# Flowering phenology influences bee community dynamics in old fields dominated by the invasive plant *Centaurea stoebe*

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## Abstract

Wild and managed bees provide critical pollination services to both native and cultivated plants, and the invasion of exotic plants can have positive or negative effects on bee communities. In this study we investigated the influence of the exotic invasive *Centaurea stoebe* ssp. micranthos (spotted knapweed) on bee species diversity and abundance in old-fields (Michigan, USA). We conducted field observations in knapweed dominated fields and adjacent fields with greater forb diversity to determine whether the bee communities foraging in each field type differed in their composition, diversity, and abundance, and to determine how bees' use of floral resources changed throughout the growing season. This was coupled with a common garden experiment that contrasted the attractiveness of *C. stoebe* to 12 native plant species, which occur in similar habitats. Both studies were conducted throughout the 2012–2013 growing seasons to examine the temporal effect of floral resource availability. *C. stoebe* was the most heavily-visited plant, in terms of total bee visitation and bee species richness in both studies. While *C. stoebe*-dominated old-fields had high floral resource levels during its peak bloom period, before and after this period these fields contained very few floral resources. In contrast, diverse fields had a number of flowering plant species that provided floral resources before, during, and after *C. stoebe* bloom. As a result, diverse fields contained significantly greater season-long floral resource availability and significantly greater season-total bee abundance, diversity and species richness. This greater species richness was driven at least in part by the ability of diverse flowering plant communities to support bee species that are active before and after the bloom period of *C. stoebe*. Our results suggest that efforts to manage *C. stoebe* should take into account the floral resources the plant is providing, and coincide with the restoration of diverse forb communities in order to enhance bee foraging habitat in old-fields.

## Zusammenfassung

Wildbienen und Imkereibienen erbringen entscheidende Bestäubungsleistungen für einheimische und angebaute Pflanzen. Das Eindringen von exotischen Pflanzen kann positive oder negative Auswirkungen auf die Bienengemeinschaften haben. Wir untersuchten den Einfluss der exotischen, invasiven *Centaurea stoebe* ssp. *micranthos* (Kleinköpfige Rispen-Flockenblume) auf die Artendiversität und Abundanz der Bienen auf Ackerbrachen (Michigan, USA). Wir führten Freilandbeobachtungen auf von der Flockenblume dominierten Flächen und benachbarten Flächen mit größerer Krautdiversität, um zu ermitteln, ob die Bienengemeinschaften, die auf den Flächen sammelten, sich in ihrer Zusammensetzung, Diversität und Abundanz unterschieden

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und wie sich die Nutzung der Blütenressourcen durch die Bienen im Laufe der Vegetationsperiode änderte. Dies wurde kombiniert mit einem 'common garden'-Experiment, in dem die Attraktivität von *C. stoebe* mit zwölf einheimischen Arten, die in ähnlichen Habitaten vorkommen, verglichen wurde. Beide Untersuchungen wurden in den Vegetationsperioden 2012 und 2013 durchgeführt, um den zeitlichen Effekt der Verfügbarkeit der Blütenressourcen zu untersuchen. In beiden Untersuchungen war *C. stoebe* die am stärksten besuchte Pflanze in Hinsicht auf den gesamten Bienenbesuch und den Artenreichtum. Während von *C. stoebe* dominierte Brachen ein hohes Blütenangebot während ihres Blühmaximums aufwiesen, gab es vor und nach dieser Periode nur wenige Blüten auf diesen Brachen. Diverse Brachen wiesen dagegen eine Reihe von Pflanzen auf, die vor, während und nach der Blütezeit von *C. stoebe* florale Ressourcen bereit hielten. Damit wiesen diverse Brachen über die Saison gerechnet signifikant höhere Blütenverfügbarkeit sowie höhere Abundanz, Diversität und Artenreichtum der Bienen auf. Dieser höhere Artenreichtum wurde mindestens zum Teil durch die Fähigkeit der diversen Blütengemeinschaften bewirkt, Bienenarten zu ernähren, die vor oder nach der Blüte von *C. stoebe* aktiv sind. Unsere Ergebnisse legen nahe, dass das Management von *C. stoebe* das Blütenangebot der Art berücksichtigen und mit der Wiederherstellung von diversen Krautgemeinschaften einhergehen sollte, um das Nahrungshabitat der Bienen auf Ackerbrachen zu verbessern.

