



Pollinator floral provisioning by a plant invader: quantifying beneficial effects of detrimental species

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ABSTRACT

Aim Although the negative effects of invasive species are globally recognized, little is known about the potential positive impacts they can have on other species in the ecosystems they invade. However, the persistence of invaders in a wide range of ecological communities may mean that they provide resources and refuge for threatened native species, or supplement ecosystem services.

Location Agroecosystems in the USA.

Methods We use a 2-year field experiment to explore the potential positive and negative impacts of an invasive thistle (*Carduus acanthoides*) on the composition of the resident community of foraging insects. The presence or absence of the thistle was the only difference in experimental and control plots comprising a background community of ten flowering annual species.

Results We demonstrate that the invasive thistle is both highly visited and strongly preferred by bees relative to other flowering species. Bee abundance was 302% higher and bee species richness 35% higher in habitat patches where the thistle was present compared to where it was absent. In addition, the abundance of *Bombus* species, a native group recently found to be in decline, was 479% higher when the thistle was present.

Main conclusions Our results suggest that, despite causing significant problems, the invasion of this non-native species may also provide crucial benefits via floral resources for pollinators. Benefits, such as the floral resources that invaders provide to pollinators, should also be taken into account in conservation and invader management plans. Eradication or complete removal of invasive species which provision insects with floral resources could have unintended negative impacts on the associated pollinator community.

Keywords

agroecosystem, biological invasions, *Carduus acanthoides*, ecosystem services, invasive species, plant–pollinator interactions, pollinator diversity, resource provisioning.

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INTRODUCTION

The negative impacts of non-native invasive species are well documented. Indeed, invasive species are known to have many detrimental effects on ecosystems (e.g. Elton, 1958; Charles & Dukes, 2007; Vilá *et al.*, 2011) and are considered to be one of the major threats to biodiversity (Williamson, 1998; Parker *et al.*, 1999; Hejda *et al.*, 2009). The costs of controlling the populations of non-native species, in addition to the costs from losses and damages, are estimated to be

billions of dollars per annum (Pimentel *et al.*, 2005). Particularly in agricultural ecosystems, management of unwanted weeds can be a costly burden, with estimates of US\$8 billion in control costs and US\$25 billion in damages and losses per year for crop and pasture weeds (Pimentel *et al.*, 2005). Given that approximately 40% of the land surface is dedicated to agriculture (Foley *et al.*, 2005), the management of these ecosystems may have far-reaching impacts.

Considerably less is known about the potential beneficial aspects of these invaders, in part because studies of invader

impact often focus on competitive effects with native species (Kumschick *et al.*, 2015). However, invader impacts are not always negative (Gurevitch & Padilla, 2004; Rodriguez, 2006; Sax & Gaines, 2008; Davis *et al.*, 2011; Schlaepfer *et al.*, 2011). In some cases, invasive species can become integral parts of the ecosystem, even to the point of providing refuge for endangered native species (Zavaleta *et al.*, 2001) or replacing lost pollination services (Junker *et al.*, 2010). Invasive species may have facilitative effects on native species, for example, by providing limited resources or habitat (Zavaleta *et al.*, 2001; Rodriguez, 2006; Stout & Morales, 2009; Gleditsch & Carlo, 2010; Davis *et al.*, 2011). The opposing negative and positive effects of invaders may lead to significant controversy (e.g. Cullen & Delfosse, 1985; Davis *et al.*, 2011; Simberloff, 2011; Richardson & Ricciardi, 2013).

One important way in which invasive species may have unrecognized beneficial effects is in providing floral resources for pollinators (Rodriguez, 2006; Stout & Morales, 2009; Gibson *et al.*, 2012). Pollination services in agroecosystems are valued in the billions of dollars (e.g. Gallai *et al.*, 2009), and to ensure sufficient pollination for crop species dependent on insect vectors, many land managers must expend resources to buy or rent hives of honeybees and colonies of other domesticated bees. At the same time, they often attempt to encourage the populations of wild bee communities by establishing patches of floral provisioning habitat (Isaacs *et al.*, 2009). This floral provisioning habitat is associated with an increase in pollinator abundance and can result in a higher crop yield (Blaauw & Isaacs, 2014). Many recent studies suggest that fragments of remnant habitat are also critical refuges for wild bee populations (Garibaldi *et al.*, 2011). These fragments, though not always thoroughly described in the literature, are likely composed of mostly hardy weed species that can persist in the face of intense agricultural practices (D. Mortensen, pers. comm.). Weed diversity has been found to enhance pollinator diversity within sunflower fields (Carvalho *et al.*, 2011), and invasive weeds can be disproportionately well visited in agricultural systems and therefore important components of the plant–pollinator community structure (Pocock *et al.*, 2012); indeed, pollen from crop species has been found to be a relatively small component of the pollen found in honeybee hives (Pettis *et al.*, 2013). This suggests that agricultural weeds have the potential to provide resources or habitat that support valuable crop pollinators.

