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2 **Unraveling the ecological and evolutionary impacts**
3 **of a plant invader on the pollination of a native plant**

4 **Wilnelia Recart** · **Diane R. Campbell**

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7 **Abstract** Interactions between a native plant species
8 and its pollinators, herbivores, or microbiome can be
9 affected by the presence of non-native plant species.
10 Non-native plant species are altering plant-pollinator
11 interactions, yet we know little about how these non-
12 native species influence natural selection. In addition,
13 year-to-year variation in flowering could influence the
14 impacts of non-native species on reproductive success
15 in native plants and the strength and direction of
16 pollinator-mediated selection. We examined whether
17 the presence of the highly invasive plant *Linaria*
18 *vulgaris* influenced average pollinator visitation,
19 species composition of floral visitors, or pollinator-
20 **AQ1** mediated selection in the native *Penstemon strictus*. In
21 the field, we conducted small scale *L. vulgaris*
22 inflorescence removals, that were repeated through 3

years. Pollinator-mediated selection on the floral trait
of platform length was examined by determining the
relationships between platform length and visitation,
between visitation and seed production, and by
calculating net selection based on seed production.
We found that the presence of *L. vulgaris* on a small
spatial scale facilitated pollinator visitation rates to *P.*
strictus but did not influence pollinator-mediated
selection on platform length. Pollinator visitation
varied across years, as did the relationship between
seed production and pollinator visitation, and the
relationship between pollinator visitation and platform
length. Although components of selection varied
across years, no net selection on platform length was
detected in any of the 3 years. Our results show how
the presence of an invasive plant and year-to-year
variation in plant-pollinator interactions affect the
pollination and components of pollinator-mediated
selection in native plants.

Keywords *Bombus* · Competition for pollination ·
Invasive · *Linaria vulgaris* · *Penstemon strictus* ·
Pollinator visitation

Introduction 45

The presence of non-native plant species can alter 46
interactions between native plants and their 47

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A2 supplementary material available at [https://doi.org/10.1007/](https://doi.org/10.1007/s10530-021-02457-z)
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48 pollinators, herbivores, or microbiomes (Traveset and
 49 Richardson 2006; Bezemer et al. 2014; Coats and
 50 Rumpho 2014). By imposing new selective pressures,
 51 plant invasions could also influence the evolution of
 52 native plant species (Oduor 2013). It is crucial to
 53 understand the potential of non-native species to alter
 54 natural selection because adaptive change, along with
 55 plasticity, could eventually influence the persistence
 56 of a native species in the face of an invasion (Berthon
 57 2015). Most studies addressing evolutionary change in
 58 native plants have focused on direct competitive
 59 impacts of the presence of the invader (Callaway
 60 et al. 2005; Goergen et al. 2011) rather than the
 61 evolutionary effects of the invader that are mediated
 62 by interactions with third-party organisms (Lau 2008),
 63 **AQ2** such as pollinators (Beans and Roach 2015).

64 Ecological impacts of invasive plants on average
 65 pollination are better studied, and these impacts range
 66 from negative to positive (Morales and Traveset 2009;
 67 Charlebois and Sargent 2017). For example, non-
 68 native plant species can negatively influence pollina-
 69 tion through decreases in average pollinator visitation
 70 rates (Brown et al. 2002; Bjerknes et al. 2007;
 71 Albrecht et al. 2016). Furthermore, if pollinators
 72 exhibit low floral constancy (i.e., they switch fre-
 73 quently between plant species in a single foraging
 74 bout), they could increase pollen wastage, or cause
 75 deposition of heterospecific pollen onto stigmas
 76 (Brown and Mitchell 2001; Bruckman and Campbell
 77 2016). In some cases this lack of floral constancy can
 78 lead to reductions in seed production of the native
 79 plant (Flanagan et al. 2009). In other instances, non-
 80 natives could facilitate the pollination of native
 81 species. For example, invasive plants can generate a
 82 larger floral display that attracts more pollinators to a
 83 patch, thus increasing the chances that a co-flowering
 84 species is visited by a pollinator (Jakobsson and
 85 **AQ3** Padrón 2014).

86 Invasive plants can also change the composition of
 87 flower visitors that are visiting native plants; for
 88 example, when only a subset of the pollinator species
 89 that visit a plant species change their visitation
 90 frequency in the presence of the invader (Albrecht
 91 et al. 2016). Additionally, changes in pollinator
 92 species composition can lead to differences in seed
 93 production if pollinators vary in effectiveness (Sahli
 94 and Conner 2007; Rafferty and Ives 2012). Thus the
 95 impact of invasive plants on the pollination of native
 96 plant species can be quite varied, and, as recent

research suggests, these effects can be highly context-
 dependent on the spatial scale and relative floral
 densities of the interacting species (Albrecht et al.
 2016; Bruckman and Campbell 2016).

Plant community composition can not only influ-
 ence the average level of pollination in a population,
 but it can also change natural selection exerted by
 pollinators on the floral traits of plants. Since the time
 of Darwin, natural selection by pollinators on floral
 traits has been viewed as critical to the evolutionary
 diversification of the Angiosperms (Harder and John-
 son 2009). Two pathways can lead to pollinator-
 mediated phenotypic selection on floral traits. Either
 the pollinator (i.e., selective agent) needs to show a
 preference (e.g., higher visitation rate) for certain trait
 values, or be more effective at transferring pollen from
 or to plants with certain trait values, such that a trait
 influences pollination success. In addition, for the trait
 to experience net selection the higher visitation or
 higher effectiveness must translate into higher fitness.
 If either of these relationships breaks down, for
 example, between visitation and fitness (Fig. 1a) or
 between the impact of a trait on pollinator visitation
 (Fig. 1b), net selection will be weakened (Fig. 1c).
 Impacts of an invasive plant species on average
 pollination and on selection of floral traits are both
 more likely for plant species that depend on animal
 pollination.

In communities of native plants, the presence of a
 competing plant species has been shown to influence
 the advantageous trait value for flowering phenology
 (Campbell 1985), daily display size (Wassink and
 Caruso 2013), selfing rate (Fishman and Wyatt 1999),
 and flower size (Caruso 2000). Similarly, invasive
 plant species could affect natural selection mediated
 by pollinators in native plants. In theory, selection in
 the presence of an invader could favor floral traits that
 enhance interspecific competitive ability through
 increasing pollinator attraction, or floral traits that
 minimize interspecific pollen transfer (Campbell and
 Motten 1985), for example by limiting access to
 specific pollinators or by altering pollen placement on
 the body of a pollinator. In addition, if stands of a
 highly invasive species attract a different set of floral
 visitors (Albrecht et al. 2016), that difference in visitor
 composition might also favor different floral trait
 values, thereby changing selection. So far, only one
 study has described the effects of an invasive plant on
 pollinator-mediated selection in a native plant species

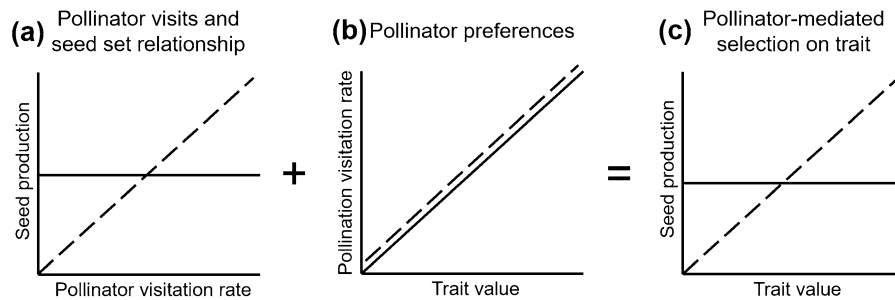


Fig. 1 Diagram showing how changes in linear relationships between pollinator visitation, plant reproduction, and floral traits lead to changes in the strength of selection. Contributions of **a** the relationship between pollinator visits and seed production, **b** pollinator trait preferences (selection based on visitation), and **c** to net selection through female function.

