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Experimental shifts in exotic flowering phenology produce strong indirect effects on native plant reproductive success

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Abstract

1. By causing phenological shifts that vary among species, climate change is altering time envelopes for species interactions, often with unexpected demographic consequences. Indirect interactions, like apparent competition and apparent facilitation, are especially likely to change in duration because they involve multiple interactors, increasing the likelihood of asynchronous phenological shifts by at least one interactor. Thus, we might observe ecological surprises if intermediaries of indirectly interacting species change their mediating behaviour.
2. We explored this possibility in a plant–pollinator community that is likely to experience asynchronous phenological shifts. We advanced and delayed the flowering phenology of two ubiquitous exotic plants of western Washington prairies, *Hypochaeris radicata* and *Cytisus scoparius*, relative to seven native perennial forb species whose phenologies remained unmanipulated. These species interact indirectly through shared pollinators, whose foraging behaviour influences plant reproductive success. We quantified impacts of experimental phenological shifts on seedset, pollinator visitation rates and visiting pollinator composition relative to an unmanipulated control. We first verified that unmanipulated indirect interactions between native and exotic plants were strong, ranging from facilitative to competitive.
3. Seedset of native plants was strongly affected by changes in exotic flowering phenology, but the magnitude and direction of effects were not predicted by the nature of the original indirect interaction (facilitative vs. neutral vs. competitive) or the change in interaction duration. The relationship between pollinator visitation and seedset changed for most species, though changes in pollinator visitation rate and pollinator composition were not as widespread as effects on native seedset.
4. **Synthesis.** Changes in pollinator foraging behaviour in response to changes in available floral resources are probably responsible for the unexpected effects we observed. Asynchronous phenological shifts have the potential to produce large and unexpected effects on reproductive success via indirect interactions.

KEYWORDS

climate change, exotic, indirect interaction, mismatch, neighbourhood effect, phenological shift, phenology, plant–pollinator interaction

1 | INTRODUCTION

Climate change is temporally reshuffling interactions between organisms (e.g. Burkle, Marlin, & Knight, 2013; CaraDonna, Iler, & Inouye, 2014; Theobald, Breckheimer, & HilleRisLambers, 2017), including groups of species that interact indirectly. Indirect interactions such as apparent competition and apparent facilitation can have important demographic and community-structuring consequences (Bonsall & Hassell, 1997; Holt & Lawton, 1994; Martinsen, Driebe, & Whitham, 1998; Orrock, Witter, & Reichman, 2008; Schmidt & Ostfeld, 2008). Given variation in phenological shifts among species, interaction time envelopes (the duration and timing of co-occurrence of interactors) are especially likely to change for indirect interactions, which involve multiple species. Yet we still know little about how phenological shifts will influence indirect interactions, and to what degree there are likely to be demographic impacts.

Previous work has demonstrated that phenological shifts frequently differ *between* trophic levels (Thackeray et al., 2010, 2016), and there is ample documentation of strong effects on

direct interactions like those between consumer and resource species (e.g. Both, Asch, Bijlsma, Burg, & Visser, 2009; Domis, Mooij, Hulsmann, Nes, & Scheffer, 2007; Ozgul et al., 2010; Post & Forchhammer, 2008). Variation *within* trophic levels (of the kind leading to altered indirect interactions) is less studied, yet no less likely. Observed climate-induced phenological shifts vary considerably within insect, plant and fungal communities (Bartomeus et al., 2013; CaraDonna et al., 2014; Fitter & Fitter, 2002; Kausarud et al., 2012; Willis et al., 2010). In addition, experiments that manipulate global change factors (e.g. temperature, CO₂, moisture) have documented wide variation in the magnitude and direction of phenological responses by plants (Cleland, Chiariello, Loarie, Mooney, & Field, 2006; Sherry et al., 2007). Since apparent competitors or facilitators are often controphic, variation in phenological responses within trophic levels increases the potential for changes in indirect interactions.

When interactors shift phenology at different rates, the interaction time envelope is altered, setting the stage for changes in outcomes (Figure 1a). For *direct* interactors, the effect of altering interaction time envelopes depends on at least two factors: the nature

