al. 2011).	Underestimates global impacts of mismatch if highly diverse or important groups are disproportionately affected. Overestimates impacts if adaptive responses are common, particularly within diverse or important groups.	Community-wide studies or simulations on responses of species to climate change that are phylogenetically controlled and examined by guilds, functional groups, or other life history traits.

Assumption	Examples	Challenges/new concepts	Effect?	Methods to address
5) All pollinators are similarly effective (as measured by pollen transferred per-visit) and effectiveness is consistent throughout the season; all plants offer similar resources to pollinators.	Gordo & Sanz 2005; Vázquez et al. 2005; Memmott et al. 2007; Kaiser-Bunbury et al. 2010; Forrest & Thomson 2011; Bartomeus et al. 2013b	Some taxa (e.g. *Bombus*) are more abundant, or effective pollinators than others (Wall et al. 2003; Thomson 2010), and effectiveness varies *within* years (Rafferty & Ives 2012). Climate change might alter nectar composition, making flowers more attractive to pollinators yet providing fewer resources (Hoover et al. 2012). Some flowers offer greater resources (Mosquin 1971).	Counting all visits as effective or beneficial can underestimate negative impacts by overestimating pollination services or benefits to pollinators. Consequences of mismatch may be overestimated or underestimated at particular times of the season.	Use highly-specialized study systems (single-pair mutualisms) and high taxonomic resolution when monitoring visitation; use controlled experiments allowing only single visits; use of appropriate controls (comparing experimental plants to plants with "open" pollination).
6) Plant reproduction is pollen-limited, and pollinator populations are limited by availability of floral resources	Kudo et al. 2004; Memmott et al. 2007; Kaiser-Bunbury et al. 2010; Rafferty & Ives 2010	Other biotic/abiotic factors limit reproduction (Harder & Aizen 2010). Many species have reproductive assurance through selfing (Knight et al. 2005) or extended flowering (Doorn 1997). Pollen limitation varies among locations, species, and years (e.g. Hegland & Totland 2008).	Overestimates the demographic impacts of mismatch.	Study drivers of pollen limitation using controls (e.g. pollen-supplementation) to verify pollen-limitation during field studies simulating mismatch. Use self-incompatible species. Manipulate floral resources and examine consequences for pollinator populations.
7) New mutualisms will not arise (or historical mutualisms will not be restored); parasitism or antagonism will remain constant	Harrison 2000; Wall et al. 2003; Kudo et al. 2004; Memmott et al. 2007; Kaiser-Bunbury et al. 2010	Interactions are flexible; new mutualisms may arise (or historical ones be restored) that preclude pollen limitation for plants (Kaiser-Bunbury et al. 2010; Olesen et al. 2011) or resource-limitation for pollinators. Species may be released from parasitic or antagonistic interactions (Parsche et al. 2011), or new ones may arise (Liu et al. 2011).	Overestimates negative consequences of mismatch by ignoring potential for network re-wiring and release from parasitism or antagonism; underestimates consequences if new antagonisms arise.	Experimentally force mismatches under field conditions and measure resulting seed set. Use choice/no-choice experiments with high taxonomic resolution for pollinators, parasites, and floral antagonists. Manipulate density in addition to identity of resources.
8) Changes to patterns of co-flowering or co-activity will not influence the effects of mismatch	Few studies to date, but identified as a key question by Miller-Rushing et al. 2010; Forrest et al. 2010; Rafferty & Ives 2012	Co-flowering displays and co-flying pollinators can be competitive OR facilitative (Goulson 2003; Dafni et al. 2005; Mitchell et al. 2009). Removing species affects interactions among remaining species (Brosi & Briggs 2013).	When flowers or pollinators compete, if co-flowering/co-flight increases, negative impacts of mismatch might be exacerbated, but this would be reversed in cases of facilitation.	Community-scale studies on competitive vs. facilitative relationships among co-flowering plants or co-flying pollinators. Separating effects of density.
9) Phenotypic plasticity or adaptive evolution cannot mitigate consequences of phenological mismatches	Harrison 2000; Kudo et al. 2004; Memmott et al. 2004, 2007	Synchronized phenology may be maintained by rapid evolution, plastic responses to changing cues, or novel interactions (Kaiser-Bunbury et al. 2010; Rafferty & Ives 2010; Singer & Parmesan 2010; Gilman et al. 2012; Bartomeus et al. 2013b).	Overestimates negative consequences of mismatch.	Experimentally force mismatches under field conditions (assessing plasticity of responses to phenological cues). Long-term studies on heritability of responses to cues, and strength of selection on cues under varying conditions.

The origins of phenological mismatch

The match/mismatch hypothesis originated in studies of marine food webs and predator-prey interactions (Table 2). Mismatches have arisen *in situ* (when interacting, diapausing species responded differently to the same set of environmental cues: Visser et al. 1998; Visser & Holleman 2001; Edwards & Richardson 2004), or by mistiming of migration (when species could not access environmental cues at their breeding grounds; Both et al. 2006). Anticipated plant-pollinator mismatches might arise either *in situ* (e.g. when ground-nesting bees respond differently to soil temperatures than do alpine flowers: Kudo et al. 2004; Kudo & Ida *in press*). Mismatches might also arise through mistimed migration (e.g. when hummingbirds migrate in response to day length, but flowers respond to temperature: McKinney et al. 2012). Pollination mismatch differs from the "classic" match/mismatch hypothesis (Table 2) because of the (usually) mutualistic instead of predatory relationship between plants and pollinators. Pollen and nectar resources impact reproductive fitness of pollinators by affecting (1) ability to mate, (2) the size and number of offspring (or relatives), and (3) survival probability (Eickwort & Ginsberg 1980). Plants rely on pollinators for sexual reproduction, with floral visitation being linked to seed set (Kearns & Inouye 1993; Vázquez et al. 2005), which can affect recruitment (e.g. Turnbull et al. 2000). While empirical studies of phenological mismatch sometimes show declines

in abundance (Table 2), many do not (Parsche et al. 2011; Iler et al. 2013; Reed et al. 2013). Empirical data on demographic consequences of plant-pollinator mismatch are lacking (Rafferty et al. *in press*), but model predictions for the future of plant-pollinator interactions can be bleak (Memmott et al. 2004, 2007). Understanding the disconnect between models and empirical data starts with examining model assumptions.