Different line types (solid and dashed) represent different years or invasive species treatments. While this figure panel describes the patterns in terms of some potential linear relationships, it is also possible for other linear, saturating, or other non-linear relationships to occur

147 (Beans and Roach 2015), finding that the native
 148 *Impatiens capensis* experienced selection for shorter
 149 corollas in the presence of the non-native *Impatiens*
 150 *glandulifera*, although whether that trait affected visit
 151 ^{AQ5} quantity or quality was not determined.

152 Impacts on both average pollination and selection
 153 mediated by pollinators may also vary with other
 154 ecological conditions. Temporal variation in pollina-
 155 tion across flowering seasons is often assumed yet not
 156 widely studied (Price et al. 2005). Pollination success
 157 can be influenced by spatiotemporal variation in
 158 pollinator species composition, pollinator effective-
 159 ness, and visitation by pollinators and pollen eaters
 160 (Herrera 1988; Horvitz and Schemske 1990; Fishbein
 161 and Venable 1996; Fenster and Dudash 2001; Price
 162 et al. 2005). Such variation in pollination success
 163 could, in turn, influence the strength and direction of
 164 pollinator-mediated selection (Benitez-Vieyra et al.
 165 2012). However, competitor effects have mostly been
 166 tested by examining the level of within-season rather
 167 than year-to-year variation in pollination success.
 168 Assessing consistency across years is critical to
 169 determine if selection consistently favors particular
 170 trait values, as fluctuating selection would weaken any
 171 ^{AQ6} evolutionary response (Grant and Grant 2002).

172 Here we assess how an invasive plant influences
 173 pollinator visitation rate and net selection through
 174 female function in a native plant species and deter-
 175 mine if these effects are consistent across 3 years. We
 176 focus on yellow toadflax (*L. vulgaris*), which is a
 177 highly invasive plant in the western mountains of the
 178 U.S. and other regions of North America and classified
 179 as a noxious weed in seven states (USDA and NRCS

2020). We examined the impact of this widespread
 180 invasive on a focal native plant species, *P. strictus*, in
 181 dry subalpine meadows in Colorado. We chose this
 182 species because it is often spatially intermixed, flowers
 183 simultaneously, and shares the same bumblebee
 184 visitors with *L. vulgaris* (Castellanos et al. 2004;
 185 Burkle et al. 2007). We experimentally removed
 186 flowers of *L. vulgaris* to test the impacts of the
 187 presence of *L. vulgaris* on *P. strictus* visitation and
 188 seed production during a growing season, and we
 189 looked at whether these effects were consistent over
 190 years. We answered the following questions. (1) Does
 191 the nearby presence of the invasive *L. vulgaris*
 192 influence the mean rate of pollinator visitation or seed
 193 production in *P. strictus*? We also tested for changes in
 194 species composition of flower visitors to address one
 195 potential mechanism that could alter natural selection.
 196 (2) Does the invasive influence the relationship
 197 between pollinator visitation and seed production
 198 (Fig. 1a)? (3) Does the invasive influence the rela-
 199 tionship of a floral trait to pollinator visitation
 200 (Fig. 1b; selection based on visitation)? (4) What are
 201 the resultant effects of the invasive on net selection
 202 through female function (Fig. 1c)? (5) How consistent
 203 are all these effects over 3 years that differed in the
 204 degree of flowering overlap between the plant species?
 205

Author Proof

206	Materials and methods	Calculating the effectiveness of <i>Penstemon strictus</i> visitors	252 253
207	Site and species description	In our study, <i>P. strictus</i> was visited by several species of hymenopterans, including <i>Anthophora terminalis</i> , <i>Bombus appositus</i> , <i>B. bifarius</i> , <i>B. californicus</i> , <i>B. flavifrons</i> , <i>Pseudomasaris vespoides</i> , and a wide variety of unidentified small solitary bees. To allow interpretation of patterns in visitation, in 2017 we measured the effectiveness of several of these visitors, in terms of seeds produced from a single visit (n = 113 single visits; n = 31 unvisited flowers), to flowers on 43 <i>P. strictus</i> plants (Online Resource 1: Methods S1).	254 255 256 257 258 259 260 261 262 263
208	Our study site was at the Lupine Trail near Nicholson Lake, Crested Butte, Colorado, United States (GPS coordinates: 38.903260, – 107.011476—WGS 84 Web Mercator). In this area, the invasive <i>Linaria vulgaris</i> Mill. (Scrophulariaceae) co-occurs and shares pollinators with the native <i>Penstemon strictus</i> Benth. (Scrophulariaceae). <i>L. vulgaris</i> is an herbaceous perennial plant that is native to Europe and Asia (Saner et al. 1995). It was introduced to North America in the nineteenth century and has spread widely, through both rhizomes and seeds, throughout the continental United States (Saner et al. 1995). Near our study site, <i>L. vulgaris</i> produces an average of 27 pale yellow flowers per flowering shoot and is pollinated by bumblebees such as <i>Bombus appositus</i> , <i>B. californicus</i> , <i>B. fervidus</i> , <i>B. flavifrons</i> , and <i>B. frigidus</i> (Burkle et al. 2007). <i>Penstemon strictus</i> , the Rocky Mountain Penstemon, is an herbaceous perennial plant native to the southern Rockies, present in Colorado, eastern Utah, eastern Arizona, southern Wyoming, and northern New Mexico (Ogle et al. 2013). This plant has a basal rosette from which one to a few inflorescences can arise (Ogle et al. 2013). Each inflorescence can have up to 50 purple flowers open at any given time and offers both pollen and nectar to its visitors (Thomson 1996). Near our field sites, <i>P. strictus</i> is visited by many insects, including wasps, solitary bees, and several species of bumblebees, including <i>Bombus bifarius</i> , <i>B. flavifrons</i> , <i>B. appositus</i> , and <i>B. californicus</i> (Thomson 1996, Wilson et al. 2004, W. Recart personal observation). In <i>P. strictus</i> , control, bagged flowers not exposed to pollinators, did not set seed, indicating that <i>P. strictus</i> is dependent upon animal visitation and does not self-pollinate in the absence of pollinators (Fig. S1; Online Resource 1: Methods S1).	Linaria removal experiment	264 265 266 267 268 269 270 271 272 273 274 275 276 277 278 279 280 281 282 283 284 285 286 287 288 289 290 291 292 293 294 295 296 297
209	The degree of flowering overlap between the two species varied across the 3 years. In 2015 and 2017 <i>L. vulgaris</i> and <i>P. strictus</i> flowered at the same time, from mid-July (approximately July 12th) through late-August (approximately August 20th). In 2016 <i>L. vulgaris</i> did not bloom during the time of our pollinator observations on <i>P. strictus</i> (Online Resource 1: Fig. S2).	We examined whether the nearby presence of the invasive <i>L. vulgaris</i> influenced mean visitation rate by floral-visitors (as a proxy for pollinator visitation), visitor composition, selection based on visitation, and net selection in the native <i>P. strictus</i> . We tested these effects in 2015, 2016, and 2017 at the Lupine Trail field site. In each year, we established experimental blocks at this site, with seven blocks in 2015, five additional blocks in 2016, and five additional blocks in 2017 (more details on the sample sizes are found in Online Resource 1: Table S1). Each block was placed over a continuous <i>L. vulgaris</i> patch. In our field site these <i>L. vulgaris</i> patches do not usually exceed the area of our block size, thus our blocks are representative of the maximum patch size that can be found in this area. Each block had two 3 by 3 m plots that were 3 meters apart, and each plot received one of the two <i>L. vulgaris</i> treatment, either <i>L. vulgaris</i> flowers present or <i>L. vulgaris</i> flowers removed by clipping inflorescences (Fig. 2a). Five potted or cut inflorescences of <i>P. strictus</i> , obtained from the Lupine trail site, were placed into each plot, arranged in the form of an X (Fig. 2a). Both cut and potted inflorescences were brought to the field site on the day pollinator observations were made and set out just prior to beginning observations. Insects sometimes visited those flowers within a few minutes of placement. Each block was at least 10 meters away from other blocks. The <i>P. strictus</i> density in the experimental blocks (0.37 <i>P. strictus</i> individuals/m ²) resembled the average density of <i>P. strictus</i> in our field site (0.36) under the assumption of a random distribution, while at the same time maximized the number of plants we	264 265 266 267 268 269 270 271 272 273 274 275 276 277 278 279 280 281 282 283 284 285 286 287 288 289 290 291 292 293 294 295 296 297