We selected a noxious invader, the plumeless thistle (*Carduus acanthoides*), which is notoriously difficult to eradicate (Zhang *et al.*, 2011), for our study. Our goal was to quantify the impacts of the thistle on the species richness and abundance of the insect community within a patch of floral provisioning habitat over the course of a single flowering season. Specifically, the thistle has a showy floral display and can produce hundreds of large purple-red flower heads over a summer. Its attraction for pollinators is noticeable (K. Shea, L. Russo, pers. obs.) and, for this reason, we hypothesized that the largest changes would be in the community of

insects that are anthophilic, especially the bees (members of the superfamily Apoidea). Using both active and passive sampling methods, we monitored the insect communities at experimental plots composed of a background community of flowering annuals with and without this thistle over 2 years.

METHODS

Study species

The plumeless thistle (*Carduus acanthoides* L. Asteraceae), native to Eurasia, was first recorded in the United States in 1879 (Desrochers *et al.*, 1988) and is invasive in North and South America, Australia and New Zealand. The thistle is widely distributed in the United States and is considered a pest in agricultural areas and roadsides (Desrochers *et al.*, 1988; Allen & Shea, 2006); in agricultural systems, it can reach extremely high densities of more than 15,000 individuals per hectare (Tipping, 1992). The thistle is actively managed, but notoriously difficult to eradicate, requiring continuous reapplication of both mechanical and chemical control methods (Desrochers *et al.*, 1988). It does not compete well in natural systems, but does persist in the face of extreme disturbances, for example, frequent mowing by farmers (Zhang *et al.*, 2011).

C. acanthoides is a monocarpic perennial and reproduces strictly by wind-dispersed seed (Skarpaas & Shea, 2007). *C. acanthoides* is self-compatible (Warwick & Thompson, 1989), but depends on insect pollinators for outcrossing pollination (Yang *et al.*, 2011). It produces hundreds of composite flower heads across its flowering season and an individual plant can have more than 200 flower heads at a given time (Yang *et al.*, 2011); each flower head can have more than 100 florets (Giurfa & Núñez, 1993) and produces up to 80 mg of nectar in a day (Giurfa & Núñez, 1992). In addition to these nectar resources, a single flower head can produce more than 125,000 grains of pollen (Costa & Yang, 2009).

Experimental design

We established eighteen paired 2 × 2 m plots in March 2009 at the Russell E. Larson Agricultural Research farm, Pennsylvania, USA. All plots were spatially separated by more than 100 m along the edges of agricultural fields and sprayed with the herbicide glyphosate ('Round-up'TM) in early April and then seeded with 3.5 g each of 10 flowering annual species (Table 1). Pairs were selected as plots that were more than 100 m apart, but less than 250 m apart and matched for surrounding habitat as much as possible, and treatments were randomly assigned within each pair. The flowering species in the background community were selected based on the following criteria: (1) they were annuals and would flower in the same summer in which they were planted, (2) they had a showy floral display attractive to pollinators, (3) we could acquire them from a local

Table 1 List of ten flowering annual plant species, as well as the invasive thistle (in bold), used as the background community in this study, sorted by family.

Species binomial	Flower colour	Bloom diameter (cm)†	Plant height (cm)‡
Asteraceae			
<i>Carduus acanthoides</i>	Pink/purple	2.5–3	89.4 ± 1.4
<i>Centaurea cyanus</i>	Blue/purple	1.5–3	45.4 ± 1.7
<i>Coreopsis tinctoria</i> *	Yellow/maroon	2.5–4	42.9 ± 1.4
<i>Cosmos bipinnatus</i>	Pink/purple	7.5–8.9	107.3 ± 6.1
<i>Gaillardia pulchella</i> *	Red/yellow	4–6	16.4 ± 3.7
<i>Helianthus annuus</i> *	Yellow	7.5–12.7	137 ± 1.6
<i>Rudbeckia hirta</i> *	Yellow	5–7.5	40.3 ± 1.9
Fabaceae			
<i>Chamaecrista fasciculata</i> *	Yellow	1.5–2	52.1 ± 0.6
<i>Melilotus albus</i>	White	0.4–0.5	2.5 ± 1.8
<i>Melilotus officinalis</i>	Yellow	0.5–0.7	2.5 ± 1.8
Malvaceae			
<i>Lavatera trimestris</i>	Pink	6–7	28.5 ± 1.8

*Species native to the study area.

†Estimated diameter range of individual flower or flower heads on the plant.

‡Height of tallest flowering stem averaged across each plot and year at the time of the destructive census (± standard error).

source, and (4) they were not considered weedy or invasive (although some were non-native). The background species presented a variety of different floral displays in terms of colour, size and morphology (Table 1).

We transplanted four second-year *C. acanthoides* rosettes (greater than 10 cm in diameter to ensure bolting) into each of the four corners of one randomly selected plot from each pair; this density falls within the naturally occurring range. After being seeded, plots were subsequently layered with mulch and watered. Maintenance of the plots included watering and weeding out any plant material that had not been planted. Because the plants in the plots were annuals, and because we destructively sampled above-ground biomass, we established eighteen new plots in the second year of the study (2010); we prepared them in exactly the same way except that we planted the thistle rosettes in the corners in the previous fall to allow them to overwinter in the plots and avoid transplant stress. These second-year plots were established directly adjacent to the former year's plots, but not on exactly the same patch of ground, to avoid any unanticipated below-ground legacy effects. In 2010, we established three additional plots with the same background community of annual plants and four thistles, also more than 100 m away from any existing plots. In these additional plots, we removed all flower heads from the thistles every other day throughout the summer, leaving other thistle biomass intact. The purpose of these floral removal plots was to allow us to distinguish whether changes in the insect community might be solely attributed to the green biomass or to the flower

heads of the thistle and also whether there were any competitive effects on the other plants in the community due to the presence of the thistle root and shoot biomass.