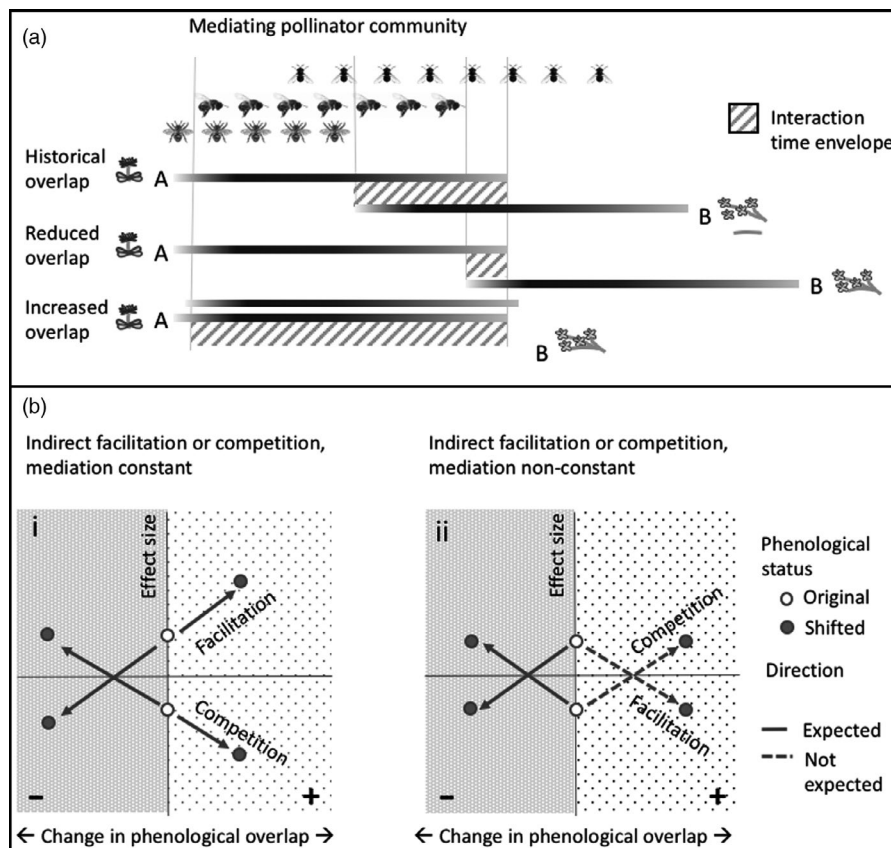


FIGURE 1 (a) Change in the time envelope for indirect interaction by phenological shifting of one interactor. Top panel shows hypothetical changes in relative phenological relationships of indirectly interacting plant species A and B and the pollinators that mediate the interaction. Length of bars shows duration of flowering phenology and shading of bar indicates floral abundance. With species A phenologically static, a shift by species B can alter the community of mediators for the interaction and create novel relative abundances of A and B that could change mediator behaviours (e.g. foraging decisions). (b) Hypothetical changes to the effect on one interactor when interaction time envelope is changed by phenological shifting. Open circles denote effect of the original (historical) relationship; shaded circles denote the effect of the relationship after an increase or reduction in interaction time duration. (i) Effects on indirect mutualists or indirect competitors when mediation by the third species remains constant over time; (ii) Potential nonlinear effects on indirect mutualists or indirect competitors when mediation is not constant over time

of the original interaction (i.e. consumer/resource, competitive or facilitative) and the magnitude and direction of change in overlap duration. The result of changing an *indirect* interaction time envelope depends on these factors plus a third: the degree to which the phenological change alters the availability and behaviour of the species that mediates the interaction (Figure 1b). Regardless of altered availability of the mediating species, altered mediating behaviour could change the strength and/or sign of the indirect relationship. Thus, asynchronous phenological shifts are likely to lead to effects on indirect interactions.

Native and exotic plants and their shared pollinators are an appropriate system in which to explore this possibility. First, interactions mediated by shared pollinators can strongly affect plant reproductive success (Kandori, Hirao, Matsunaga, & Kurosaki, 2009; Traveset & Richardson, 2006; Waters, Eshe, & HilleRisLambers, 2014). One plant species can exert indirect competitive or facilitative effects on another plant species by affecting pollinator foraging choices, thereby altering seedset (Goodell & Parker, 2017; Moeller, 2004; Morales & Traveset, 2009). Second, changes in the duration of native/exotic flowering overlaps are likely as the two plant interactors shift at different rates with warming. For example, exotic plants tend to shift their flowering phenology in response to climate more readily than native plants (e.g. Willis et al., 2010; Wolkovich et al., 2013; Zettlemoyer, Schultheis, & Lau, 2019), and many exotic plant species expanding into new ranges show phenological flexibility in flowering time across latitudinal gradients (Dlugosch & Parker, 2008; Montague, Barrett, & Eckert, 2008; Weber & Schmid, 1998) or generally greater phenotypic plasticity (Davidson, Jennions, & Nicotra, 2011). Finally, both compositional and behavioural changes in mediating pollinators are likely, because pollinator community composition changes seasonally, and many pollinators tailor foraging behaviours to the composition and density of floral resources (Jha & Kremen, 2013; Kunin, 1997; Stout, Allen, & Goulson, 1998). Asynchronous phenological shifts of plants alter the suite of floral resources available at a given time point (Figure 1a), so foraging decisions are likely to change. For all of these reasons, native and exotic insect-pollinated plants are indirect interactors that may (a) experience future changes in interaction time envelopes, (b) experience differences in the composition or behaviour of the mediating pollinator community and (c) respond with changes in reproductive output that could have demographic consequences.

We used a native/exotic plant–pollinator system to explore how asynchronous phenological shifts may affect the strength and direction of indirect interactions. We did this by manipulating the phenology of the exotic plant species and examining the effect on pollinator-mediated interactions with multiple native plants. Specifically, we asked how (a) native seedset, (b) the rate of pollinator visitation to native plants and (c) the composition of pollinators visiting native plants were altered by the phenological shifts of co-occurring exotic plants. Our hypothesis was that the effects of asynchronous shifts depend on the sign of the existing indirect interaction and changes in interaction time envelopes. For example, when a native/exotic plant interaction was competitive, we expected that increasing the interaction time envelope (through advancing or

delaying exotic phenology) should lead to lower pollinator visitation, fewer shared pollinators and lower seedset for natives (Figure 1bi). Using identical logic, we expected that when the original native/exotic plant interaction is facilitative, increasing the interaction period should lead to higher pollinator visitation, more shared pollinators and higher seedset for natives (Figure 1bi). Alternatively, the interaction sign and change in interaction period might be insufficient to predict the direction of change if mediating organisms change in abundance or behaviour (Figure 1bii). In this case, changing phenology of one interactor could produce novel effects (new interactions between species that have not previously overlapped) or emergent effects (when a change in existing overlap duration produces an unexpectedly large change in interaction strength).

2 | MATERIALS AND METHODS

2.1 | Study site and species

We explored the effect of flowering phenology on pollinator-mediated indirect interactions in a Puget Trough prairie (western Washington, USA). Many exotic forbs in this system flower later than the majority of natives, (S. Waters, unpubl. data), so advancing exotic phenology would produce new phenological overlaps between native and exotic flowers and result in novel choices for pollinators. We focused on two widespread exotic prairie species, *Cytisus scoparius* (Fabaceae) and *Hypochaeris radicata* (Asteraceae). *Cytisus scoparius* is a European shrub that flowers for 3–4 weeks beginning in May. Flowers can be handled only by heavy-bodied bees (e.g. *Bombus* spp., *Apis mellifera*) and provide pollen but no nectar reward (Parker, 1997). *Hypochaeris radicata* is a dandelion-like forb that begins to bloom in early June, continuing for 5–6 weeks. Its flowers provide nectar and pollen rewards and are visited by a wide assortment of solitary bees, bumblebees, honeybees and flies (S. Waters, unpubl. data).