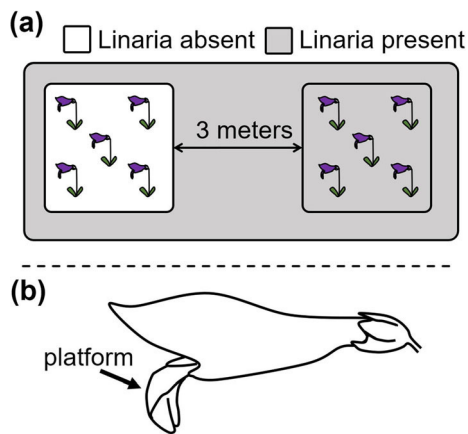


Fig. 2 **a** Diagram of the experimental design applied and replicated during the 3 years of the experiment. Gray space represents areas where *L. vulgaris* is present. The bigger outer square represents the block and the inner two squares represent the plots containing the *L. vulgaris* treatment: removed (white square) or present (gray square). The plots are three meters by three meters and are three meters apart. Inside the plots there are five *P. strictus* individuals—represented by each green rosette with a purple flower. **b** Flower of *P. strictus* showing the landing platform—the floral trait of interest in this experiment

298 were able to observe at each plot (details on density
299 calculation in Online Resource 1: Methods S2).
300 During 2016, only a few individuals of *L. vulgaris*
301 bloomed at the field site and they did so later in the
302 summer (early August through late August) than *P.*
303 *strictus* (see Online Resource 1: Fig. S2). Thus, we
304 were not able to implement the *L. vulgaris* removal in
305 2016. We still collected data during this year and used
306 the same experimental design (without conducting the
307 *L. vulgaris* removal but keeping two observation plots
308 within each block) and data collection protocol
309 (Fig. 2a).

311 Some methodological details differed across the 3
312 years (Online Resource 1: Table S2). In 2015 we used
313 cut inflorescences only, allowing measurements of
314 pollinator visitation but not of seed production. Cut
315 inflorescences were placed in floral picks with water,
316 and floral traits were measured immediately after
317 pollinator observations were complete. In 2016 we
318 used potted *P. strictus* individuals. In 2017 two of the
319 blocks contained cut inflorescences, and the other
320 three contained potted *P. strictus* individuals. By using
321 cut and potted *P. strictus* individuals we eliminated
322 belowground inter- and intra-specific competition
323 with other plants. All potted *P. strictus* plants were
324 overwintered at the Rocky Mountain Biological

Laboratory and placed in a pollinator-free greenhouse
to prevent visitation by pollinators. Plants needed to be
overwintered since the shock of transplantation pre-
vented them from blooming during the same flowering
season. *P. strictus* plants were placed in 4L pots and
planted using soil from our field site, where they were
collected.

In all 3 years, pollinators were observed on *P.*
strictus for three hours at both plots (*L. vulgaris*
present or removed) in each block to determine plot
level visitation rate (visits per open flower per hour)
and species composition of the flower visitors of *P.*
strictus. Pollinators were assigned to one of the two
following groups, *Bombus* spp. or non-*Bombus* insect
group. The distinction between *Bombus* spp. and non-
Bombus insects was made because bumblebees were
the most common and effective pollinator group (see
Results on Effectiveness). In the *Bombus* group,
bumblebees were identified as *B. bifarius* or not-*B.*
bifarius. We did this further distinction in the *Bombus*
group because *B. bifarius* was the most common floral
visitor to *P. strictus*. We observed plots simultane-
ously when two observers were in the field. When
there was only one observer in the field, the observer
alternated every hour between the two plots. Pollinator
observations were completed on each block before
conducting pollinator observations in another block.
Using this protocol, it took one or two days to fully
complete the three hours of pollinator observations for
both plots in a single block. Thus, before moving to the
next block we collected data from a plot where *L.*
vulgaris was removed and one where *L. vulgaris* was
present. More details on the duration of the pollinator
observations can be found in the Online Resource 1:
Fig. S2. Pollinator observations were conducted
during sunny days (no overcast or rain) and during
the day (9:00–16:00). The entire experiment included
102 plot-hours of observation. Each individual (potted
or cut inflorescence) was observed only once for three
hours during the experiment. We calculated seed
production per flower and per fruit from all the flowers
open during the pollinator observations from the
potted *P. strictus* individuals (data only available in
2016 and 2017). When potted *P. strictus* individuals
were not used for pollinator observations they were
inside a pollinator-free enclosure.

We used the abovementioned experimental setup to
assess the impact of *L. vulgaris* on pollinator-mediated
phenotypic selection on the trait of platform length

(Fig. 2b). We focus on pollinator visitation, as one component of fitness (Arnold and Wade 1984; Campbell et al. 1991) and refer to that relationship as “selection based on visitation” (Campbell et al. 1996). We also document female fitness as estimated by seed production and use the shorthand “net selection” to refer to the impact of a trait on seed production, recognizing that selection can also occur through male fitness (Stanton et al. 1986) or be influenced by events after seed formation (Campbell et al. 2017). We chose platform length because a landing platform is present in bee-pollinated *Penstemon* species and absent in hummingbird-pollinated *Penstemon* spp. (Castellanos et al. 2003; Wilson et al. 2004), suggesting it could be a trait under strong selection by bees, which are the shared pollinators with *L. vulgaris*. Pilot pollinator observations on *P. strictus* showed that bumblebees interacted with the platform by hanging on to this surface to access the nectar or pollen rewards present inside the flower. Experimentally reducing platform size reduced bumblebee visitation to *P. strictus* in a previous study, demonstrating selection on that trait, and so did restricting corolla tube width (Zung et al. 2015). We recognize that these two traits—corolla tube width and platform size—could be correlated, such that we cannot unambiguously distinguish between selection on the two traits. Platform length was measured with a digital caliper, from the split of the fused petals to the end of the platform (Fig. 2b), and averaged across three measured flowers for each *P. strictus* individual. To estimate selection, we examined the effects of platform length on both pollinator visitation rate (i.e., selection based on visitation) and seed production (i.e., net selection).

