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RESEARCH ARTICLE

# Better reproductive success of an invasive thistle than its native relative under pollinator exclusion

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## ABSTRACT

- Invasive plants often can self-pollinate and have higher reproductive outputs than native counterparts. Pollinator declines may exacerbate disparities in reproductive output by negatively impacting native plants more than invasives.
- To determine how pollinator availability affects reproductive success of two species (one native, one invasive), we conducted a pollinator exclusion experiment for two functionally similar species: the invasive musk thistle *Carduus nutans* and native field thistle *Cirsium discolour*. We manipulated pollinator access to flowers by partially or completely excluding pollinators and evaluated how pollinator visitation rates and community composition influenced reproductive success.
- Both thistle species received pollinators from all seven functional groups that we considered, but pollinator community composition differed by thistle species and treatment. Sweat bees and butterflies were important drivers in community differences between the *Ca. nutans* and the *Ci. discolour* flower heads. Complete pollinator exclusion resulted in a higher probability of total reproductive failure; 55% of total pollinator exclusion flowers failed while <7% failed in other treatments. When flower heads produced at least one viable achene, any level of pollinator exclusion resulted in lower seed output, but germination success did not differ from the control.
- Overall, *Ca. nutans* had higher reproductive success per flower head than native *Ci. discolour* in control and partial pollinator exclusion due to higher seed output rather than higher germination rates. While pollinator loss will be detrimental to reproduction of both species, our study provides evidence that reproductive losses in invasive *Ca. nutans* will be lower than the native *Ci. discolour*.

## INTRODUCTION

In recent years, there has been growing concern about the loss of insect populations due to a variety of anthropogenic factors, including habitat destruction and pesticide use. While highly variable, many studies estimate declines in insect abundance to be between 1% and 2% annually (Wagner *et al.* 2021), with cumulative losses as high as 75% since 1989 (Hallmann *et al.* 2017). For wild plants, the majority depend on insect pollination to set fruit and seed, and even when pollinator populations are robust, plants may be pollen-limited (Burd 1994; Potts *et al.* 2010). Therefore, any reductions to insect pollinator populations may further exacerbate pollen limitation in plant populations. Pollinator losses, and the subsequent effects on plant reproduction, have resulted in public interest in insect conservation, as seen in popular initiatives in Northern temperate zones, such as "Save the bees" (www.savethebees.com) and "No Mow May" (https://www.plantlife.org.uk/campaigns/nomowmay/).

Concurrent with insect declines, expanding invasive plant populations pose a major challenge to native plant communities. Invasive plants directly compete with native plants for pollinators, and can be preferred by pollinators in their introduced range over closely related native species (Brown *et al.* 2002). Invasive plants may also reduce connectivity in pollination webs, causing further disruptions to native plant pollination (Aizen *et al.* 2008). In the face of declining insect populations, invasive plants are likely more resilient to pollinator losses because they employ other means of reproduction, such as self-fertilization and vegetative reproduction (Baker 1955). Indeed, traits associated with self-compatible reproductive approaches are more common in invasive and naturalized species outside their native range (Razanajatovo *et al.* 2016). When coupled with evidence that invasive plants thrive in a wider range of conditions than native plants (Van Kleunen *et al.* 2010), pollinator decreases may result in further advantages to invasive plants, since their reproduction may not be as severely impacted by pollinator losses.

Understanding how pollinator loss impacts plant population growth is critical as insect populations continue to decline globally. We were interested in understanding how pollinator reductions differentially impact closely related and functionally similar native and invasive plant pairs, given the dearth of such studies. The musk thistle (*Carduus nutans*) was introduced from Eurasia in the mid-1800s and has invaded much of North America (McWhorter 1971; Sezen *et al.* 2016). *Ca. nutans* can

outcompete native thistles, causing biodiversity loss among native plant communities (Zouhar 2002). *Ca. nutans* produces showy flower heads that attract a diversity of pollinators, from hummingbirds to sweat bees, similar to native thistles. *Ca. nutans* co-occurs with the closely related field thistle (*Cirsium discolour*; open habitats including prairies, savannas, and open woodlands), and presumably the two species compete for resources as they are similar in growth form and flower characteristics.

Little is known about how pollinator communities vary between these two thistle species despite their overlap in distribution throughout much of North America. Pollinator communities may differ as temporal separation in flowering periods can result in varying pollinator activity when flowers are present. However, pollinator communities may converge after pollinator declines if pollinator loss leads to the dominance by relatively few pollinator species or functional groups. In addition to pollinator community differences, reproductive output of the two thistle species under current and reduced pollination conditions remains unclear. As such, we addressed two questions using a pollinator reduction experiment: (a) how do pollinator communities visiting the native (*Ci. discolour*) and invasive (*Ca. nutans*) thistles vary under control and pollinator exclusion treatments, and (b) how do pollinator exclusion treatments impact reproductive output for the two species?

