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Fitness costs and benefits of a non-native floral resource for subalpine solitary bees

Charlotte M. Cahill[1,2], Paul J. CaraDonna[2,3,4] and Jessica R. K. Forrest[1,2]

[1]Department of Biology, University of Ottawa, Ottawa, ON, Canada
[2]Rocky Mountain Biological Laboratory, Crested Butte, CO, USA
[3]Chicago Botanic Garden, Glencoe, IL, USA
[4]Plant Biology and Conservation, Northwestern University, Evanston, IL, USA

Correspondence: Jessica R. K. Forrest (jforrest@uottawa.ca)

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Organisms inhabiting seasonal environments must fit their life cycle into a limited time window while also synchronizing periods of resource consumption with timing of resource availability. Introduced non-native species, which often differ in phenology from natives, can alter and expand the seasonal window of resource availability for native consumers, providing potential fitness benefits. However, if these non-native resources are nutritionally unsuitable for native consumers, their presence could elicit foraging behaviour that proves maladaptive – i.e. they could act as an ecological trap. Here, we used multi-year field observations and a laboratory experiment to investigate the impacts of a common non-native plant species on two components of fitness in three solitary bee species (all specialist consumers of pollen from the plant family Asteraceae) native to the Colorado Rocky Mountains. First, we tested whether individual bees that collect pollen from the non-native common dandelion *Taraxacum officinale* produce more offspring than those that do not, thanks to the unusually early flowering phenology of the non-native. Second, we compared survival of bee larvae experimentally reared on *Taraxacum* pollen to that of larvae reared on native Asteraceae pollen. Bees that used at least some non-native *Taraxacum* pollen produced more potentially viable offspring, but larval survival was significantly reduced for bee larvae experimentally fed provisions dominated by *Taraxacum* pollen. Therefore, survival costs may negate the potential fitness benefits of early nesting, indicating that non-native floral resource use may act as an ecological trap for native bees. Using a series of simple simulations informed by our results, we explore the fitness effects of non-native floral resource use, demonstrating that the net cost or benefit depends on how bees respond to resource shortages. Our results highlight the importance of considering organisms' full life cycles when evaluating the fitness consequences of resource availability and species introductions.

Keywords: ecological trap, invasive species, life history, *Osmia* (Megachilidae), phenology, plant–pollinator interactions

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Introduction

A challenge faced by many organisms is the need to fit the life cycle into a limited seasonal time window while also synchronizing periods of resource consumption with timing of resource availability (Perrins 1970, Varpe et al. 2007, Post 2019, Wong and Forrest 2021). For example, in seasonal environments, where favourable abiotic and biotic conditions are temporally limited, organisms with earlier activity may have a competitive advantage and more time to gather resources, develop, and reproduce relative to those with later activity (Varpe et al. 2007, Weis et al. 2015, Wong and Forrest 2021). However, the potential benefits of earlier activity will only be realized if the resources available are of sufficient quantity and quality to support later parts of the life cycle.

The fitness costs and benefits of early or late activity might be altered by the introduction of novel, non-native species that can be used as resources. Non-native plants often have phenologies that differ from those of native vegetation, and many non-native plant species flower early in the growing season, occupying a temporal niche when few native species are in bloom (Wolkovich and Cleland 2011, Wolkovich et al. 2013, Durham et al. 2017, Zettlemoyer et al. 2019). The distinct phenologies of native and non-native plants could complement one another to expand the foraging season for consumers, including pollinators such as bees, which rely exclusively on floral resources for food. Indeed, native bees have been observed to exploit non-native floral resources when the opportunity arises (Williams et al. 2011, Gillespie et al. 2017, Koyama et al. 2018, Seitz et al. 2020). Non-native plants might be particularly beneficial to consumers living in highly seasonal ecosystems, where short growing seasons limit the time available for foraging and reproduction (Bergman et al. 1996, Shibata and Kudo 2020, Wong and Forrest 2021). A prolonged availability of potentially suitable floral resources, which may arise with the introduction of non-native plants, could provide notable fitness benefits to floral consumers whose foraging is not only limited by time, but also restricted to certain host plants (i.e. floral specialists). However, non-native resources also have the potential to act as ecological traps (Dwernychuk and Boag 1972) by attracting consumers but reducing their fitness (Chew 1977, Schmidt and Whelan 1999, Horne et al. 2023).

Here, we investigate the fitness consequences of a non-native floral resource for three mason bee species that are common in subalpine ecosystems in the Colorado Rocky Mountains, USA: *Osmia coloradensis*, *O. montana* and *O. subaustralis*. Like many other bee species (Hurd et al. 1980, Larkin et al. 2008, Müller and Kuhlmann 2008), these three are dietary specialists that collect and consume pollen only from plants in the sunflower family (Asteraceae). We have observed that offspring mortality in these three species is greater with later nesting and activity dates, because offspring born from late-laid eggs often fail to complete larval development before the onset of winter (Fig. 1). However, the widely distributed, non-native common dandelion *Taraxacum officinale* (hereafter *Taraxacum*) is among the first wildflowers to bloom in spring in our study system (Esser 1993), departing from the typical late-season flowering schedule of most other Asteraceae species (Kochmer and Handel 1986). Therefore, foraging from early-blooming, non-native *Taraxacum* could provide bees a longer reproductive season in which to lay eggs, as well as more time for larval development. But, it is unclear whether non-native *Taraxacum* pollen is a suitable food resource for developing bees; available evidence suggests the pollen may be toxic or nutritionally poor (Roulston and Cane 2000, Vanderplanck et al. 2020, Bain 2023). If *Taraxacum* pollen inhibits offspring development, then any reproductive benefits it might provide via earlier foraging might be outweighed by survival costs. With these potential tradeoffs in mind, we asked: 1) whether bees that collect and consume non-native *Taraxacum* pollen produce more offspring due to the earlier nesting opportunity it provides during the short growing season and 2) whether non-native *Taraxacum* pollen provides a suitable food resource for developing bee larvae. Then, based on our empirical results, 3) we created an exploratory model to investigate whether and under what circumstances this common invasive plant confers a net benefit or cost to the native bees with which it now co-occurs.

Material and methods

Overview

Our first objective was to determine whether non-native *Taraxacum* pollen usage by three subalpine solitary bee species was associated with increased reproductive output via earlier nesting phenology. To address this objective, pollen samples taken from nests in the field were used to quantify *Taraxacum* pollen usage by individual female bees. These data on pollen usage were then compared with the timing of first nesting and brood cell production from the same individuals. Our second objective was to determine whether non-native *Taraxacum* pollen provides an adequate substrate for larval development. Here, bee eggs were reciprocally transferred between food provisions dominated by *Taraxacum* pollen and those dominated by pollen of other Asteraceae species. We then monitored larval survival on these different pollen provisions. Finally, we used our observational and experimental results to calculate the net effects of *Taraxacum* pollen usage under different behavioural scenarios. These methods are described in detail below.