We examined pollinator-mediated interactions between these exotic species and seven common native forbs with a diversity of floral traits, whose peak flowering phenology ranges from April to July (Figures S1 and S2): *Ranunculus occidentalis* (Ranunculaceae), *Camassia quamash* (Liliaceae), *Microseris laciniata* (Asteraceae), *Lupinus lepidus* (Fabaceae), *Eriophyllum lanatum* (Asteraceae), *Prunella vulgaris* (Lamiaceae) and *Campanula rotundifolia* (Campanulaceae). Six of the native forbs are known to share pollinators with *H. radicata*, and five share pollinators with *C. scoparius* (S. Waters, unpubl. data).

2.2 | Experimental design

We established forty-eight 5 × 5 m plots in Glacial Heritage Preserve in Littlerock, Washington. Plots were organized in a randomized block design, with eight blocks each containing one plot for each of six phenology treatments. Within blocks, plots were randomly located, with the constraint that they must contain at least six naturally occurring

individuals of each of the native species. While other forb species were present in plots, they never occurred at high densities relative to focal species (Figure S3). Naturally occurring *C. scoparius* was absent from all plots, and naturally occurring *H. radicata* was present in all plots. We established plots to be at least 10–16 m apart, to reflect foraging neighbourhoods (floral patches) that are probably treated as distinct by most pollinators at our location (Jakobsson, Lazaro, & Totland, 2009; Waser, 1986); plots are not separated by enough distance to represent non-overlapping pollinator communities.

Control plots were unmanipulated, while flowering greenhouse-grown potted exotic plants were placed in experimental plots. Management actions had largely removed *C. scoparius* from the surrounding plant community, so the potted plants represented a 'reinvasion' for *C. scoparius*, while for *H. radicata*, treatments amplified an existing invasion. Pots were placed with the desired timing ('Ambient', 'Advanced' and 'Delayed'), to impose phenological treatments (1 potted *C. scoparius* shrub = 152 ± 23 flowers added, or four pots of large *H. radicata* = 56 ± 4 capitulas added; Figure S4). There were thus two kinds of controls: exotic absent and exotic present with 'ambient' timing. The appropriate control is different depending on the species pair: for native species that had no initial flowering overlap with the neighbouring exotic, the appropriate comparison is exotic absent (control) versus 'Advanced' or 'Delayed' exotic phenology. By contrast, the appropriate comparison for plants that already overlapped with the exotic (before manipulation of exotic phenology) would be 'Ambient' exotic phenology versus 'Advanced' or 'Delayed' exotic phenology. Example sets of treatments for species that do and do not have initial flowering overlaps with the focal exotic species are shown in Figure S1.

Using potted plants allowed us to isolate pollinator-mediated effects from direct competitive/facilitative effects that occur below-ground. Pots were typically at least ~0.75 m away from focal native individuals, so shading was minimal. In the absence of specific predictive information on phenological shifting by these exotic species, we chose a shift that would be large, but likely within the scope of possible future change. Wolkovich et al. (2013) found up to ~10 days of phenological advance had occurred in exotic plants, while Lindh, MacGahan, and Bluhm (2018) detected ~2.5 days advancement per decade since 1958 and Reed et al. (2019) found up to ~25 days of advancement in some forb species in a warming experiment in Pacific Northwest prairies. We therefore altered exotic phenology by adding pots at the onset of the species' natural flowering at nearby sites for Ambient treatments, ~3 weeks before ambient flowering for Advanced treatments, or ~3 weeks later than ambient flowering for Delayed treatments. We were unable to delay flowering of *C. scoparius*, so the Delayed treatments were used only for *H. radicata*. Note that in addition to manipulating presence/absence and timing of flowering, these treatments also affect the total floral density of the neighbourhood.

2.3 | Measurements

We quantified seedset of three individuals of each focal native species within plots, representing three phenological stages to capture

phenological spread in the native population: Early (first individuals of the species to bloom in plot), Peak (blooming during maximum conspecific floral density) and Late blooming (site wide, >80% of conspecifics with mostly senescing flowers). We selected only plants that were estimated to be in 'full bloom' (i.e. bearing multiple flowers/inflorescences), haphazardly chose one newly opening inflorescence on each of these individuals and bagged the inflorescence when it had senesced to ensure seed capture. To quantify pollinator dependence, we also excluded pollinators on one additional individual of each native species using a breathable bag, and collected seed after senescence. When counting seed from pollinator-excluded and naturally pollinated flowers, we also recorded evidence of pre-dispersal seed predator activity that might reduce seed counts (insect presence or seed residues).

We observed pollinator visitation to each focal native species three times per plot per plant species during the bloom season (=24 observations per plant species per treatment)—early, peak, and late. Observations were performed for 15 min on sunny days $\geq 15.5^\circ\text{C}$. Visiting insects were netted in sites once a week for 3 weeks and preserved in reference collections; specimens were classified into visually recognizable morphospecies, and further observations used these morphospecies designations without collecting specimens. We counted visits to the focal native individuals, identified each visitor and recorded the number of conspecific floral units (flowers or inflorescences) within the 1×1 m subplot where the focal plants were located to quantify floral patch size. Visits were counted only if there was contact between the visitor and flower stigmas or anthers. We surveyed floral richness and abundance biweekly in all plots as a covariate, by counting open inflorescences in six randomly chosen 1×1 m subplots per 5×5 m plot.

2.4 | Analysis

We analysed native species individually, since each species was exposed to a different subset of exotic phenological treatments. Four native species (*M. laciniata*, *E. lanatum*, *P. vulgaris* and *C. rotundifolia*) overlapped with altered phenology treatments for only one exotic species, while three (*R. occidentalis*, *C. quamash* and *L. lepidus*) overlapped with both.