Assumption 1: Dates of first flowering or activity provide reliable estimates of phenology for populations

Before studies can assess whether populations of plants and pollinators are matched or mismatched with respect to phenology, appropriate ways of measuring phenology must be established. One ecological response to climate change has been advancing dates of first flowering (DFF) for some plants or dates of first activity, flight, or arrival (DFA) for some pollinators (Sparks & Yates 1997; Fitter & Fitter 2002; Figure 1a). Historical DFF or DFA are often used to assess baseline phenology and quantify phenological shifts through time (Gordo & Sanz 2005, 2006; Willis et al. 2008; Rafferty & Ives 2011; Figure 1a). However, DFF and DFA are unreliable representations of phenology for populations when sampling effort or abundance change (Van Strien et al. 2008; Ellwood et al. 2012). Also, phenological synchrony (and thus mismatch) is defined as the relative

TABLE 2. A brief and generalized history of developments in the match/mismatch hypothesis. Inter-trophic mismatches have been shown to occur in many systems (see Donnelly et al. 2011 for a thorough review).

Study System	Value	Reference
Marine: recruitment success of juvenile herring was linked to the degree of temporal coupling between larval fish and cycles of abundance in copepods as a limiting food source	Proposed that mismatches in phenology among interacting trophic levels, driven by climatic events, could have a limiting effect on populations that were directly dependent on a food source belonging to a lower trophic level	Cushing 1990
General hypothesis: "combined effects of elevated CO_2 and other aspects of climate change, such as rising temperature, may cause large shifts in phenology such that the activities of the plants and their pollinators become decoupled"	First proposed that climate change could lead to the occurrence of phenological mismatches between plants and pollinators	Bazzaz 1990
Recruitment of Great Tits, *Parus major*, depended on availability of insects for food in the spring, specifically on their breeding grounds	Highlighted the importance of environmental cues in determining to what degree synchrony would be possible between breeding schedules and food availability for offspring	Visser et al. 1998
Larval recruitment of moths, *Operophtera brumata*, depended on timing of bud-burst in their host oak tree, *Quercus robur*	Demonstrated potential for disruption of phenological cues under climate-warming	Visser & Holleman 2001
Marine: members of open-water plankton communities responded differently through time to changes to climate, and these emerging differences in phenology could affect higher trophic levels through changes in the abundance of prey	Linked occurrence of match/mismatch to long-term changes to climate	Edwards & Richardson 2004
Pied Flycatchers, *Ficedula hypoleuca,* and their caterpillar prey responded to different cues, causing dramatic declines in Dutch populations of these birds	Attributed population declines to inter-trophic mismatch	Both et al. 2006

timing of a *peak* in requirement for pollination of plants, and availability of pollen or nectar for pollinators (Singer & Parmesan 2010). Phenological patterns in populations are better described as variation around a mean, constrained by first and last dates of flowering or activity (Figure 1b), but the true mean and variance are rarely measured, and flowering curves can be skewed (Thomson 1980; Forrest & Miller-Rushing 2010; Forrest & Thomson 2010), or vary among years and species (Figure 1c). Assessing phenological synchrony or asynchrony among interacting species requires quantifying overlap of the area under flowering or activity curves for plants and pollinators (Figure 1b). Inferring mismatch from disparity in DFF and DFA assumes that DFF and DFA represent flowering or activity curves, which may not always be true (Figure 2a).

Shapes of phenological curves may differ between pollinators and plants due to differences in their physiologies (Table 1; Figure 1d). Flowering times follow curved distributions, subject to physiological cues for early-season development (e.g. snow-melt, growing degree-days), and constrained by time needed after pollination for seeds to mature (Galen & Stanton 1993). However, bumble bees in temperate environments continue emerging and pollinating until it becomes too cold. Rather than declining gradually, abundance of foraging bees can increase until an abrupt die-off when only reproductives overwinter (Goulson 2010; Thomson 2010). Similarly, breeding hummingbirds should be most abundant before fall migration, after fledging. Analyses based on DFF and DFA fail to consider pollination interactions in the tail of the flowering curve.

Shapes of flowering curves can also depend on whether flowers are pollinated (Table 1) (Doorn 1997; Fründ et al. 2011; Willmer 2011). Flowering duration can be driven by pollinator behaviour (and vice versa) in addition to abiotic factors (Doorn 1997; Fründ et al. 2011), confounding pollination and phenology.

How it affects predicted consequences of mismatch

Focusing on DFF or DFA underestimates the risk of mismatch if mid or late-season deficits in pollination or floral resources are what limits populations of plants or pollinators (e.g. Aldridge et al. 2011). If pollinator abundance increases through the season instead of declining, ignoring the tail of the flowering curve for the plant community ignores a period when pollinators are highly available for relatively few plants (Mosquin 1971; Thomson 2010; Figure 1d, shaded area). In some systems, flowering and foraging are both higher toward the end of the season.
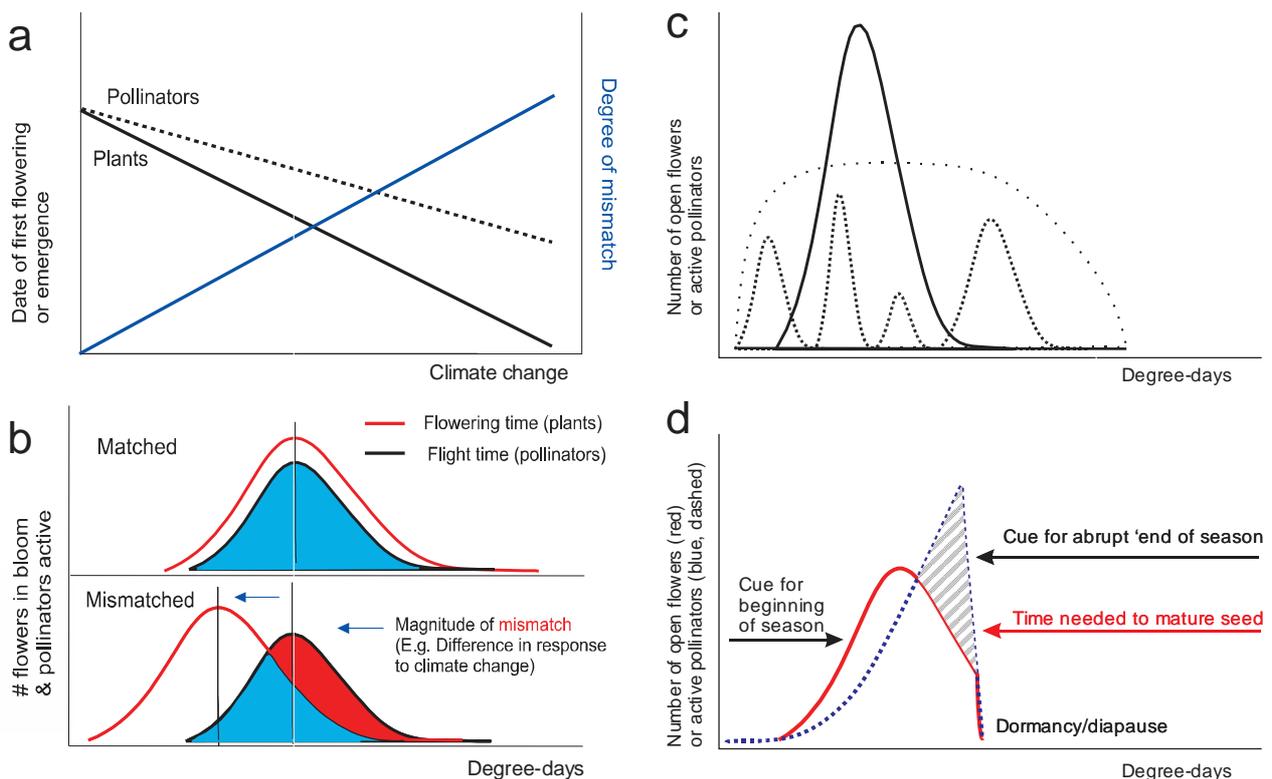
FIGURE 1. Simplified representations of (a) increasing phenological mismatches (space between lines) between plants and pollinators occurring when their changes in timing respond differently to climatic drivers through time, and (b) predicted consequences in relation to historical plant-pollinator overlap (blue) that can no longer occur (red). In this example, plants have advanced their flowering times more than pollinators have shifted their flight times. (c) Possible variation in shapes of phenological curves among species or years (following Willmer 2011). (d) Alternative shapes of phenological curves for flowers (red) and pollinators (blue) in seasonal environments. Both are constrained by conditions (e.g. snow, low temperatures, frost) at the beginning and end of the curve, but plants are additionally constrained by time needed for seeds to mature. Many insects, in contrast, can continue to reproduce until an abrupt die-off forces a switch to the dormant state.