Data collection

In both years, we sampled plots for insects every other week from late May through early September. At each sampling period, we observed plots for 5 min to record floral visitors, vacuumed for 1.5 min with a Bioquip insect vacuum and passively sampled with a composite insect trap, which included cone, malaise, flight intercept and pan components (Russo *et al.*, 2011). We sampled each plot six times in each summer, for a total experiment-wide sampling time of 19.5 observation hours and 5.85 vacuum hours.

The observations have the advantage of recording interactions on particular plant species, but lose resolution in insect identification to groupings of solitary bee (SB), bumblebee (BB), honeybee (HB), syrphid fly (SF), carpenter bee (CB) and Lepidoptera (Lep). In contrast, we identified all bee specimens collected in the vacuum to the species level, but do not have information about the specific plants they were visiting when they were captured.

We completed three plant censuses each year by recording the stem number, tallest stem and number of flowering stems of each species in each plot (Table S1). We terminated the experiment in early September of each year by collecting, drying and weighing all above-ground plant biomass. We counted the number of flowers of each species for every sampling period.

Insect identification

We identified all collected insect specimens to the order level and all hymenopteran specimens to the family level (voucher specimens at the Pennsylvania State University). Within Hymenoptera, we identified all members of the superfamily Apoidea to the species level (voucher specimens for each species are at the Pennsylvania State University) and all identifications were confirmed by Leo R. Donovall at the Pennsylvania Department of Agriculture.

Data analysis

We tested differences in plant biomass, insect counts at the order, family and species level between plots with and without thistles for significance using generalized linear regression models using the R package *LME4* (R Development Core Team 2011). We assumed the count data to be Poisson distributed, and the individual bee genera and species to follow a zero-inflated Poisson distribution. Random effects included sampling date, plot location and year, while the treatment was the presence of the invasive thistle. Full details on each model are included in the supporting information (see Appendix S1 in Supporting Information). To compare the relative proportion of bee species and genera found only in

thistle plots, only in non-thistle plots, or found in both, we used a single-sample chi-square test. We also used a two-way chi-square test to compare the proportion of specimens in thistle and non-thistle plots for hymenopteran families that include natural enemies of agricultural pests. We used the two-way test in this case because we were interested in the association between many independent variables (hymenopteran families) in thistle versus non-thistle plots, while we used a single-sample chi-square for the first test because we were only interested in the response of one independent variable (i.e. bee species or genera richness) in thistle versus non-thistle plots.

RESULTS

Observational data

We observed a total of 1903 insect visitors to flowers in the plots. There was a higher average number of observed pollinator visits at the plot level in thistle plots across both years ($P < 0.01$, Fig. 1A). However, there was no significant impact on the visitation rates to other plants in the plots (i.e. no significant difference between the visitation to plots without thistles as compared to thistle plots, excluding visits to thistles, $P > 0.05$, Fig. 1A). Bumblebees, solitary bees and lepidopterans were found in significantly higher numbers when the thistle was present ($P < 0.01$, Fig. 1B). Syrphid flies, honeybees and carpenter bees did not respond significantly to the thistle, although each of these groups was slightly more abundant in thistle plots ($P > 0.05$, Fig. 1B). The presence of the thistle

did not affect the frequency of visits by these groups to other plants in the plots (i.e. there was no difference between the number of visits received by non-thistle plants in plots without thistles and plots with thistles, $P > 0.05$, Fig. 1B).

Vacuum collections

We collected 3008 insects, of which 432 were bees, with the vacuum over the 2 years. These collections included twenty-eight bee species (Fig. 2, Table S3). The vacuum collections follow a similar pattern to the observations. There were more than four times as many bee specimens collected in thistle plots relative to non-thistle plots over the 2 years (346 vs. 86), and significant increases in both bee abundance ($P < 0.01$, average number of bee specimens collected per plot sample, Fig. 3A) and species richness ($P < 0.05$, average number of bee species collected per plot sample; Fig. 3B). The genera *Bombus* and *Ceratina* responded especially strongly, with almost 6 and 12 times as many specimens, respectively, collected in thistle plots over the 2 years (110 vs. 19 and 83 vs. 7, $P < 0.01$). The genus *Lasioglossum* ($P < 0.05$, Fig. 2) and the species *Augochlora pura*, *Bombus bimaculatus*, *Bombus impatiens*, *Ceratina calcarata* and *Ceratina dupla* ($P < 0.01$, Fig. 2) were also more abundant in thistle plots. There were no bee species that were in significantly lower abundance in thistle plots, although three bee species were found in low abundance in non-thistle plots that were not found in thistle plots.