Study system

Field work took place near the Rocky Mountain Biological Laboratory (RMBL) in western Colorado, USA (38°57'30"N, 106°59'18"W, 2900 m a.s.l.). Climate in this area is characterized by heavy winter snowfall, an early-summer dry period, and late summer monsoons. In 2013–2014, we established seven long-term study sites in subalpine meadows around the RMBL (Supporting information). The meadows contain

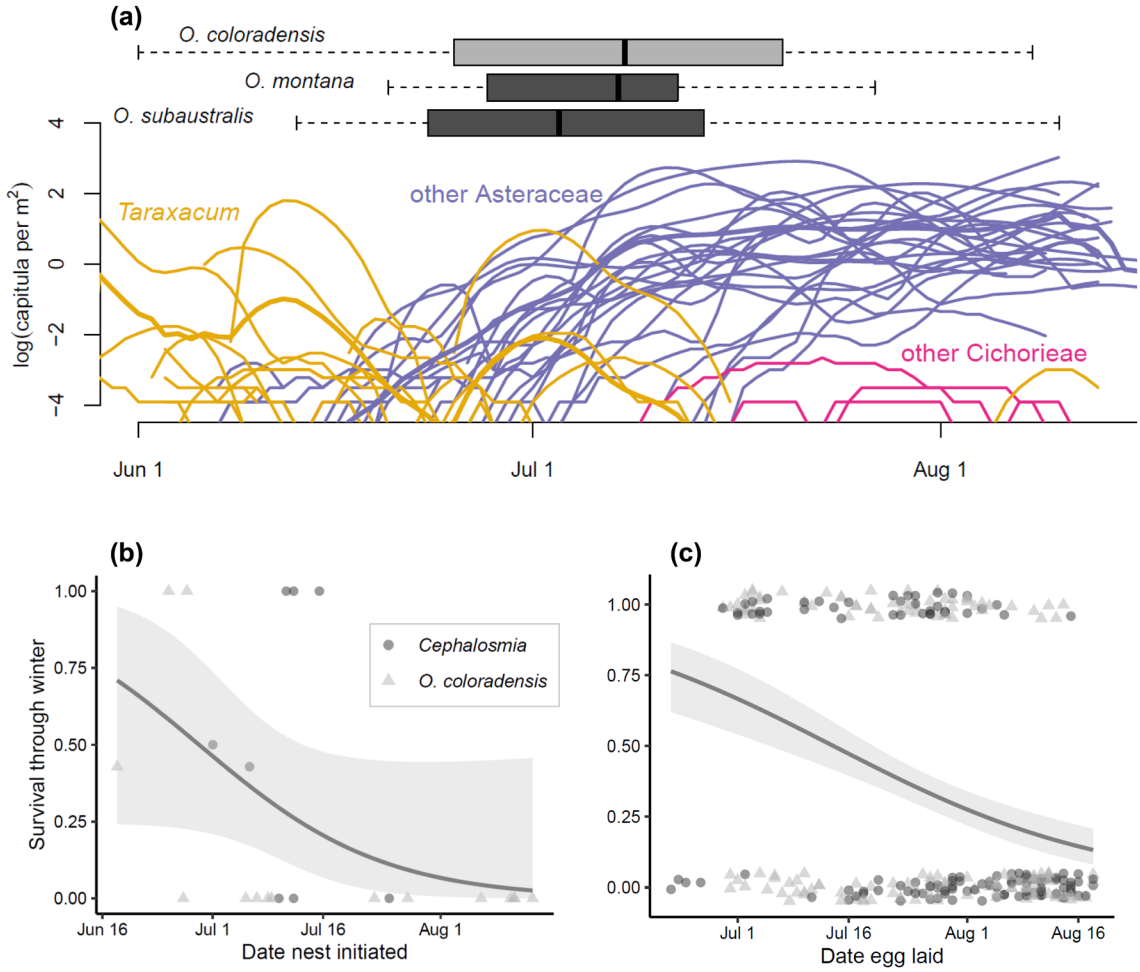

Figure 1. Phenology of flowering and bee nesting at study sites (a), and relationship between date of nest initiation (b) or egg laying (c) and larval survival of Asteraceae-specialist *Osmia* bees. Fine lines in (a) are the daily densities (interpolated between sampling days) of *Taraxacum officinale* (gold), all non-Cichorieae Asteraceae (purple) and other (non-*Taraxacum*) Cichorieae (pink) at each of six sites in each year (2016–2019); thick lines represent the average density (across sites and years) for each plant taxon. (Some lines are not visible because densities were < 0.02 m^{-2}.) Boxplots in (a) show the distributions of first nesting dates for all individual bees of each species, across all six sites, 2016–2019. Boxes show medians and interquartile ranges; whiskers show the full ranges. Datapoints in (b) represent 23 nests constructed by 17 individual bees at 5 sites in a single year (2017); datapoints in (c) represent 271 individual brood cells in 50 nests constructed by 31 mother bees at a single site over three years (2013–2015). For (b) and (c), there is a significant negative relationship between overwinter survival and date (binomial GLMM; $|z| > 2.3$, $p < 0.02$). *Cephalosmia* spp. = *O. montana* and *O. subaustralis*. See the Supporting information for details on data used to generate (b) and (c).

a diverse assemblage of mostly native perennial forbs and grasses (RMBL 2016), but they have been invaded to varying extents by non-native *Taraxacum officinale* (Asteraceae: Cichorieae [=Lactuceae]; 'common dandelion', hereafter '*Taraxacum*'). *Taraxacum* was introduced to North America from Eurasia and is now widely distributed across the continent (Brouillet 2006). The species was introduced to the study region at some point before 1889, and it was apparently abundant in roadside meadows at the RMBL by 1963 (Supporting information). In the western USA, *Taraxacum* is among the first wildflowers to bloom in spring (Esser 1993).

At each of our long-term study sites, we attached 12–24 artificial nesting structures ('trap-nests'; MacIvor and Packer 2015) to dead or dying trees (aspen, spruce or fir) at approximately 1 m above ground level. We used these trap-nests to monitor the activity of three species of wild solitary bees: *Osmia (Helicosmia) coloradensis*, *O. (Cephalosmia) montana* and *O. (Cephalosmia) subaustralis* (Hymenoptera: Megachilidae). Each trap-nest contained ten drilled holes (approximately 14 cm deep and 4.5–8.2 mm in diameter) lined with paper straws (Custom Paper Tubes, Cleveland, OH, USA) that represent suitable nesting locations for these cavity-nesting bees (Supporting information). The straws allowed for the temporary removal of nests to observe nesting progress and sample pollen. Bee individuals build multiple brood cells along the length of the straw, each consisting of one pollen-and-nectar provision and one egg, and partitioned from one another by walls of mud or masticated leaves.

