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Pollinator Behavior Mediates Negative Interactions between Two Congeneric Invasive Plant Species

Suann Yang,* **Matthew J. Ferrari, and Katriona Shea**

Pennsylvania State University, University Park, Pennsylvania 16802

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ABSTRACT: Simultaneously flowering plant species may indirectly interact with each other by influencing the quantity of pollinator visitation and/or the quality of pollen that is transferred. These effects on pollination may depend on how pollinators respond to floral resources at multiple levels. In this study, we demonstrate pollinator-mediated negative interactions between two invasive plants, *Carduus acanthoides* and *Carduus nutans.* Using constructed arrays of the two species, alone and in mixture, we quantified pollinator visitation at the patch and individual plant levels and measured seed production. We found that co-occurrence of our species led to a shift in pollinator services at both levels. Greater interference occurred when arrays were small and spacings between neighboring plants were large. A spatially explicit movement model suggests that pollinator foraging behavior, which mediates the interactions between plants, was driven by floral display size rather than species identity per se. Pollinator behavior significantly reduced the proportion of seed set for both species relative to that in single-species arrays. Overall, the dependence of pollinator behavior on patch size, spacing between plants, and patch composition can lead to pollinator-mediated plant interactions that range from facilitative to competitive.

Keywords: Carduus acanthoides, *Carduus nutans*, gravity model, indirect interactions, invasional interference, pollination.

Introduction

Simultaneously flowering plant species often share generalist pollinators with each other, which can lead to indirect positive or negative interactions within the plant community (e.g., Rathcke 1983; Waser et al. 1996; Mitchell et al. 2009). Outcomes of these interactions may depend on how the quantity (e.g., Campbell and Motten 1985; Chittka and Schürkens 2001; Flanagan et al. 2009) and quality (e.g., Waser 1978; Campbell et al. 2002) of pollination are affected by patch and plant characteristics (Mitchell et al. 2009). To understand the variation in these outcomes, we need to identify the underlying mechanisms by focusing explicitly on the pollinators, specifically their behavioral responses to patch and plant characteristics and how that behavior translates to an effect on pollination quantity and quality.

An extensive literature on pollinators and native plants exists, detailing how a foraging pollinator's decisions to visit patches of plants and to move within and between those plants are influenced by the distribution of floral resources at two levels: the patch and the individual plants within that patch. These studies primarily investigate behavior in single-species patches; however, the patterns would be expected to be similar for multispecies patches. Patches with large, aggregated floral displays tend to have high pollinator visitation (e.g., Sih and Baltus 1987; Ågren 1996; Waites and Ågren 2004). Individual plants with large floral displays also receive more visits (e.g., Robertson and Macnair 1995; Mitchell et al. 2004; Hegland and Totland 2005); these plants can also facilitate visitation to the entire patch (e.g., Moeller 2004). A net competitive effect may occur if pollinators exhibit a preference for individuals of one species (e.g., Brown et al. 2002), even if larger patches attract more pollinators overall (reviewed in Ghazoul 2005). In addition, floral display may interact with the spatial arrangement of plants within a patch, because pollinators may spend more time visiting inflorescences within a plant when distances between plants are large (e.g., Klinkhamer and de Jong 1990; Cresswell 1997; Kunin 1997; Mustajärvi et al. 2001), and thereby enforce pollinator preferences for individuals of large floral display. Although floral constancy of pollinators may prevent movements between coflowering species (e.g., Feldman 2008), phenotypic similarity tends to erode constancy and promotes heterospecific movements (e.g., Thomson 1981; Bell et al. 2005). Clearly, the quantity and quality of pollinator visits are linked to the distribution of floral resources at more than one level.

In this study, we focus on the pollinator-mediated interactions between the two congeneric invasive thistles *Carduus acanthoides* (plumeless thistle) and *Carduus nu-*

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* Corresponding author; e-mail: suy14@psu.edu.