## MATERIAL AND METHODS

### Study site and experimental design

The study was conducted in a 20-ha restored tallgrass prairie located in the Western Pennyroyal Karst Ecoregion near Clarksville, Tennessee, USA (Griffith *et al*. 1998). This site was under row-crop agriculture for at least a century, but prairie restoration efforts began in July 2020 when the site was seeded with a mix of 77 species of native forbs, legumes, and grasses. By the time of the study in 2022, the site contained 166 native forbs and grasses, but non-native or invasive plant species like *Sorghum halepense*, *Trifolium campestre*, and *Ca. nutans* were present. Preliminary surveys at the site documented over 100 pollinating insect species, suggesting pollinator communities were robust for a restoration site. *Ci. discolour* and *Ca. nutans* were distributed throughout the site, and individual plants were often within several meters of individuals of each species. For additional site details and information about the plant and pollinator community see LeFevre (2023).

Compiled lists (e.g., https://illinoiswildflowers.info/) of the known pollinator community in North America of invasive *Ca. nutans* include bumblebees, other long-tongued bees, butterflies, and skippers, whereas the native *Ci. discolour* pollinator community includes bumblebees, digger bees (*Melissodes* spp., including the *Cirsium* spp. specialist *Melissodes desponsa*), leaf-cutting bees (*Megachile* spp.), and butterflies. *Ca. nutans* blooms in early to late summer while the native *Ci. discolour* blooms in late summer to early fall, limiting the period when both species are simultaneously blooming. Although highly variable, both species usually have 4–6 capitulescences (i.e., flower heads) per plant, each containing 100–1000 disk florets (i.e., flowers) (https://www.illinoiswildflowers.info/index.htm). The flower heads of *Ca. nutans* are slightly larger than those of *Ci. discolour*. *Ca. nutans* pollinator visitation rates have been documented (Yang *et al*. 2011; Russo *et al*. 2020), but to our knowledge visitation rates to *Ci. discolour* have not been published prior to this study.

Beginning in spring 2022, we located and marked 18 invasive *Ca. nutans* and 13 native *Ci. discolour* plants prior to blooming. On individual plants, we selected three flower heads within 10 vertical centimetres of each other and subjected them to one of three pollinator treatments: control, partial pollinator exclusion, and total pollinator exclusion. Partial pollinator exclusion was achieved by covering flower heads with a wire cage covered with a 2.54 cm aperture mesh netting designed to exclude some pollinators of all body sizes but likely disproportionately excluded large-bodied pollinators, as they could not fit through the mesh. The higher exclusion of large-bodied insects is not ideal but is an artefact of methodological limitations. We are unaware of any approach that would lower pollinator abundance equally across all morphological types or body sizes. However, recent evidence does suggest that large-bodied pollinators like butterflies are at higher risk of extinction in North America than smaller bodied flower beetles and flies so this approach may mimic patterns of realized pollinator loss (Cornelisse *et al*. 2025). Total pollinator exclusion was achieved by covering flower heads with fine mesh window screen (1.13 mm aperture; Fig. S1). Treatments were applied before flower heads bloomed, and plants were between 1 and 434 m apart.

### Pollinator community

Marked flower heads of *Ca. nutans* bloomed between 12 June and 6 July, while *Ci. discolour* bloomed between 17 August and 8 October. Once flowers were in peak bloom, we observed all flower heads once for a period of 20 min, with observation periods for each species stratified between 08:00 and 15:00 h, a period during which pollinators are most active. We recorded the identity, number of visits, the time spent by pollinators on flower heads. Floral visitors were identified to the highest taxonomic resolution possible (62.5% to genus or species) using photographs and later categorized into seven functional groups (beetle, bumblebee, butterfly, carpenter bee, fly, other long-tongued bee, sweat bee).

### Reproductive output

In the early stages of senescence, we measured flower heads (involucre length and diameter) and placed them inside screen bags (constructed from window screen and wire) to prevent escape of wind-dispersed achenes. Once the plants had completely senesced, we cut the heads and stored them until the achenes could be counted. All achenes were counted and placed into one of three categories: mature (filled and tan-coloured), undeveloped (shrivelled and brown), or medium (somewhere in between mature and undeveloped).

