



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

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Abstract Interactions between a native plant species and its pollinators, herbivores, or microbiome can be affected by the presence of non-native plant species. Non-native plant species are altering plant-pollinator interactions, yet we know little about how these non-native species influence natural selection. In addition, year-to-year variation in flowering could influence the impacts of non-native species on reproductive success in native plants and the strength and direction of pollinator-mediated selection. We examined whether the presence of the highly invasive plant *Linaria vulgaris* influenced average pollinator visitation, species composition of floral visitors, or pollinator-mediated selection in the native *Penstemon strictus*. In the field, we conducted small scale *L. vulgaris* 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.

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Introduction

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

pollinators, herbivores, or microbiomes (Traveset and Richardson 2006; Bezemer et al. 2014; Coats and Rumpfo 2014). By imposing new selective pressures, plant invasions could also influence the evolution of native plant species (Oduor 2013). It is crucial to understand the potential of non-native species to alter natural selection because adaptive change, along with plasticity, could eventually influence the persistence of a native species in the face of an invasion (Berthou 2015). Most studies addressing evolutionary change in native plants have focused on direct competitive impacts of the presence of the invader (Callaway et al. 2005; Goergen et al. 2011) rather than the evolutionary effects of the invader that are mediated by interactions with third-party organisms (Lau 2008), such as pollinators (Beans and Roach 2015).

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

Invasive plants can also change the composition of flower visitors that are visiting native plants; for example, when only a subset of the pollinator species that visit a plant species change their visitation frequency in the presence of the invader (Albrecht et al. 2016). Additionally, changes in pollinator species composition can lead to differences in seed production if pollinators vary in effectiveness (Sahli and Conner 2007; Rafferty and Ives 2012). Thus the impact of invasive plants on the pollination of native 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 influence 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 Johnson 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

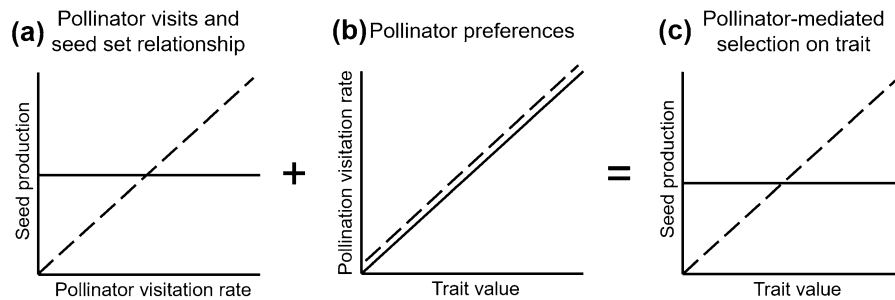


Fig. 1 Diagram showing how changes in linear relationships between pollinator visitation, plant reproduction, and floral traits lead to changes in the strength of selection. Contributions of **a** the relationship between pollinator visits and seed production, **b** pollinator trait preferences (selection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

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

Impacts on both average pollination and selection mediated by pollinators may also vary with other ecological conditions. Temporal variation in pollination across flowering seasons is often assumed yet not widely studied (Price et al. 2005). Pollination success can be influenced by spatiotemporal variation in pollinator species composition, pollinator effectiveness, and visitation by pollinators and pollen eaters (Herrera 1988; Horvitz and Schemske 1990; Fishbein and Venable 1996; Fenster and Dudash 2001; Price et al. 2005). Such variation in pollination success could, in turn, influence the strength and direction of pollinator-mediated selection (Benitez-Vieyra et al. 2012). However, competitor effects have mostly been tested by examining the level of within-season rather than year-to-year variation in pollination success. Assessing consistency across years is critical to determine if selection consistently favors particular trait values, as fluctuating selection would weaken any evolutionary response (Grant and Grant 2002).