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tans (musk thistle). Most studies of pollinator-mediated interactions focus on interactions among native plants or between native and invasive plants. In contrast, very few studies examine pollinator-mediated interactions between invasive plants (but see Suehs et al. 2006; Molina-Montenegro et al. 2008). However, it is becoming increasingly common for communities to be invaded by multiple species, which may or may not have interacted (directly or indirectly) in their respective native ranges; this novel context of interactions among invaders can provide insights into the process of invasion. Here, we apply the current understanding of how pollination quantity and quality can be affected by plant and patch characteristics (Mitchell et al. 2009) to address pollinator-mediated interactions among invaders. Pollinator-mediated competition often occurs between native and invasive plants that are phenotypically similar (Morales and Traveset 2009). As these two *Carduus* species have very similar, showy floral displays, we predicted competition for (rather than facilitation of) pollinator services; such a negative interaction has never before been demonstrated between two invasive species. To test this prediction, we examined how the quantity and quality of pollinator visits depend on the plant and patch distribution of floral resources in these two *Carduus* thistles.

Methods

Study System: Carduus *Thistles*

Carduus acanthoides L. and *Carduus nutans* L. (Asteraceae) are introduced Eurasian weeds of major economic importance (Skinner et al. 2000). They are invasive worldwide, with one or both species now in North and South America, southern Africa, New Zealand, and Australia (Allen and Shea 2006). These two species have sympatric populations across the United States and southern Canada (McCarty et al. 1980). The two thistles are similar in appearance and life history but nevertheless have obvious physical and ecological differences (Desrochers et al. 1988), which may make a difference to pollinator behavior. Although the two are of similar height (*C. nutans*: 130.5 ± 4.5 cm; *C. acanthoides*: 126.9 ± 4.8 cm), *C. nutans* possesses relatively few (18.2 ± 2.1), large (1.5–4.5 cm in diameter), solitary heads, whereas *C. acanthoides* flower heads are numerous (208.3 ± 35.5), small (1.2–1.6 cm in diameter), and solitary or clustered (see fig. 1*A*; R. Zhang and K. Shea, unpublished data). In central Pennsylvania, they flower simultaneously in June and July and are common in grazed pastures and disturbed roadsides. In typical pasture communities, grazing animals avoid foraging on spiny thistle leaves, which results in a simple floral landscape consisting nearly entirely of thistles in a matrix of cropped vegetation. Both hermaphrodites, *C. nutans* and *C. acanthoides* are pollinated by insects such as bees and butterflies (Giurfa and Núñez 1992). Although both plant species are similarly self-compatible (Warwick 1987; Warwick and Thompson 1989), geitonogamous and outcrossing pollination is accomplished through their insect pollinators (Jessep 1990).

Experimental Design

In 2007 and 2008, we constructed arrays of potted thistles within the 2,000 pasture/crop acres of Pennsylvania State University's Russell E. Larson Agricultural Research Farm in Rock Springs, Pennsylvania. Using potted plants allowed us to control for belowground interactions. In 2007, our arrays were of three sizes (1, 4, and 16 plants), two spacings between plants (0.5 and 1 m), and three compositions (pure *C. nutans*, pure *C. acanthoides*, and a 1 : 1 evenly distributed mixture of both), for a total of 14 different arrays (fig. 2). These arrays were replicated four times for a total of 56 sites, with each group of 14 arrays designated as a block and located in the same general locale on the farm. Arrays were separated from each other by at least 200 m of thistle-free vegetation. We assume that this distance is large enough that the observed patch behavior of pollinators is not influenced by neighboring patches (Karron et al. 1995). Thistles were raised from seed in a greenhouse, transplanted to overwinter in the ground outdoors (vernalization is required for flowering; Popay and Medd 1990), and then repotted just as bolting initiated. Potted plants were watered abundantly. We repeated this design in 2008, with two exceptions. We increased the upper interplant spacing to 2.0 m, to strengthen the effect of this factor. In addition, because not all individuals in an array flower simultaneously throughout the season, any plant that was not flowering in an array was replaced by a flowering individual from a large reserve pool of plants. This replacement permitted us to maintain array sizes, ensuring that behavioral observations could be replicated across array sizes, but prohibited us from meaningful seed collection at the end of the season. Thus, all seed set data are from 2007, and all behavioral data are from 2008. We analyzed the seed set data and behavioral data separately (see "Data Analysis") and made the assumption that the seeds produced in 2007 resulted from pollinator behavior similar to that observed in 2008.