## Introduction

Declines in wild and managed bee populations have recently triggered investigation of the factors that allow robust communities of bees to persist in a landscape. Recent declines in wild bee populations have been linked to habitat fragmentation (Potts et al. 2010), disease (Cameron et al. 2011), pesticides (Fischer & Moriarty 2014), loss of floral resources (Kleijn & Raemakers 2008), and climate-change (Kerr et al. 2015). Because bees often use many habitats within a landscape (Williams & Kremen 2007), increasing the concentration and quality of resource-rich habitats (i.e., habitats containing abundant floral resources) enhances native bee abundance and diversity within a given landscape (Kremen, Williams, Bugg, Fay, & Thorp 2004). Native bee community structure is largely determined by the types and diversity of flowering plants available within a habitat, and increasing flowering plant species richness is linked to increasing bee species richness (Moroń et al. 2009; Wilson, Messinger, & Griswold 2009; Grundel et al. 2010).

While the relationship between flowering plant diversity and bee diversity has been clearly demonstrated, the mechanisms that drive this relationship in regions where the majority of bees are generalists are not completely understood (Fründ, Linsenmair, & Blüthgen 2010). Increasing plant diversity generally allows more animal species to coexist via niche partitioning (Vellend 2008), and bees may be able to avoid competition by visiting different forb species when other bee species are present (Fründ, Dormann, Holzschuh, & Tscharntke 2013). Additionally, visiting multiple forb species may help certain generalist bee species obtain the complete balance of nutrients their offspring require for development (Alaux, Ducloz, Crauser, & Le Conte 2010). Whatever the mechanistic causes of this relationship, the loss or alteration of diverse plant communities has major implications for bee conservation.

Invasive weeds have been widely demonstrated to decrease the abundance, diversity, and fitness of native plant species (Vila et al. 2010). Their impact on native bees is less straightforward, and likely depends on the land-use history of a landscape. In "novel ecosystems" in which invasive species compose a large proportion of the biotic community, they may sustain ecosystem services that native species can no longer provide (Hobbs, Higgs, & Harris 2009). For instance, invasive plants have been shown to provide native bees with floral resources where native plants are no longer abundant (Williams, Cariveau, Winfree, & Kremen 2011). In landscapes with more intact native plant communities, invasives can have a negative impact on bees: Moroń et al. (2009) found that the invasion of the goldenrods *Solidago canadensis* L. and *Solidago gigantea* Aiton in Poland caused a significant decrease in the abundance, species richness, and evenness of bees in wet meadows. Overall, the impacts of invasive plants are complex, and insufficient research has been performed to make specific predictions about the impacts of invasive plants on bees (Vanbergen 2013).

*Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek (spotted knapweed) (Asteraceae) (hereafter *C. stoebe* or knapweed) is an invasive forb with the potential to impact native and managed bee communities. The plant was introduced to North America in the 1890s, and has since become a widespread invasive species throughout much of the continent's temperate zone (Sheley, Jacobs, & Carpinelli, 1998). In Michigan, *C. stoebe* dominates many disturbed sites including old-fields, and threatens intact natural areas with invasion (Albert 1999; Cohen 2000; Kost 2004; Lee 2007). Because of its negative impacts, *C. stoebe* is the target of management efforts including hand pulling, cultivation, and chemical or biological controls (Carson, Bahlai, & Landis 2015). While the negative impacts of *C. stoebe* on native plant communities are significant, this species is highly valued by beekeepers. Its relatively long bloom period, attractiveness,

nectar quality, and abundance in the landscape all contribute to its importance as a floral resource for honey bees (Watson & Renney, 1974). Because of their propensity to form monotypic stands, invasive flowering plants such as *C. stoebe* often comprise the most abundant floral resources in degraded systems (Williams et al. 2011). Eighty-four bee species were observed visiting its invasive congener *Centaurea solstitialis* L. in Oregon (McIver, Thorp, & Erickson 2009), and it is likely that *C. stoebe* is also providing floral resources to native bee species, especially those that are generalist foragers.