Plants that remain open longer when not pollinated could buffer against phenological mismatch because their date of last flowering (and thus flowering period) depends on pollination rather than DFF or responses to abiotic cues. Models predicting mismatch based on DFF ignore this buffering capacity.

Methods for addressing

Assessing phenology for random flowers, plots, or repeated measures on individuals can represent wider populations, and may prove more reliable than historical records (e.g. Hocking 1968; Miller-Rushing et al. 2008). Recording multiple phenological stages could control buffering effects of flowers that remain open when not pollinated. Monitoring post-flowering development helps estimate seed set and future recruitment (Galen & Stanton 1993). Degree-days above a physiological threshold for development are more relevant units of time than calendar days for assessing phenological shifts (e.g. Lindsey & Newman 1956; Schemske et al. 1978), since degree-days can mechanistically link phenology with physiology and climate change.

Assumption 2: "Optimal" matches are measured correctly; perceived mismatches are not merely short-term measurement of longer-term adaptive strategies

Once phenology has been defined and measured, how can phenological synchrony of plant-pollinator communities be assessed? How synchronized must populations be? Time-series data can detect long-term phenological shifts in response to changing climate. Examining relative shifts among interacting species may establish relevant baselines for assessing changing synchrony (Visser & Both 2005; Parmesan 2006). However, precise synchrony (100% overlap of flowering and activity curves) may not be the baseline (i.e. pre anthropogenic climate change) or optimal state (Table 1; Mayer et al. 2011). Instead, poor synchrony could be the norm in some systems, driven by tradeoffs in other life history components.

Emergence of *Euphydryas editha* caterpillars has historically been poorly synchronized with seasonal availability of their host plants, *Plantago* and *Castilleja* (Singer & Parmesan 2010). This may be an adaptive strategy for living in fluctuating climates, where phenology of host plants is unpredictable (Hocking 1968). In some locations, interannual variation in shapes of flowering curves, and co-flowering might exceed the variation from long-term phenological shifts (Hocking 1968; Bartomeus et al. 2013b). Phenology varies over small (<100 m) areas in mountains, where it is driven by snowmelt and temperature (Willmer 2011). Late in a season, early-flowering species might bloom at high elevation, north-facing slopes, or patches with accumulated snow while late-flowering species might bloom at low elevation, south-facing, or snow-free areas (with wind, rock, or avalanches). By bet-hedging emergence time, populations of female caterpillars experience trade-offs between the ability to grow large during the feeding season and produce many offspring, and risk of death due to incomplete development (Singer & Parmesan 2010). In

Erythronium, earlier snowmelt may lead to earlier flowering, but late-season frost may preclude seed-set in early-flowering individuals (Thomson 2010). Considering tradeoffs complicates assessing whether shifting plant/pollinator synchrony might represent truly maladaptive mismatches with demographic consequences.

How it affects predicted consequences of mismatch

The severity of mismatch could be overestimated if synchrony is not as important as assumed and other factors limit the vital rates of plant and pollinator populations. However, disruptions of systems with poor baseline synchrony could have severe impacts when some level of synchrony is necessary (Singer & Parmesan 2010). Local variation in phenology could mitigate effects of mismatch if pollinators are highly mobile (e.g. in mountains).

Methods for addressing

The importance of plant-pollinator synchrony could be assessed using multi-year studies with synchrony as an independent variable, and repeated measures of reproductive success on individual plants as the dependent variable. Synchrony can be manipulated by moving plants with advanced or delayed flowering into the field (e.g. Waser 1979; Rafferty & Ives 2011). Ideally, studies should measure reproductive success and lifetime fitness to determine which tradeoffs maximize fitness, and consider how interactions besides pollination affect reproductive success. Optimal synchrony could be assessed by raising pollinators, seed-predators, and plants in a series of growth chambers simulating climate variability (e.g. temperature, moisture) to examine how this variability affects the degree of matching and reproductive success. Such experiments would encounter logistical challenges (e.g. keeping pollinators alive for multiple generations on limited floral resources), but supplementing pollinator diet with a fixed amount of nectar could ensure survival while preserving biologically significant differences in success between matched and mismatched pollinators. Optimal synchrony could also be estimated from demographic models combined with mathematical simulations where synchrony and abundance of resources are manipulated, and realistic constraints are placed on phenology (e.g. date of last spring frost, time needed for development, and onset of fall frost).