We conducted two types of behavioral observations in order to capture behavior across resource levels: (1) measuring visitation rates to an array (behavior at patch level) and (2) recording movements within and between plants along entire visitation sequences (behavior at plants within patch level). All observations were conducted on dry days from 0800 to 1700 hours during peak flowering (June–

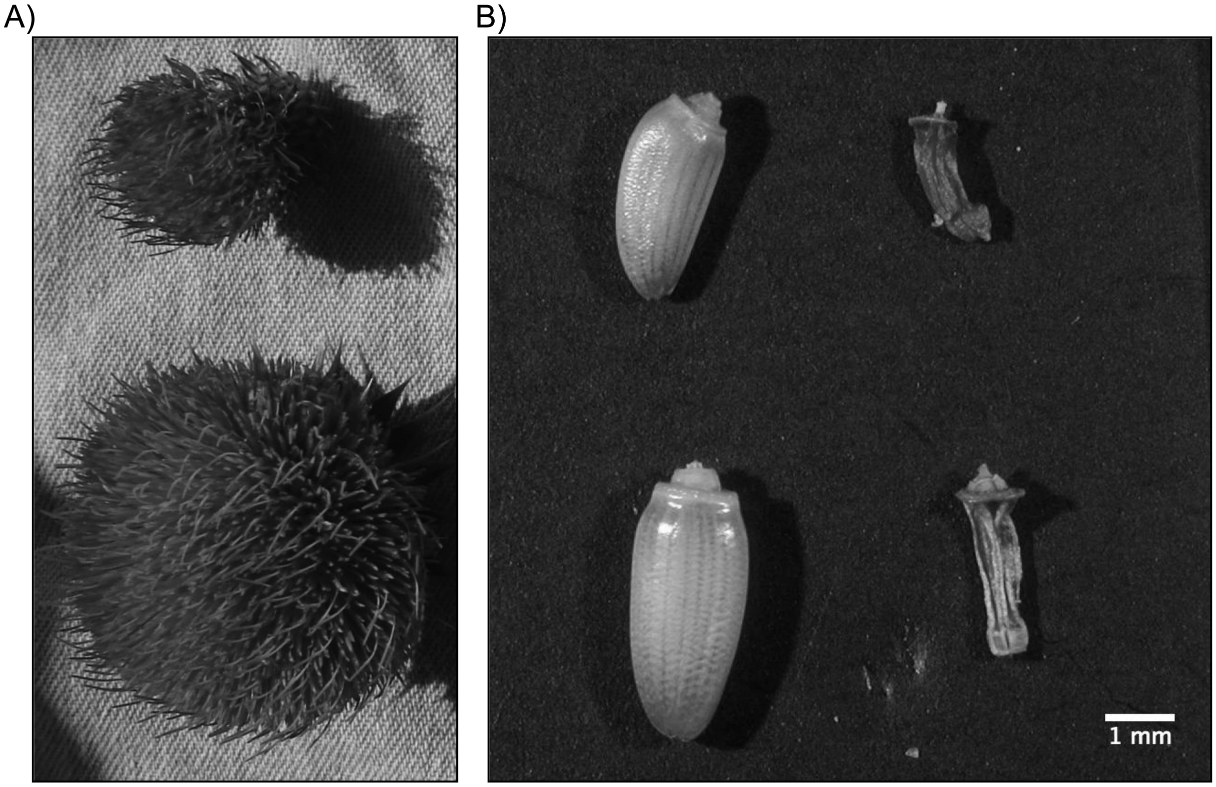

Figure 1: *A*, Flower heads of *Carduus acanthoides* (*top*) and *Carduus nutans* (*bottom*). *B*, Filled (*left*) and unfilled (*right*) seeds of *C. acanthoides* (*top*) and *C. nutans* (*bottom*). Filled seeds were counted as ovules that were successfully pollinated and produced a live embryo. A color version of this figure is available in the online edition.

July). We used two teams of three observers and one recorder; consistency between teams was ensured by training and calibration sessions. Binoculars were used to aid in identifying small insects. In addition, herbivory was qualitatively measured, but as minimal herbivory was observed, we do not mention it further.