Due to the interest of natural areas managers in controlling *C. stoebe*, understanding how pollinator communities are influenced by floral abundance, attractiveness, and diversity in *C. stoebe*-dominated landscapes is essential to inform management and restoration efforts. The overall goals of our work are to understand the role *C. stoebe* plays in supporting bee abundance and diversity, and to understand how forb diversity influences native bee communities in old-field habitats. We conducted an observational study that paired knapweed-dominated fields with fields that contained a more diverse flowering plant community (of which *C. stoebe* was still a substantial member), within a larger landscape context. The objective of this experiment was to determine whether the bee communities foraging in each field type differed in their composition, diversity, and abundance, and to determine how bees' use of floral resources changed throughout the growing season. We coupled this study with a common garden experiment that contrasted bee visitation to *C. stoebe* and 12 native plant species in a landscape largely devoid of *C. stoebe*. The reason for this experiment was two-fold. First, it allowed us to compare the inherent attractiveness of *C. stoebe* to a subset of co-occurring native plant species while controlling for their abundance in the landscape. The second purpose was more applied: as land managers decrease the density of *C. stoebe*, it is important to identify native plant species that can replace the floral provisioning service *C. stoebe* formerly provided.

## Materials and methods

### Field-level floral diversity study

This study was conducted at Orion Oaks County Park in Oakland County, Michigan ($42.75°$ N, $-85.29°$ E). The park contains remnant oak barrens, mesic hardwood forest, and a variety of wetlands. The uplands primarily consist of well-drained sandy soil, and the majority of the non-forested upland habitat has been invaded by *C. stoebe*. We selected four upland fields within the park where *C. stoebe* was the predominant blooming species (hereafter knapweed-dominated) and four nearby fields (i.e., within 250 m) that contained a diversity of flowering plant species, including *C. stoebe*. The diverse fields had undergone significant management over the past decade, including controlled burns and over-seeding. The fields were paired to account for spatial variation in bee community composition throughout the park, and each field

pair was a minimum of 600 m from the other three pairs and separated by forest (Appendix A: Fig. 1). This allowed us to contrast floral visitation by bees in both knapweed-dominated and more diverse plant communities. The fields ranged from $60\,m \times 60\,m$ to $100\,m \times 100\,m$ in size. A two-person team sampled each field three times during 2012 (August 2, August 21, and September 17) and four times during 2013 (July 10 or 11, July 22 or 30, August 19, and September 11). In both years, *C. stoebe* blooms were present in small numbers in the beginning of July, reaching peak abundance by August 1st, and becoming nearly absent by the 10th of September. Thus in 2012, we sampled twice during peak bloom and once after senescence, and in 2013 we sampled once prior to peak bloom, twice during peak bloom, and once after senescence. Bee observation occurred between 10:00 and 16:00 on sunny days when the temperature was a minimum of $21\,°C$. Air temperature and percent cloud cover were recorded at the beginning of each sampling period using a smart phone application (The Weather Channel, Apple Iphone). Floral sampling was conducted immediately following bee sampling in each field.

### Floral community sampling

Two permanent 20 m sampling transects were established in each field. Because the purpose of the study was to examine the effect of increasing floral resource diversity in old fields dominated by *C. stoebe*, the transects were placed in locations that contained most of the plant species present in each field, and were at least 20 m from the field edges. In 2012, observers placed a $2\,m \times 2\,m$ quadrat at the 0 and 10 m positions on each transect and counted the number of inflorescences of each forb species present in each quadrat. In 2013, sampling efforts were doubled, with quadrats placed at the 0, 5, 10, and 15 m positions on each transect.