To further investigate the reproductive success of *Ca. nutans* and *Ci. discolour* according to pollinator treatment and species, we planted up to 10 randomly chosen mature/medium achenes from every flower head that produced at least one mature/medium achene inside a climate-controlled greenhouse with uniform sunlight conditions. Achenes were planted 1 cm deep in commercially purchased potting soil and maintained under standard greenhouse conditions. When flower heads produced fewer than 10 mature achenes, we planted the

number of mature/medium achenes available. When more than 10 mature achenes were produced, we discarded medium achenes and only planted mature achenes. Achenes were watered twice daily and monitored for germination every 3 days for 6 weeks after initial planting. Mature achenes of both species germinated within 2–3 weeks of planting, but we allowed 6 weeks for germination to ensure accurate germination estimates. An achene was classified as germinated if cotyledons were visible. An achene with no visible leaves after the germination period was recorded as failed. For flower heads that did not yield any mature achenes, we planted undeveloped achenes as a means of validating our visual separation of achenes into mature and undeveloped categories.

### Statistical analysis

*Pollinator community*

We used R v. 4.2.3 to perform all analyses (R Core Team 2023). While direct measurement of stigmatic pollen deposition is a more robust method to determine pollinator efficiency, it is logistically impractical in many cases, and pollinator behaviours such as visitation or visit duration can serve as a suitable proxy (Ne'eman *et al.* 2010). We estimated pollination rates using both visitor count and visit duration metrics, and the results were qualitatively similar. We present analyses of visitor count as each visitor may be carrying pollen from another flower and this should better represent the likelihood of successful pollination. For this analysis, we excluded total pollinator exclusion flower heads as this treatment was effective in excluding visitors and therefore all these flower heads had a count of zero visitors. We therefore modelled visitor count by treatment (only control and partial exclusion), thistle species, and their interaction using a generalized linear model with a Poisson distribution. We then conducted model selection following Burnham & Anderson (2002) by comparing all subsets of the global model. Models were considered competing when they were within two ΔAIC units of the best ranked model. The simplest model was then chosen when multiple competing models were considered. The chosen model was checked by examining residual plots and overdispersion metrics.

To assess if the pollinator communities differed among pollinator treatments and thistle species identity, we applied a permutational multivariate analyses of variance from the "vegan" package (Oksanen *et al.* 2022). As in our analysis of visitor count, we removed the total pollinator exclusion treatment since no pollinators could access the flower heads. We also ran a Simper analysis using *simper* to identify the pollinator functional groups that drove differences in pollinator communities among treatment–species combinations. We visualized differences in pollinator communities using non-metric multidimensional scaling (NMDS).

*Reproductive output*

To investigate how pollinator exclusion treatment and species identity impacted reproductive output, we analysed fruit production and germination success. Many flower heads, especially in the total pollinator exclusion treatment, produced zero achenes creating zero-inflation in our dataset. Therefore, we analysed fruit production using a two-component model, one component for modelling zeros and another for modelling counts of achenes. For these analyses, all treatments (control, partial and total pollinator exclusion) were included. The *hurdle* function in the (Jackman 2020) "pscl" package was used to fit two-component models for achene count data with a hurdle component that models the zero counts with a logit link and a truncated count component for positive counts (Zeileis *et al.* 2008). For the zero-count process, we included fixed effects of treatment, species identity, and their interaction on total flower head failure with a binomial distribution. We used the same model structure for positive counts (at least one mature achene produced) with a truncated Poisson distribution. We then conducted model selection and validation as outlined above.

The proportion of seeds germinated per flower head was not zero inflated because often at least one seed could germinate if seeds were produced. Therefore, germination success was modelled using a generalized linear model on the proportion of seeds germinated per flower head with fixed effects of treatment, species identity, and their interaction with a binomial distribution. We then conducted model selection and validation as outlined above.

## RESULTS

### Pollinator community

A total of 489 individual pollinators were observed visiting flower heads of both species. Both the native thistle *Ci. discolour* and the invasive *Ca. nutans* received pollinators from all seven functional groups. No pollinators were observed to penetrate the screen bags in the total pollinator exclusion treatment, indicating that the treatment effectively eliminated pollinators. The best selected model of visitor counts included treatment and species identity, but not their interactions (Table S1). The partial exclusion resulted in fewer visitors relative to the control treatment ($P < 0.001$; Table S2), and native species had fewer visitors relative to the invasive plant ($P < 0.001$).