Seventy percent of all bee species and 77% of all bee genera were more common in thistle plots relative to non-thistle

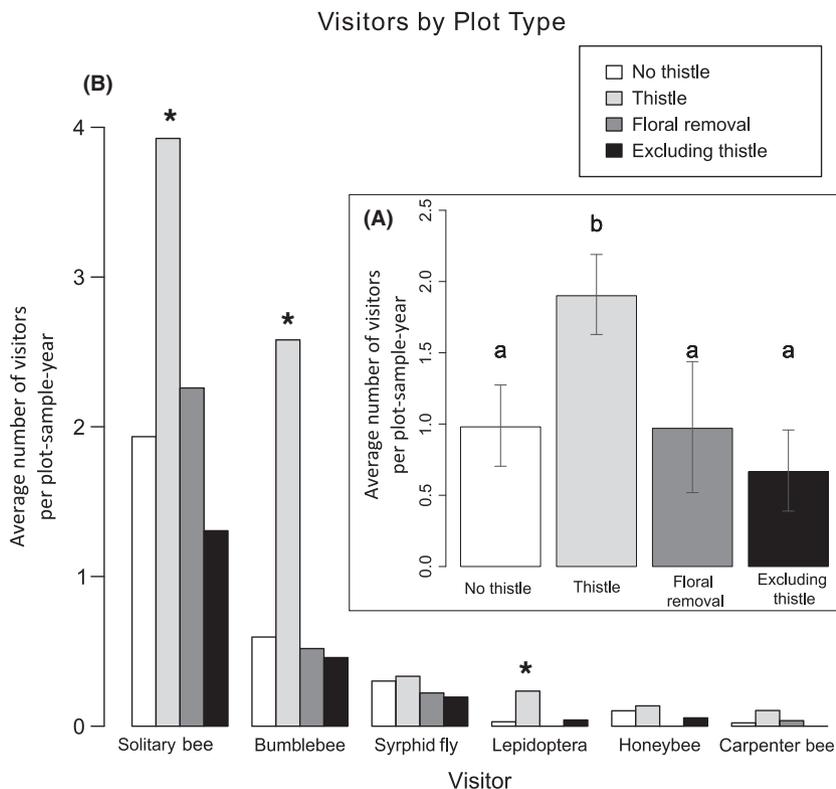


Figure 1 The average number of insect visitors per plot-sample-year observed in experimental plots, organized by plot type. The average sum (A) of all visitors to plots with no thistle (white), thistle present (light grey) and floral removal plots (dark grey), as well as the average sum of visitors in thistle plots excluding visits to the thistle (black), with error bars representing the standard error. The thistle plot has a significantly higher number of visitors on average, while the other plot types are not significantly different from each other. The average number of visits sorted by insect group (B) shows that there were significantly more bumblebees, solitary bees and lepidopterans in thistle plots, while the other plot types are not significantly different from each other. The asterisk (*) represents statistical significance ($P < 0.01$).

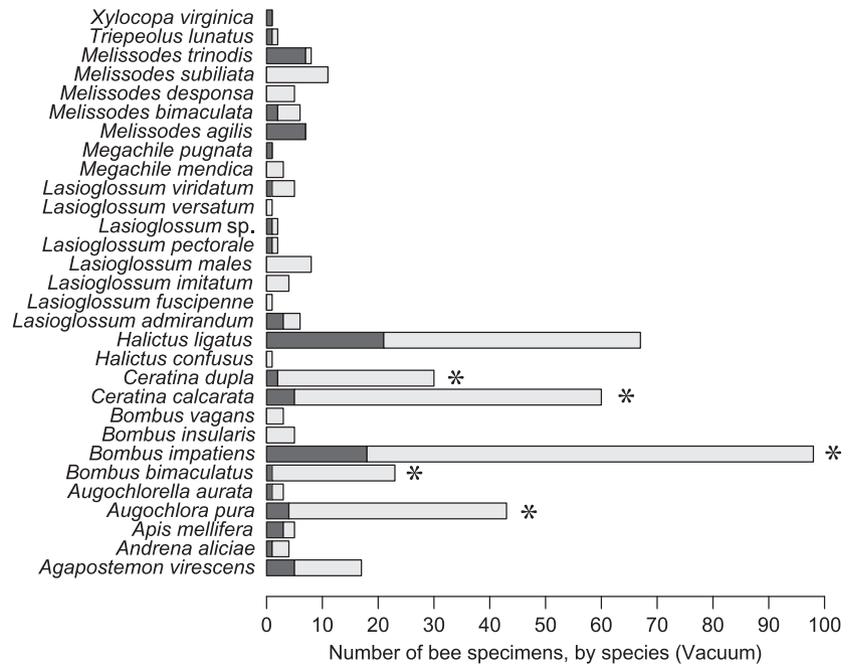


Figure 2 The total number of bee specimens collected in vacuum traps, arranged by bee species. The number of specimens is separated by those that were collected in thistle (light grey) and non-thistle (dark grey) plots, with significant ($P < 0.01$) differences between the treatments indicated by an asterisk (*). See Table S2 for numbers.