In the field, natural replicates of early, peak, and late flowering "cohorts" can be followed using spatial variation in flowering (Kameyama & Kudo 2009). The scale at which mismatches are simulated affects results. Highly mobile pollinators could make treatments represent phenological shifts for patches, rather than entire ecosystems (Kudo & Hirao 2006; Kameyama & Kudo 2009). The result would test pollinators' abilities to find resources in heterogeneous landscapes, rather than representing responses to mismatch. Latitudinal variation in phenology can be used to simulate mismatch by transplanting plants among phenological contexts (Waser 1979). Mate availability must be controlled (Hegland et al. 2009), but this is possible with flight cages (Fründ et al. 2012), or arrays of flowers, set apart from habitat (Rafferty & Ives 2011, 2012).
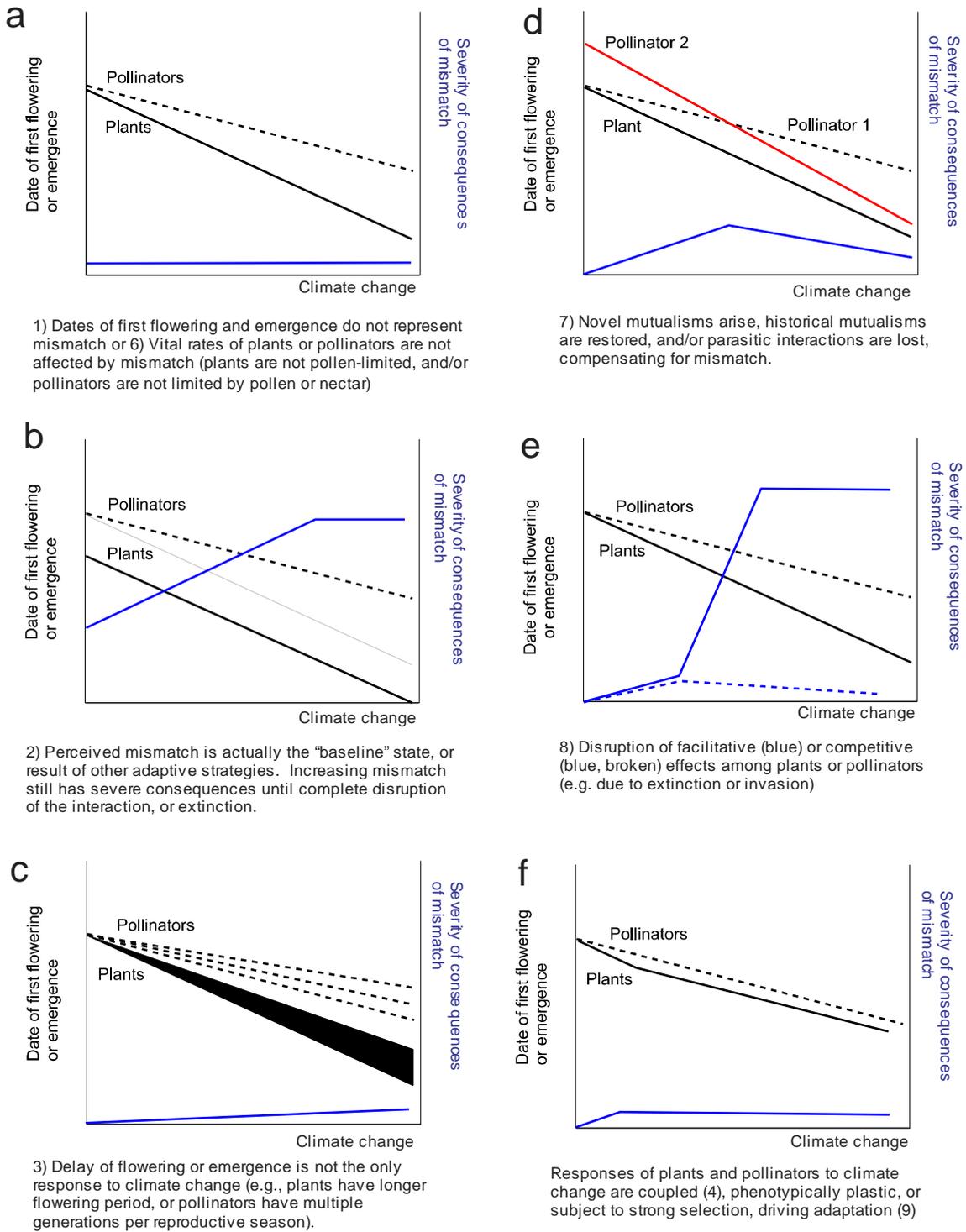
FIGURE 2. Some possible outcomes in terms of plant-pollinator mismatch under scenarios where common assumptions about mismatch are violated. Numbers correspond to assumptions discussed in text, summarized in Table 1.

Assumption 3: Advancement of phenology will be the primary response of plants and pollinators to climate change

Advancement is not the only phenological response to climate change (Table 1; Figure 2b). Experimental warming has caused community-level advancement of early flowers

and delay of late flowers in tall grass prairies (Sherry et al. 2007). Early and late flowers have responded divergently to warming over ~50-150 years in the UK and Washington D.C., likely because of physiological differences in vernalization requirements (Cook et al. 2012). Species-dependent advancements or delays in flowering time have occurred at Rocky Mountain Biological Laboratory

(RMBL), Colorado, USA, between 1974 and 2009 (Aldridge et al. 2011). Divergence in flowering times among species meant a shift from one flowering peak to multiple peaks. Bimodality (distinctiveness of peaks) increased most in mesic habitats, while time between early and late flowering peaks increased everywhere (Aldridge et al. 2011).

It is not clear whether responses to climate change will diverge among early and late-emerging pollinators. However, number of flight periods per year (voltinism) has changed in Lepidoptera (Altermatt 2010a) (Table 1, Figure 2b). We did not find papers describing altered voltinism in bees and flies, but it could occur for multivoltine *Megachile* (Kim & Thorp 2001) and Syrphidae (Iler et al. 2013), or *Bombus*, which produce multiple broods of workers throughout summer (Goulson 2010). Warming is predicted to decrease generation time and increase generations per year for many genera (Bale et al. 2002).

How it affects predicted consequences of mismatch

Advancement or delay of flowering could exacerbate the effects of mismatch when plants encounter other factors that limit reproduction (see assumption 2), but restrictions to phenological shifts could preclude severe mismatches. Advancement of early-flowering species is constrained by exposure to frost in temperate regions (Inouye 2000, 2008). Late-flowering species can be vulnerable to late-season drought (Forrest 2011), and constrained by the time needed for seeds to develop, although growing seasons are also extending (Thórhallsdóttir 1998). If pollinators do not advance or delay phenology with plants, shifts from one flowering peak to multiple peaks could create mid-season periods with low floral resources for pollinators (Aldridge et al. 2011). The likelihood and impacts of mismatch could be underestimated if mid-season deficits in floral resources are ignored.

Increased voltinism expands the period of resource-requirements for pollinators in multiple peaks (Cartar & Dill 1990) but could mitigate pollinator-deficiency by ensuring pollinators are always present – a phenomenon seen during mild European winters (Stelzer et al. 2010). Fewer flights per year could create "gaps" where pollinators are absent, creating pollination deficits and reducing seed set.