### Bee community sampling

The order in which field pairs were sampled was rotated on each sampling date to minimize potential bias caused by diurnal patterns of pollinator activity. Pollinator observations were conducted by two observers walking each of the two 20 m transects for 10 min. Observers walked parallel to each other on opposite sides of the transect line, and all bees visiting flowers within 1.5 m of the transect were documented. Bees were collected in a modified hand-held vacuum cleaner (Bioquip model 2820GA; hereafter "bee vacuum"), and the plant visited documented as *C. stoebe* or "other". In 2013, we intensified collection efforts to obtain more complete host-plant visitation data. Most transects only contained a few species of plants that were both in bloom and being actively visited, but there were often more plants being visited than one person could keep track of. To collect floral visitation data, during the first 10 min transect observation each observer collected from half of the plant species present. To minimize bias, during the second 10 min transect the observers switched which half of the plant species they focused on. Thus, each plant species was collected off

of for a total of 20 min per field on each sampling day. After each 20 m transect, the bees were killed using ethyl acetate and returned to the lab for pinning and identification. All identifications of captured bees were made to the species level using keys in published revisions (Mitchell 1960, 1962; LaBerge 1961, 1967; Laverty & Harder 1988; Gibbs 2011; Rehan & Sheffield 2011, Sheffield, Ratti, Packer, & Griswold 2011) in conjunction with online keys available from www.Discoverlife.org. For the purposes of this study, we defined specialists as bee species that focus on plant species occurring in a single plant family and generalists as species documented to use plants from multiple families. We used host plant records from DiscoverLife.com to determine the diet breadth of the bee species in our study. In both 2012 and 2013, we also recorded visual observations of bee morphogroups (honey bee, bumble bee, or solitary bee) and what plant species they were visiting. This was to account for bees that evaded capture in our visitation estimates, as our insect vacuums did not have a long range and bees often had moved off the transect by the time we reached them. We chose these three morphogroups based on ecologically relevant differences in their overall life-history strategies. We did our best to avoid double-counting individuals, though bees that revisited the transect after flying away may have been counted twice. Sixty minutes total, or 120 person-minutes, was spent at each field in 2012, and 80 min, or 160 person-minutes was spent in each field in 2013.

### Data analysis

We used floral density as the metric in all of our analyses to account for the differing amount of nectar and pollen provided by plant species with varying inflorescence sizes. Among the plant species in our study the total size of the inflorescence closely correlates to the number of individual flowers within that inflorescence. To standardize the size of floral display of different species, we measured the inflorescence diameter of all individuals of each species present in several quadrats. For inflorescences that were not radially symmetrical (ex. *Solidago* sp.) we estimated the mean floral area in square centimeters. On the assumption that each plant species' floral area follows a normal distribution, we used the series of measured flower heads to estimate the mean floral area for each plant species. Using this mean we calculated the floral area of each plant species in each quadrant. We used this to estimate the floral density ($cm^2$ floral area/$m^2$) of each plant species in each field on each sampling date by dividing the observed floral area by the total area surveyed in each field ($16 m^2$ in 2012 and $32 m^2$ in 2013). These data were used to calculate the Shannon diversity index (Shannon 1948) of each field on each sampling date, with floral density serving as the abundance metric.