2.4.1 | Pollinator dependence and pre-dispersal seed predation

We first verified that seedset for each native species was pollinator dependent by comparing seedset in pollinator exclusion and pollinator open treatments. We tested the seedset response variable for over-dispersion and zero inflation by fitting a series of null models with varying distributions, with and without zero inflation term, in the GLMMTMB package in R (Brooks et al., 2017). Comparing AIC values of these null models led to selecting zero-inflated Poisson GLMs. Further comparison of glms with glmers that included block as a random

effect led to selecting null models (glmers) that included block. We then compared this null with alternative models (which included pollinator treatment). We accounted for the effect of pre-dispersal seed predation by adding a binary variable to these models ('infested'; presence or absence of an insect or damaged seeds inside collected seed bags). All seedset data, including data from inflorescences that were bagged to exclude pollinators, were included in the tests of pollinator exclusion and pre-dispersal seed predation effects. For all other tests, pollinator exclusion replicates were excluded. To test whether pre-dispersal seed predation itself was responding to phenology treatments (thereby affecting our ability to detect any phenology treatment-sensitive pollination effects), we modelled infestation (yes/no) as a function of phenology treatment, with binomial glms. In this and all cases, we performed model selection on nested null and alternative models using likelihood ratio tests and compared AIC values to choose the best-fit model.

2.4.2 | Phenology treatments and seedset

We tested whether seedset for each native varied in response to exotic phenology treatment (Ambient/Advanced/Delayed) using zero-inflated Poisson glms with block as a random effect. We included native phenology status (Early/Peak/Late) and infestation (yes/no) as additional explanatory variables and compared a series of nested null and alternative models using AIC. We used post hoc Tukey multiple comparison tests to test for individual effects of treatment levels. Model selection was complicated by the fact that some native–exotic treatment combinations were relevant only for a phenological subset of natives in the control. We therefore performed two parallel analyses: (a) using all native plant data (relevant to population-level responses); (b) including only native plants at phenological stages present in all treatments being compared (e.g. if data from Early, Peak and Late natives were available in the control plots, but only Early overlapped with exotic flowers in the Advanced treatment plots, we included only Early when comparing the two treatments). These phenologically equivalent native cohorts were nevertheless overlapping with a different stage of exotic bloom in different treatments. We report both results in Table S4, but focus on the analysis of the full dataset in the remainder of our discussion, since exotic phenology treatment remained significant in both analyses. We used Benjamini–Hochberg adjustments to correct post hoc *p* values for separate tests of exotic phenology effects on multiple species (Waite & Campbell, 2006).

We used Fisher's exact test to assess whether the sign of the change in seedset for each realized native–exotic pair was in the expected direction (i.e. extending the duration of facilitative relationships increases seedset).

2.4.3 | Phenology treatments and pollinator activity

We used zero-inflated Poisson glms with block as a random effect to test whether the number of pollinator visits to a native species

during an observation varied in response to exotic phenology treatments. We used the zero-inflated Poisson structure based on comparison of null models that varied in distribution and inclusion or exclusion of a zero inflation term, as described above. Patch size for observed individuals, conspecific floral density and heterospecific floral density were included as covariates to distinguish phenological effects from the effects of floral abundance. For conspecific and heterospecific floral density, floral counts were averaged for each plot on each observation date, over six 1 × 1-m subsamples. We used likelihood ratio tests to ascertain the best-fit model from nested models via AICs and used post hoc Tukey multiple comparison tests to test for individual effects of phenology treatment levels. Again, we used Benjamini–Hochberg adjustments to correct *p* values for separate tests on multiple species (Waite & Campbell, 2006).

In three native–exotic pairings (*L. lepidus*/Advanced *C. scoparius*, *P. vulgaris*/Advanced *H. radicata* and *M. laciniata*/Advanced *H. radicata*), unseasonably cold weather and a short duration of native–exotic overlap resulted in an inadequate number of observations for analysis of visitation. These pairs were still included in seedset analyses as described above.

To examine the effect of the same variables and covariates on composition of pollinator assemblages visiting a given native species, we performed perMANOVAs, using Bray–Curtis distance measures to accommodate pollinator richness differences between samples. We standardized visits by each visitor type to a proportion of the total visits per plot and relativized pollinator types by pollinator morphospecies maxima (by setting the maximum morphospecies value in the column to 1 and converting all other values proportionally to a value between 0 and 1). Because many plots received zero visits during observations, we added a dummy species with a value of 1 to each plot to ensure a non-zero denominator. We created models with factors in all possible orders to determine whether sequential sums of squares influenced the significance level of any of our explanatory variables and performed 9,999 permutations. Finally, we used zero-inflated Poisson glms to examine the effect of phenology treatment on the relationship between visitation and seedset and included infestation (yes/no) as a covariate. Data were limited to species for which visitation data were adequate (see above). We performed model selection of nested models with AIC and used post hoc Tukey multiple comparison tests to test for individual effects of treatment levels. We also used Benjamini–Hochberg corrections in this case.

3 | RESULTS

All native forb species showed strong dependence on pollination for seedset (Table S2). Pre-dispersal seed predation had a significant impact on measured seedset for four species, but was not related to phenology treatment (Tables S2 and S3).

Cytisus scoparius and *Hypochaeris radicata* both interacted indirectly with focal native forbs before phenological manipulation, via facilitative indirect effects on some species and competitive indirect

effects on others. The effect of *C. scoparius* on co-flowering native forbs was facilitative or neutral, with seedset of *L. lepidus* and *C. quamash* increasing in Ambient *C. scoparius* plots over control plots (which did not contain *C. scoparius*; Figure 2a). *Hypochaeris radicata* reduced seedset of *E. lanatum* in Ambient plots, increased seedset of *M. laciniata*, *P. vulgaris* and *C. rotundifolia*, and did not affect *L. lepidus* (Figure 2b).