Methods for addressing

To predict phenological responses of plants and pollinators to climate change, phenology should be linked with the physiological mechanisms that determine how species respond to environmental cues. Factorial experiments manipulating multiple cues (e.g. snowmelt, precipitation, temperature, and sunlight) in the field or microcosms can link cues with phenology (Dunne et al. 2003). Long-term data on phenological shifts of pollinating insects are needed to determine whether climate change is changing voltinism, or creating gaps between early and late-emerging pollinators. Meta-analyses should consider phenological shifts within subsets of communities (e.g. early versus late-flowering plants, or plants with different pollinators: e.g. Miller-Rushing & Primack 2008; Davis et al. 2010; Cook et al.

2012) to understand what drives overall trends (Bartomeus et al. 2011). Consequences of mid-season pollen deficits for box-nesting pollinators could be tested by experimentally forcing mid-season deficits in pollen availability where there normally are none (e.g. mowing fields or removing flowers). Impacts of naturally-occurring deficits could be tested if provisioning rates (the rate at which pollen is accumulated) of nesting bees are estimated at peak flowering for early and late species, and again in the mid-season trough in flower abundance. The impact of gaps in pollinator abundance could be estimated by passively estimating pollinator abundance (e.g. Malaise trapping, coloured pan traps), and repeating pollen-limitation experiments (bagging, and pollen-supplementation) during early, peak, and late-flowering (e.g. Ackerman 1989). Pollination gaps can be artificially induced by temporarily removing pollinators from field sites (e.g. Inouye 1978; Brosi & Briggs 2013) or microcosms (Fründ et al. 2012).

Assumption 4: Responses of plant and pollinator species to climate change will be independent for each species

Species may respond in a variety of ways to climate change, but what determines the response? Can responses be predicted, and can species with high risk of mismatch be identified? Some groups of species respond to similar cues, and are disproportionately affected by climate change in terms of shifting phenology and declining abundance (Willis et al. 2008; Davis et al. 2010; Bartomeus et al. 2013a). Related species are more likely to have similar physiology, and interact with the same mutualists. Responses to climate change might be correlated among species with similar traits (e.g. flowering time, diet breadth, body size) or phylogeny (Davis et al. 2010; Bartomeus et al. 2013a), but closely-related species can respond divergently (Miller-Rushing & Primack 2008; Elwood et al. 2012).

Syrphid flies tracked interannual phenological variation of flowers in the alpine over 20 years (Iler et al. 2013). European Lepidoptera feeding on deciduous woody vegetation responded to 150 years of climate warming with larger advancements in flight periods and smaller increases in number of flights per year than herbivores specializing on evergreen herbaceous vegetation (Altermatt 2010b). Stronger selective pressure is predicted to maintain high synchrony with hosts among insects feeding on woody vegetation because new leaves are all produced at once, and are chemically vulnerable for short, seasonal bursts (Altermatt 2010b). Importance of synchrony for pollinators, and consequences of mismatch, might similarly be related to duration of flowering. "Pulse" resources that are highly abundant for short periods of time can be distinguished from "press" resources, which are available with similar abundance for an extended time (Bender et al. 1984; Figure 1c). Selection on phenological schedules (and thus, likelihood of mismatch) might apply differently to pollinators that rely on early-spring "pulses" (e.g. species with one short-lived flower, or "mass blooming") versus late-season "presses" (e.g. species with multiple long-lived flowers) (Willmer 2011).

How it affects predicted consequences of mismatch

If ecologically important or diverse pollinators (e.g. *Bombus*) or plants (e.g. Rosaceae) have high risk of mismatch, or if responses of related species are correlated, the global impacts of mismatch may have been underestimated. If important pollinators or plants have lower risk of mismatch, the impacts of mismatch may have been overestimated. Depending on which species are prone to mismatch, there might be no extinctions, single-species extinctions (resulting from asymmetrical interactions), co-extinctions of paired mutualists (Memmott et al. 2004), or cascading co-extinctions (Koh et al. 2004).

Methods for addressing

Community-level simulations of mismatch (e.g. Memmott et al. 2007, Kaiser-Bunbury et al. 2010) and experimentally-induced mismatches (e.g. Rafferty & Ives 2011) should ideally use diverse communities (see Bartomeus et al. 2013b), be phylogenetically controlled, and consider life history traits (e.g. guilds, functional groups, pollination syndrome, or flowering time). However, the labour and expertise required for understanding effectiveness of all pollination interactions in terms of pollen delivery and contribution to reproduction of pollinators is enormous (e.g. Vázquez et al. 2005).

Assumption 5: All pollinators are similarly effective, and all plants offer similar resources to pollinators

If some species are more prone to mismatch than others, which species will have the greatest impacts when mismatches occur? Researchers are aware that effectiveness of pollination interactions varies among species, yet effectiveness is rarely considered with respect to consequences of mismatch (Willmer 2012). Most studies use frequency of interactions to estimate importance (Vázquez et al. 2005), and focus on pollinators that previous studies find most effective, such as *Bombus* (e.g. Wall et al. 2003; Thomson 2010) or hummingbirds (Waser 1979; McKinney et al. 2012). However, some plants can be disproportionately important, offering massive rewards to pollinators, saturating the pollinator community with floral resources, and possibly negating resource-limitation during that period (e.g. "cornucopian" flowers referred to by Mosquin 1971). Flies are generally less effective pollinators than bees per visit, but effectiveness varies among species; flies are important pollinators for plants adapted to fly-pollination, when bees are scarce, and at higher latitudes (Motten et al. 1981; Kearns & Inouye 1994; Kudo et al. 2004). Few studies consider how nectar and pollen from different species contribute to the total energy and proteins necessary for reproductive success of bees (but see Cartar & Dill 1990; Vázquez et al. 2005; Hoover et al. 2012), and to mating, nesting, and provisioning young.

Rafferty & Ives (2012) limited focal flowers to single visits by pollinators, and found that effectiveness of the same pollinating species varied throughout a season. The perceived consequences of mismatch could therefore vary depending on when they are measured. Species diversity could be important in maintaining pollination services if abundance and effectiveness varies within and among years (Mosquin 1971, Olesen et al. 2008). Demographic impacts of climate change could result from shifts in effectiveness as opposed to (or in addition to) frequency of interactions. Warming, elevating CO_2, and adding nitrogen to *Cucurbita* led to floral nectar compositions that attracted more bees, but provided lower-quality nectar, reducing bumble bees' survival despite increased visitation rates (Hoover et al. 2012). Conversely, some interactions could become more beneficial, but this possibility, and its potential to mitigate the effects of mismatch, has not been explored.

How it affects predicted consequences of mismatch

Mismatches could have greater impact if they affect disproportionately abundant or effective pollinators, or plants that offer disproportionately important or abundant floral resources. Counting all visits as effective or beneficial overestimates negative impacts of mismatch. Estimating effectiveness or abundance at one time (e.g. when most pollinators are relatively scarce, or when one species is most abundant) may overestimate or underestimate importance of that interaction, leading to biased estimates of the consequences of mismatch. Failing to consider disproportionately important plants or effective pollinators could underestimate impacts of mismatch if those plants or pollinators are prone to mismatch. The consequences of climate change could be underestimated if mismatches are compounded by reduced effectiveness of pollination interactions.