Patch-level visitation rates were quantified on Palm Tungsten E2 personal digital assistants (PDAs) using EZRecord (http://cas.bellarmine.edu/tietjen/) to record all new visits to an array in 10 min. We examined behavior at the plant level, using the same arrays but on different days, and recorded visitation sequences within and between plants. These data were recorded with our PDAs and the Outdoor Explorer (BIOBSERVE) software, which allows for the recording of within- and between-plant movement. During each 20-min observation period, a team followed the visitation sequence of the first newly arriving insect visitor, waiting for the current visitor to complete its sequence before following another visitor. Individual pollinator moves were classified as selfing moves (to another inflorescence on the same plant), outcrossing moves (to another plant of the same species), heterospecific moves (to another plant of the other species), or moves away from the array. To account for weather and time-of-day variation, we randomized the order in which arrays were observed within each block of 14 arrays. We repeated both types of observations for each array at least five times, for a total of 94.7 h of sequence observations and 46.5 h of visitation rate observations from all arrays across the entire season.

To examine the difference in pollination success across the array configurations, seeds were collected from each plant at the end of the 2007 season, and the filled (fertilized, containing a live embryo) and unfilled (unfertilized) seeds were counted (fig. 1*B*). The sum of filled and unfilled seeds is approximately equal to the number of florets, and therefore the number of ovules, produced (S. Yang, personal observation). Thus, this sum represents the maximum possible seed set. Deviations from this theoretical maximum are attributable to pollinator-mediated interactions and/or resource limitation (Stephenson 1981). As our plants were maintained in separate, identical pots, seed set differences were unlikely to be from resource limitation. Therefore, we considered any differences in the proportion

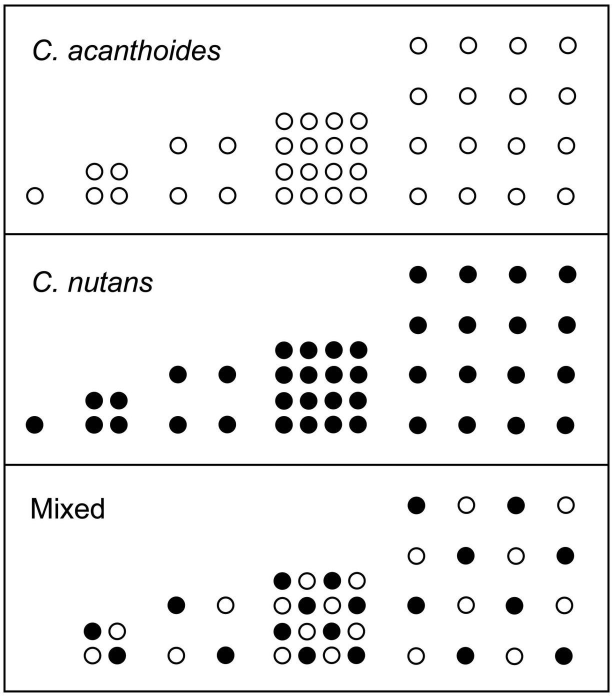

Figure 2: Schematic of potted array design. In 2007, spacing between plants was 0.5 and 1.0 m. In 2008, spacing between plants was 0.5 and 2.0 m.

(i.e., seed-to-ovule ratio) or number of filled seeds to reflect the outcome of interactions for pollinators, because of our treatment factors.

Data Analysis

We used general linear mixed-effects models (GLMMs; Crawley 2005) that used the lmer function in R (R Development Core Team 2010) with Poisson errors and block and sampling date as random effects to test for the effect of species composition, array size, and plant spacing on the quantity of visits to an array (patch level) and to a plant made within an array (plant level). To examine the quality of visits at the plant level, we used a similar linear mixed-effects model (but with binomial errors) on the proportion of outcrossing moves to individual plants (outcrossing moves/(selfing + outcrossing moves)). In order to compare visits for each species between pure and mixed arrays, analyses were conducted separately for *C. nutans* and *C. acanthoides.* We selected the most likely models by using Akaike's Information Criterion (AIC; Akaike 1974). To identify the effects of individual floral display and plant spacing on movements of pollinators, we also analyzed the data on individual moves within arrays, using a spatially explicit movement model (Ferrari et al. 2006). The details of this model are described in appendix A in the online edition of the *American Naturalist.* To test for the effect of array configuration on pollination success, we used a GLMM with the lmer function in R and quasi-binomial errors to test for the effect of array species composition, array size, and spacing between plants (with block and flower head size as random effects) on the proportion of filled seeds. To test the effect of these factors on the total number of filled seeds, we used a GLMM with negative binomial errors and the glm.nb function in R. Again, AIC was used to select the most likely model.