Altering *C. scoparius* and *H. radicata* flowering phenology led to four kinds of outcomes for native seedset among the 10 native–exotic species pairs that could be compared (Table 1; Figure 2): (a) emergent indirect effects, where native species originally flowered synchronously with one of the exotic species, but did not show any measurable effect on seedset until exotic phenology was shifted (three native–exotic species pairs); (b) novel indirect effects, where native species did not originally flower synchronously with an exotic species, but showed a response in seedset when exotic phenology was shifted (one native–exotic species pair); (c) reversals, loss or change in strength of indirect effects (four native–exotic species pairs) and (d) no effect (three native–exotic species pairs). For example, advancing *H. radicata* flowering produced an emergent indirect effect in *L. lepidus*, which typically blooms earlier than *H. radicata* but overlaps with it later in the season. Shifting *H. radicata* earlier increased flowering overlap, with a significant increase in *L. lepidus* seedset (Figure 2; Table 1). A similar emergent effect (though a decrease) occurred in *R. occidentalis* when *C. scoparius* flowering was advanced. Advancing *H. radicata* also produced novel

indirect effects when a novel temporal overlap was created between *H. radicata* and *C. quamash*. Seedset was reduced for *C. quamash* in comparison with control plots (Figure 2; Table 1). Advancing *C. scoparius* and *H. radicata* also strengthened or weakened indirect effects on *C. rotundifolia*, *L. lepidus*, *M. laciniata*, *P. vulgaris* and *E. anatum* (Table 1). Finally, exotic phenology shifts did not alter native seedset in all cases; for example, the novel overlap between *H. radicata* and *R. occidentalis* produced no change in *R. occidentalis* seedset (Table 1).

Pollinating insects also changed visitation patterns in response to exotic phenology treatments for some species, but not all. Conspecific and heterospecific floral density helped explain variation in overall pollinator visitation rate in four of the eight native–exotic pairs with adequate visitation data; in three of these pairs, phenology treatment added significant explanatory power, suggesting that visitation was influenced by both changes in native floral density over time and the novel exotic timing (Table S6; Figure S5). In addition, the slope of the relationship between pollinator visitation and seedset changed for four of the eight pairs (Table 2; Table S5). The relationship was strengthened for some species pairs (suggesting improved average effectiveness of pollinating visits) and weakened for others (Table 2). We did not detect relationships between exotic phenology treatments and overall visiting pollinator composition (with the exception of *P. vulgaris*, for which the effect size was small; Table 2).

Changes in native/exotic overlap duration (interaction period) were not accompanied by proportional changes in native seedset,

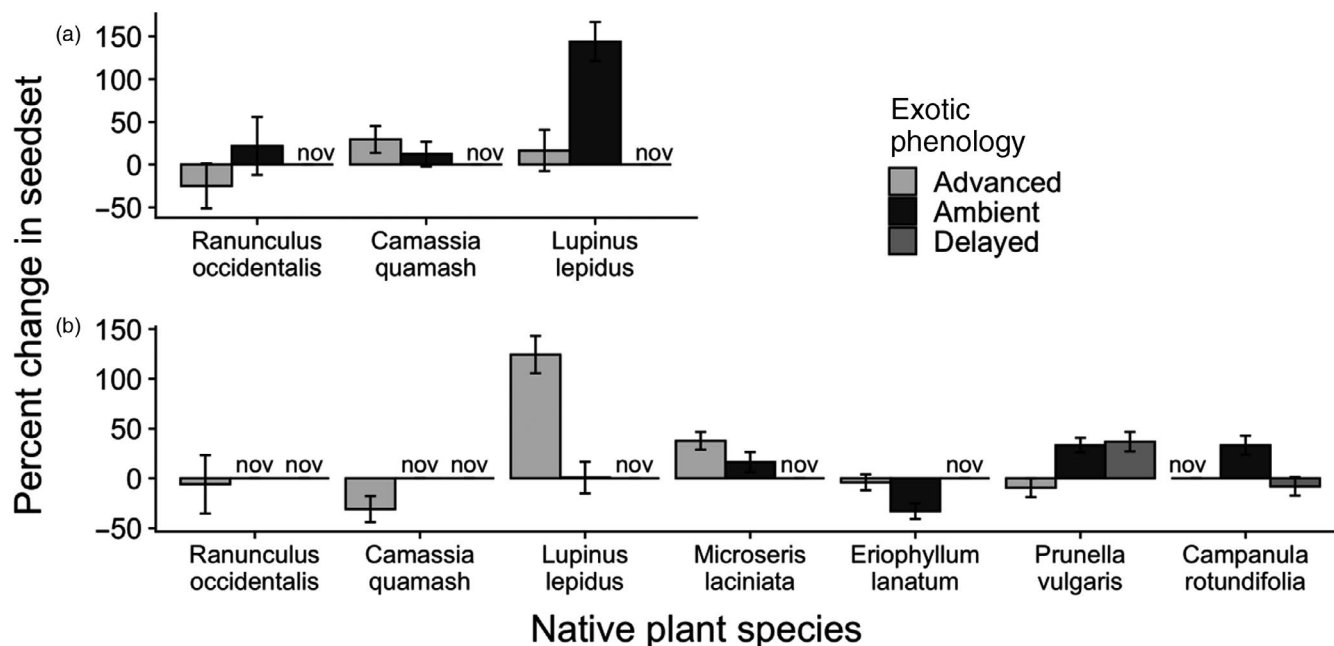


FIGURE 2 Mean percent change in seedset of seven native forbs (early, peak and late-blooming individuals pooled) in the presence of neighbouring exotic species (a) *C. scoparius* or (b) *H. radicata*, compared to seedset in exotic-absent plots (zero line). Percent change in seedset is shown when exotic flowering phenology is experimentally advanced or delayed, versus timed in synchrony with ambient (unmanipulated) exotic flowering (native forbs: *Ranunculus occidentalis* (RANOCC), *Camassia quamash* (CAMQUA), *Lupinus lepidus* (LUPLEP), *Microseris laciniata* (MICLAC), *Eriophyllum lanatum* (ERILAN), *Prunella vulgaris* (PRUVUL) and *Campanula rotundifolia* (CAMROT). Error bars represent 95% confidence intervals for the difference between means (treatment and control). nov: no overlap in flowering between the native species and the exotic phenology treatment

TABLE 1 Types and magnitudes of effects on native plant seedset when flowering phenology of neighbouring exotic plants is shifted. Native species are listed in order of flowering onset. Bold values are significant to $p < 0.05$ according to Tukey post hoc tests on mixed effects models of the impact of exotic phenology treatments on native seedset. Forbs are listed phenologically within each category