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

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

Materials and methods

Site and species description

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 *Linaria vulgaris* Mill. (Scrophulariaceae) co-occurs and shares pollinators with the native *Penstemon strictus* Benth. (Scrophulariaceae). *L. vulgaris* 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, *L. vulgaris* produces an average of 27 pale yellow flowers per flowering shoot and is pollinated by bumblebees such as *Bombus appositus*, *B. californicus*, *B. fervidus*, *B. flavifrons*, and *B. frigidus* (Burkle et al. 2007). *Penstemon strictus*, 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, *P. strictus* is visited by many insects, including wasps, solitary bees, and several species of bumblebees, including *Bombus bifarius*, *B. flavifrons*, *B. appositus*, and *B. californicus* (Thomson 1996, Wilson et al. 2004, W. Recart personal observation). In *P. strictus*, control, bagged flowers not exposed to pollinators, did not set seed, indicating that *P. strictus* is dependent upon animal visitation and does not self-pollinate in the absence of pollinators (Fig. S1; Online Resource 1: Methods S1).

The degree of flowering overlap between the two species varied across the 3 years. In 2015 and 2017 *L. vulgaris* and *P. strictus* flowered at the same time, from mid-July (approximately July 12th) through late-August (approximately August 20th). In 2016 *L. vulgaris* did not bloom during the time of our pollinator observations on *P. strictus* (Online Resource 1: Fig. S2).

Calculating the effectiveness of *Penstemon strictus* visitors

In our study, *P. strictus* was visited by several species of hymenopterans, including *Anthophora terminalis*, *Bombus appositus*, *B. bifarius*, *B. californicus*, *B. flavifrons*, *Pseudomasaris vespoides*, 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 *P. strictus* plants (Online Resource 1: Methods S1).

Linaria removal experiment

We examined whether the nearby presence of the invasive *L. vulgaris* 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 *P. strictus*. 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 *L. vulgaris* patch. In our field site these *L. vulgaris* 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 *L. vulgaris* treatment, either *L. vulgaris* flowers present or *L. vulgaris* flowers removed by clipping inflorescences (Fig. 2a). Five potted or cut inflorescences of *P. strictus*, 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 *P. strictus* density in the experimental blocks (0.37 *P. strictus* individuals/m²) resembled the average density of *P. strictus* in our field site (0.36) under the assumption of a random distribution, while at the same time maximized the number of plants we

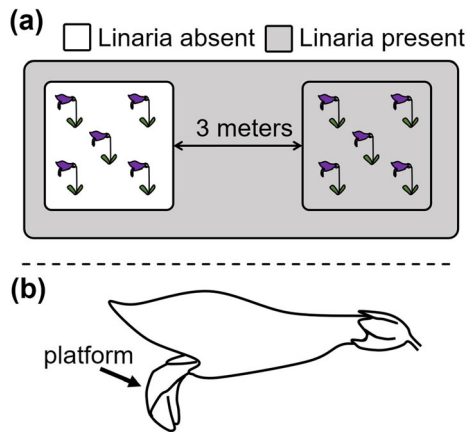


Fig. 2 **a** Diagram of the experimental design applied and replicated during the 3 years of the experiment. Gray space represents areas where *L. vulgaris* is present. The bigger outer square represents the block and the inner two squares represent the plots containing the *L. vulgaris* treatment: removed (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

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

Some methodological details differed across the 3 years (Online Resource 1: Table S2). In 2015 we used cut inflorescences only, allowing measurements of pollinator visitation but not of seed production. Cut inflorescences were placed in floral picks with water, and floral traits were measured immediately after pollinator observations were complete. In 2016 we used potted *P. strictus* individuals. In 2017 two of the blocks contained cut inflorescences, and the other three contained potted *P. strictus* individuals. By using cut and potted *P. strictus* individuals we eliminated belowground inter- and intra-specific competition with other plants. All potted *P. strictus* plants were

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 prevented 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 simultaneously 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).

Statistical analysis

All data analysis was performed using the R statistical program version 3.4.4 (R Core Team 2018). All pollinator visitation data were analyzed for the following categories: all pollinator visitors, only bumblebee pollinators, and only non-bumblebee pollinators. All seed production data were analyzed as seeds per flower (total seeds divided by the number of open flowers). For all statistical analyses, normality of the residuals was tested using the Shapiro–Wilks test (shapiro.test function), and pollinator visitation rate

was square-root transformed in order to achieve normality of the residuals.