Each straw represents one nest, containing 1–13 brood cells (mean = 5.1, SD = 3.2 cells per nest). A female bee may build multiple nests in succession at one site (mean = 1.4 nests per female in our trap-nests; range = 1–7), constructing up to two brood cells (though typically < 1) per day. The female builds these nests over a period of typically 2–3 weeks and dies by the end of the summer. Each larva develops within its brood cell during the summer and spins a cocoon before overwintering within the nest. All three bee species appear to be uniformly semivoltine in our study area, meaning they spend their second summer undergoing pupation and emerge as adults the following spring (Forrest and Thomson 2011, Tepedino et al. 2022). The two bee subgenera can be distinguished using nest characteristics, as the two *Cephalosmia* species (*O. montana* and *O. subaustralis*) fill cells completely with pollen and nectar, burying each egg within the pollen provision (Torchio 1989), while *O. coloradensis* leaves a space before the outer cell wall, laying each egg atop the pollen provision.

Field methods

Between 2013 and 2019, we monitored bee nesting activity and flowering phenology at our long-term study sites throughout the growing season (early June to mid- or late August). Six of the seven long-term sites were visited approximately twice per week throughout the nesting season and once per week late in the season when bee activity slowed. The seventh, highest-elevation site was visited approximately weekly throughout the summer. At each visit, all trap-nest holes were checked for occupancy and the number of completed brood cells per nest was counted. The date of construction of each cell was estimated by interpolation (as in Forrest and Chisholm 2017). We estimated floral density (capitula per m^2) for the most common Asteraceae taxa at our study sites on each site visit using the plotless method described by Forrest and Chisholm (2017) and in further detail by Forrest (2024). We initially surveyed only the most common native Asteraceae genera (full list of taxa in Forrest 2024), but in 2016 we added *Taraxacum officinale* to the list of surveyed taxa, and in 2018 we began surveying all other cichorioid Asteraceae, both native (*Agoseris* spp.) and non-native (*Tragopogon dubius*, *Cichorium intybus*), as an additional taxon. Five additional Asteraceae taxa (*Achillea, Artemisia, Chrysanthemum, Chrysothamnus, Cirsium*) were present at a subset of our study sites but excluded from surveys because we judged them to be relatively unimportant as resources for bees owing to their particularly late flowering time (late July–August), sometimes in combination with anemophilous flowers (*Artemisia*) or low abundance (*Chrysanthemum, Cirsium, Achillea*).

To monitor bee nesting activity, nesting bees were identified to species based on adult morphology and nest characteristics (Rust 1974, Torchio 1989), and a paint mark (Testors hobbyist's paint; Vernon Hills, IL, USA) was applied to the mesosoma of each to distinguish individuals (Supporting information). A subset of nests (41 out of 305) were constructed entirely between site visits, such that we were unable to identify or mark the mother; these nests, and the 94 brood cells they contained (= 8% of the total), were excluded from analyses. To determine pollen usage, we cut flaps approximately 1 mm wide into the straw at the locations of the pollen provisions and used forceps to collect pollen samples from the inner and outer brood cells (or just the inner cell if there were fewer than four total brood cells in the nest). The straw was then patched with tape and returned to the hole from which it had been taken. Each pollen sample was melted on a slide with fuchsin stain (Kearns and Inouye 1993; melting dispersed the pollen grains across the slide) and returned to the laboratory for examination (*Taraxacum usage*, below).

Trap-nests were established at three additional sites within 1 km of the RMBL in 2018 and 2019 to obtain nests for the egg-transfer experiment (Supporting information). These sites were visited weekly. During each visit, nests were identified to subgenus as described above. We could not determine whether *Cephalosmia* nests belonged to *O. montana* or *O. subaustralis* unless we saw the mother, so the two species were treated as a single taxon for the egg-transfer experiment. During each site visit, we marked the observation date on the outside of the straw at the outermost edge of the nest so that we could estimate the date on which each egg was laid (either by interpolation, if multiple dates were recorded on the same straw, or by assuming a progress rate of one brood cell per day, similar to the rate obtained by interpolation). Completed Asteraceae-specialist nests were collected for lab experiments. To increase sample sizes for the experiments, we also used a subset of nests collected from five of the seven long-term sites, in addition to those obtained from the three short-term sites established just for the lab experiment in this study.

Taraxacum usage in the field

To determine whether bees that collect *Taraxacum* pollen begin nesting earlier and produce more brood cells, we quantified pollen usage, nesting phenology, and reproductive output for the three aforementioned Asteraceae-specialist bee species nesting at the long-term study sites between 2013 and 2019. To quantify pollen usage, each slide-mounted pollen sample was examined under a compound microscope at ≥ 100× magnification. Within each sample, we examined four field-of-view transects, each starting at a haphazardly selected location within the sample. The first 20 pollen grains in each transect (moving in a vertical line up or down the slide) were identified as *Taraxacum*, other Asteraceae, or other plant families (Supporting information). For each marked bee, we calculated the proportion of *Taraxacum* pollen in each sample and then calculated an average across all samples for that bee (i.e. 1–2 per nest × as many nests as that bee constructed). The date of first nesting was the date on which an individual's first brood cell was estimated to have been constructed. We then calculated lifetime reproductive output for each bee as the sum of all completed brood cells across all nests constructed by that bee.

Taraxacum pollen is distinct from that of all the most common native Asteraceae in our study area, but we were unable to distinguish it from that of other Cichorieae

species. However, other Cichorieae species are much less abundant than *Taraxacum* at most of our study sites, and all flower much later in the season than *Taraxacum* (Fig. 1), so we do not expect them to bias our results. Non-cichorioid Asteraceae were grouped as 'other Asteraceae' because we could not reliably distinguish pollen of the multiple genera (e.g. *Arnica*, *Erigeron*, *Helianthella*, *Heliomeris*, *Heterotheca*, *Hymenoxys*, *Pyrrocoma*, *Senecio*, *Solidago*, *Wyethia*) occurring in our study area. We have observed marked individuals of our focal bee species collecting pollen from several of these genera (*Arnica*, *Heliomeris*, *Senecio*, *Pyrrocoma*), indicating they do not restrict foraging to an individual tribe.

Egg-transfer experiment

To determine whether *Taraxacum* pollen provides a suitable substrate for developing bee larvae, we conducted a reciprocal egg-transfer experiment in 2018 wherein we compared bee larval development on *Taraxacum* pollen provisions to that on other Asteraceae pollen provisions (similar to the approaches of Praz et al. 2008, Sedivy et al. 2011). We repeated the experiment in 2019 to increase sample size. Completed bee nests were collected from the field and divided into individual brood cells, consisting of one pollen provision and one egg, using a scalpel and a pair of microscissors. Individual brood cells were placed in 2.0 × 1.0 cm wells drilled into the side of 30.8 × 3.7 cm wood blocks (Supporting information). The first 100 pollen grains from a sample of each provision were identified along random transects of microscope slides, as described above. Since use of natural nests, which are rarely 100% one pollen type, was preferable for testing survival on different provision types, the provisions were classified as either '*Taraxacum*' or 'other Asteraceae' if greater than 80% of the identified grains belonged to either taxon. Ultimately, the 'other Asteraceae' treatments contained at most a few *Taraxacum* pollen grains, while the '*Taraxacum*' treatments contained up to 20% other Asteraceae. A metal spatula was used to transfer eggs between *Taraxacum* pollen provisions and other Asteraceae provisions in a reciprocal transplant design; in other words, eggs originating on each type of pollen provision were transferred onto a provision of the same type or of the other type. Treatments were distributed alternately throughout the wood blocks to avoid any positional effects. We attempted to achieve a balanced design, with equal numbers of each bee subgenus originating from and transferred to each provision type, and with equal proportions of conspecific and heterospecific transfers. However, since all but one of the bees that collected *Taraxacum*-dominated pollen provisions were *O. coloradensis*, not all combinations of each taxon originating on each provision type could be included in the transfer design (Supporting information).