Type of effect	Native species	Exotic species	Shift in exotic phenology	Effect of shifted-exotic versus ambient exotic phenology		Effect of shifted-exotic versus control (native only, no exotic)	
				Percent change in native seedset	p	Percent change in native seedset	p
Novel indirect effect: Native and exotic species bloom synchronously for the first time	<i>C. quamash</i>	<i>H. radicata</i>	Advanced	NA	NA	-36.8	<0.02
Emergent indirect effect: Native and exotic species currently bloom synchronously, but did not show any interaction until exotic phenology was shifted	<i>R. occidentalis</i>	<i>C. scoparius</i>	Advanced	-48.4	0.006	-28.7	0.33
	<i>L. lepidus</i>	<i>H. radicata</i>	Advanced	79.9	<0.001	80.8	<0.001
	<i>P. vulgaris</i>	<i>H. radicata</i>	Delayed	38.3	<0.001	31.5	<0.001
Loss, reversal or change in strength of existing indirect effect	<i>L. lepidus</i>	<i>C. scoparius</i>	Advanced	-73.7	<0.001	15.2	0.353
	<i>M. laciniata</i>	<i>H. radicata</i>	Advanced	16.8	<0.014	-32	<0.001
	<i>E. lanatum</i>	<i>H. radicata</i>	Advanced	35.9	<0.001	4.1	0.643
	<i>C. rotundifolia</i>	<i>H. radicata</i>	Delayed	37.2	<0.001	-8.3	<0.380
No effect	<i>C. quamash</i>	<i>C. scoparius</i>	Advanced	-14.2	0.351	-25.8	0.059
	<i>P. vulgaris</i>	<i>H. radicata</i>	Advanced	-5.7	0.643	-10	0.28
	<i>R. occidentalis</i>	<i>H. radicata</i>	Advanced	NA	NA	-6.1	0.722

Note: NA: These native forbs did not flower simultaneously with exotic forbs until experimental manipulation of exotic flowering phenology.

TABLE 2 Impacts of exotic phenology treatments on pollinator visitation to six^a (of seven studied) native forb species. Effects of shifted-exotic phenology on assemblages of pollinator morphospecies foraging on native species were evaluated with perMANOVA (R^2 and p -values based on 999 permutations). Effects of shifted-exotic phenology on the relationship between pollinator visitation rate and seedset of native species were evaluated with a Tukey post hoc test of linear mixed effects models with exotic phenology treatment as a fixed effect. Bold values are significant to $p < 0.05$

Native species	Relevant overlapping exotic species	Phenology treatments compared	perMANOVA R^2	perMANOVA p	Visitation-seedset slope (ambient)	Visitation-seedset slope (shifted)	p for change in slope
<i>R. occidentalis</i>	<i>H. radicata</i>	Advanced, Native control [new overlap]	0.05	0.063	1.68	1.65	0.848
<i>C. quamash</i>	<i>H. radicata</i>	Advanced, Native control [new overlap]	0.04	0.375	2.57	1.98	<0.001
<i>L. lepidus</i>	<i>H. radicata</i>	Advanced, Ambient	0.07	0.189	2.15	3.77	<0.001
<i>E. lanatum</i>	<i>H. radicata</i>	Advanced, Ambient	0.05	0.526	3.78	3.91	<0.249
<i>P. vulgaris</i>	<i>H. radicata</i>	Delayed, Ambient	0.09	0.005	4.37	4.73	<0.001
<i>C. rotundifolia</i>	<i>H. radicata</i>	Delayed, Ambient	0.02	0.838	3.90	2.83	<0.001
<i>R. occidentalis</i>	<i>C. scoparius</i>	Advanced, Ambient	0.05	0.093	2.00	1.56	0.160
<i>C. quamash</i>	<i>C. scoparius</i>	Advanced, Ambient	0.01	0.898	2.47	3.25	0.066

^aOne native forb, *M. laciniata*, does not appear because a short flowering duration led to an inadequate number of pollinator observations for analysis, although seed data were collected.

although our ability to detect a pattern was limited because the number of interactions was small (Figure 3; Fisher's exact test, $n = 9$, odds ratio = 8.355, $p = 0.206$). Specifically, seedset of focal native

species that competed with exotics neither consistently benefited from a decreased phenological overlap nor consistently suffered from increased phenological overlap, though results trended in that

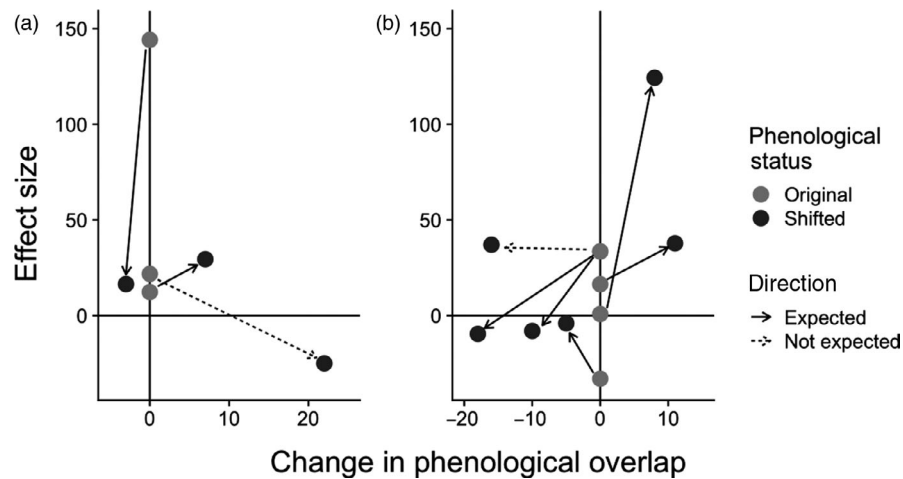


FIGURE 3 Effect sizes of changes in native forb seedset as a function of experimentally induced changes in duration of synchronous flowering with (a) exotic *C. scoparius*, (b) exotic *H. radicata*. Flowering phenology overlaps with each exotic plant species are shown for seven native plant species (realized only for a subset of the seven with respect to each exotic species; novel overlaps not shown). An effect size of zero represents no difference from native seedset in control plots. Light grey points represent native seed production under ambient exotic phenology; a y value different from zero indicates a competitive (if negative) or facilitative (if positive) original effect of the exotic plant on native seedset. Dark grey points show changes in flowering phenology overlaps and effect sizes when exotic flowering phenology is experimentally advanced or delayed. Dotted lines indicate results that did not conform to the expected direction of changes in seedset given the original sign of the interaction, including positive or negative changes if the original interaction was neutral

direction. Similarly, seedset of native species initially facilitated by exotics did not consistently benefit from increased overlap or consistently suffer from decreased overlap (Figure 3).