For analyses we pooled 2012 and 2013 data. To test for differences in the dependent variables of floral and bee diversity and visitation, we used analysis of deviance. To do this we built a series of models that included the factors of sampling year, day of year, field pair, and field type (knapweed-dominated or diverse) and a field type by day of year interaction. Including these factors accounted for the variance they contribute to the observed dependent variables. Models testing the continuous variables of floral density and floral and bee diversity used a linear structure. Models for count variables bee visitation and richness used a Poisson structure or negative binomial structure, depending on fit (i.e., models initially used a Poisson structure, but in cases where the residual deviance was greater than the residual degrees of freedom using this structure, the model was re-run using a negative binomial structure). In our analyses of bee visitation we used on-the-wing observed visits rather than captured bees, and investigated total observed bee visits and observed bee visits by morphogroup (honey bee, bumble bee, solitary bee). Where significant interactions were observed between field type and day of year in analysis of deviance analysis, we performed a post hoc pair-wise *t*-test that was Holm-adjusted for multiple comparisons. All analyses were performed in R 3.03 (R Development Core Team 2014), and the script and data used have been made publically available on Github (https://github.com/cbahlai/Carson2015).

## Common garden experiment

This experiment was conducted on a private farm in Ingham County, Michigan (42.608° N, −84.382° W) where *C. stoebe* was nearly absent in the surrounding landscape, allowing us to test its inherent attractiveness in comparison to other species (i.e., without flower constancy interactions). Native plant species were selected based on their potential to thrive in dry sandy soils that support *C. stoebe*, and ability to provide floral resources for bees (Appendix A. Table 1). We also considered the bloom period of candidate species, and chose species that overlapped with *C. stoebe* bloom. Because the experiment was located in an area with clay-dominated soils, all of the plant species tested in the common garden were relatively rare in the surrounding landscape.

### Planting design

Four replications of 15 forb species (Appendix A. Table 1) were grown in a randomized complete block design. The blocks were laid out on a rectangular grid, with each block consisting of three rows of five plant species each. Each species plot consisted of a cluster of three plants of a single species, planted 0.5 m apart in a triangle. Each plot was spaced 2 m from the next, and was the basic experimental unit. The placement of each species' plot within each block was randomized. Rooted plant material was obtained from Wildtype Nursery, Mason, MI. The garden was planted on May 15, 2012, and watered up to three times a week for the first month of establishment. Plants that died in the first four weeks were replaced. The first blooms were observed July 2 at which time bee observations were initiated. Two species did not survive in high enough proportion and were excluded from bee observations, changing the total from 15 to 13 forb species (see Fig. 4).

## Bee observations

2012 sampling occurred from July 2 to September 19, and 2013 sampling occurred from June 20 to September 27. Each plant species was sampled once per week beginning at its first bloom, continuing until its last bloom of the season. Only plant species with actively blooming flowers were observed. When a plot had at least one individual in bloom, that species was observed in all four blocks. All of the blooming plant species in a block were observed before moving on to the next block. The order that blocks were sampled was rotated each week so that no one block received all of its observations at the same time of day. Bee observation occurred between 10:00 and 16:00 on sunny days when the temperature was above 15.5 °C. Each plant cluster was observed for 6 min during each data collection period (24 min total per species per week). During this time, we attempted to capture every bee that landed on a flower. Bees were collected using a bee vacuum. All bee visits were recorded as either "honey bees" or "other bees," regardless of whether each bee was successfully collected. Bees were killed, pinned, labeled and identified as described above.

## Data analysis

To understand whether *C. stoebe* is inherently attractive on a per-unit basis or whether it plays an important role in pollinator dynamics simply because it is so abundant in the landscape, we used the common garden visitation data to calculate each plant species' relative attractiveness on a per-flower and per-individual basis. To estimate the attractiveness of the basic unit of floral display, we divided the total bee visitation each plant species received by the total area of floral display ($cm^2$) that species presented throughout the season. To calculate floral area we calculated an average area for each plant species' inflorescence and used this to convert inflorescence counts to floral area. For analysis we pooled 2012 and 2013 data. Because each plant species represented a unique treatment and not all plant species were blooming simultaneously, pairwise comparisons would be statistically misleading, thus, we did not include formal statistical analyses for this experiment. To estimate the attractiveness of each plant as a whole, we divided the number of bee visits to a species plot by the number of individual plants in bloom in that plot at the time of observation (bees/plants in bloom/6 min observation). By averaging this metric for each species within each month of the summer, we were able to compare the relative attractiveness of each plant species that was in bloom for July, August, and September.