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

Mean rate of pollinator visitation to *P. strictus* ($n = 24$ plots) was analyzed using a linear mixed effects model (hereafter LME; using lme4 package, lmer function) with *L. vulgaris* treatment and year as fixed crossed effects and block as a random effect nested within year (Bates et al. 2015; statistical models summarized in Online Resource 1 Table S3). Mean seed production for a plot ($n = 6$ plots) was analyzed using *L. vulgaris* treatment as a fixed effect and block as a random effect using only the 2017 data. We analyzed the effect of *L. vulgaris* treatment on *P. strictus* visitor composition ($n = 24$ plots) using MANOVA on visitation rate by *B. bifarius*, bumblebees other than *B. bifarius*, and non-bumblebee pollinators, with block identity as an additional factor.

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

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

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

To examine selection based on visitation and its dependency on the invasive species (Question 3), we used a LME where each data point consisted of a *P. strictus* individual for which we had a mean platform length value and a pollinator visitation rate value as the fitness components ($n = 103$ plants). We set platform length, *L. vulgaris* treatment and year as

fixed crossed effects and block identity was nested within year. In cases where we did not detect an interaction between platform length and presence of *L. vulgaris*, we then performed a standard analysis of covariance in which we removed the interaction term to determine the overall slope of the fitness component on platform length. Lastly, to enable comparisons of selection in this study with those of other plant species, we expressed the strength of selection as a standardized selection differential. A standardized selection differential is the change in the average value of the trait due to phenotypic selection, expressed in units of standard deviation of the trait. To estimate standardized selection differentials, we repeated the ANCOVA using untransformed pollinator visitation rate relative to the mean as the dependent variable and platform length standardized to a mean of zero and standard deviation of one (Kingsolver et al. 2001).

Net selection (Question 4) was examined by repeating the analyses described for estimating selection based on visitation and standardized selection differentials but using seed production per flower as the dependent variable ($n = 15$ plants).

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

To analyze the effects of year on mean pollinator visitation and on selection, we took out the *L. vulgaris* treatment from the statistical analysis allowing us to analyze all years of data collection (2015 through 2017; Online Resource 1: Table S4). The effect of year on mean plot pollinator visitation rate was analyzed using a LME with year as a single fixed effect and the random effect of plot identity nested within year ($n = 34$ plants).

The relationship between pollinator visitation rate and seed production was analyzed for 2016 and 2017—when we had both pollinator visitation data and seed production data, by using a LME with year as a fixed effect crossed with pollinator visitation, and seed production per flower set as the dependent variable ($n = 74$ plants).

We used a LME to determine whether the year (data from 2015 to 2017) influenced the relationship between platform length and pollinator visitation rate (selection based on visitation). For this model, each data point consisted of a *P. strictus* individual for which we had a mean platform length value and a

pollinator visitation rate value ($n = 148$ plants), with year and platform length set as fixed crossed effects and plot identity nested within year. We also calculated standardized selection differentials using the same approach as detailed for Question 3.

We used a linear model to determine whether the year (2016 or and 2017) influenced the relationship between platform length and seed production (net selection; $n = 60$ plants). Selection differentials were calculated as described previously using seeds per flower as the dependent variable.

Results

Effectiveness of *Penstemon strictus* visitors

A visit to *P. strictus* by *Bombus* spp. yielded three times more seeds than did a visit by a non-*Bombus* insect, making the bumblebees a more effective pollinator group (Online Resource 1: Table S5 and Fig. S1). The results below focus on the following categories: all flower visitors, *Bombus* spp., and *B. bifarius* (the most common bumblebee visitor). Analysis on non-*Bombus* insects for this and subsequent sections are reported in the online resource file (Online Resource 1: Results S1).