Methods for addressing

Ideally, studies on mismatch should use highly-specialized pollination systems (single-pair mutualisms, which often include morphological specialization) or high taxonomic resolution when monitoring visitation to verify that flower visitors are legitimate pollinators. Per visit effectiveness at pollen transfer, and floral fidelity, should be assessed. This can be done with controlled experiments allowing only single visits (e.g. Rafferty & Ives 2012), use of appropriate controls (comparing pollen-supplemented plants to plants with bagged and open pollination), inspecting pollen loads of species visiting flowers, and watching pollinators move among plants (Kearns & Inouye 1993; Proctor et al. 1996; Dafni et al. 2005; Brosi & Briggs 2013).

Assumption 6: Plant reproduction is pollen-limited, and pollinator populations are limited by availability of floral resources

How important is it that plants and pollinators avoid phenological mismatch? Negative demographic consequences of plant-pollinator mismatch are predicted by assuming reproduction of plants is pollen limited, and pollinator populations are limited by availability of floral resources (Miller-Rushing et al. 2010). However, few studies on phenological mismatch quantify pollen limitation of plants (Kameyama & Kudo 2009, Forrest & Thomson 2010; Thomson 2010; Rafferty & Ives 2012; Kudo & Ida 2013).

We could not find any studies that showed how pollen limitation or lack of floral resources resulting from mismatch affects recruitment of plants or pollinators.

Pollen limitation is affected by synchrony between flowering time and emergence or visitation rates of important pollinators of *Erythronium grandiflorum* (Thomson 2010) and other spring ephemerals (Kameyama & Kudo 2009; Kudo & Ida 2013). However, many studies show that pollen limitation is context-dependent (Burd 1994; Ashman et al. 2004; Dafni et al. 2005; Knight et al. 2005; Hegland & Totland 2008; Harder & Aizen 2010). Factors driving pollen limitation vary in space and time (e.g. Ehrlén 1992; Totland 2001; Dafni et al. 2005) and are frequently confounded with other forms of reproductive limitation (Kodric-Brown & Brown 1979; Dafni et al. 2005; Knight et al. 2005). Though pollen-supplementation sometimes increases seed set, many species have reproductive assurance through selfing (Knight et al. 2005), which could preclude pollen-limitation under mismatched conditions. Reproductive success of long-lived, perennial plants in matched (or "good") years might also compensate for reproductive failure in mismatched ("bad") years. Forgoing reproduction in favour of growth in years with poor conditions could increase later reproductive output, and conditions up to two years prior can affect fruit set (Krebs et al. 2009). Variation in reproductive success between years can explain the persistence of some plants in marginal habitats.

Inter-annual impacts of mismatch via pollinator recruitment have never been demonstrated in the field. However, availability of floral resources early in the flowering season can affect pollinator abundance (and therefore visitation rates) later in the season. The foraging success of early-emerging queen bumble bees affects quality and quantity of successive broods of workers (Bowers 1985, 1986). The leafcutting bee *Megachile* produces more and larger offspring after periods of abundant floral resources (Kim & Thorp 2001).

How it affects predicted consequences of mismatch

If availability of pollination or floral resources does not limit reproduction of plants or pollinators (or if other factors are more important as "limiting factors"), then consequences of mismatch might be overestimated (Bond 1994). Conversely, consequences of mismatch might be underestimated for sites or species that are frequently and severely pollen-limited. Early-season mismatch could cause negative effects on pollination later in the season by reducing within-season recruitment.

Methods for addressing

More studies are needed to understand interactions among local drivers of pollen limitation, and how pollen limitation affects recruitment. One approach would be measuring pollen limitation repeatedly across an altitudinal gradient at one field site, and monitoring how the pollinator community varies with abiotic conditions over space and time. Controls (e.g. bagging or pollen-supplementation)

should be used to test pollen-limitation during field studies that simulate mismatch. Verifying pollen-limitation for each study of mismatch is labour-intensive, but necessary. A strategy might be combining results of studies from researchers working simultaneously to answer different ecological questions at one intensively-studied location (e.g. RMBL, Colorado, USA). Conducting experiments using self-incompatible and/or dioecious plants, or obligate pollinators (e.g. syrphid flies) assures that there is a direct link between pollination interactions and survival or reproduction. Using annual species with short-lived seeds simplifies linking pollen limitation with lifetime fitness and recruitment.

Assumption 7: New mutualisms will not arise, and parasitism or antagonism will remain constant

If phenological mismatches occur in the future, the demographic consequences for plants and pollinators cannot be predicted without considering flexibility of interactions among species (Table 1; Figure 2e). Predicted consequences of phenological shifts emphasize reproductive declines through loss of mutualistic interactions (pollination and foraging) (Memmott et al. 2004, 2007; Kaiser-Bunbury et al. 2010), however reproductive increases due to loss of parasitic interactions are also possible. Phenological shifts may release plants from floral antagonists such as robbers of nectar or pollen, florivores, or seed-predators (Parsche et al. 2011). Phenological shifts may also separate pollinators from deceptive plants that offer no rewards, though deceptive plants might be predicted to shift along with rewarding "models". Conversely, antagonistic interactions may arise, which could decrease reproductive rates of "losing" partners (Liu et al. 2011).

Fewer extinctions are predicted when pollinators are allowed to switch food sources in simulated mismatch (Kaiser-Bunbury et al. 2010, but see Brosi & Briggs 2013). High species richness of pollinators ensures apples still receive visits from pollinators during peak flowering even when individual pollinator species shift their phenology at different rates (Bartomeus et al. 2013b). Dietary flexibility or "re-wiring" theoretically increases stability of pollination networks, with the caveats that (1) a baseline level of species diversity and abundance is needed to prevent networks from collapsing (Kaiser-Bunbury et al. 2010) and (2) pollination may decline with loss of a single species if it alters interactions in a way that decreases effectiveness (Brosi & Briggs 2013).

How it affects predicted consequences of mismatch

The negative consequences of mismatch are overestimated when potential for network re-wiring (formation of novel or restoration of historical mutualisms) is ignored, and when release from antagonistic interactions (thieving, robbing, herbivory, and deception) is ignored. Release from parasitic interactions (e.g. seed-predators) can compensate for reduced visitation by pollinators through a net increase in seed survival (Parsche et al. 2011). Conversely, population declines resulting from phenological shifts could be underestimated if deleterious interactions are

exacerbated. Declining efficacy of interactions and failure of networks to re-wire could increase the demographic impacts of phenological mismatch between plants and pollinators.