For *O. coloradensis,* bees were often transferred at the larval stage, as their eggs are more fragile than those of the other two species. Larvae were transferred no later than 17 days from the estimated egg lay date, to ensure that they had only consumed small amounts of their original pollen provision. (Eggs eclosed approximately 10 days after the date laid, and we assumed that larvae less than seven days old would have consumed little pollen, since most of the provision remains at this time.) All transferred bees, whether transferred at the egg or larval stage, are referred to as eggs for simplicity.

Transferred eggs were kept in a dark growth chamber that ramped daily between approximately 5.0 and 25°C (in 2018 and part of 2019) or in an opaque container in a shaded outdoor enclosure (for the remainder of 2019). Both situations mimic the natural environment larvae experience within the nesting blocks and natural cavities. Survival and developmental progress of the transferred eggs and eclosed larvae were monitored every other day using a hand lens or a dissecting microscope. Observations for each bee began immediately after transfer and ended once the individual completed its cocoon or died (or upon our departure from the research station, 23 August 2018 and 6 September 2019). Larvae that survived to the end of the observation period in 2018 were stored in the shaded outdoor enclosure and examined on 3 June and 15 August 2019 to assess survival and developmental status (by cutting a flap into the cocoon wall when necessary).

Statistical analysis

Analyses were conducted in R ver. 4.1.1 (www.r-project.org).

Taraxacum usage in the field

Taraxacum usage was treated as a binary variable ('yes' for at least one *Taraxacum* pollen grain; 'no' for no *Taraxacum* pollen grains) for analysis because the data were heteroscedastic when *Taraxacum* usage was treated as a proportion. However, except where reported, our results are qualitatively unchanged by using proportion data instead (i.e. proportion of *Taraxacum* pollen grains in the sample relative to other Asteraceae pollen, pooled across all brood cells scored for each individual bee).

We first tested whether *Taraxacum* usage by individual bees predicted the timing of nesting (first day of year of nesting) using a linear mixed model (R package 'lme4'; Bates et al. 2015) that included bee species as an additional fixed factor, and site and year as random factors (each with seven levels). Next, we used a negative binomial generalized linear mixed model to evaluate the relationship between first day of year of nesting (rescaled using the R package 'scales'; Wickham and Seidel 2019) and offspring production. Here, the response variable was the number of brood cells produced by each individual bee. Bee species, site, and year were included as in the previous model. Finally, using a second negative binomial mixed model, we tested whether *Taraxacum* usage predicted offspring production (not accounting for nesting phenology). Bee species, site, and year were included as before. Analyses were limited to brood cells produced before 1 August, as high mortality of eggs laid after this date suggests that they will not contribute to maternal fitness (Fig. 1). Nevertheless, we re-ran the analyses including all brood cells (even those produced after 1 August) and found that most results are robust to the assumption of complete mortality of late-laid eggs (Supporting information).

We used the 'lmerTest' package in R (Kuznetsova et al. 2017) to evaluate significance of the fixed factors in linear mixed models. To evaluate significance in generalized linear mixed models, we used Wald *z* tests (for continuous variables) and likelihood-ratio tests (for categorical variables). In all cases, we assessed collinearity by calculating variance inflation factors using the *vif* function in the 'car' package (Fox and Weisberg 2019), and we used the 'DHARMa' package (Hartig 2021) to check for violations of model assumptions. All squared $GVIF^{1/(2df)}$ values (the equivalent of VIFs for models with categorical predictors) were less than 1.1. Because interactions between predictors were not significant, and because interaction terms sometimes introduced collinearity problems, they were not included in the models. In addition, because one particularly productive bee (an *Osmia coloradensis* who produced a total of 63 brood cells, 53 of these before 1 August) was a clear outlier in analyses involving numbers of offspring, we ran those models with and without this individual. Significance of results was unchanged by exclusion of this bee, so we report the results including all individuals. Aside from this outlier, we detected only one violation of model assumptions, which we note in the relevant section of the Results, below. Our total sample for these analyses comprised 189 individual bees, with a range of 1–12 bees (mean 3.2) per species, site, and year, in 60 unique species-site-year combinations.

Egg-transfer experiment

We analyzed the survival of experimentally transferred eggs using Cox mixed-effects proportional hazards models (function *coxme* in the 'coxme' package (Therneau 2019)). We initially modelled survival as a function of provision type (*Taraxacum* or other Asteraceae) and year of experiment (coded as categorical); we also included bee subgenus (*Cephalosmia* or *Helicosmia*) and the interaction between subgenus and provision type as factors in analysis to account for the apparently greater fragility of *O. (Helicosmia) coloradensis* eggs and larvae. (We could not include species as a factor because nests were identified to subgenus only.) However, the interaction term was not significant, and a model without this term had a lower AIC value, so we report only the results for the simpler model with main effects of provision type, year, and subgenus. The source nest from which the egg originated was included as a random factor. Because virtually all eggs originating on *Taraxacum* provisions came from *O. coloradensis* nests, we could not account for subgenus in the analysis along with origin pollen type. Instead, we analyzed the effects of origin and destination pollen types, and their interaction, for *O. coloradensis* alone. Here, the interaction term tests whether larvae of mother bees that choose to collect *Taraxacum* pollen are better able to survive on this pollen type than larvae of mothers that did not use *Taraxacum* pollen.