Pollinator community composition differed by thistle species identity (native or invasive; $R^2 = 0.22$, $P = 0.001$) and treatment ($R^2 = 0.03$, $P = 0.045$; Figs. 1 and 2) but not their interaction. Sweat bees, for instance, made up a large proportion of visitors to the invasive *Ca. nutans*, while a more even distribution of individuals across functional groups visited the native *Ci. discolour* flower heads (Fig. 1). While treatment explained little of the difference in community composition ($R^2 = 0.03$), it was nevertheless significant. We observed that sweat bees, butterflies, and other long-tongued bees were more abundant in the control than in the partial exclusion treatment for both thistle species (Fig. 1). The Simper analysis supported these patterns (Table 1), showing that sweat bees consistently played an important role in differentiating the pollinator assemblage. For example, sweat bees were the most important functional group contributing to dissimilarity between five of the six possible treatment–species combination comparisons. Under the control treatment, sweat bees contributed between 57.0% and 73.8% to the dissimilarity to other treatment–species pairs and, under the partial exclusion treatment, contributed between 47.3% and 73.8% to the dissimilarity (Fig. 1). Butterflies differentiated the *Ci. discolour* control pollinator assemblage from *Ci. discolour* partial exclusion (29.0% dissimilarity) and *Ca. nutans* controls (15.8% dissimilarity), with butterflies being most abundant on native-control flower heads. Meanwhile bumblebees were more abundant in the *Ci.*

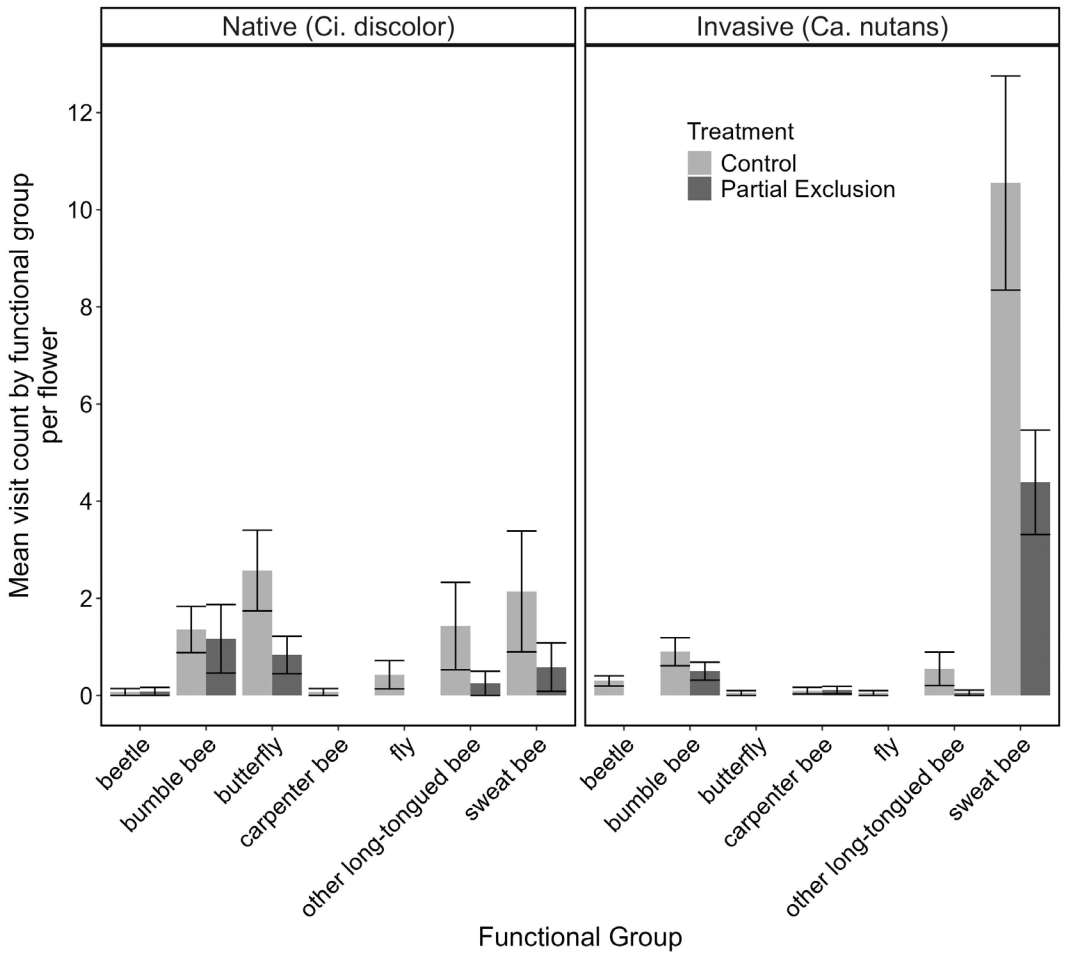


**Fig. 1.** Composition of pollinator visitors observed over 20-min periods at *Ci. discolour* (native) and *Ca. nutans* (invasive) under a control and a partial pollinator exclusion treatment ($n_{Ci.\ discolor}$ = 13; $n_{Ca.\ nutans}$ = 18). Visitor count (mean ± SE) was significantly different among exclusion treatments ($P < 0.05$). Note total pollinator exclusion is not included as the treatment was effective at preventing any pollinator from reaching the flower heads.