408 Statistical analysis

409 All data analysis was performed using the R statistical
410 program version 3.4.4 (R Core Team 2018). All
411 pollinator visitation data were analyzed for the
412 following categories: all pollinator visitors, only
413 bumblebee pollinators, and only non-bumblebee pol-
414 linators. All seed production data were analyzed as
415 seeds per flower (total seeds divided by the number of
416 open flowers). For all statistical analyses, normality of
417 the residuals was tested using the Shapiro–Wilks test
418 (shapiro.test function), and pollinator visitation rate
419 was square-root transformed in order to achieve
420 normality of the residuals.

Effects of Linaria vulgaris on pollinator visitation, 421
visitor composition, and seed production (Question 1) 422

Mean rate of pollinator visitation to *P. strictus* (n = 24 423
plots) was analyzed using a linear mixed effects model 424
(hereafter LME; using lme4 package, lmer function) 425
with *L. vulgaris* treatment and year as fixed crossed 426
effects and block as a random effect nested within year 427
(Bates et al. 2015; statistical models summarized in 428
Online Resource 1 Table S2). Mean seed production 429
for a plot (n = 6 plots) was analyzed using *L. vulgaris* 430
treatment as a fixed effect and block as a random effect 431
using only the 2017 data. We analyzed the effect of *L.* 432
vulgaris treatment on *P. strictus* visitor composition 433
(n = 24 plots) using MANOVA on visitation rate by *B.* 434
bifarius, bumblebees other than *B. bifarius*, and non- 435
bumblebee pollinators, with block identity as an 436
additional factor. 437

Effects of Linaria vulgaris on the relationship 438
between visitation and seed production (Question 2) 439

The relationship between pollinator visitation rate and 440
seed production (3 blocks, n = 26 plants) was only 441
analyzed with 2017 data, as that was the only year with 442
appropriate data (see Online Resource 1: Table S2). 443
Due to the small sample size, we could not analyze the 444
full LME with block nested within *L. vulgaris* 445
treatment. Instead, we first ran a linear model deter- 446
mining whether block identity influenced seed pro- 447
duction. Since we detected no effect of block, we then 448
ran a linear model to determine whether pollinator 449
visitation rate and *L. vulgaris* treatment interacted in 450
their effects on seed production. 451

Effects of Linaria vulgaris on pollinator-mediated 452
selection (Question 3 and 4) 453

To examine selection based on visitation and its 454
dependency on the invasive species (Question 3), we 455
used a LME where each data point consisted of a *P.* 456
strictus individual for which we had a mean platform 457
length value and a pollinator visitation rate value as 458
the fitness components (n = 103 plants). We set 459
platform length, *L. vulgaris* treatment and year as 460
fixed crossed effects and block identity was nested 461
within year. In cases where we did not detect an 462
interaction between platform length and presence of *L.* 463
vulgaris, we then performed a standard analysis of 464

465	covariance in which we removed the interaction term	511
466	to determine the overall slope of the fitness component	512
467	on platform length. Lastly, to enable comparisons of	
468	selection in this study with those of other plant species,	513
469	we expressed the strength of selection as a standard-	514
470	ized selection differential. A standardized selection	515
471	differential is the change in the average value of the	516
472	trait due to phenotypic selection, expressed in units of	517
473	standard deviation of the trait. To estimate standard-	518
474	ized selection differentials, we repeated the ANCOVA	
475	using untransformed pollinator visitation rate relative	519
476	to the mean as the dependent variable and platform	
477	length standardized to a mean of zero and standard	
478	deviation of one (Kingsolver et al. 2001).	
479	Net selection (Question 4) was examined by	
480	repeating the analyses described for estimating selec-	
481	tion based on visitation and standardized selection	
482	differentials but using seed production per flower as	
483	the dependent variable (n = 15 plants).	
484	<i>Yearly variation in pollinator visitation and seed</i>	
485	<i>production (Question 5)</i>	
486	To analyze the effects of year on mean pollinator	
487	visitation and on selection, we took out the <i>L. vulgaris</i>	
488	treatment from the statistical analysis allowing us to	
489	analyze all years of data collection (2015 through	
490	2017; Online Resource 1: Table S3). The effect of year	
491	on mean plot pollinator visitation rate was analyzed	
492	using a LME with year as a single fixed effect and the	
493	random effect of plot identity nested within year	
494	(n = 34 plants).	
495	The relationship between pollinator visitation rate	
496	and seed production was analyzed for 2016 and	
497	2017—when we had both pollinator visitation data	
498	and seed production data, by using a LME with year as	
499	a fixed effect crossed with pollinator visitation, and	
500	seed production per flower set as the dependent	
501	variable (n = 74 plants).	
502	We used a LME to determine whether the year (data	
503	from 2015 to 2017) influenced the relationship	
504	between platform length and pollinator visitation rate	
505	(selection based on visitation). For this model, each	
506	data point consisted of a <i>P. strictus</i> individual for	
507	which we had a mean platform length value and a	
508	pollinator visitation rate value (n = 148 plants), with	
509	year and platform length set as fixed crossed effects	
510	and plot identity nested within year. We also	
	calculated standardize selection differentials using	511
	the same approach as detailed for Question 3.	512
	We used a linear model to determine whether the	513
	year (2016 or and 2017) influenced the relationship	514
	between platform length and seed production (net	515
	selection; n = 60 plants). Selection differentials were	516
	calculated as described previously using seeds per	517
	flower as the dependent variable.	518
	Results	519
	Effectiveness of <i>Penstemon strictus</i> visitors	520
	A visit to <i>P. strictus</i> by <i>Bombus</i> spp. yielded three	521
	times more seeds than did a visit by a non- <i>Bombus</i>	522
	insect, making the bumblebees a more effective	523
	pollinator group (Online Resource 1: Table S5 and	524
	Fig. S1). The results below focus on the following	525
	categories: all flower visitors, <i>Bombus</i> spp., and <i>B.</i>	526
	<i>bifarius</i> (the most common bumblebee visitor). Anal-	527
	ysis on non- <i>Bombus</i> insects for this and subsequent	528
	sections are reported in the online resource file (Online	529
	Resource 1: Results S1).	530
	Effects of <i>Linaria vulgaris</i> on pollinator visitation,	531
	visitor composition, and seed production	532
	(Question 1)	533
	In the removal experiments, the presence of <i>L.</i>	534
	<i>vulgaris</i> increased by 50% the mean visitation rate	535
	by all flower visitors to <i>P. strictus</i> ($\bar{x} \pm 1SE$:	536
	present = 0.95 ± 0.15 , removed = 0.64 ± 0.08 ;	537
	$F_{1,10} = 6.87$, $P = 0.03$, Fig. 3). This increase in	538
	visitation was likely driven by a 76% increase in	539
	visitation by <i>B. bifarius</i> ($F_{1,10} = 3.94$, $P = 0.07$) and a	540
	57% increase in visitation by other visitors	541
	($F_{1,10} = 3.73$, $P = 0.08$). Visitor composition was	542
	not influenced by the presence of <i>L. vulgaris</i>	543
	(MANOVA: $F_{1,21} = 0.57$, $P = 0.64$). Even with only	544
	3 blocks in 2017 available for testing the impact on	545
	seed production, there was a trend for the presence of	546
	<i>L. vulgaris</i> to increase the seed production per flower	547
	of <i>P. strictus</i> by 80% ($\bar{x} \pm 1SE$: pre-	548
	sent = 18.44 ± 4.92 , removed = 10.23 ± 2.68 ;	549
	$F_{1,2} = 13.34$, $P = 0.07$).	550
		551