Calculating net effects of *Taraxacum* usage

Given the apparent positive and negative effects of *Taraxacum* usage on native bees, we explored the likely net effects of its usage with a simple mathematical model (described in detail in the Supporting information). This analysis investigates four ecological scenarios, all parameterized with values from our empirical findings. Specifically, the analysis investigates the number of brood cells produced by a bee as a function of the timing (day of year) of first nesting, the availability of native Asteraceae and non-native *Taraxacum* flowers during the nesting period, and the net effect of using these resources (on brood production and offspring survival), under each of the model scenarios. In other words, in all cases, for an Asteraceae-specialist bee that begins nesting on any given day of the nesting season, the model calculates the total number of brood cells expected to survive winter as our measure of the net effect of *Taraxacum* presence or absence. Our first scenario 1) assumed that *Taraxacum* is available in the environment for bees to use in proportion to its abundance, and that its pollen has no effect on larval survival. Our second scenario 2) also assumed that *Taraxacum* is present and used by bees in proportion to its abundance, but here there is a survival cost to using this pollen, consistent with our empirical findings. For our third and fourth scenarios 3A–B), we assumed that *Taraxacum* is absent, so that bees can only use other Asteraceae pollen (which is scarce or absent in early summer). Here, we considered two possibilities for how an Asteraceae-specialist bee might respond to scarcity of its host flowers: 3A) the bee produces fewer brood cells; or, 3B) the bee takes longer to complete each brood cell, with the time taken to complete each cell inversely proportional to the availability of host pollen (in other words, brood production is faster when the availability of host pollen is greater). Yet another option would be that the bee switches to non-host pollen in the absence of host flowers, but, as we see no evidence that this occurs among our study species, we do not explore it further.

Results

We observed 189 bee individuals across seven years (2013–2019), seven sites, and three species. *Taraxacum* occurred at all study sites, making up between 0.1 and 59% of the total density of surveyed Asteraceae capitula, depending on the site, and all three bee species used *Taraxacum* pollen to some extent (Fig. 2). Overall, 57 individuals (30%) used at least some *Taraxacum* pollen (mean ± SD *Taraxacum* content for these individuals = 23 ± 33% of pollen grains sampled), and three *O. coloradensis* individuals used exclusively *Taraxacum* pollen. In 15% of all pollen provisions examined (including provisions constructed by 13 *O. coloradensis* and 3 *O. subaustralis* individuals), *Taraxacum* pollen made up more than 50% of the total. *Taraxacum* pollen usage by the three bee species appeared to roughly track the relative abundance of *Taraxacum* capitula at the study sites (Supporting information).

Is *Taraxacum* usage associated with greater offspring production in the wild?

Bees that included non-native *Taraxacum* pollen in their provisions began nesting on average 10 days earlier than bees that did not ($F_{1,183.8} = 21.8$, $p < 0.0001$; Fig. 3a). Earlier

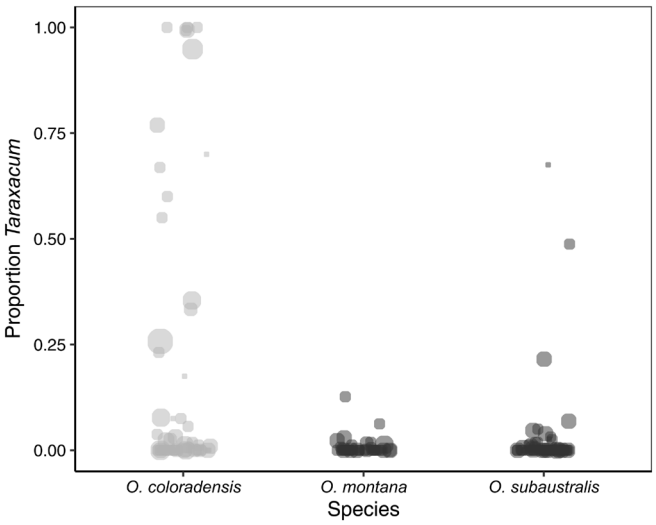

Figure 2. *Taraxacum* pollen usage by the three study species (2013–2019). Points show the proportion of Cichorieae (primarily *Taraxacum*) pollen grains in samples taken from brood cells; >99% of the remainder was pollen of other Asteraceae taxa. Each point represents an individual bee, with point size scaled to the number of brood cells sampled for that individual (the smallest point represents a single brood cell; the largest represents 12 brood cells). Point shading indicates bee subgenus (light grey = *Helicosmia*; dark grey = *Cephalosmia*). Points have been jittered horizontally to reduce overlap. n = 62 *O. coloradensis*, 55 *O. montana*, 72 *O. subaustralis*.

nesting was strongly associated with increased production of offspring (brood cells) prior to 1 August ($z = -10.0$, $p < 0.0001$; Fig. 3b), with a 10-day advance in timing (relative to the mean first nesting date) yielding an expected 47% increase in brood cell production (from 5.6 to 8.2). It should be noted that residuals from this model suggested poor fit, due in part to the series of '0' values for fitness of bees that began nesting after 1 August; however, no reasonable changes to the model solved the issue, nor did they change the conclusion that earlier-nesting individuals produce more offspring before 1 August. We therefore suggest readers draw their own conclusions based on Fig. 3b. Bees that used *Taraxacum* pollen produced on average 55% more brood cells before 1 August compared to bees that did not use *Taraxacum* (7.7 versus 5.0; $z = 3.2$, $p = 0.0014$; Fig. 3c). The positive association between *Taraxacum* usage and production of brood cells before 1 August remains significant if *Taraxacum* usage is measured as a proportion ($z = 2.2$; $p = 0.030$).

Is *Taraxacum* a suitable resource for developing larvae?

In total, 154 egg transfers were completed; of these, 138 survived at least one day as a larva after being transferred and were included in the analysis. Of these, 68 were transferred onto *Taraxacum* provisions (34 bees originating on *Taraxacum* provisions and 34 originating on other Asteraceae provisions) and 70 were transferred onto provisions consisting of other Asteraceae pollen (34 bees originating on *Taraxacum* and 36 originating on other Asteraceae; Supporting information).

Survival of bee larvae during their first summer of development was reduced on a diet of *Taraxacum* pollen relative to a diet consisting of other Asteraceae pollen (hazard ratio = 1.56, $p = 0.024$; Fig. 4). This hazard ratio corresponds to a 1.56 × greater risk of dying on *Taraxacum* pollen than on the pollen of other, native Asteraceae flowers. Survival of *O. coloradensis* larvae was also much poorer than that of *Cephalosmia* (*O. montana* and *O. subaustralis*) larvae (hazard ratio = 2.9, $p = 0.00005$; Fig. 4). Survival after the first summer was also reduced for bees reared on *Taraxacum* provisions: Of the 12 bees reared on other Asteraceae pollen that survived to the end of the experiment in 2018, all survived the ensuing winter, and 83.3% (10) had pupated by the end of summer 2019. In contrast, of the five bees reared on *Taraxacum* pollen that survived to the end of 2018, only 40% (2) survived the winter, and none had pupated by the end of summer 2019.

Within *O. coloradensis* specifically, larvae reared on *Taraxacum* provisions (n = 48) had reduced survival compared to those reared on other Asteraceae provisions (n = 41; hazard ratio = 3.5, $p = 0.037$). In addition, *O. coloradensis* bees that originated on *Taraxacum* provisions (n = 66) had significantly lower survival than those originating on other Asteraceae provisions (n = 23; hazard ratio = 4.4, $p = 0.011$). Finally, there was no significant interaction between source and destination provision type (hazard ratio = 0.39, $p = 0.14$, n = 89), suggesting that bees whose mothers had provided *Taraxacum* pollen for them were no better than other bees at surviving on a *Taraxacum*-pollen diet.