Results

Pollinators

We observed that 80% of visitors to our arrays were bees: bumblebees (*Bombus* sp.), small, short-tongued, solitary bees (e.g., *Colletes* sp., *Lasioglossum* sp.), and carpenter bees (*Xylocopa* sp.). Other species less commonly observed included hoverflies (11%; e.g., *Allograpta obliqua*) and butterflies (4%; e.g., *Danaus* sp., *Papilio* sp., and *Speyeria* sp.).

Quantity of Visits to Arrays. Pure *Carduus acanthoides* arrays received more visitors in 10 min than mixed arrays (general linear mixed model [GLMM] with Poisson errors: $z = 3.068$, $P = .002$), and mixed arrays received more than pure *Carduus nutans* arrays (GLMM: $z = -6.831$, $P < .0001$; fig. 3*A*). Larger arrays received more visits than smaller ones (GLMM: $z = 14.734$, $P < .0001$). Spacing also had a significant positive effect on visitation rate (GLMM: $z = 5.580$, $P < .0001$), although there was a significant size × spacing interaction (GLMM: $z = -5.261$, $P < .0001$): 2.0-m-spaced arrays received approximately one more visit per observation period, on average, than those with 0.5-m spacing in four-plant arrays, while the 0.5-m-spaced arrays received approximately one more visit than those with 2.0-m spacing in 16-plant arrays.

Quantity and Quality of Visits to Plant within Arrays. In general, the number of pollinator moves within an array increased with array size (GLMM: $z = 15.597$, $P < .0001$) and decreased with spacing (GLMM: $z = -5.407$, $P = .0424$), regardless of species composition. Individual *C. nutans* plants received more visits in a pure *C. nutans* array than in a mixed array (GLMM: $z = 9.235$, $P < .0001$). Individual *C. acanthoides* plants received fewer visits in mixed arrays than in pure arrays, although this relative reduction in visitation is smaller for the four-plant arrays than for the 16-plant arrays (composition × size interaction; GLMM: $z = -3.951$, $P < .0001$; fig. 3*B*). Also, the positive effect of array size for individual *C. acanthoides*