# Results

## Field-level floral diversity study

### Floral community sampling

In diverse fields, the plant species with the greatest floral area, in decreasing order, were: *Solidago speciosa, Monarda*
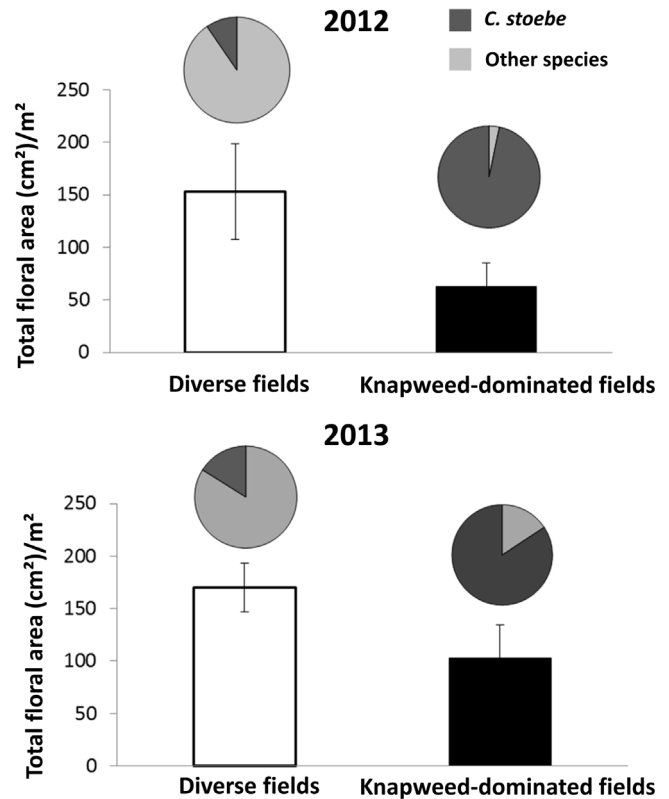


**Fig. 1.** Mean season-long floral bloom density ($cm^2/m^2$) ±SE in diverse and knapweed-dominated fields in 2012 and 2013, and the contribution of *C. stoebe* blooms to the total floral area in each field type (Oakland Co, Michigan).

*fistulosa, C. stoebe, Solidago juncea, Solidago nemoralis, Achillea millefolium*, and *Asclepias tuberosa* (Table 1). In knapweed-dominated fields the vast majority of floral area was represented by *C. stoebe*. The mean season-long floral resource diversity, calculated as Shannon's H′ of species' floral area, was significantly higher in the diverse versus knapweed-dominated fields across sampling years (diverse field mean = 0.99 ± 0.08; knapweed-dominated field mean = 0.4 ± 0.1; deviance = 9.251, df = 42, $p < 0.001$). All reported deviance values reflect the main effect of field type.

The total season-long floral area density was also higher in diverse versus knapweed-dominated fields across sampling years (diverse field mean = 26 ± 3 $cm^2/m^2$; knapweed-dominated field mean = 14 ± 4 $cm^2/m^2$; deviance = 13,131, df = 42, $p = 0.011$) (Table 1; Fig. 1). In 2012 *C. stoebe* represented 10% and 96% of the total measured floral area in diverse and knapweed-dominated fields, respectively, and in 2013 *C. stoebe* represented 16% and 84% of the total measured floral area in diverse and knapweed-dominated fields, respectively.