*discolour* partial exclusion pollinator assemblage than the *Ca. nutans* partial exclusion (25.7% dissimilarity) or *Ci. discolour* control (15.1% dissimilarity).

### Reproductive output

We counted 7854 mature and medium achenes from 77 flower heads that produced at least one mature achene (Table 2). Sixteen flower heads never produced an achene, with 13 of these failed flower heads being in the total pollinator exclusion treatment. Two *Ca. nutans* flower heads in the partial pollinator exclusion treatment failed to produce a mature achene, while one *Ca. nutans* control flower head failed to produce a mature achene. Averaged across all treatments, *Ca. nutans* yielded higher mature fruit production per flower head than *Ci. Discolour*, with mean mature achene production of 152 (±23.82 SE) and 107 (±14.80 SE), respectively. While it is possible seed production under the total pollinator exclusion treatment does not reflect self-fertilization, the small mesh used made these flowerheads inaccessible to any potential pollinators, and wind pollination has not been documented in either genus (Camara *et al.* 2003; Nouroozi *et al.* 2012). Therefore, we contend that total pollinator exclusion flower reproduction represents self-fertilization. Both species displayed variable self-fertilization potential in the total exclusion treatment. Eleven invasive (61%) and three native (23%) flower heads produced at least one mature achene under total exclusion, with a mean mature achene output of 24 (±7.03) in *Ca. nutans* and 19 (±9.34) in *Ci. discolour* flower heads. When investigating fruit set among treatment and species identity, the zero-count process of the two-component model showed that total flower head failure was best explained by treatment alone (Table S3). Highest failure occurred in the total pollinator exclusion treatment, lowest failure in the control, and partial pollinator exclusion was somewhere in between (Table 3). Species identity did not play a role in determining flower head failure. The count process model showed that species identity and treatment interacted to explain the variation in mature achene output (Table 3, Fig. 3). *Ca. nutans* produced more seeds per flower head than *Ci. Discolour*, and the pollinator exclusion treatments reduced mature achene output relative to the control for both species. However, the interaction indicated that the native *Ci. discolour* had a larger relative decline in achene production in the partial pollinator exclusion treatments than in *Ca. nutans*.

Across all treatments, 66% of 711 mature achenes germinated, resulting in a mean germination proportion of 0.55

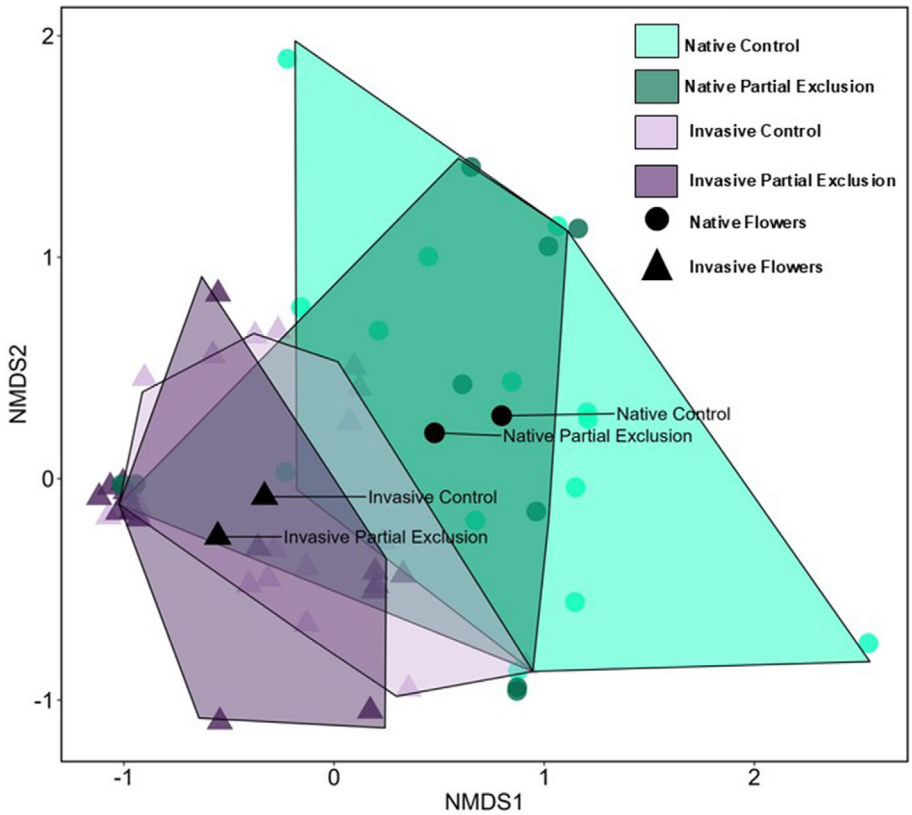


**Fig. 2.** NMDS ordination as visualization of differences of pollinator communities by functional group. Each point in the plot represents one flower head from native *Ci. discolour* (circles) and invasive *Ca. nutans* (triangles). Colour indicates control (light green and light purple) and partial exclusion (darker green and dark purple) treatments. The distance between points is proportional to the distance between pollinator communities, measured by Bray–Curtis dissimilarity. Community clustering was significantly different between species and treatment, measured using PERMANOVA, $P < 0.05$.