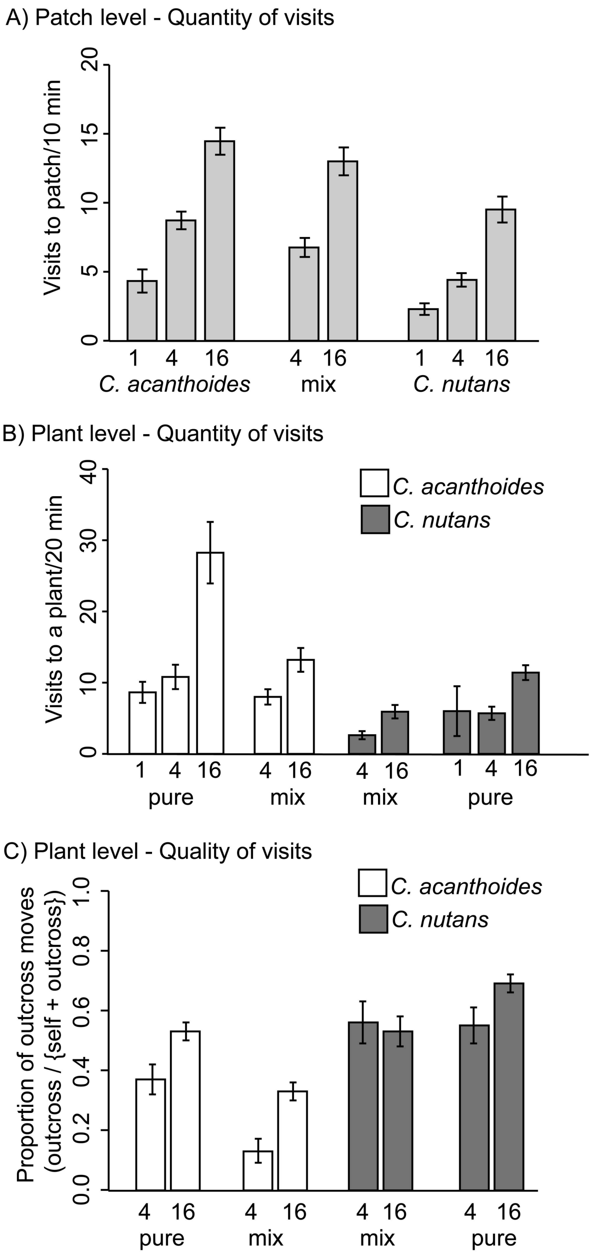

Figure 3: Quantity and quality of pollinator visits at the patch (array) and plant levels. All error bars denote standard errors. Array configurations are arranged by size (1, 4, or 16 plants) and composition. *A*, Patch-level quantity of visits as mean visitation rate of arrays. Mixed arrays receive an intermediate quantity of visitation, compared to pure arrays. *B*, Within arrays, quantity of visits to individual plants. Individual plants receive fewer visits in mixed arrays. *C*, Within arrays, quality of visits. A greater proportion of moves within plants (self moves) occurs in mixed than in pure arrays for *Carduus acanthoides* but not for *Carduus nutans*.

plants was diminished at the larger spacing (size × spacing interaction; GLMM: $z = -2.727$, $P = .0063$).

In terms of visit quality, the proportion of moves to *C. acanthoides* that were outcrossing moves was greater in pure than in mixed arrays. Outcrossing moves were more common in large patches and relatively more so in mixed arrays (size × composition interaction; GLMM: $z = -2.319$, $P = .020$). In addition, a greater proportion of outcrossing moves occurred when plants were closer together (GLMM: $z = -2.004$, $P = .006$). In contrast, the proportion of outcrossing moves to *C. nutans* did not differ between pure and mixed arrays (GLMM: $z = 0.522$, $P = .602$). For *C. nutans*, only spacing significantly affected the proportion of outcrossing moves (GLMM: $z = -1.914$, $P = .056$; fig. 3*C*).

The number of heterospecific moves from *C. acanthoides* to *C. nutans* within mixed arrays was smaller for large spacing (GLMM: $z = -2.312$, $P = .021$) but was not affected by array size (GLMM: $z = 0.661$, $P = .509$). In contrast, although the number of moves from *C. nutans* to *C. acanthoides* was negatively affected by spacing (GLMM: $z = -3.582$, $P = .0003$), the number of this type of move increased with array size (GLMM: $z = 3.081$, $P = .0020$).

Movement Model. We analyzed the individual moves of pollinators within arrays by using a spatially explicit model to identify the effect of distance and plant characteristics on pollinator movement (see app. A for full analysis). In general, pollinators made more moves in *C. acanthoides* arrays than in mixed or *C. nutans* arrays, and short-distance moves were more likely across all array types. The probability of selfing moves increased with plant floral display size across all array types and spacings. In contrast, outcrossing moves did not favor larger floral displays, except in the *C. acanthoides* arrays at the 0.5-m spacing.

In mixed arrays, we assessed whether the display size (see app. A) or the plant species was the better predictor of outcrossing moves to a plant. We fitted competing models where the probability of a move to a plant was a function of the plant species (a binary variable), the plant display size (a continuous variable), or an interaction between the two (app. A). The model with display size alone was better supported than a model that accounted for the species of the destination plant (AICs of −54.8 and −42.1, respectively). Thus, while there were relatively more moves to *C. acanthoides* than to *C. nutans* in the mixed arrays, our analysis suggests that the bias arose from a preference for larger floral displays (mean display size ± SE = 27.6 ± 0.52 for *C. acanthoides* and 16.3 ± 0.88 for *C. nutans*) rather than a preference for *C. acanthoides* per se.

Pollination Success

A higher proportion of seeds was produced by plants in larger arrays for both *C. acanthoides* (general linear mixed-effects model [GLMM] with quasi-binomial errors: $z = 2.733$, $P = .0063$) and *C. nutans* (GLMM: $z = 4.620$, $P < .0001$). In addition, the proportion of seed set was significantly lower in mixed than in pure arrays for both *C. acanthoides* (GLMM: $z = -3.196$, $P = .0014$) and *C. nutans* (GLMM: $z = 5.260$, $P = .0003$; fig. 4), with more severe reductions in smaller arrays (*C. acanthoides*: −21.3% for 4 plants and −6.8% for 16 plants; *C. nutans*: −19.9% for 4 plants and −4.6% for 16 plants). Interestingly, while there was a strong effect on the proportion of seed set, there was no significant difference between the total number of seeds produced per plant in pure arrays and that in mixed arrays (*C. acanthoides*, GLMM with negative binomial errors: $z = -1.859$, $P = .060$; *C. nutans*, GLMM: $z = 0.209$, $P = .242$). There was a significant positive effect of array size (9% increase; GLMM: $z = 2.155$, $P = .028$) and a significant negative effect of spacing (11% decrease; GLMM: $z = -2.264$, $P = .024$) on the total seeds per plant for *C. nutans*; neither size nor spacing was included in the most likely model for *C. acanthoides*.