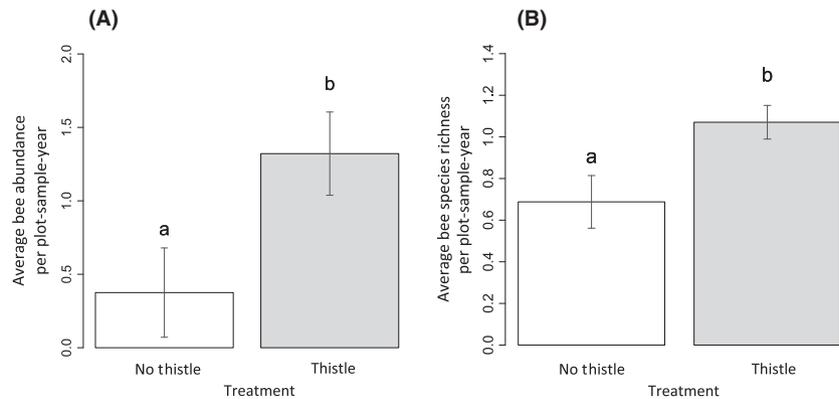


Figure 3 The average abundance (A) and species richness (B) of bee species collected by vacuum traps in thistle (grey) and non-thistle (white) plots. The error bars represent the standard error. The thistle plots had both significantly higher species richness ($P < 0.05$) and abundance ($P < 0.01$).

plots (Table 2, $P < 0.01$). Ten bee species (including two species of *Bombus*) were only found in thistle plots, while three species were only found in non-thistle plots (Fig. 2).

Composite insect trap data

The composite insect trap collected a total of 24,852 insect specimens over the 2 years, but did not detect significant differences in the number of insects between thistle and non-thistle plots for any taxonomic group and is therefore described further only in the supporting information (Appendix S2). Rather than targeting insects specifically visiting small habitat patches, the composite traps are more likely to capture a background community of insects in the landscape (Cane *et al.*, 2000; Russo *et al.*, 2011); thus, it is not surprising that these traps did not detect a difference between our small plots.

Other insect groups

At the order level, we collected fewer Diptera in thistle plots, but more Hymenoptera overall ($P < 0.05$, Fig. S1). We did not detect a difference in any other insect order collected ($P > 0.05$, Fig. S1). Within the Hymenoptera, we did not detect significant differences in the abundance of any non-Apoidean family, or in the number of families collected between thistle and non-thistle plots ($P > 0.05$, Table S4). We looked specifically at 18 families of Hymenoptera that contain natural enemies of agricultural pest species, but did not detect a significant difference in their abundance in thistle plots relative to non-thistle plots ($P > 0.05$, Table S5).

Plot data

The presence of the thistle did not add significantly to plant biomass, stem counts, species richness or flower counts in

Table 2 Number and proportion of species/genera and their distribution in thistle/non-thistle plots, with one-way chi-square comparison and two degrees of freedom.

	Species				Genera			
	Proportion of total	Number	χ^2	<i>P</i> value	Proportion of total	Number	χ^2	<i>P</i> value
More individuals in thistle plots	0.7	21	12.1	–	0.77	10	7.41	–
Fewer individuals in thistle plots	0.17	5	2.5	–	0.15	2	1.26	–
Same number of individuals in thistle/non-thistle plots	0.13	4	3.6	–	0.08	1	2.56	–
Total	–	30	18.2	< 0.01	–	13	11.23	< 0.01

either year, likely due to a large amount of variation between plots ($P > 0.05$, Tables S1 and S2, and Fig. S5 in Supporting Information).

DISCUSSION

Recent research increasingly highlights the beneficial impacts that invaders can have on native species (Rodriguez, 2006; Davis *et al.*, 2011; Schlaepfer *et al.*, 2011). For example, invasive species can provide resources in disturbed and managed ecosystems (Gleditsch & Carlo, 2010) and habitat for threatened species (Zavaleta *et al.*, 2001). As we demonstrate here, an invasive species may provide useful floral resources for the resident pollinator community over the scale of a flowering season, and be particularly attractive to key native bee species.

Our study shows that the insect community within an agroecosystem responds over short times and small spatial scales to the presence of an invasive thistle, demonstrating that the presence of non-native plants can result in a significant localized increase in the abundance and species richness of resident pollinator species. The order Hymenoptera as a whole was significantly more abundant in thistle plots, although there was no significant difference in the non-Apoidean families collected, suggesting that this effect was largely driven by the increased abundance of the bee species. Our results show that this noxious invader is highly attractive to bee species relative to a selection of ten other flowering annuals. The strong response of the bee community is distinct from that of the rest of the insect community, which suggests that bees as a group are attracted to thistles in a way that other insects are not. We did not detect significant differences at the order level of Hemiptera (true bugs), Coleoptera (beetles) or Lepidoptera (butterflies, skippers and moths), although it is possible that individual species within these orders responded. The order Diptera (flies) was significantly less abundant in thistle plots. We did not detect a significant difference in any insect group using passive trapping methods (see Appendix S2), in agreement with studies that show such traps collect the background community of insects at a larger spatial scale rather than those actively visiting flowers or foraging in small patches of habitat (Cane *et al.*, 2000). This information, coupled with the fact that bees were not in higher abundance in plots where thistle flowers had been removed, suggests that bees are responding

to the floral resources (i.e. nectar and pollen) provided by thistles.