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

In the removal experiments, the presence of *L. vulgaris* increased by 50% the mean visitation rate by all flower visitors to *P. strictus* ($\bar{x} \pm 1\text{SE}$: present = 0.95 ± 0.15 , removed = 0.64 ± 0.08 ; $F_{1,10} = 6.87$, $P = 0.03$, Fig. 3). This increase in visitation was likely driven by a 76% increase in visitation by *B. bifarius* ($F_{1,10} = 3.94$, $P = 0.07$) and a 57% increase in visitation by other visitors ($F_{1,10} = 3.73$, $P = 0.08$). Visitor composition was not influenced by the presence of *L. vulgaris* (MANOVA: $F_{1,21} = 0.57$, $P = 0.64$). Even with only 3 blocks in 2017 available for testing the impact on seed production, there was a trend for the presence of *L. vulgaris* to increase the seed production per flower of *P. strictus* by 80% ($\bar{x} \pm 1\text{SE}$: present = 18.44 ± 4.92 , removed = 10.23 ± 2.68 ; $F_{1,2} = 13.34$, $P = 0.07$).

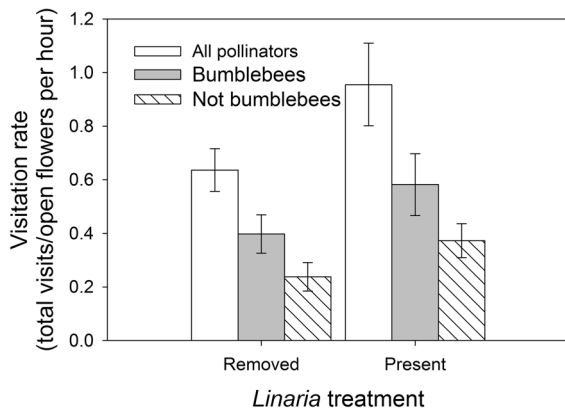


Fig. 3 Pollinator visitation rates to *P. strictus* in the removal or presence of *L. vulgaris* sorted by different pollinator groups. Means and standard errors are shown, based on the means of visitation rate grouped by *L. vulgaris* treatment and pollinator group

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

In 2017, we detected a positive relationship between visitation rate by all visitors and seed production per flower ($F_{1,22} = 13.43$, $P = 0.001$, Fig. 4a). This relationship was not affected by the presence of *L. vulgaris* (interaction term: $F_{1,22} = 0.10$, $P = 0.75$, Fig. 4a), as slopes were similar whether *L. vulgaris* was present (slope = 1.78) or removed (2.49). Since pollinator visitation was markedly reduced in the absence of *L. vulgaris*, visitation rate in that situation has a smaller range, but there was no evidence for any curvature in the relationship (quadratic term $P = 0.63$ in quadratic regression of seed production on visitation in presence of *L. vulgaris*). Seed production also increased with higher bumblebee visitation ($F_{1,22} = 4.94$, $P = 0.04$). This pattern was seen for visitation specifically by *B. bifarius* ($F_{1,22} = 5.59$, $P = 0.03$), but not for other bumblebee visitors ($F_{1,22} = 0.05$, $P = 0.82$), suggesting that the increase in bumblebee visitation was driven by an increase in *B. bifarius* visitation. The relationship between seed production and bumblebee visitation was not influenced by the presence of *L. vulgaris* (interaction term $F_{1,22} = 0.01$, $P = 0.92$). The presence of *L. vulgaris* also did not