4 | DISCUSSION

Our results suggest that asynchronous phenological shifts, as expected with climate change, could have large and diverse effects on plants in this system. Native and exotic plant species interacted indirectly both competitively and facilitatively, and altering the time envelope for interaction led to a wide range of effects on native seedset (Figure 2; Table 1). Shifts in exotic flowering phenology also led to changes in pollinator visitation to natives, suggesting that pollinator behaviour may play a mediating role. However, the direction and magnitude of change in seedset could not be predicted by the initial nature of the interaction (competitive or facilitative).

4.1 | Strong effects of asynchronous shifts on seedset and pollinator visitation

We found that phenological change by exotic plants can strongly influence native plants. Seedset for all seven focal native forb species was altered in at least one exotic phenology treatment, despite variation in initial native–exotic interactions (facilitation vs. competition) and native phenologies. This result complements other studies that have observed changes in seedset of plants whose flowering phenology was artificially shifted (Gezon, Inouye, & Irwin, 2016; Rafferty & Ives, 2011), by showing that even plants whose flowering time has not changed can be affected by phenological changes

in neighbours. We detected significant changes in native seedset in several situations: novel interactions (in which the native and exotic species never previously overlapped in flowering; e.g. *C. quimash* and *H. radicata*), emergent interactions (in which the native and exotic species originally overlapped without measurable interaction, e.g. *L. lepidus* and *H. radicata*) and cases where an interaction was reduced or lost (e.g. *L. lepidus* and *C. scoparius*; Figure 2). In addition, exotic phenology shifts had no effect on seedset of some natives (e.g. *R. occidentalis* and *H. radicata*; Figure 2). Overall, however, flowering phenology of neighbouring exotic plants tended to have strong effects on native seedset.

Exotic phenological shifts also affected foraging behaviour by intermediary pollinators in some cases, though the responses were far from uniform. The relationship between overall visitation rate and native seed production was altered by exotic phenology treatment for half of native–exotic species pairs (Table 2). This change in the relationship between visitation and seed production could happen via at least three different behavioural mechanisms. First, pollinator species of different intrinsic effectiveness for a given plant species (i.e. depositing pollen at different rates because of variation in degree of trait matching with the flower) could be foraging at different rates in control and shifted-exotic treatments. For example, Waters et al. (2014) observed that solitary bees and syrphid flies, which are likely to have very different intrinsic pollination effectiveness for most flowers due to differing anatomical and behavioural traits, showed different responses to changes in floral neighbourhoods. Similarly, Bruckman and Campbell (2014) found that *Apis mellifera* and *Bombus* sp., which differed in their pollination effectiveness for a focal plant, responded differently to changing characteristics of a floral neighbourhood (density of non-native flowers). Anecdotally, we observed several cases of individual

pollinator species appearing to forage preferentially in some phenology treatments, but not always with the same preferences: for example, *Drymeia* sp. appeared to prefer to visit *R. occidentalis* in Advanced *C. scoparius* treatments over controls, while *Bombus mixtus* and *Bombus vosnesenskii* appeared to favour *Lupinus lepidus* in Ambient over Advanced treatments.

Second, realized pollinator effectiveness could be contingent on exotic phenology treatment, if changes to the floral neighbourhood alter local foraging decisions that lead to pollinators carrying changed proportions of conspecific and heterospecific pollen. By adding exotic flowers to plots at novel times, we altered floral composition, floral diversity and exotic floral density (e.g. Figure 1a; compare scenarios 1 and 3). All of these factors are known to affect pollinator foraging behaviour, changing the probability that a pollinator will visit a native inflorescence and arrive bearing conspecific pollen (Jha & Kremen, 2013; Stout et al., 1998). For example, Rafferty and Ives (2012) observed changes in the effectiveness of individual pollinator taxa when they experimentally shifted the flowering phenology of a focal plant. Likewise, Miller, Barrett, and Dickinson (2018) found that the abundance of introduced flowers predicted the proportion of introduced pollen carried by pollinators visiting focal native flowers, which can in turn change seedset via multiple mechanisms. Realized pollinator effectiveness could therefore be altered by the floral neighbourhood changes created by phenological shifting.

Third, asynchronous phenological shifts could influence behaviour of some key pollinators through priority effects on pollinator learning. Eusocial bees learn to 'handle' specific floral resources, and individuals can demonstrate floral constancy once they have mastered harvesting from a particular floral architecture (Waser, 1986). Changing the timing of exotic flowering alters the suite of floral resources available when individual pollinators emerge, so individuals might specialize on a flowering species they would not otherwise choose. The impact could depend on when native/exotic overlap first takes place. An individual bee might maintain a preference for an early blooming native plant if its flowers are available first (phenological precedence), even if a temporally novel set of floral choices occurs a week later; but if the same novel choices occur without earlier availability of the native flower, the outcome might be different (e.g. Figure 1a, historical overlap vs. increased overlap). Priority effects on foraging behaviour could feed back to affect native seedset by influencing the likelihood that an arriving pollinator bears conspecific pollen. Ultimately, any or all of these mechanisms could help explain why the sign and strength of the original plant–plant indirect interactions mediated by pollinators do not predict how seedset changes in response to altered interaction time envelopes.

4.2 | Possible demographic effects

Our results suggest that changes in indirect interactions have the potential to influence demography when conditions are right.