Some bee species responded particularly strongly to the presence of the thistle. Five native bee species were found in significantly higher abundance, and nine were only found where the thistle was present (Fig. 2). This higher abundance was not only significant, but large for several groups. For example, the genus *Ceratina* was 12 times more common in thistle plots. In addition, we collected almost six times as many bees of the genus *Bombus* in thistle plots. Two of the bumblebee species in our study were only detected in plots where the thistle was present and the other two species were both significantly more abundant. Our observational data corroborate this result; we observed much higher visitation rates of *Bombus* specifically to thistles in thistle plots, without affecting their visitation to other plant species in the plots. This result may be of interest because bumblebees have recently been shown to be in decline and therefore of conservation concern (Bartomeus *et al.*, 2013). Although the species found in our study are not among the most threatened, this larger bodied genus has been shown to be more vulnerable overall, relative to other bee species (Bartomeus *et al.*, 2013).

In otherwise identical plots, we found the total abundance of bees to be four times higher in plots where the thistle (*C. acanthoides*) was present. Over the short time-scale of the study, the thistle is more likely to be attracting these bees from elsewhere in the landscape than to be directly affecting the population size. One possibility is that these non-native flowers are competing for pollinators and attracting them away from other species at a larger temporal or spatial scale (Chittka & Schürkens, 2001; Brown *et al.*, 2002; Gibson *et al.*, 2013; Traveset & Richardson, 2014).

On the other hand, there is little evidence to support the claim that invasive species have a negative effect on the pollination of adjacent species (Bjerknes *et al.*, 2007; Nielsen *et al.*, 2008). Indeed, resources from managed native flower strips on field margins have been shown to increase the abundance of native bees and the pollination services provided to adjacent crop species (Blauw & Isaacs, 2014). The use of a highly attractive species to increase visitation rates to other species is known as a magnet effect (Molina-Montenegro *et al.*, 2008). Given the value of crop pollination services (Gallai *et al.*, 2009), and the relationship between

pollinator diversity and crop yields (Garibaldi *et al.*, 2013), the presence of a plant attractive to pollinators may be advantageous to land managers. At the scale of our study, we found that the presence of the thistle did not alter visitation rates of insects to other plant species present, suggesting that the thistle has neither a magnet species effect nor a competitive effect in terms of pollinator visitation over short time periods or small spatial scales.

In contrast to the negative impacts of invasive species, which, in agricultural systems, largely seem to manifest via resource competition with crop species or through reduction of available forage in pasturelands (Pimentel *et al.*, 2005), the potential benefits of invasive species may be seen in the trophic subsidy they provide to resident species (Rodríguez, 2006). This trophic subsidy may result in the provisioning of floral resources for bees, as our study suggests, but it also has the potential to provide resources for natural enemies of pests (Landis *et al.*, 2000). Although we did not detect significant differences in hymenopteran families of natural enemies between thistle and non-thistle plots, other agricultural weeds might be more attractive to them. Indeed, there is the potential for many non-native species to provide resources to insects (Carvalho *et al.*, 2011; Schlaepfer *et al.*, 2011; Pockock *et al.*, 2012).

Many other species may also provide resources for agricultural pollinators (Pettis *et al.*, 2013), especially those with a phenology complementary to the crop species requiring pollination (Russo *et al.*, 2013). Thus, there is potentially an added complexity to the impact of an invasion: an undesirable species may also have desirable effects. In the context of a resource-poor agroecosystem, the presence of flowering weeds may provide an essential supply of resources for pollinators such as bees when the crops are not in flower, or when a non-flowering crop is in rotation. As such, weeds may support pollinator populations in the longer term, although this hypothesis remains to be tested.

This study is restricted in its temporal and spatial scale. Thus, we observed short-term changes in bee foraging behaviour rather than long-term changes in population dynamics. An important future direction will be to assess whether the floral resources provided by the thistle will lead to an increase in the size of the populations of some bee species in the longer term. In addition, the floral resources provided by the thistle or other non-native weeds may prove to be either competitive or facilitative; the net effect on longer spatial and temporal scales remains to be quantified.

The invasive thistle *C. acanthoides* is already ubiquitous in agricultural regions throughout North America, and it is invasive in South America, New Zealand and Australia. It is a persistent, noxious weed, yet the very fact that it is difficult or impossible to eradicate may mean that it also provides reliable resources and habitat in regions of high-intensity agriculture. In addition, this plant species is highly generalist, attracting abundant numbers of many species of bees. Models suggest that such generalist species (in both the number and frequency of their interactions) tend to have a much larger impact on the structure of plant–pollinator communities

than specialist invasive species (Russo *et al.*, 2014). We do not suggest that the thistles (or any other invader) be planted deliberately, only that, in the calculation of the negative impacts of non-native species, the potential indirect and facilitative effects of their presence also be accounted for. Our work shows that native pollinators are strongly associated with invaded habitat and that, on a restricted spatial and temporal scale, the entire pollinator community is positively impacted by invader presence. Thus, our results suggest that agricultural weeds may provide undocumented resources for a broad range of crucial crop pollinators, in turn potentially buffering a key ecosystem service. It is possible that some pollinators may depend on the weedy habitat fragments that pervade agroecosystems (Pettis *et al.*, 2013). Floral resource provisioning has been shown to lead to increased crop yields (Blaauw & Isaacs, 2014); weed populations adjacent to crop fields may provide a similar service to these deliberate plantings.