**Table 1.** Top three functional groups contributing to community differences between pollinator exclusion treatment and species pairs (*Cirsium discolour* or *Carduus nutans*).

| | top contributor | | | | | |
|---|---|---|---|---|---|---|
| pair | functional group | contribution (%) | functional group | contribution (%) | functional group | contribution (%) |
| ***Ci. discolour* Control** vs. *Ci. discolour* Partial Exclusion | Butterfly | 29.00 | Bumble bee | 25.75 | Sweat bee | 21.74 |
| ***Ca. nutans* Control** vs. *Ci. discolour* Control | Sweat bee | 56.98 | Butterfly | 15.80 | | |
| ***Ca. nutans* Control** vs. *Ca. nutans* Partial Exclusion | Sweat bee | 73.78 | | | | |
| ***Ca. nutans* Partial Exclusion** vs. *Ci. discolour* Partial Exclusion | Sweat bee | 54.44 | Bumble bee | 19.71 | | |

Bolded variables indicate the treatment in which the first listed functional group is most abundant (e.g., butterflies are most abundant in the *Ci. discolour* control treatment relative to the native partial exclusion).

(±0.40). The proportion of germination from flower heads that produced at least one mature achene was best explained by the null model (Table S3). This suggests that there was no difference in germination success among treatments nor in species identity (Fig. 4).

## DISCUSSION

Global pollinator declines and invasive plants pose serious threats to native species and rare prairie communities (Cariveau *et al.* 2020). Current theory on the success of invasive plants suggests that invasive plants may be more resilient to pollinator loss than their native relatives, but experimental evidence is limited (Van Kleunen *et al.* 2015). Here, we manipulated pollinator communities on flower heads and followed reproductive success in a native thistle (*Ci. discolour*) and a closely related, widespread North American invasive thistle (*Ca. nutans*). Under control conditions, we found that pollinator communities differed between the two thistle species (partially driven by non-overlapping flowering periods) and that mature seed production per flower head was higher for the invasive thistle. Under partial pollinator exclusion, both species

**Table 2.** Fruit set and germination of mature achenes per flower head of *Cirsium discolour* and *Carduus nutans* in response to pollinator exclusion treatments at a restored prairie in Clarksville, TN, USA.

| species | treatment | flower head count | proportion of failed flowers | mean mature achene count ± SE | mean germination proportion ± SE |
|---|---|---|---|---|---|
| *Cirsium discolour* | Control | 13 | 0 | 106.62 ± 14.80 | 0.69 ± 0.06 |
| *Cirsium discolour* | Partial Exclusion | 13 | 0 | 75.92 ± 11.79 | 0.62 ± 0.09 |
| *Cirsium discolour* | Total Exclusion | 13 | 0.62 | 19.40 ± 9.34 | 0.52 ± 0.22 |
| *Carduus nutans* | Control | 18 | 0.06 | 152.29 ± 23.82 | 0.64 ± 0.07 |
| *Carduus nutans* | Partial Exclusion | 18 | 0.11 | 122.69 ± 16.70 | 0.67 ± 0.08 |
| *Carduus nutans* | Total Exclusion | 18 | 0.28 | 23.62 ± 7.03 | 0.69 ± 0.10 |

**Table 3.** Fitted regression terms for the selected two-component model of mature fruit set in *Cirsium discolour* and *Carduus nutans* collected at a restored prairie in Clarksville, TN.

| process | model structure | model term | estimate (± SE) | *P*-value |
|---|---|---|---|---|
| Zero | Total flower head failure (0 mature achenes) ~ treatment | (Intercept) | −3.40 ± 1.02 | **<0.001** |
| | | Partial exclusion | 0.73 ± 1.25 | 0.561 |
| | | Total exclusion | 3.08 ± 1.08 | **0.004** |
| Count | Mature achenes produced (>0) ~ species × treatment | (Intercept) | 4.67 ± 0.03 | **<0.001** |
| | | *Ca. nutans* | 0.36 ± 0.03 | **<0.001** |
| | | Partial Exclusion | −0.34 ± 0.042 | **<0.001** |
| | | Total Exclusion | −1.70 ± 0.12 | **<0.001** |
| | | *Ca. nutans* × partial exclusion | 0.12 ± 0.05 | **0.016** |
| | | *Ca. nutans* × total exclusion | −0.16 ± 0.12 | **0.187** |

The zero-count model assessed total flower head failure as a binary factor (0 = no achenes produced, 1 = at least one achene produced) and included treatment as a fixed effect. The positive count-process models assess how many achenes non-failed flower heads produced and included species identity × treatment as fixed effects. Values in bold are significantly different from zero, $P < 0.05$.