Net effects of *Taraxacum* usage

Our analysis suggests that *Taraxacum* usage can be an ecological trap (i.e. reduce maternal fitness, despite its apparent benefits), but only under certain conditions. First, unsurprisingly, if we assume there is no survival cost to using *Taraxacum* pollen, and if not having *Taraxacum* available simply results in no reproduction, then bee fitness is improved by having access to *Taraxacum* (Fig. 5; compare scenario 1 and 3A). Furthermore, even if there is more than a 50% survival cost to using *Taraxacum* pollen – consistent with our empirical results – it is better to use *Taraxacum* than not, assuming the alternative is no reproduction (Fig. 5; compare scenario 2 and 3A). However, if the consequence of not using *Taraxacum* is merely slower brood production, then this is ultimately better than using *Taraxacum*, given its survival cost (Fig. 5; compare scenario 2 and 3B; although note the uncertainty in model estimates).

Discussion

This work demonstrates the importance of considering the effects of novel resources on all facets of animal fitness – from reproductive phenology and reproductive output to successful offspring development – to gain a comprehensive picture

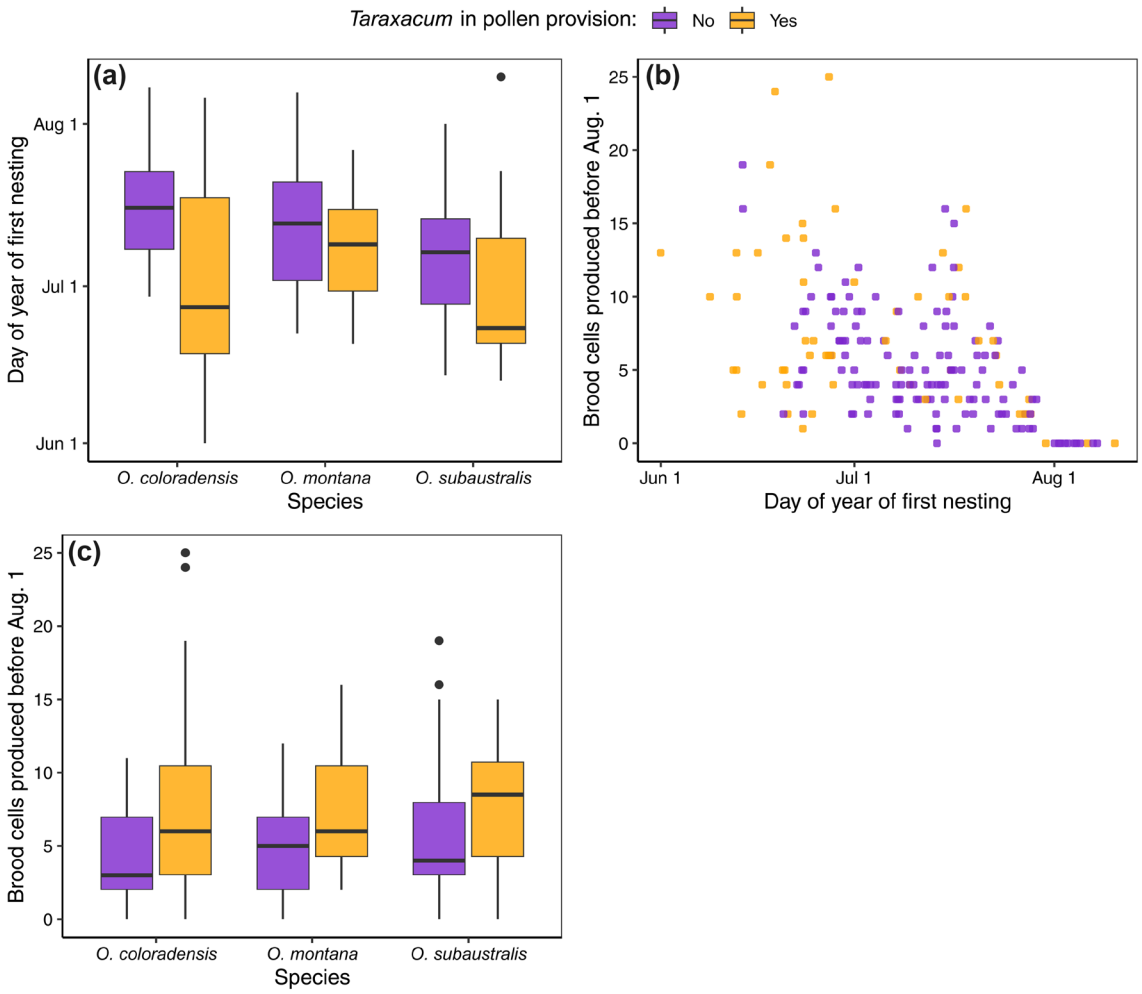

Figure 3. Relationship between *Taraxacum* pollen usage (treated here as binary, Yes/No), date of first nesting, and brood cell production in three *Osmia* species. (a) Bees that incorporate *Taraxacum* pollen in their provisions begin nesting earlier. (b) Early nesting appears associated with increased production of brood cells before 1 August. (c) Bees that incorporate *Taraxacum* pollen in their provisions produce 2 to 3 more brood cells, on average, than those that do not. Boxes show medians and interquartile ranges; whiskers extend to the furthest point within 1.5 × the interquartile range. Sample sizes as in Fig. 2, except that one outlier (an *O. coloradensis* that used *Taraxacum* and produced 53 brood cells) is omitted from (b) and (c).

of their impacts. For the Asteraceae-specialist bees in our subalpine study area, there is limited early-season availability of floral resources among the native flora. The early flowering time of the non-native *Taraxacum officinale* appears to mitigate resource constraints for Asteraceae-specialist bees by filling an early-season niche when the flowers of native Asteraceae are less abundant. Indeed, we found that the native bees that used at least some non-native *Taraxacum* pollen began nesting earlier than those that did not, and these early-nesting bees produced more potential offspring. These results suggest that non-native *Taraxacum* gives the bees that use it a fitness advantage – on the order of a 50% increase in potential reproductive output (Fig. 3). Critically, however, we found that all three Asteraceae-specialist bees had lower larval survival when experimentally reared on a diet dominated by non-native *Taraxacum* pollen instead of native Asteraceae pollen. In fact, the magnitude of this effect – on the order of a 50% reduction in survival – seems sufficient to negate the apparent fitness benefits of *Taraxacum* usage observed in the field.