Methods for addressing

Experimentally forcing mismatches under field conditions can test whether species interaction networks re-wire. Identifying whether new species of pollinators visit artificially mismatched species, and then tracking the consequences for seed set, is a priority for future research (Rafferty & Ives 2011). Potential for network re-wiring might be tested using choice/no-choice experiments (Box 1). If pollinators are not exposed to systematically manipulated communities of available plants, their *preferences* are known, but which plants they could use under duress (i.e. natural or experimentally-induced mismatch) remain unclear. Studies should consider the balance of mutualisms and parasitisms faced by plants or pollinators under altered phenological scenarios predicted by climate change, or created through artificial mismatch.

Assumption 8: Changes to patterns of co-flowering or co-flight will not influence the effects of phenological mismatch

Biotic interactions (competition and facilitation) could affect the consequences of mismatch. Climate change is predicted to alter patterns of co-flowering or co-flight (Forrest et al. 2010), which might increase competition among plants for pollinators (Mitchell et al. 2009) or competition among pollinators for floral resources (Potts et al. 2010; Schweiger et al. 2010). However, it remains unclear to what extent vital rates of populations are limited by competition (Figure 2f). Co-flying pollinators that forage on different parts of flowers can be complementary, increasing seed set (Chagnon et al. 1993). Co-flowering plants can be facilitative, attracting shared pollinators (Waser & Real 1979; Thomson 1981; Rathcke 1983; Proctor et al. 1996; Mitchell et al. 2009) (Table 1; Figure 2f). Experimental removal of one pollinator species from subalpine study plots at RMBL affected competition, causing remaining pollinators to shift to more generalized diets (Brosi & Briggs 2013). Floral fidelity, efficiency of pollen transfer among flowers, and seed production of *Delphinium barbeyi* (Ranunculaceae) were reduced (Brosi & Briggs 2013). Relative density or abundance of plants and pollinators affects whether they compete or facilitate (Brown & Kodric-Brown 1979; Willmer 2011) but what if density remains constant? Identity, physiology, and behaviour (i.e. competitive ability) are important (Mosquin 1971), as are abiotic conditions. At high elevation (with increased wind, cold, and aridity), cushion plants are facilitators, attracting higher densities of pollinators (Reid & Lortie 2012), but competition is predicted to be more important under less harsh conditions.

How it affects predicted consequences of mismatch

If climate-driven phenological shifts increase competition or decrease facilitation between co-flowering plants or co-flying pollinators, the impacts of climate change may be underestimated. Conversely, if climate change decreases competition, or increases facilitation, the impacts of climate change may be overestimated. Climate change will affect abiotic conditions and may affect density of floral resources, which determine whether interactions are facilitative or competitive.

Methods for addressing

Most studies on facilitation in pollination communities have used two or three species, and examined effects of competition between native and invasive plants or pollinators (Kearns et al. 1998). This might emphasize good competitors rather than species likely to undergo phenological shifts. Mismatches have been experimentally induced using arrays of flowers (e.g. Rafferty & Ives 2011), or large enclosures with planted communities and added pollinators (e.g. Parsche et al. 2011). A next step would be manipulating density, abundance, and identity of flowers and pollinators (e.g. Brosi & Briggs 2013) to determine how these factors affect competition or facilitation.

Assumption 9: Phenotypic plasticity or evolution cannot mitigate the consequences of phenological mismatches

Can evolution or phenotypic plasticity of traits determining phenology for plants and pollinators prevent mismatches associated with climate change? Heritable variation and/or plasticity for the trait of flowering (e.g. Widén 1991) or emergence times, or for physiological responses to environmental cues, could enable species to cope with changing conditions. Species with potential for rapid evolution (Franks et al. 2007) could shift phenological schedules in response to changing phenology of species with which they interact (Visser 2008; Figure 2c). Mutualistic plants and pollinators are expected to respond adaptively to shifting phenology because of strong selective pressures to maintain synchrony (Augspurger 1981; Widén 1991). The concern is the rate at which microevolution can occur, not whether it will (Yang & Rudolf 2010; Gilman et al. 2012). Rates of microevolution are affected by population size and density, existing genetic diversity and variation in flowering or activity time, life history characteristics such as generation time and reproductive output, and strength of selection (Yang & Rudolf 2010; Gilman et al. 2012).

Some species might respond adaptively to climate change, while others might not. Species that responded plastically to warming experiments by advancing flowering times performed better (in biomass, percent cover, number of flowers, or growth) under warmer conditions (Cleland et al. 2012). Species that did not advance flowering performed worse under warmer conditions (Cleland et al. 2012), although reproductive success or recruitment were not assessed. Plants that had naturally advanced their flowering times to earlier in the season over 70 years in Wisconsin, USA did not suffer reduced visitation from pollinators under experimentally-induced mismatch (an artificial advancement); plants that had not historically advanced flowering received fewer visits under induced mismatch (Rafferty & Ives 2011). Hungarian orchids may have responded adaptively to climate change, since pollination

Box 1. Choice/no-choice experiments.

Choice/no-choice experiments have been used by behavioural ecologists for decades, and are fundamental in clarifying specialization with respect to trophic interactions (Johnson 1980). This tool is under-used in studies of plant-pollinator interactions. Figure 3 shows a simple choice/no choice experiment. The full range of possible trophic interactions among species cannot be assessed by field observations alone. Field observations are realized interactions, which may result from complex decision-making processes or tradeoffs, and represent foraging preferences under specific conditions. Long-term, high-resolution studies of pollination networks have been published that provide the basis for constructing models of plant-pollinator interactions (e.g. Bascompte et al. 2003, Memmott et al. 2004, 2007, Olesen et al. 2008, 2011). However, predictions generated by most models assume all possible interactions are considered. Separating obligate from facultative relationships is fundamental to predicting consequences of climate-driven mismatch between plants and pollinators; treating facultative relationships as obligate overestimates the negative consequences of mismatches.

Experiments like the one depicted in Figure 3 may appear logistically difficult for non-domesticated species. Nevertheless, presence or absence of flowering plants could be manipulated by placing plants from greenhouses into the field (e.g. Rafferty & Ives 2011), by transplanting flowers into "novel" situations and observing whether or not they are pollinated under mismatched conditions (e.g. Waser 1979), or by deliberately removing species or sets of species from a community (e.g. Inouye 1978; Brosi & Briggs 2013).