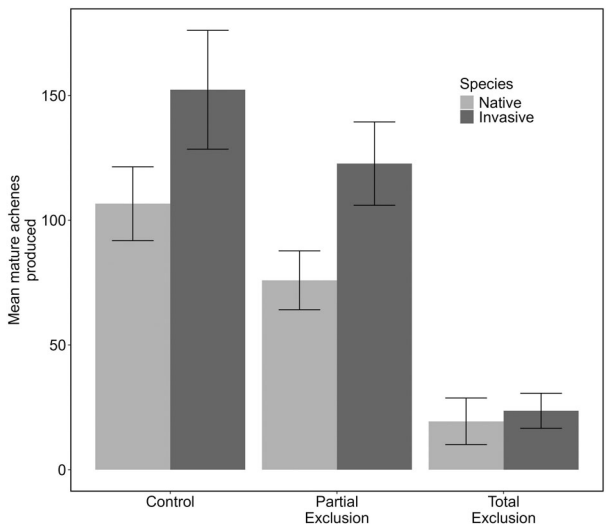


**Fig. 3.** Mature achenes produced (mean ± SE) per flower head by species identity and treatment. Light grey bars indicate native *Ci. discolour* and dark grey bars indicate invasive *Ca. nutans*. Failed flowers (0 mature achenes produced) were excluded from this figure.

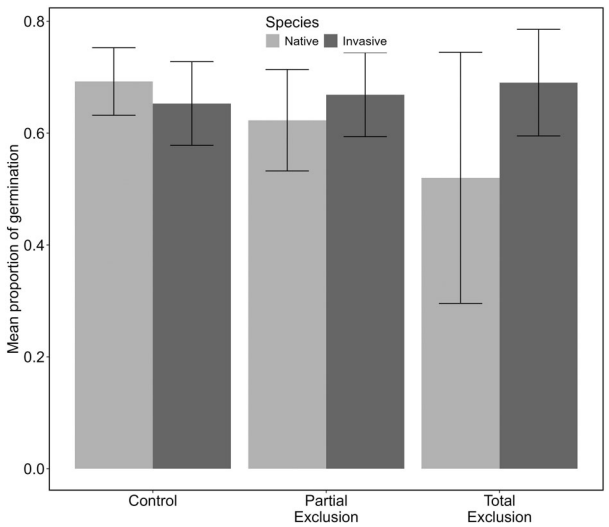


**Fig. 4.** Proportion of germination (mean ± SE) by treatment and species identity. Light grey bars indicate native *Ci. discolour* and dark grey bars indicate invasive *Ca. nutans*.

had reduced pollinator visitation, which led to decreased fruit production. However, the decrease in fruit production was more severe for the native *Ci. discolour* than for invasive *Ca. nutans* under partial pollinator exclusion. Moreover, total pollinator loss led to high total reproductive failure in both species. Collectively, we found that the pollinator loss negatively impacted both species, but the detrimental effects of fewer

pollinators was more severe in the native than in the invasive species.

Overlapping pollinator communities can increase competition between native and invasive species, reducing pollination and seed set, while maintaining different pollinator communities allows native species in highly invaded communities to maintain pollination and seed set (Thijs *et al*. 2012). Temporal separation in bloom time can be one mechanism by which interspecific competition for pollinators is reduced (Oleques *et al*. 2017; Jensen *et al*. 2019). In our system, the pollinator community visiting flower heads differed between the native and invasive thistle, with sweat bees and butterflies seemingly driving this difference. Differences in abundance of these two main functional groups is partially explained by the time of year each species produces flowers. In early summer, sweat bees are highly abundant on the site, but their abundance decreases later into the summer. *Ca. nutans* blooms earlier in the year, coinciding with the peak in sweat bee abundance. Meanwhile, *Ci. discolour* blooms in late summer and early fall when sweat bees are in decline, but fall migration is beginning for butterflies. This means small-bodied sweat bees that could easily access partial pollinator exclusion treatments were abundant during the invasive *Ca. nutans* bloom time but less abundant during the native *Ci. discolour* flowering period. It is therefore important to consider not only the total amount of pollinator loss in a system, but relative loss rates among different pollinator groups and potential temporal patterns in pollinator loss. Shifting pollinator abundance over the flowering season variably affects visitation rates and seed set (Ashman & Stanton 1991; Aizen 2001), suggesting that future pollinator losses may exacerbate natural seasonal variation in pollinators, and thus preferentially reduce the pollination of *Ci. discolour*.