Discussion

Carduus acanthoides and *Carduus nutans*, when co-occurring, reduced the quantity and quality of pollinator services each received at both the array and the individual-plant

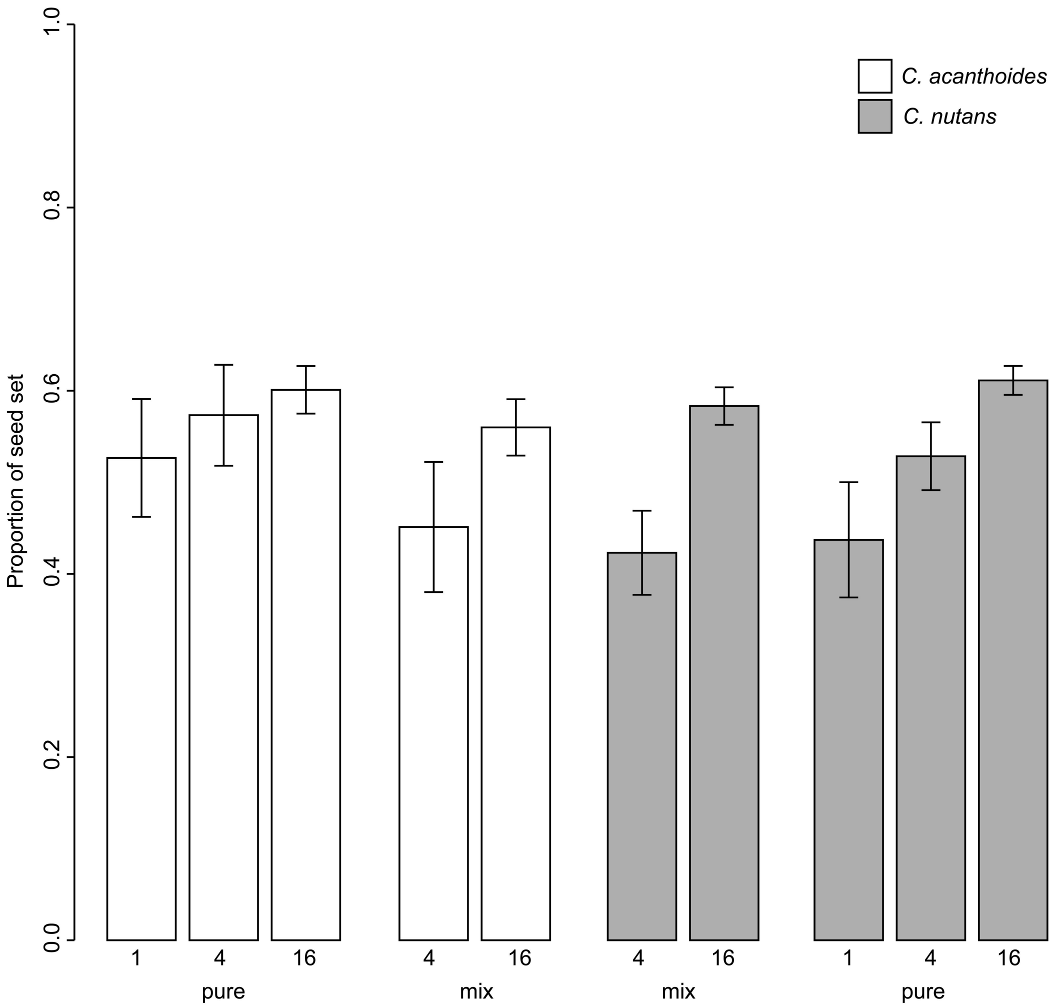

Figure 4: Proportion of filled seeds per plant. *White bars*, *Carduus acanthoides*; *gray bars*, *Carduus nutans*. Array compositions are arranged by size (1, 4, or 16 plants) and composition. Error bars show standard errors.