Integrating these empirical findings into a simple mathematical model revealed that using non-native *Taraxacum* as a resource can be a net cost or benefit to bees, depending on how bees respond to resource shortages. If bees respond to the absence of early-summer floral hosts by delaying reproduction – a scenario we think is plausible – then their populations would likely be better off without *Taraxacum*. This is because the reproductive gains that come from using *Taraxacum* as an early-season resource are outweighed by survival costs later in the life cycle. Thus, under these conditions, *Taraxacum* would indeed present an ecological trap by providing an attractive novel resource whose consumption in fact reduces fitness. Furthermore, expending energy to begin nesting early in the season could mean that bees who use *Taraxacum* are less able to construct nests later in the season when flowers of native Asteraceae species become more abundant – a tradeoff that

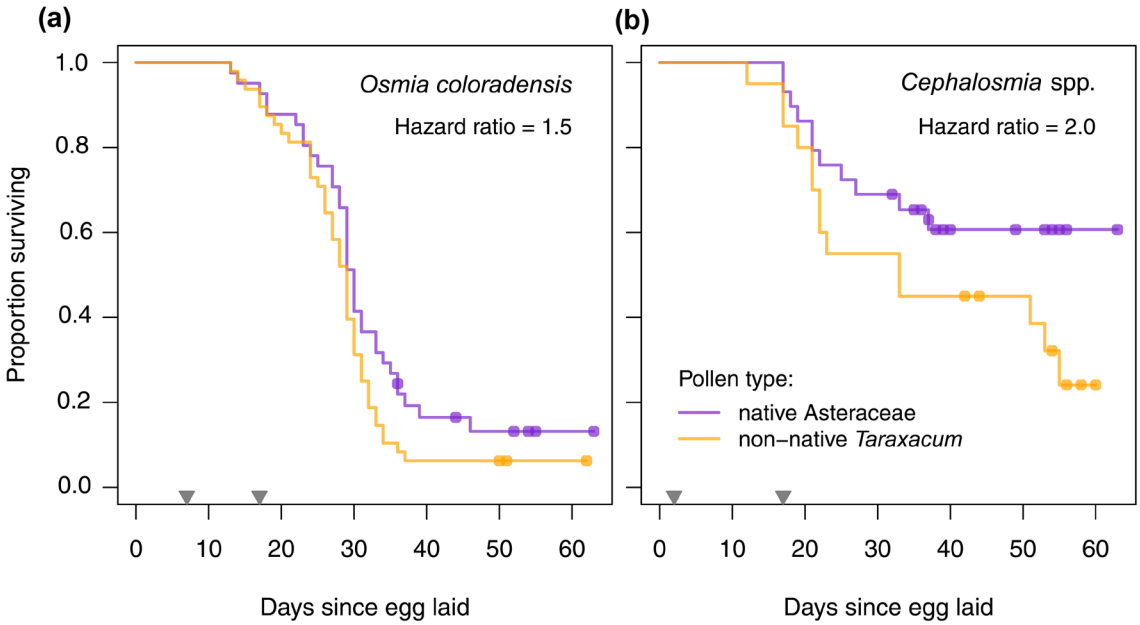

Figure 4. Kaplan–Meier survival curves for bee larvae transferred onto *Taraxacum* or other (native) Asteraceae pollen provisions. (a) *Osmia coloradensis*; n = 48 + 41; (b) bees in the subgenus *Cephalosmia* (*O. montana* and *O. subaustralis*); n = 20 + 29. Points indicate censored data (cocoon completion or the end of observation). Grey triangles along x-axes indicate minimum and maximum ages at which eggs of each subgenus were transferred. Hazard ratios are from Cox mixed-effects models of the form 'Survival ~ Pollen.type + (1|Nest)', run separately for each subgenus.

would intensify the severity of the trap. Regardless, this trap only becomes apparent by examining the costs and benefits of novel resource use for each part of the life cycle.

Our egg-transfer experiment suggests that the ecological trap may be even more severe than our calculations indicate: *O. coloradensis* eggs that originated on *Taraxacum* pollen provisions had poor survival regardless of what pollen type the larvae were ultimately reared on, suggesting that *Taraxacum* ingestion in the first few days as larvae, or perhaps even contact with *Taraxacum* pollen at the egg stage, may reduce survival. We therefore suspect that if we had been able to transfer all eggs before hatching, the disparity in survival between the two pollen types would have been even greater, making the net negative effect of *Taraxacum* on bee fitness greater. In addition, probabilities of survival to adulthood for bees developing on *Taraxacum* may be even lower than the hazard ratio from our experiments with larvae suggest, given that no bees reared on *Taraxacum* pollen provisions in our 2018 experiment survived to pupation. From observations of unmanipulated nests in the field, we know that *O. coloradensis* larvae fed *Taraxacum* pollen by their mothers occasionally survive to the pupal stage, but we have yet to observe any successfully reach adulthood, and we have too few datapoints to estimate diet-specific survival rates in the field. Our results raise the question why *Osmia* bees in our study area have not evolved to better tolerate *Taraxacum* pollen in their diets, given the seemingly strong selective advantage such tolerance would confer, and given that *Taraxacum* has apparently been abundant in the area for at least 30 (two-year) bee generations.

Poor larval survival on *Taraxacum* pollen relative to other Asteraceae pollen suggests the presence of chemical or physical properties that make it an unsuitable food source. Asteraceae pollen in general has been hypothesized to possess deterrent qualities that may function to reduce its collection by pollen consumers, particularly bees (Müller and Kuhlmann 2008, Vanderplanck et al. 2020). Yet, based on our results, *Taraxacum* pollen appears to be a poor food source even for bee species that can tolerate other Asteraceae pollen. Vanderplanck et al. (2020) argued that chemical properties of *Taraxacum* pollen, such as the presence of toxic compounds or nutrient deficits, were the most likely explanation for the noxious effects of this pollen on bees; and the finding that *Taraxacum* pollen can have allelopathic effects on neighbouring plants (Loughnan et al. 2014) supports the hypothesis that it contains toxins. The nutritional composition of *Taraxacum* pollen also appears unusual (low in P, K and Fe) even compared to other Asteraceae (Filipiak 2019), and it may be deficient in certain essential amino acids (Auclair and Jamieson 1948, Loper and Cohen 1987). For example, on a diet consisting only of *Taraxacum* pollen, young honeybees failed to rear brood (Herbert et al. 1970), and adults died sooner (Knox et al. 1971) than those reared on other pollen diets. The addition of a missing essential amino acid (L-arginine) to *Taraxacum* pollen restored honeybee development and reproductive success (Herbert et al. 1970), supporting the notion that nutrient deficiencies contribute to the poor dietary quality of this pollen. Egg-transfer experiments accompanied by nutrient supplementation of *Taraxacum* and non-*Taraxacum* pollen provisions would help to determine the mechanisms by which *Taraxacum* as a resource affects larval bee survival.