More general insights also arise; although the potential beneficial services provided by invaders do not counter their negative impacts, non-native species often become integrated into ecological communities and may have important implications for a wide range of conservation, restoration and land management issues (Schlaepfer *et al.*, 2011). Indeed, non-native species that integrate into ecological communities may become a key component of the ecosystem services those communities provide. The potential beneficial aspects of non-native species documented here are not unprecedented; they have been demonstrated in other systems as well and the potential unintended negative impacts of their eradication have been noted (Zavaleta *et al.*, 2001; Gleditsch & Carlo, 2010). Only with clear quantification of beneficial, as well as negative, effects in a diversity of different invaded systems can the true impacts of invasive species on resident communities be assessed fairly and thus addressed in conservation and agricultural management plans.

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REFERENCES

- Allen, M.R. & Shea, K. (2006) Spatial segregation of congeneric invaders in central Pennsylvania, USA. *Biological Invasions*, **8**, 509–521.

- Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M. & Winfree, R. (2013) Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences USA*, **110**, 4656–4660.
- Bjerknes, A., Totland, O., Hegland, S.J. & Nielsen, A. (2007) Do alien plant invasions really affect pollination success in native plant species? *Biological Conservation*, **138**, 1–12.
- Blaauw, B.R. & Isaacs, R. (2014) Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, **51**, 890–898.
- Brown, B.J., Mitchell, R.J. & Graham, S.A. (2002) Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology*, **83**, 2328–2336.
- Cane, J.H., Minckley, R.L. & Kervin, L.J. (2000) Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. *Journal of the Kansas Entomological Society*, **73**, 225–231.
- Carvalho, L., Veldtman, R., Shenkute, A., Tesfay, G., Pirk, C., Donaldson, J. & Nicolson, S.W. (2011) Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters*, **14**, 251–259.
- Charles, H. & Dukes, J.S. (2007) Impacts of invasive species on ecosystem services. *Biological invasions* (ed. by W. Nentwig), pp. 217–237. Springer-Verlag, Berlin.
- Chittka, L. & Schürkens, S. (2001) Successful invasion of a floral market. *Nature*, **411**, 653.
- Costa, C.M. & Yang, S. (2009) Counting pollen grains using readily available, free image processing and analysis software. *Annals of Botany*, **104**, 1005–1010.
- Cullen, J.M. & Delfosse, E.S. (1985) *Echium plantagineum*: catalyst for conflict and change in Australia. *Proceedings of the VI International Symposium on the Biological Control of Weeds* (ed. by E.S. Delfosse), pp.19–25. Agriculture Canada, Vancouver.
- Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Tredici, P.D., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J. & Briggs, J.C. (2011) Don't judge species on their origins. *Nature*, **474**, 153–154.
- Desrochers, A.M., Bain, J.F. & Warwick, S.I. (1988) The biology of Canadian weeds: *Carduus nutans* L. and *Carduus acanthoides* L. *Canadian Journal of Plant Science*, **68**, 1053–1068.
- Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570–574.
- Gallai, N., Salles, J.M., Settele, J. & Vaissière, B.E. (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, **68**, 810–821.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C. *et al.* (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, **14**, 1062–1072.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R. *et al.* (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, **339**, 1608–1611.
- Gibson, M.R., Richardson, D.M. & Pauw, A. (2012) Can floral traits predict an invasive plant's impact on native plant-pollinator communities? *Journal of Ecology*, **100**, 1216–1223.
- Gibson, M.R., Pauw, A. & Richardson, D.M. (2013) Disruption of a native flower-insect interaction by an invasive tree in the Cape Floristic Region. *Biological Conservation*, **157**, 196–203.
- Giurfá, M. & Núñez, J.A. (1992) Foraging by honeybees on *Carduus acanthoides*: pattern and efficiency. *Ecological Entomology*, **17**, 326–330.
- Giurfá, M. & Núñez, J.A. (1993) Efficient floret inspection by honeybees in capitula of *Carduus acanthoides*. *Ecological Entomology*, **18**, 116–122.
- Gleditsch, J.M. & Carlo, T.A. (2010) Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. *Diversity and Distributions*, **17**, 244–253.
- Gurevitch, J. & Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution*, **19**, 470–474.
- Hejda, M., Pyšek, P. & Jarošík, V. (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, **97**, 393–403.
- Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M. & Landis, D. (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment*, **7**, 196–203.
- Junker, R.R., Bleil, R., Daehler, C.C. & Blüthgen, N. (2010) Intra-floral resource partitioning between endemic and invasive flower visitors: consequences for pollinator effectiveness. *Ecological Entomology*, **35**, 760–767.
- Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J.M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T.M., Dick, J.T.A., Evans, T., Hulme, P.E., Kühn, I., Mrugala, A., Pergl, J., Rabitsch, W., Richardson, D.M., Sendek, A. & Winter, M. (2015) Ecological impacts of alien species: quantification, scope, caveats and recommendations. *BioScience*, **65**, 55–63.
- Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, **45**, 175–201.
- Molina-Montenegro, M.A., Badano, E.I. & Cavieres, L.A. (2008) Positive interactions among plant species for pollinator service: assessing the 'magnet species' concept with invasive species. *Oikos*, **117**, 1833–1839.