level. *Carduus acanthoides* consistently suffered negative effects on quantity and quality across both levels of observation, but the negative effect for *C. nutans* was apparent only in terms of the quantity of visits at the plant level. The degree of interference depended on the number and spacing of neighboring plants in an array, with greater interference at smaller array sizes and larger plant spacing. Our model allowed us to go beyond these coarse effects of array size and spacing between neighbors to examine finer-scale effects on pollinator movement within arrays. The distance between plants in an array, together with the floral display size (but not species identity) of individual plants, was an important influence on the types of moves made by pollinators within an array. By examining multiple levels of resource distribution, we were able to capture the shift in pollinator behavior that caused this change in pollinator services.

Our study suggests that competition among plants eliminated any benefit from joint attraction at the patch level, in contrast to studies documenting interspecific facilitation (e.g., Moeller 2004; Ghazoul 2006). Like other researchers documenting negative effects of pollinator-mediated interactions (e.g., Brown et al. 2002; Kandori et al. 2009), we found that the species with larger floral display diverted pollinators away from the less showy species. Surprisingly, the more attractive *C. acanthoides* suffered as well, because pollinators were more likely to make selfing rather than outcrossing moves in mixed arrays. Although deposition of heterospecific pollen may also contribute to interference between species (e.g., Brown and Mitchell 2001; Morales and Traveset 2008), hybrid incompatibility between our two species (Warwick et al. 1989) likely contributed very little to the interference we observed, because we saw fewer heterospecific than conspecific moves (fig. B1 in the online edition of the *American Naturalist*).

Pollinator-mediated interactions between these two *Carduus* thistles reduced an individual thistle's ability to attain maximal seed production. Because individual variation in ovule production was high, however, the extension of our findings to population growth and spread is somewhat limited as measured here. Without a significant decrease in fecundity (i.e., total rather than proportional seed set) due to co-occurrence with congeners, demographic models will not project differences in population growth rates or spatial spread. However, other measures of fitness may still allow us to consider population-level consequences. In particular, the offspring produced by individuals in mixed arrays may have lower fitness than their counterparts from pure arrays. As noted above, *C. acanthoides* received relatively more selfing moves in mixed arrays (a potential cost of large floral display). Unlike self-incompatible species, where pollinator visitation results in outcrossing, self-compatible species may experience differing or interacting effects of visitation quantity and quality (such as when visitation leads to increased selfing). Highly inbred offspring may suffer in their ability to establish and reproduce (Charlesworth and Charlesworth 1987; Husband and Schemske 1996; Crnokrak and Barrett 2002). These alternative measures of fitness will be fruitful avenues for additional research.

Clearly, competition between native and invasive plants for pollinators is a problem for native communities (Bjerknes et al. 2007; Morales and Traveset 2009), but given the existence of disturbance-prone communities with many co-occurring invasive plant species, negative interactions between invaders may be an underappreciated factor in determining invasion success. Much attention has been paid to the "invasional meltdown" hypothesis, that invasive species can facilitate each other's invasion success (Simberloff and Von Holle 1999; Simberloff 2006). However, as we have documented in our study, "invasional interference" may also occur by way of direct or indirect antagonistic interactions within the community. The increase in pollen limitation that accompanies co-occurrence with congeners may have consequences for the invasion process, although the magnitude of such effects remains to be evaluated.

Our results reveal indirect interactions between invaders to be a previously overlooked phenomenon that has the potential to reduce the success of plant invasions. More generally, we have shown that the behavioral responses of pollinators to the distribution of floral resources at both patch and plant levels translate to effects on both quantity and quality of pollination. Thus, the outcome of a pollinator-mediated interaction between plant species can be highly dependent on ecological context. Overall, our study underscores that the context dependence of pollinator behavior is an important mechanism that determines whether pollinator-mediated plant interactions will be facilitative or competitive.

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Invasive plumeless thistle with bumblebee pollinator. Because bumblebees also visit the invasive musk thistle (not shown), both thistles are likely to experience reduced reproduction when they grow together. Photograph by Suann Yang.