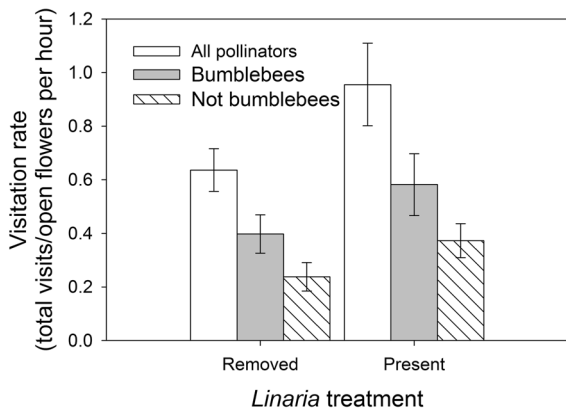


Fig. 3 Pollinator visitation rates to *P. strictus* in the removal or presence of *L. vulgaris* sorted by different pollinator groups. Means and standard errors are shown, based on the means of visitation rate grouped by *L. vulgaris* treatment and pollinator group

552 Effects of *Linaria vulgaris* on the relationship
 553 between visitation and seed production (Question
 554 2)

555 In 2017, we detected a positive relationship between
 556 visitation rate by all visitors and seed production per
 557 flower ($F_{1,22} = 13.43, P = 0.001$, Fig. 4a). This
 558 relationship was not affected by the presence of *L.*
 559 *vulgaris* (interaction term: $F_{1,22} = 0.10, P = 0.75$,
 560 Fig. 4a), as slopes were similar whether *L. vulgaris*
 561 was present (slope = 1.78) or removed (2.49). Since
 562 pollinator visitation was markedly reduced in the
 563 absence of *L. vulgaris*, visitation rate in that situation
 564 has a smaller range, but there was no evidence for any
 565 curvature in the relationship (quadratic term $P = 0.63$
 566 in quadratic regression of seed production on visita-
 567 tion in presence of *L. vulgaris*). Seed production also
 568 increased with higher bumblebee visitation ($F_{1,22} =$
 569 $4.94, P = 0.04$). This pattern was seen for visitation
 570 specifically by *B. bifarius* ($F_{1,22} = 5.59, P = 0.03$), but
 571 not for other bumblebee visitors ($F_{1,22} = 0.05,$
 572 $P = 0.82$), suggesting that the increase in bumblebee
 573 visitation was driven by an increase in *B. bifarius*
 574 visitation. The relationship between seed production
 575 and bumblebee visitation was not influenced by the
 576 presence of *L. vulgaris* (interaction term $F_{1,22} = 0.01,$
 577 $P = 0.92$). The presence of *L. vulgaris* also did not
 578 influence the relationship between visitation by *B.*
 579 *bifarius* and seed production ($F_{1,22} = 0.11, P = 0.74$).
 580

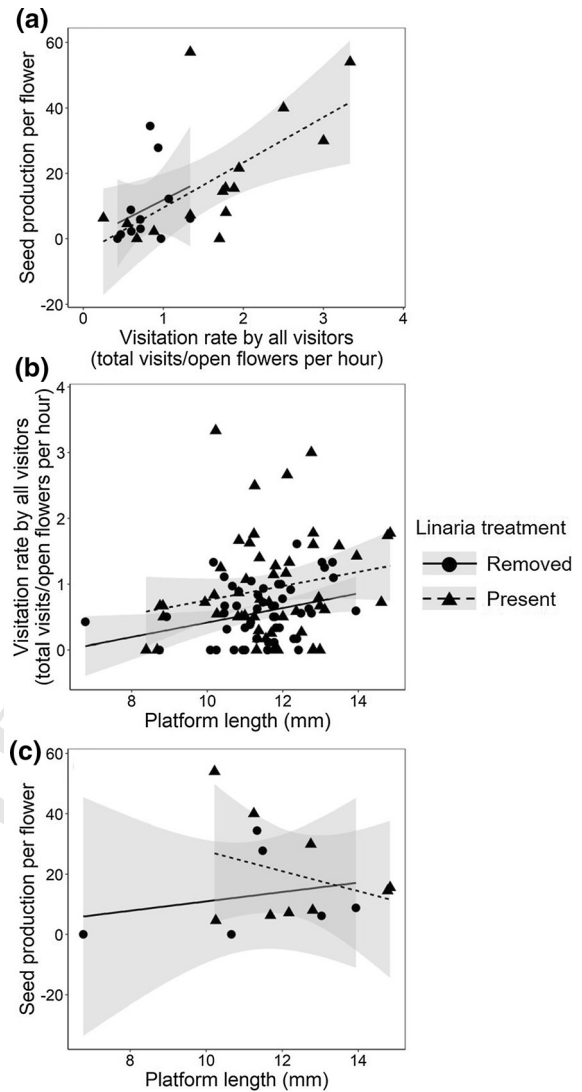


Fig. 4 Relationships in the removal and presence of *L. vulgaris* between **a** pollinator visitation rate and seed production per flower in *P. strictus*, **b** *P. strictus* platform length and visitation rate by all pollinators, and **c** *P. strictus* platform length and seed production per flower. Gray shading around each regression line represents 95% confidence intervals

Effects of *Linaria vulgaris* on pollinator-mediated selection (Question 3 and 4) 581 582

The presence of *L. vulgaris* did not detectably alter the slope of pollinator visitation on the trait of platform length ($F_{1,90} = 0.83, P = 0.37$, Fig. 4b). Plants with longer platforms had higher visitation rate by all flower visitors combined ($F_{1,95} = 4.41, P = 0.04$), with a standardized selection differential equal to 0.09 583 584 585 586 587 588

(Fig. 4b). This relationship between platform length and visitation rate was lost, however, when looking at any given visitor group (*Bombus* spp.: $F_{1,93} = 1.58$, $P = 0.21$; non-*Bombus* spp.: $F_{1,92} = 2.67$, $P = 0.11$; *B. bifarius*: $F_{1,90} = 1.39$, $P = 0.24$; other *Bombus* spp.: $F_{1,92} = 0.35$, $P = 0.56$). In the 2017 experiment manipulating *L. vulgaris*, net selection did not differ detectably from zero ($F_{1,11} = < 0.001$, $P = 0.99$, Fig. 4c). That net selection strength did not differ depending on whether *L. vulgaris* was present (interaction $F_{1,11} = 1.0811$, $P = 0.32$) and that remained so after removing the one outlier that made the ranges of platform length different across the two treatments ($P = 0.95$).