Although the timing and duration of the shifts we created do not reflect a specific prediction for future native–exotic overlaps, they represent reasonable high-end estimates for shifts based on change observed in other systems (e.g. Wolkovich et al., 2013) and in warming experiments in Pacific Northwest prairies (Reed et al., 2019). The changes in seedset we observed could have demographic effects in plant species if population growth rate is sensitive to reproductive rate, which is not always the case (Iler et al., 2019). Demographic effects would also depend on how phenological shifts influence other processes (e.g. seed predation, dispersal, germination), as well as effects on other interaction mediators like shared herbivores or flower predators (Brody, 1997; Parsche, Fründ, & Tschardtke, 2011; Price, Campbell, Waser, & Brody, 2008). In addition, the *direct* effects of shifting species on non-shifting species will complicate any demographic response to *indirect* interactions. For example, abiotic cues leading to accelerated flowering phenology might also accelerate other life-history stages, such as seed maturation and germination (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011), and affect the dynamics of competition between shifting and non-shifting species.

4.3 | Generalizing effects of asynchronous phenological shifts is elusive

In contrast to our primary hypothesis, several lines of information about (a) the sign of the original pollinator-mediated indirect interaction (competitive vs. facilitative) and (b) the magnitude of change in the overlap of native/exotic phenology were insufficient to predict the amount or even the sign of change in native seedset (Figure 3). For example, *H. radicata* had a competitive effect on *E. lanatum* seedset under Ambient phenology. If mediation of the interaction remained constant, seedset would be predicted to diminish as this phenological overlap—and presumably the time available to compete—increased under the advanced *H. radicata* treatment, yet the opposite occurred. In general, the change in overlap did not lead to the expected increase or decrease in interaction strength (Figure 3). In short, shifted-exotic flowering phenology led to ecological surprises with unexpected indirect effects on native plant seedset, implying that nonlinear pollinator responses play an important role in mediating impacts of phenological shifts.

Alternative explanations for the seedset patterns we observed are possible, but less likely. Removal of seed by pre-dispersal seed predators affected our counts in some species, but adding an effect of phenology treatment improved models even when seed predation was significant (Table S4). Seed production itself can be affected by factors that change naturally through the season, such as plant resource status and pollinator community composition (Campbell & Halama, 1993), but we controlled for these factors. For example, earlier and later blooming individuals are expected to differ in seedset even if pollination services are identical, because they have accumulated different levels of resources with which to produce seed. Likewise, pollinator

communities vary in composition and abundance seasonally (Olesen, Bascompte, Elberling, & Jordano, 2008), so shifting the native/exotic indirect interaction time envelope might result in a different communitywide assemblage of pollinators available to mediate the interaction. However, when we performed an analysis to compare native seedset in exotic phenology treatments with seedset *only* of the contemporaneously blooming fraction of native plants in the control treatment, we found results comparable to analysis of the full dataset (Table S4). Native plant resource status and available pollinator community in that analysis are expected to be similar across treatments. Consequently, changes in pollinator foraging behaviour are the best explanation for the patterns we observed. One caveat is that we cannot rule out the potential effects of differences in floral reward between the earlier (and younger) potted exotic flowers used in Advanced treatments, and the later (and older) individuals used in other treatments on pollinator behaviour. Finally, floral visitation can also be a poor predictor of actual pollination success (King, Ballantyne, & Willmer, 2013), so measurement of pollinator effectiveness is necessary to fully interpret the mechanisms that underlie our results.

4.4 | Pollinator-mediated interactions and native plant restoration

Our study is one of many to show that the interactions between exotic and native plants are complex, and not always negative. We observed both facilitative and competitive indirect effects of exotic flowers on native seedset (before phenological manipulation; Figure 2). This result is similar to other studies that have reported changes in pollinator foraging behaviour and native seedset in response to exotic forbs (reviewed Morales & Traveset, 2009). The presence of strong indirect interactions between native and exotic species, with unpredictable mediating behaviour by pollinators, implies that future efforts at native restoration and management may meet with extra demographic surprises.

5 | CONCLUSIONS

Would we generally expect ecological surprises to emerge with asynchronous phenological shifts when species interact indirectly? We believe so, but there are caveats to applying our results more broadly. First, we manipulated the flowering phenology of two abundant exotic species, leaving native flowering phenology static. Although exotic plant species may have more flexible phenological responses to climate change on average than native species (Willis et al., 2010; Wolkovich et al., 2013), our manipulations created a set of interaction time envelopes that may be different than those that will occur under future warming, and our study thus represents a 'proof of concept' rather than any predictive capability. Second, *pollinator* phenology obviously may also shift (Bartomeus et al., 2011; Burkle et al., 2013; Forrest & Thomson, 2011). Our experimental design did not reflect pollinator shifting,

the rate and extent of which are unknown for pollinators in our system. Third, our experiment shifted the onset of exotic flowering, but did not extend flowering duration. Climate change has led to extended flowering duration as well as phenological shifts in many cases (e.g. Kauseurud et al., 2012; Sherry et al., 2007). Finally, the 'temporal transplant' nature of our experiment (Forrest, 2015) produces islands of altered phenological neighbourhoods surrounded by unaltered prairie, and our plots are likely not to be entirely independent units (pollinators can move between them). This means that our results reflect behavioural changes that are difficult to generalize to the population level. Nonetheless, the surprising magnitude and diversity of changes in seedset demonstrate that individualistic phenological shifting by one plant species can have large indirect impacts.

Understanding how changes in phenological overlap alter indirect interactions is important, given that future changes in interaction time envelopes are likely (Thackeray et al., 2010, 2016). We suggest several directions for future research: (a) How demographically important are phenologically induced changes in indirect interactions, relative to direct interactions? (b) Does phenological breadth of an interactor affect the likelihood that changes in overlap duration will have strong effects? (c) How historically common is year-to-year 'flipping' of phenological precedence between two indirect interactors? (d) Do intermediary species typically change their mediating behaviours in response to changes in phenological precedence, making priority effects important in indirect interactions? We suggest that many indirect interactions will be profoundly affected by changing the phenological timing of interactors, and that answering these questions will improve our capacity to anticipate some of the important biological impacts of climate change.

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AUTHORS' CONTRIBUTIONS

S.M.W. and J.H.R.L. designed research; W.-L.C.C. and S.M.W. collected the data; S.M.W. led data analysis and manuscript writing; J.H.R.L. contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

Archived data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gqnk98sj0> (Waters, Chen, & HilleRisLambers, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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