Our experiment compared only *Taraxacum*-dominated and *Taraxacum*-free pollen provisions, but might bees have gained

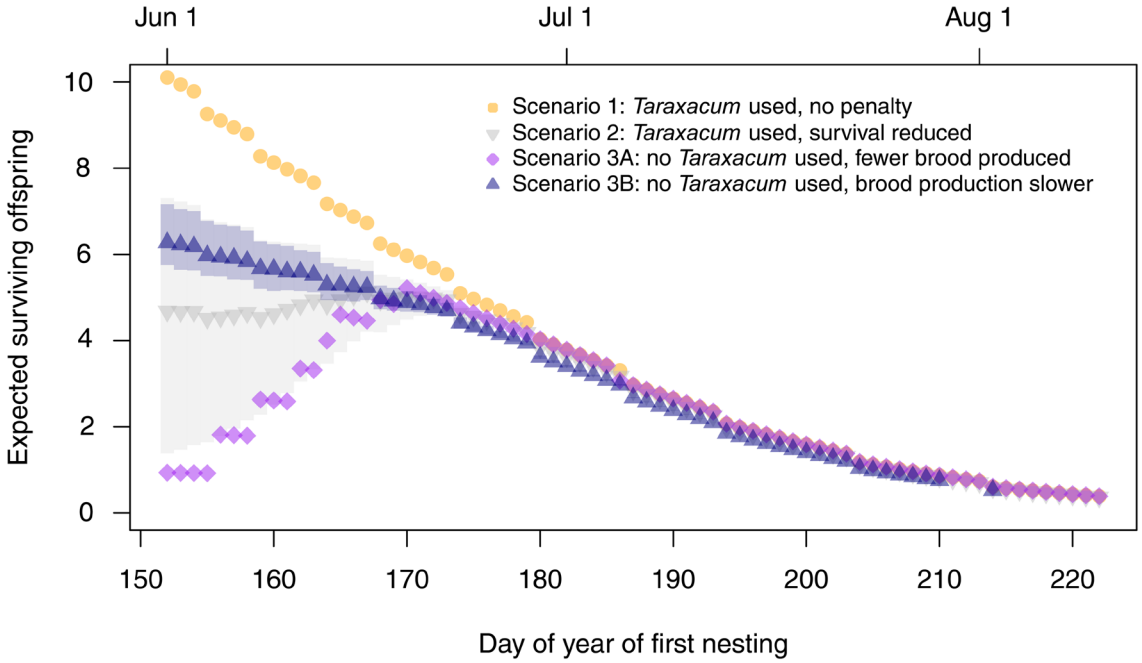

Figure 5. Results of simulation showing expected numbers of surviving offspring as a function of first nesting date, under four different scenarios. Scenario 1 (gold circles): bees use *Taraxacum* pollen interchangeably with other Asteraceae pollen, and their offspring suffer no fitness penalty related to *Taraxacum* usage. The number of progeny expected to survive to adulthood decreases with later nest initiation because later-nesting bees produce fewer offspring, and later-produced offspring have less chance of surviving winter (as in Fig. 3b and 1b-c). Scenario 2 (grey inverted triangles): bees use *Taraxacum* pollen in proportion to its availability, but offspring survival probability is reduced as a function of the *Taraxacum* content of the pollen provision (as in Fig. 4). Scenario 3A (purple diamonds): bees do not use *Taraxacum* pollen and instead use only native Asteraceae pollen; this reduces offspring production in proportion to the lost resource. Scenario 3B (blue triangles): bees do not use *Taraxacum* pollen; this causes production of each brood cell to take longer than the usual 3.6 days, in proportion to the lost resources, up to a maximum duration of 15 days per brood cell. Grey shading indicates the range of likely values under scenario 2 (based on ± 1 SE of the model-estimated survival cost of *Taraxacum* pollen usage). Blue shading indicates the range of likely values under scenario 3B, based on upper and lower estimates for the maximum duration of brood cell construction. Functions are not smooth because the number of eggs produced by a female bee can only take integer values. In all scenarios, impacts of *Taraxacum* usage are experienced only by individuals that begin nesting early in the season, when *Taraxacum* is in flower. See the Supporting information for additional information on parameter values.

some of the benefits of *Taraxacum* pollen usage without the apparent costs by mixing some amount of non-*Taraxacum* pollen into their provisions? In principle, this seems a reasonable hypothesis, particularly if non-*Taraxacum* pollen could compensate for any nutrient deficiencies or neutralize toxins in the *Taraxacum* pollen (Eckhardt et al. 2014). However, *Taraxacum* is often the only Asteraceae pollen resource available at the beginning of the season, in our study area and elsewhere, such that early bee nests can be dominated by this pollen (Supporting information). Consequently, the early-season offspring that are responsible for the greater reproductive output of *Taraxacum*-using bees are also likely to be exposed to a *Taraxacum*-dominated diet – and any survival costs that entails.

It is possible that greater pollen resource diversity in our 'native Asteraceae' treatment, rather than the absence of *Taraxacum*, was responsible for the higher observed survival in that treatment (Foley et al. 2012, Filipiak 2019). While our *Taraxacum* pollen treatment included only provisions containing > 80% *Taraxacum* pollen, the 'native Asteraceae' provisions likely contained a mixture of floral resources, since the pollens of the various non-cichorioid genera in our study area are not easily distinguished from one another. More diverse pollen mixtures might be more likely to support larval development if they provide complementary nutrients or vary in toxin composition. Our experiment reflects the reality that pollen type and pollen diversity are often confounded in nature, given the seasonal transition from an early-season floral resource landscape dominated by *Taraxacum* to a later-season resource landscape containing a diversity of co-flowering native Asteraceae. Testing larval survival on multiple monofloral pollen diets could disentangle these confounds, revealing whether a lack of pollen diversity or harmful attributes of *Taraxacum* pollen specifically causes the reduced fitness of *Taraxacum*-reared bees.

Taken together, our research highlights the importance of considering the impacts of non-native resources on consumers' entire life cycles to gain a more complete picture of the costs and benefits associated with novel interspecific interactions. In particular, we demonstrate that the positive effects of using non-native resources at one part of the life cycle can be overridden by negative effects later in the life cycle. While we caution against generalizing to all native bee–non-native plant relationships, our results suggest that poor larval survival on non-native *Taraxacum* makes usage of this plant

an ecological trap for North American Asteraceae-specialist bees. The broader ecological impacts of *T. officinale* on our study area are unknown, likely because it became established long ago and is no longer exhibiting rapid range expansion. However, like other successful invaders, *T. officinale* can competitively displace native plants (Molina-Montenegro et al. 2013) and interfere with reproduction of native relatives (Muñoz and Cavieres 2008, Matsumoto et al. 2010) elsewhere in its invasive range. Such effects on the floral and vegetative landscape must be considered in any comprehensive assessment of the ecological impacts of non-native species.

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Author contributions

Charlotte M. Cahill: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Investigation (lead); Methodology (supporting); Visualization (equal); Writing – original draft (lead); Writing – review and editing (supporting). **Paul J. CaraDonna**: Conceptualization (supporting); Funding acquisition (supporting); Investigation (supporting); Supervision (supporting); Visualization (supporting); Writing – review and editing (equal). **Jessica R. K. Forrest**: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (supporting); Methodology (lead); Project administration (lead); Resources (lead); Supervision (lead); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cc2fqz6g9 (Forrest et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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