Yearly variation in pollinator visitation and seed production (Question 5)

When grouping all the data by year independently of the *L. vulgaris* treatment we found that mean visitation rate by all flower visitors (averaged by plot identity) to *P. strictus* varied greatly across years ($\bar{x} \pm 1\text{SE}$: 2015 = 0.70 ± 0.11 , 2016 = 2.36 ± 0.38 , 2017 = 0.93 ± 0.16 ; $F_{2,14} = 9.71$, $P = 0.002$, Fig. 5). Visitation rate by all visitors was 195% higher in 2016, the year of non-overlap, than in 2015 and 2017 (Tukey-HSD test $P \leq 0.001$). This increase in visitation rate was not due to grouping together visitation rate independently of *L. vulgaris* treatment (for 2015 and 2017 data); when we analyzed visitation rate using data only from one treatment at a time (either *L. vulgaris* present or *L. vulgaris* removed) along with

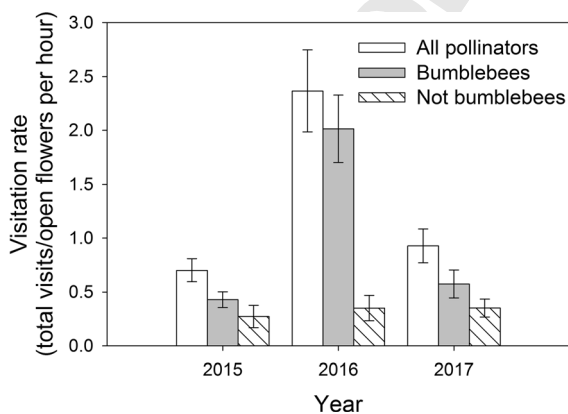


Fig. 5 *Penstemon strictus* pollinator visitation rate from 2015 to 2017. Means and standard errors are shown, based on the means of visitation rate grouped by year and pollinator group

the 2016 visitation data, we saw the same patterns reported above. Visitation rate by bumblebees also varied across years ($F_{2,14} = 13.30$, $P \leq 0.001$, Fig. 5), with bumblebee visitation being 310% higher in 2016 than in 2015 and 2017 (Tukey-HSD test $P \leq 0.001$). Visitation by *B. bifarius* (the most frequent visitor to *P. strictus*) did not vary detectably across years ($F_{2,14} = 0.98$, $P = 0.40$). In contrast, visitation by other species of *Bombus* changed across years ($F_{2,14} = 17.94$, $P \leq 0.001$) and was highest in 2016 when compared to 2015 and 2017 (Tukey-HSD test $P \leq 0.001$). Seed production per flower did not differ significantly between 2016 and 2017 ($\bar{x} \pm 1\text{SE}$: 2016 = 9.65 ± 1.59 , 2017 = 14.34 ± 3.11 ; $F_{1,6} = 1.64$, $P = 0.25$).

Seed production per flower increased with the visitation rate by all flower visitors in 2017 but did not change detectably in 2016 (interaction of year \times visitation rate, $F_{1,70} = 9.84$, $P = 0.002$, Fig. 6a). This was also the case when using visitation by bumblebees only (interaction term $F_{1,50} = 11.27$, $P = 0.001$) and when looking at *B. bifarius* visitors (interaction term $F_{1,70} = 16.69$, $P = 0.0001$). There was no relationship between visitation rate and seed production per flower for other bumblebee species ($F_{1,70} = 2.01$, $P = 0.16$).

Yearly variation in pollinator-mediated selection (Question 5)

Total visitation by all flower visitors increased with platform length in *P. strictus* indicating selection based on visitation ($F_{1,140} = 5.66$, $P = 0.02$, Fig. 6b [showing 2016 and 2017 data]), with a standardized selection differential of 0.06. That selection on platform length was similar across the 3 years of the experiment (interaction of trait \times year, $F_{2,140} = 0.46$, $P = 0.63$, Fig. 6b [showing 2016 and 2017 data]). A similar pattern was seen when only looking at the bumblebee visitors; the interaction between year and visitation rate was not detectable ($F_{2,137} = 1.75$, $P = 0.18$) and there was a positive effect of platform length on visitation rate by bumblebees ($F_{1,137} = 3.86$, $P = 0.05$). Interestingly, platform length had no detectable effect on *B. bifarius* visitation ($F_{1,32} = 0.33$, $P = 0.56$), but it did positively influence visitation by other bumblebees ($F_{1,137} = 6.13$, $P = 0.01$). We also detected a significant interaction between platform length and year on visitation by other



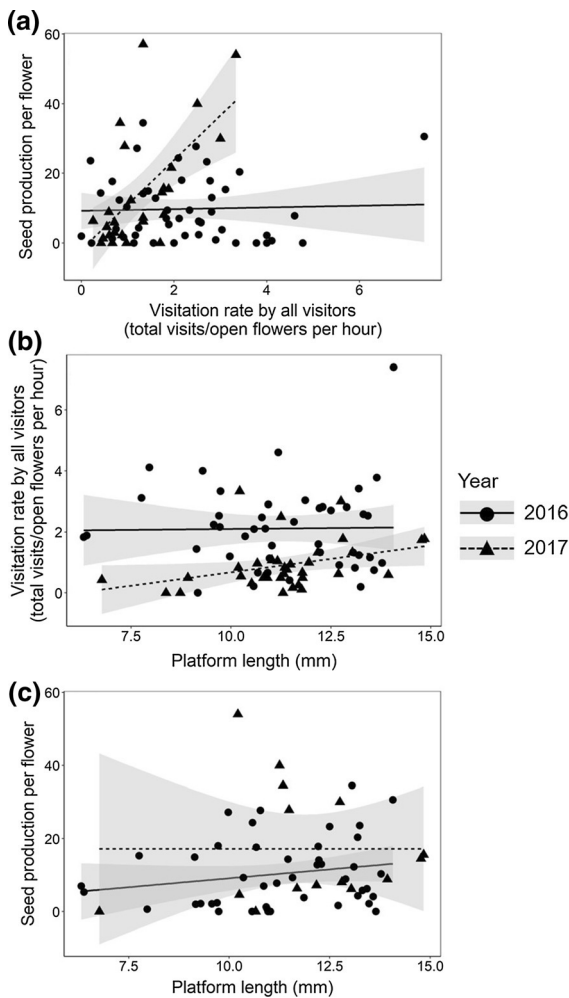


Fig. 6 Relationships in 2016 and 2017 between **a** visitation rate by all visitors to *P. strictus* and seed production per flower, **b** *P. strictus* platform length and visitation rate by all pollinators, and **c** *P. strictus* platform length and seed production per flower. Gray shading around each regression line represents 95% confidence intervals

666 bumblebees ($F_{2,137} = 5.51$, $P = 0.005$) with a steeper
 667 relationship in 2016. There was no detectable relation-
 668 ship between platform length and seed production
 669 within or across years (standardized selection differ-
 670 ential = 0.12, $F_{1,56} = 3.02$, $P = 0.09$; Fig. 6c), mean-
 671 ing that net selection was not detected throughout this
 672 experiment.
 673

Discussion

We saw two main patterns in average pollinator
 675 visitation and seed production. First, the nearby
 676 presence of the invasive plant *L. vulgaris* increased
 677 pollinator visitation rate and seed production of *P.*
 678 *strictus*. Second, these measures of average reproduc-
 679 tive success varied considerably across 3 years of the
 680 study. The first pattern indicates facilitation, which
 681 could be partially driven by the small spatial scale at
 682 which the non-native plant was manipulated. It is
 683 plausible that the non-native *L. vulgaris* serves as a
 684 magnet species, attracting pollinators to patches with
 685 *L. vulgaris* which then leads to an increase in
 686 pollinator visitation to *P. strictus*. Such facilitative
 687 effects are more commonly reported when the distance
 688 between control and removal treatments is small
 689 (Albrecht et al. 2016; Bruckman and Campbell 2016;
 690 Charlebois and Sargent 2017).
 691