- Nielsen, C., Heimes, C. & Kollmann, J. (2008) Little evidence for negative effects of an invasive alien plant on pollinator services. *Biological Invasions*, **10**, 1353–1363.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Holle, B.V., Moyle, P.B., Byers, J.E. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.
- Pettis, J.S., Lichtenberg, E.M., Andree, M., Stitzinger, J., Rose, R. & vanEngelsdorp, D. (2013) Crop pollination exposes honey bees to pesticides which alters their susceptibility to the gut pathogen *Nosema ceranae*. *PLoS One*, **8**, e70182.
- Pimentel, D., Zuniga, R. & Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273–288.
- Pocock, M.J.O., Evans, D.M. & Memmott, J. (2012) The robustness and restoration of a network of ecological networks. *Science*, **335**, 973–977.
- R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, Available at: <http://www.R-project.org>.
- Richardson, D.M. & Ricciardi, A. (2013) Misleading criticisms of invasion science: a field-guide. *Diversity and Distributions*, **19**, 1461–1467.
- Rodriguez, L.F. (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions*, **8**, 927–939.
- Russo, L., Stehouwer, R., Heberling, J.M. & Shea, K. (2011) The composite insect trap: an innovative combination trap for biologically diverse sampling. *PLoS One*, **6**, e21079.
- Russo, L., DeBarros, N., Yang, S., Shea, K. & Mortensen, D. (2013) Supporting crop pollinators with floral resources: network-based phenological matching. *Ecology and Evolution*, **3**, 3125–3140.
- Russo, L., Memmott, J., Montoya, D., Shea, K. & Buckley, Y. (2014) Patterns of introduced species interactions affect multiple aspects of network structure in plant–pollinator communities. *Ecology*, **95**, 2953–2963.
- Sax, D.F. & Gaines, S.D. (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences USA*, **105**, 11490–11497.
- Schlaepfer, M.A., Sax, D.F. & Olden, J.D. (2011) The potential conservation value of non-native species. *Conservation Biology*, **25**, 428–437.
- Simberloff, D. (2011) Non-natives: 141 scientists object. *Nature*, **475**, 36.
- Skarpaas, O. & Shea, K. (2007) Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles. *The American Naturalist*, **170**, 421–430.
- Stout, J.C. & Morales, C.L. (2009) Ecological impacts of invasive alien species on bees. *Apidologie*, **40**, 388–409.
- Tipping, P.W. (1992) Density of *Carduus* and *Cirsium* thistles in selected areas of Maryland. *Weed Technology*, **6**, 434–436.
- Traveset, A. & Richardson, D.M. (2014) Mutualistic interactions and biological invasions. *Annual Review of Ecology, Evolution & Systematics*, **45**, 89–113.
- Vilá, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702–708.
- Warwick, S.I. & Thompson, B.K. (1989) The mating system in sympatric populations of *Carduus nutans*, *C. acanthoides* and their hybrid swarms. *Nature Heredity*, **63**, 329–337.
- Williamson, M. (1998) Invasions. *Ecography*, **22**, 5–12.
- Yang, S., Ferrari, M.J. & Shea, K. (2011) Pollinator behavior mediates negative interactions between two congeneric invasive plant species. *The American Naturalist*, **177**, 110–118.
- Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution*, **16**, 454–459.
- Zhang, R., Heberling, M.J., Haner, E. & Shea, K. (2011) Tolerance of two invasive thistles to repeated disturbance. *Ecological Research*, **26**, 575–581.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supporting statistical information.

Appendix S2 Tables and Figures (Tables S1–S5; Fig. S1–S5).

Table S1 The average number of flowering and non-flowering stems of the annual species in floral removal, no thistle, and thistle plots.

Table S2 Total biomass and flower counts of background plant species.

Table S3 List of bee species collected.

Table S4 Counts of non-Apoidean families.

Table S5 Counts of natural enemies.

Figure S1 The average abundance of the four most abundant insect orders.

Figure S2 The absolute abundance of bee species in experimental and control plots.

Figure S3 The average abundance and species richness of bees.

Figure S4 Estimates for species richness and abundance of non-Apoidean families.

Figure S5 Average floral species richness in plots.

BIOSKETCHES

Laura Russo studies the interactions between plants and insects, with an emphasis on mutually beneficial relationships. Her interests revolve around interaction structure, co-evolution and conservation.

Christina Nichol is training to be a veterinarian. She worked with invasive plants and insects as an undergraduate, with a special focus on Japanese Beetles.

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Author contributions: L.R. and K.S. designed the experiment, L.R. conducted the experiment and collected the data, L.R. and C.N. analysed the data and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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