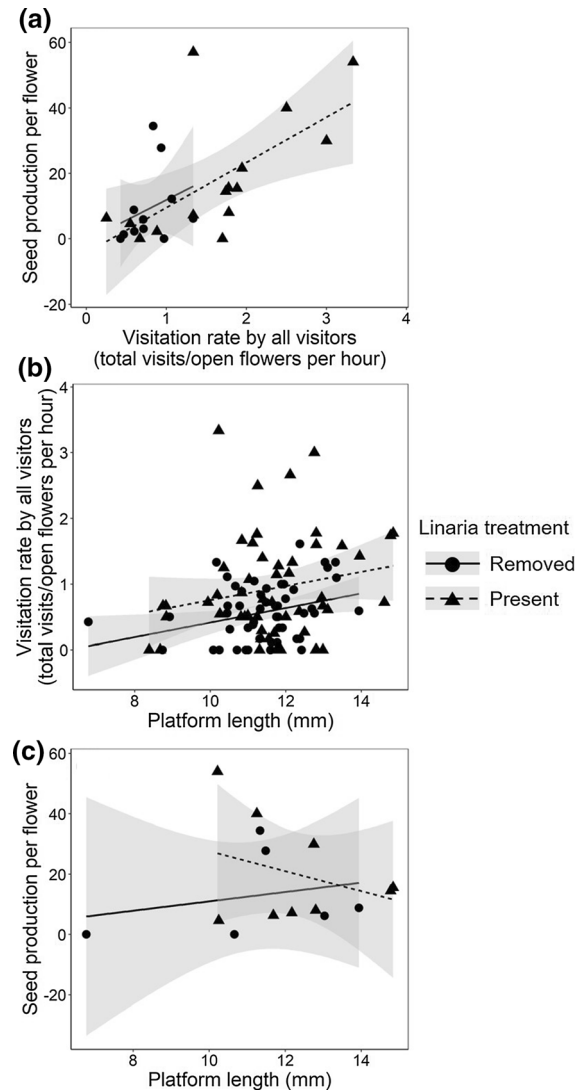


Fig. 4 Relationships in the removal and presence of *L. vulgaris* between **a** pollinator visitation rate and seed production per flower in *P. strictus*, **b** *P. strictus* platform length and visitation rate by all pollinators, and **c** *P. strictus* platform length and seed production per flower.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

influence the relationship between visitation by *B. bifarius* and seed production ($F_{1,22} = 0.11$, $P = 0.74$).

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

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 (Fig. 4b). However, this relationship between platform length and visitation rate was lost 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 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

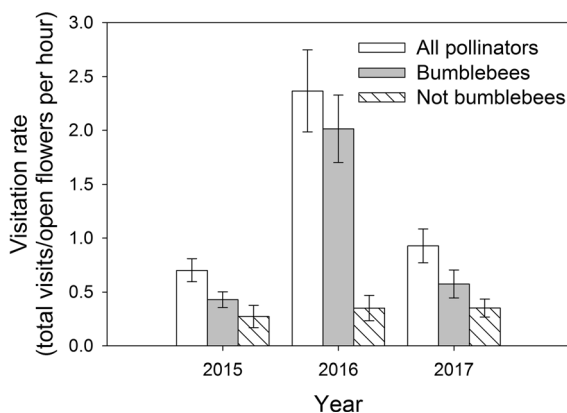


Fig. 5 *Penstemon strictus* pollinator visitation rate from 2015 to 2017. Means and standard errors are shown, based on the means of visitation rate grouped by year and pollinator group

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 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 ($F_{1,137} = 6.13$, $P = 0.01$).