Although we saw facilitation in our small-scale
 692 manipulation of *L. vulgaris*, our comparison across 3
 693 years suggests that *L. vulgaris* may successfully
 694 compete for pollination at a scale larger than our
 695 removals. In our second pattern, *P. strictus* exhibited
 696 higher visitation rates in a year (2016) of non-overlap
 697 in flowering compared to 2 years when *L. vulgaris* was
 698 present. Since 2016 did not have higher abundances of
 699 bumblebees than in 2015 (Ogilvie et al. 2017), it is
 700 unlikely that the temporal pattern is explained simply
 701 by temporal variation in bee abundances, as can be
 702 common in other systems (Horvitz and Schemske
 703 1990). In contrast, it could be due to competition for
 704 pollination over a much wider spatial scale. One recent
 705 study found negative effects of heterospecific density
 706 at a community-wide scale even though they were
 707 absent at a finer neighborhood spatial scale (Albor
 708 et al. 2019). Our results suggest that even though the
 709 invasive *L. vulgaris* facilitates local visitation, it may
 710 have overall negative impacts on pollination over a
 711 much wider spatial scale.
 712

We expected the *L. vulgaris* treatment to strongly
 713 influence the visitation rates by shared pollinators
 714 (e.g., *Bombus* spp.) when compared to non-shared
 715 pollinators, yet this was not the case. In our system we
 716 saw increase in visitation by both shared and non-
 717 shared pollinators in the presence of nearby *L. vulgaris*.
 718 Contrastingly, in other systems, the shared pollinator
 719 group was the pollinator guild that exhibited variation
 720 in visitation rate with the invasive treatment (Albrecht
 721

et al. 2016; Bruckman and Campbell 2016). One possibility is that pollinators cue on *L. vulgaris* flowers to identify flowering patches and once near these patches they forage for suitable flowers (Hegland et al. 2009). If this is the case, we should expect a relationship between *L. vulgaris* flowering density and pollinator visitation rate to *P. strictus*. While the nearby presence of *L. vulgaris* increased visitation by all pollinators, we did detect an increase by bumblebees other than *B. bifarius* in the year when *L. vulgaris* was not co-flowering with *P. strictus*, in 2016. This *Bombus* group (bumblebees other than *B. bifarius*) are effective pollinators to *P. strictus* (based on seeds produced from a single visit; Online Resource 1 Fig. S1), and thus the temporal absence of *L. vulgaris* should have positively influenced the seed production of *P. strictus*. Nevertheless, we detected no difference in seed production between 2016 and 2017. One explanation for this pattern is that we did not detect a positive relationship between visits by this specific pollinator group and seed production in either 2016 and 2017 even though we did for some other pollinator types in 2017.

The invasive plant (*L. vulgaris*) increased both pollinator visitation and seed production per flower to the native plant (*P. strictus*), but did not alter the relationship between these two variables, visitation and seed production. It is conceivable that we would have detected a difference with larger sample sizes, especially when the invasive was removed and the range of visitation values was smaller, but there was no evidence that the relationship was non-linear. Thus, the increase in seed production in the presence of *L. vulgaris* is unlikely due to changes in pollinator effectiveness but instead to simple increase in pollinator visitation. This result aligns with other research studying ‘magnet species’ where the presence of another species increases both pollinator visitation and seed production in the target species (Molina-Montenegro et al. 2008). In addition, visitation by all *Bombus* species was more strongly and positively correlated with seed production, when compared to that by other pollinator groups—even though this was the pollinator group that was shared between the two species. This pattern has also been detected in another system, where a native co-flowering species increased visitation rates and seed production of another native co-flowering species (Yang et al. 2013). In this system, the authors hypothesized that the lack of interspecific

pollen transfer was due to differences in flower morphology between the two species and a high pollinator flower constancy (Yang et al. 2013). Both differences in floral morphology between *L. vulgaris* and *P. strictus* and pollinator flower constancy could be factors that in our system maintained the high effectiveness of the shared pollinator group, *Bombus* spp., although we did not measure the degree of constancy.

In contrast, the relationship between pollinator visitation and seed production varied across years, suggesting that visitation data alone is not always a reliable measure of impacts on reproduction, despite its common use in studies of competition or facilitation for pollination (Charlebois et al. 2017). This change in the relationship between visitation and seed production held not only for all visitors combined but also for *B. bifarius*. This temporal variation could be due to variation in pollen quality and quantity, or to changes in maternal resources. Since all potted plants were overwintering in the ground it is theoretically possible that differences in snowmelt timing between the 2 years could have influenced soil moisture (Blankinship et al. 2014) and altered resource allocation in these plants, however the 2 years only differed by 5 days in snowmelt at a nearby weather station in Gothic, Colorado (<http://gothicwx.org>). Changes in water availability throughout the flowering season between the 2 years could not be responsible since for both years we used potted plants subject to the same watering regime. It is also possible that pollen quality or quantity was different across the 2 years. For example, in *Phacelia parryi*, variation in water availability to conspecific pollen donors influenced seed production, presumably by affecting pollen quality (Recart et al. 2019). Differences in pollen production across years have been suggested to explain differences in the relationship between pollinator visitation and seed production for *Ipomopsis aggregata*, a common species at our field sites (Waser and Price 2016). Additional studies are needed to determine whether changes in the relationship between pollinator visitation and seed production are driven by changes in maternal resource limitation, pollinator behavior, pollen quantity, pollen quality or a combination.

In the *L. vulgaris* manipulation, selection based on visitation favored longer platforms, with a strength (standardized selection differential = 0.09) indicating

820 that the average trait value could be changed by up to
 821 0.09 SD in a generation. That strength of selection is
 822 similar to that seen on average in studies of selection
 823 on flower size that used pollination success as a fitness
 824 measure (Harder and Johnson 2009). The removal of
 825 *L. vulgaris* did not appear to influence selection based
 826 on visitation on *P. strictus*. This lack of effect could be
 827 in part due to a lack of change in the visitor
 828 composition with *L. vulgaris* treatment. If visitor
 829 composition had changed and pollinators were track-
 830 ing different floral traits or trait values, then we should
 831 have seen a change in selection based on visitation in
 832 the removal versus presence of *L. vulgaris*. Alterna-
 833 tively, pollinators could change their floral preferences
 834 due to changes in floral neighborhood and thus
 835 influence selection based on visitation (Caruso 2000;
 836 Beans and Roach 2015). Our data suggest that the
 837 pollinators retain their trait preferences independently
 838 of the presence or removal of the invader, with the
 839 caveat that we only studied one trait. In a previous
 840 study, the invasive plant *Impatiens glandulifera* influ-
 841 enced pollinator-mediated selection experienced by
 842 the native plant *Impatiens capensis* (Beans and Roach
 843 2015). The two species of *Impatiens* had more similar
 844 flower morphology compared to the species in our
 845 study. This flower shape similarity could have
 846 increased interspecific pollen transfer, leading to a
 847 change in selection in the presence of the invader. In
 848 two other studies looking at interactions between two
 849 native species, results have varied, with *Castilleja*
 850 *linariaefolia* altering selection on corolla length of
 851 *Ipomopsis aggregata* (Caruso 2000), while *Mimulus*
 852 *ringens* did not alter selection on corolla lobe length,
 853 corolla tube length, stigma–nectary distance or petal
 854 color in *Lobelia siphilitica* (Wassink and Caruso
 855 2013).