Partial pollinator exclusion shifted pollinator communities in unexpected ways. We observed that this treatment reduced the overall number of visits by pollinators across all functional groups and not just large-bodied groups. Interestingly, flies like the hoverfly, *Allograpta obliqua*, that were abundant at the site and small enough to access the partial pollinator exclusion flower heads did not visit either thistle species under this treatment. Since this insect is small enough to access thistle flower heads through the net, we propose the partial-exclusion device presents a visual deterrent to floral visitation. Bumble bees, by contrast, were nearly as abundant on partially excluded *Ci. discolour* flower heads as control flower heads, despite their body size being roughly the same size as the mesh opening. This curious trend may be explained by the impressive body awareness of bumble bees, allowing them to access the flowers despite a potential physical barrier (Brebner & Chittka 2021). For the remaining functional groups, the partial exclusion treatment reduced the number of visitors to flowers of both species. In *Ca. nutans*, the mean number of sweat bees decreased by half under partial exclusion, whereas *Ci. discolour* saw a 20% decrease. Nevertheless, *Ci. discolour* flower heads may be disproportionately impacted by any pollinator reduction since the control community for *Ci. discolour* featured fewer pollinator individuals than the invasive species' pollinator community.

Paralleling the reduced pollinator visitation rates and pollinator community in *Ci. discolour*, reproductive output was also reduced more severely in *Ci. discolour* than in *Ca. nutans*. Unlike in previous greenhouse experiments with *Ca. nutans* (Warwick & Thompson 1989), wild populations of both thistle species in this study had low rates of self-fertilization and thus rely on insect pollinators to reproduce successfully. This evidence is reflected in the high rates of flower head failure for both species in the total pollinator exclusion treatment. However, a higher rate of self-pollination was observed in *Ca. nutans* than in *Ci. discolour*. When considering flower heads that produced at least one mature achene, we saw important reproductive differences between the two thistle species. *Ca. nutans* produced more mature achenes per flower head than *Ci. discolour* for the control and partial pollinator exclusion treatments. Both species had decreased fruit production under partial pollinator loss treatments, but the reduction was more severe in the native *Ci. discolour* than the invasive *Ca. nutans*, suggesting that even when faced with poor pollination rates for both species, *Ca. nutans* can still produce more mature achenes than its native counterpart. Fruit production for an individual depends on many additional factors, such as the number of flower heads produced and how often they flower. To obtain a complete picture of fruit production, additional work is needed to quantify whole plant fruit output through time.

Even though differences existed in mature achene production across species identity and pollinator treatment, neither of these factors seemed to impact the germination success of mature achenes. Taken together, our findings show that reductions in reproductive output are attributed to total flower head failure and changes to fruit production, rather than germination and establishment. Germination success did not vary between the two species, indicating that *Ca. nutans* does not produce inherently superior achenes, but rather it is more resilient to pollinator loss due to the smaller decrease in fruit output when faced with a reduced pollinator community.

Our comparison of closely related native and invasive thistles (i.e., within the Carduinae subtribe) has important implications for the ongoing management of invasive plants in remnant and restored habitats under global change scenarios. The invasive *Ca. nutans* is already a dangerous competitor due to a broader thermal niche, higher growth rates, and high establishment success relative to *Ci. discolour*. In addition, climate change may exacerbate this competitive advantage as *Ca. nutans* grows taller at elevated temperatures, increasing fruit dispersal capacity (Drees & Shea 2023). We show here that reduced pollinator communities can negatively impact both thistle species, but the negative consequences are more severe in *Ci. discolour* than in *Ca. nutans*.

## AUTHOR CONTRIBUTIONS

GLeF and ER contributed to study conception and design. GLeF conducted the experiment and led writing of the manuscript. GLeF and ER analysed the data. GLeF, DE, and ER contributed critically to the drafts, and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

## DATA AVAILABILITY STATEMENT

Data and analysis code will be available on GitHub prior to publication.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Model selection of pollinator visitor counts across species and pollinator exclusion treatment for *Cirsium discolor* and *Carduus nutans*.

**Table S2.** Model estimates of the best selected model of pollinator visitor counts across species and pollinator exclusion treatment for *Cirsium discolor* and *Carduus nutans*.

**Table S3.** Model selection for fruit set and germination proportion across species and pollinator exclusion treatment for *Cirsium discolor* and *Carduus nutans*.

**Fig. S1.** Depiction of pollinator exclusion treatments on a *Carduus nutans* plant.

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