Moving one species at a time from a greenhouse to another location (a greenhouse with pollinators, or a field site) where only that species is blooming (enforceable by clipping or mowing) would represent a no-choice experiment for resident pollinators. Moving an array of species to the same setting would provide a choice. Using potted plants can control for density effects and provide a local source of pollen (e.g. Rafferty & Ives 2011). Here, the choice scenario (an array of species) would represent the phenological shift of an entire community of flowering plants, or a control in which no shifts occurred. The no-choice scenarios would indicate consequences of phenological shifts of a single species (to a time when all other plants were not blooming), or a shift of all other species resulting in availability of only one species for pollinators. Species could be "removed" temporarily by selectively pruning flowering heads over a given study area, which could simulate a no-choice scenario with a single remaining species. This could be compared to scenarios presenting the full range of choices for pollinators in sites (or plots) where no species (or only some) were pruned. Consequences of changes to species composition of flowering plant communities could be inferred by measuring the relative rates at which pollinators visit plant species under various scenarios. Resulting visitation rates or reproductive success could indicate consequences of phenological mismatch for pollinators and plants.

While it is more difficult to manipulate pollinator communities than it is to move plants, capturing and removing bumblebees to reduce their local abundance affects foraging behaviour of other species (Inouye 1978; Brosi & Briggs 2013), and bees introduced into flight cages of eight square metres apparently forage and behave normally (Fründ et al. 2012). Forrest & Thomson (2011) "transplanted" pollinating bees by moving nesting-boxes to different locations along an altitudinal gradient. Future experiments could use nesting-boxes warmed by incubators to alter emergence times. This could simulate a phenological response to climate change by the insects, the consequences of which could be measured by following success of individuals using the nesting boxes (suggested by Forrest & Thomson 2011). Individual bees have never been followed for long periods because of logistical constraints. This might be done using chemically marked (or individually genotyped) bees, which could re-nest in nest-boxes if their ranges for foraging or dispersal are small, or if they complete their life cycles in flight cages that contain nest boxes. Methods have also been developed for quantifying an animal's preference for one resource over others (see Roa 1992). Such methods could help predict the resilience of pollination networks to changes in synchrony.
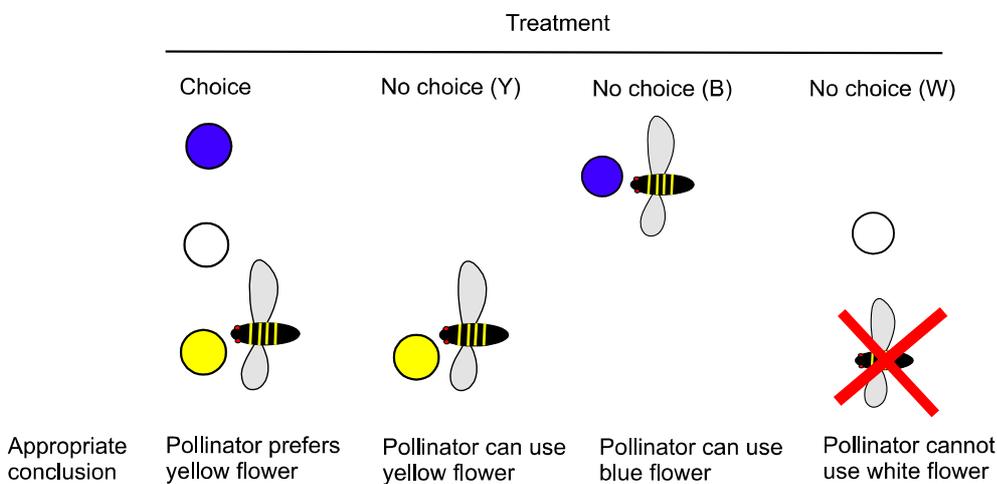
FIGURE 3. A simple choice/no choice experiment with four treatments. The pollinator is offered yellow (Y), blue (B), and white (W) flowers. This pollinator visits yellow flowers when all flowers are available. It could survive in the absence of yellow flowers IF blue flowers are available, but could not survive if only white flowers are available.

mechanisms (selfing, deceptive, or nectar-producing) seemed to explain the magnitude of phenological shifts over 50 years (Molnár et al. 2012). Self-pollinating species were more likely to advance flowering than insect-pollinated species, which would be predicted if advancement in flowering was constrained by flight times of insects (Molnár et al. 2012). However, no link was made to changes in phenology of pollinators with which the orchids interacted (Molnár et al. 2012).

How it affects predicted consequences of mismatch

The likelihood of mismatches may be overestimated if plants or pollinators are highly plastic for the traits that determine responses to changing cues (i.e. physiological responses), or if they rapidly and adaptively respond to changing conditions in ways that maintain synchrony.

Methods for addressing

Studies could observe reproductive fitness of individual plants over multiple years to determine the effect of plasticity in phenological responses to varying abiotic conditions (Forrest & Thomson 2010; Thomson 2010; Yang & Rudolf 2010). Phenological cues can be manipulated in the field or greenhouse (e.g. warming, watering, shading, or transplant experiments; Dunne et al. 2003) to assess plasticity or heritable variation in responses to cues for phenology. Applying multiple treatments to the same individuals or using common garden experiments can separate plasticity from heritable variation. Population-genetic studies are needed to determine heritability of traits that could facilitate rapid evolution of phenology in plants and pollinators. Working with short generation times (e.g. annual plants with many seeds) improves chances of detecting evolutionary change. Comparing reproductive success between past genotypes stored in the form of propagules, and individuals from the present (e.g. Franks et al. 2007) could test whether adaptive shifts are occurring.

CONCLUSION

Demographic consequences of mismatched plant-pollinator interactions remain unclear, but this is a new and fast-moving area of research. There is evidence that plant-pollinator mismatch is not fully or accurately described by dates of first-flowering or activity (Forrest & Thomson 2010), that the range of species and community responses to climate change is poorly understood (Diez et al. 2012), and that these responses tend not to be random or independent among species (Rafferty & Ives 2011). Populations of plants and pollinators are regulated by processes besides the frequency of their interactions: *effectiveness* of interactions is the best measure of pollination success, but it is difficult to measure (Rafferty & Ives 2012).

Further, plant populations are not always limited by pollination, and pollinators are not always limited by food. Pollen limitation of reproduction due to competition and facilitation is context-specific (e.g. Harder & Aizen 2010), and not all interactions are equally beneficial (e.g. Wall et al. 2003). Negative demographic consequences of mismatch

might be mitigated by phenotypic plasticity and adaptive evolution of phenology, generalization, properties of pollination networks (specifically, their nested, asymmetrical structure), habitat heterogeneity combined with dispersal ability, and the emergence of novel (or restoration of ancient) interactions. Pollination ecologists are poised to make important discoveries as all these assumptions are examined. Although the potential consequences of plant-pollinator mismatches may be enormous (Steffan-Dewenter et al. 2005), it is encouraging to note that there are many ways in which negative effects of mismatch might be mitigated. Because these have not been studied in sufficient detail, there may still be good news to keep us humming along.

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