856 Even though pollinator visitation and seed produc-
 857 tion of *P. strictus* were affected by the presence of *L.*
 858 *vulgaris*, we were unable to detect differences in
 859 pollinator-mediated selection on platform length.
 860 While platform length is a floral trait involved in the
 861 evolution of hummingbird and bee-visited *Penstemon*
 862 species (Castellanos et al. 2003; Wilson et al. 2004), it
 863 is plausible that other floral traits related to nectar and
 864 pollen accessibility could have been selected for
 865 differently in the presence of *L. vulgaris*. With only
 866 a few case studies of how invasive species influence
 867 pollinator-mediated selection, we still cannot gener-
 868 alize about when such effects will be common. Future

869 research should address whether the presence of
 870 pollinator sharing, and shared pollinator-attractive
 871 trait values are characteristics that promote changes in
 872 pollinator-mediated selection. Net selection was not
 873 detected in either the presence or removal of *L.*
 874 *vulgaris*. This lack of detection could be due to a
 875 relatively small sample size and low statistical power
 876 rather than an absence of net selection since both the
 877 relationships between platform length and visitation,
 878 and between visitation and seed production were
 879 present in that experiment.

880 Selection based on visitation was present in all 3
 881 years. Ultimately, this selection based on visitation did
 882 not translate to detectable net selection in 2016 or
 883 2017, as seen by a lack of a significant relationship
 884 between platform length and seed production even
 885 though the estimate of net selection was as high as for
 886 selection based on visitation (0.12 vs. 0.09; Fig. 6b).
 887 The apparent lack of net selection was most likely due
 888 to a lack of a positive relationship between pollinator
 889 visitation rate and seed production in 2016 and an
 890 overall weak relationship between visitation and
 891 platform length in 2016 and 2017. For selection based
 892 on visitation to translate into net selection based on
 893 female fitness there needs to be a correlation between
 894 visitation rate and seed production as reported from
 895 some other plant–pollinator systems (e.g., Galen 1989;
 896 Gómez 2000) but seen only inconsistently through the
 897 years here.

898 Studies looking at the evolutionary effects of non-
 899 native plant species that are mediated by plant enemies
 900 or mutualists are scarce (Lau 2008, 2012; Beans and
 901 Roach 2015). As non-native plant species become
 902 increasingly embedded in native ecosystems their
 903 evolutionary impacts on other species become ever
 904 more pressing to document. Most such studies have
 905 focused on direct impacts of the non-native plant on
 906 selection in the native (Oduor 2013) rather than the
 907 possibility of diffuse selection (sensu Iwao and
 908 Rausher 1997), in which presence of the non-native,
 909 such as another plant, influences selection mediated by
 910 another organism, such as a pollinator. Here we
 911 showed how an invasive plant impacted average
 912 pollinator visitation and seed production but not
 913 natural selection on a plant trait mediated by pollina-
 914 tors. Our study also illustrates how year-to-year
 915 variation in the presence of a plant invader can
 916 influence the outcomes of interactions between native
 917 plant species and other trophic levels.

918	Conclusion		
919 920 921 922 923 924 925 926 927 928 929 930 931 932 933 934 935 936 937 938 939 940 941	The long-term impacts of invasive species may depend on evolution in response to the new biotic conditions, but little is known about whether, or how, invasive plants influence selection mediated by pollinators. The non-native <i>L. vulgaris</i> facilitated the pollination of nearby <i>P. strictus</i> but did not influence the relationship between visits and seed production, or pollinator-mediated selection based on visitation. In 1 year, seed production related strongly to visitation, with a weak yet detectable pollinator preference for the trait of platform length. In another year, pollinators preferred long platforms, but there was no relationship between visitation and seed production. Different elements of the selection process were stronger in different years, but in neither year did the focal trait have an overall net detectable effect on seed production. These results emphasize the importance of measuring multiple mechanisms that can contribute to net selection. They furthermore provide an illustration of year-to-year variation in the impacts of invasive species on interactions between native species, emphasizing the need for longer studies of impacts mediated by pollinators.	effectiveness measurements. Results S1: Findings when analyzing data in terms of visitation by pollinators that are not bumblebees.	963 964 965
942	Online supplementary materials		
943 944 945 946 947 948 949 950 951 952 953 954 955 956 957 958 959 960 961 962	Online supplementary resource materials are all in a single file containing the following information. Figure S1: Effectiveness of a single visit by different pollinator groups to the seed production per flower of <i>P. strictus</i> . Methods S1: Methods for calculating pollinator effectiveness to <i>P. strictus</i> . Figure S2: Summary of phenology data collected during the experiment and the timeframe of the pollinator observations. Methods S2: Estimate of <i>P. strictus</i> density at the Lupine Trail near Nicholson Lake, Crested Butte, Colorado. Table S1: <i>P. strictus</i> sample sizes divided by year, <i>L. vulgaris</i> treatment, and data collection type. Table S2: Data collected during the 3 years of the experiment. Table S3: Models generated to evaluate the ecological and evolutionary effects of the presence of <i>L. vulgaris</i> . Table S4: Models generated to evaluate the ecological and evolutionary effects of year-to-year variation in plant-pollinator interactions. Table S5: Sample size of single visits observed on <i>P. strictus</i> by <i>Bombus</i> species to calculate	Acknowledgements We thank Ashley Morse, Alexandra Faidiga, M. Kate Gallagher, Hannah Clements, Paula Sosenski, Victoria Luizzi, Victor Prestinary, Amanda Barth and Judith Trunschke for aiding with data collection, and M. Kate Gallagher, Heather Briggs, Steve Weller, John Powers, and two anonymous reviewers for providing feedback on this manuscript. We thank the Rocky Mountain Biological Laboratory for providing access to facilities and instrumentation and the Crested Butte Land Trust for access to the field sites. This work was supported by the Rocky Mountain Biological Laboratory Graduate Student Research Fellowships, Colorado Mountain Club Foundation Student Research Awards, Botanical Society of America Graduate Student Research Award, National Science Foundation Graduate Research Fellowship under Grant No. [DGE-1321846], and the University of California Eugene Cota-Robles Fellowship.	966 967 968 969 970 971 972 973 974 975 976 977 978 979 980 981
		Author contributions WRG developed the questions; WRG and DRC contributed to the experimental design; WRG conducted fieldwork experiments and collected data; WRG and DRC contributed to the data analysis and interpretation; WRG led the writing of the manuscript, with revisions by DRC. Both authors gave final approval for publication.	982 983 984 985 986 987
		Funding This work was supported by the Rocky Mountain Biological Laboratory Graduate Student Research Fellowships, Colorado Mountain Club Foundation Student Research Awards, Botanical Society of America Graduate Student Research Award, National Science Foundation Graduate Research Fellowship under Grant No. [DGE-1321846], and the University of California Eugene Cota-Robles Fellowship.	988 989 990 991 992 993 994
		Data availability Data will be deposited in Dryad.	995
		Compliance with ethical standards	996
		Conflict of interest The authors declare that they have no conflict of interest.	997 998 999
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