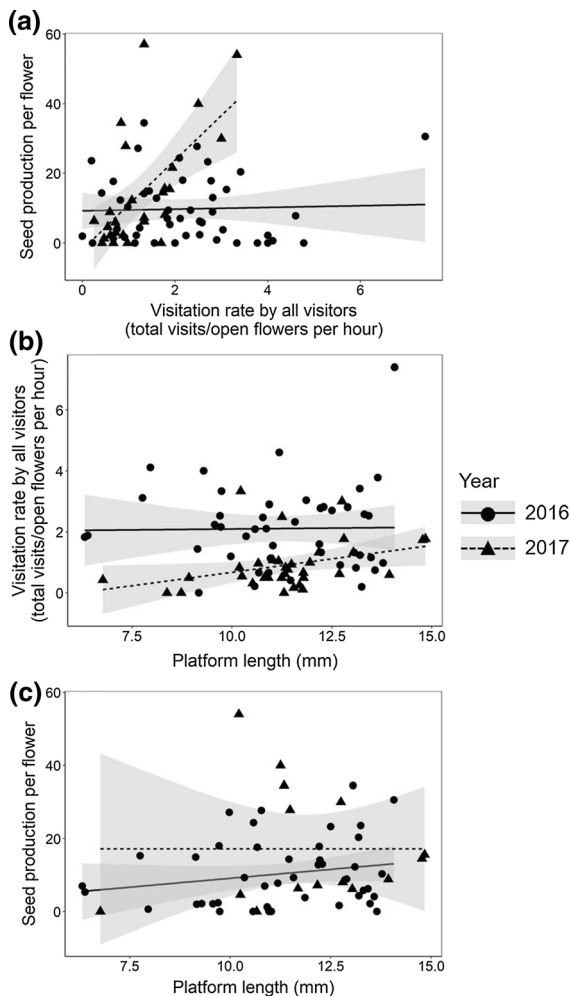


Fig. 6 Relationships in 2016 and 2017 between **a** visitation rate by all visitors to *P. strictus* and seed production per flower, **b** *P. strictus* platform length and visitation rate by all pollinators, and **c** *P. strictus* platform length and seed production per flower. Gray shading around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

We also detected a significant interaction between platform length and year on visitation by other bumblebees ($F_{2,137} = 5.51$, $P = 0.005$) with a steeper relationship in 2016. There was no detectable relationship between platform length and seed production within or across years (standardized selection differential = 0.12, $F_{1,56} = 3.02$, $P = 0.09$; Fig. 6c), meaning that net selection was not detected throughout this experiment.

Discussion

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

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

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

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 and Sargent 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 standardized selection differential = 0.09 indicating that the average

trait value could be changed by up to 0.09 SD in a generation. That strength of selection is similar to that seen on average in studies of selection on flower size that used pollination success as a fitness measure (Harder and Johnson 2009). The removal of *L. vulgaris* did not appear to influence selection based on visitation on *P. strictus*. This lack of effect could be in part due to a lack of change in the visitor composition with *L. vulgaris* treatment. If visitor composition had changed and pollinators were tracking different floral traits or trait values, then we should have seen a change in selection based on visitation in the removal versus presence of *L. vulgaris*. Alternatively, pollinators could change their floral preferences due to changes in floral neighborhood and thus influence selection based on visitation (Caruso 2000; Beans and Roach 2015). Our data suggest that the pollinators retain their trait preferences independently of the presence or removal of the invader, with the caveat that we only studied one trait. In a previous study, the invasive plant *Impatiens glandulifera* influenced pollinator-mediated selection experienced by the native plant *Impatiens capensis* (Beans and Roach 2015). The two species of *Impatiens* had more similar flower morphology compared to the species in our study. This flower shape similarity could have increased interspecific pollen transfer, leading to a change in selection in the presence of the invader. In two other studies looking at interactions between two native species, results have varied, with *Castilleja linariaefolia* altering selection on corolla length of *Ipomopsis aggregata* (Caruso 2000), while *Mimulus ringens* did not alter selection on corolla lobe length, corolla tube length, stigma–nectary distance or petal color in *Lobelia siphilitica* (Wassink and Caruso 2013).

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

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

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

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

Conclusion

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 *L. vulgaris* facilitated the pollination of nearby *P. strictus* 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.

Online supplementary materials

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 *P. strictus*. Methods S1: Methods for calculating pollinator effectiveness to *P. strictus*. Figure S2: Summary of phenology data collected during the experiment and the timeframe of the pollinator observations. Table S1: *P. strictus* sample sizes divided by year, *L. vulgaris* treatment, and data collection type. Methods S2: Estimate of *P. strictus* density at the Lupine Trail near Nicholson Lake, Crested Butte, Colorado. 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 *L. vulgaris*. 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 *P. strictus* by *Bombus*

species to calculate effectiveness measurements. Results S1: Findings when analyzing data in terms of visitation by pollinators that are not bumblebees.

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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.

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Data availability Data is available in Dryad <https://datadryad.org/stash/dataset/doi:10.7280/D1JM40>.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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