### Bee community sampling

Table 1 shows the total number of bee visitors each plant species received during 2013 transect sampling. In knapweed-dominated fields, *C. stoebe* received 235 bee

**Table 1.** Showing the proportion of the observed population in bloom on each sampling date[a], the total # of bee species observed visiting that plant species, total season-long floral area (STFA; total area of that species' flowers over all observations that season (cm$^2$)), total season-long bee visitation, and the total bee visits divided by that species' total floral area (visits/cm$^2$). Plant species observed in diverse and knapweed-dominated fields in 2013 (Oakland Co, Michigan).

| Plant species | Sampling date | | | | | Diverse fields | | | Knapweed-dominated fields | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10-July | 30-July | 19-August | 11-September | # Bee species | STFA (cm$^2$) | Total visits | Visits/cm$^2$ | STFA (cm$^2$) | Total visits | Visits/cm$^2$ |
| *Achillea millefolium* L. | +++ | ++ | + | − | 5 | 290 | 7 | 0.024 | 18 | 0 | 0 |
| *Asclepias syriaca* L. | +++ | − | − | − | 0 | 3 | 0 | 0 | 0 | 0 | NA |
| *Asclepias tuberosa* Torr. | +++ | + | − | − | 2 | 194 | 5 | 0.026 | 0 | 0 | NA |
| *Berteroa incana* (L.) DC.* | +++ | +++ | + | + | 4 | 25 | 4 | 0.16 | 109 | 9 | 0.083 |
| *Centaurea stoebe* L. | + | +++ | ++ | − | 22 | 437 | 125 | 0.286 | 1382 | 235 | 0.17 |
| *Daucus carota* L.* | +++ | ++ | ++ | − | 0 | 7 | 0 | 0 | 6 | 0 | 0 |
| *Dianthus armeria* L.* | +++ | − | − | − | 1 | 1 | 0 | 0 | 1 | 1 | 1 |
| *Erigeron strigosus* Muhl ex. Willd | +++ | +++ | ++ | − | 3 | 51 | 6 | 0.118 | 10 | 1 | 0.1 |
| *Euphorbia corollata* L. | ++ | +++ | + | − | 1 | 0 | 0 | NA | 59 | 1 | 0.017 |
| *Euthamia graminifolia* (L.) Nutt. | − | − | − | +++ | 0 | 1 | 14 | 14 | 0 | 0 | NA |
| *Hypericum perforatum* L.* | +++ | ++ | + | + | 2 | 28 | 5 | 0.179 | 12 | 3 | 0.25 |
| *Leucanthemum vulgare* Lam.* | +++ | − | − | − | 0 | 3 | 0 | 0 | 0 | 0 | NA |
| *Medicago lupulina* L.* | +++ | + | − | − | 0 | 0 | 0 | NA | 3 | 0 | 0 |
| *Monarda fistulosa* L. | ++ | +++ | + | − | 11 | 449 | 106 | 0.236 | 5 | 1 | 0.2 |
| *Potentilla recta* L.* | +++ | + | − | − | 3 | 0 | 0 | NA | 10 | 4 | 0.4 |
| *Solidago canadensis* L. | ++ | +++ | + | − | 0 | 5 | 0 | 0 | 0 | 0 | NA |
| *Solidago juncea* Ait. | − | ++ | +++ | − | 7 | 420 | 18 | 0.043 | 1 | 0 | 0 |
| *Solidago nemoralis* Ait. | − | − | − | +++ | 9 | 276 | 48 | 0.174 | 0 | 0 | NA |
| *Solidago speciosa* Nutt. | − | − | − | +++ | 9 | 471 | 96 | 0.204 | 19 | 0 | 0 |
| *Symphyotrichum ericoides* (L.) G.L. Nesom | − | − | − | +++ | 3 | 39 | 6 | 0.154 | 0 | 0 | NA |
| *Verbascum thapsis* L.* | − | +++ | − | − | 0 | 0 | 0 | NA | 1 | 0 | 0 |
| *Vicia villosa* Roth* | +++ | ++ | + | − | 2 | 21 | 7 | 0.333 | 10 | 0 | 0 |
| Total | | | | | | 2721 | 447 | | 1646 | 255 | |

[a] +++ indicates that the floral area >80% of the maximum floral area observed for that species. ++ indicates that the floral area was between 30% and 80% of that species' observed maximum. + indicates that the floral area was <30% of that species' observed maximum. − indicates that that species had no blooms present. *Indicates non-native species.
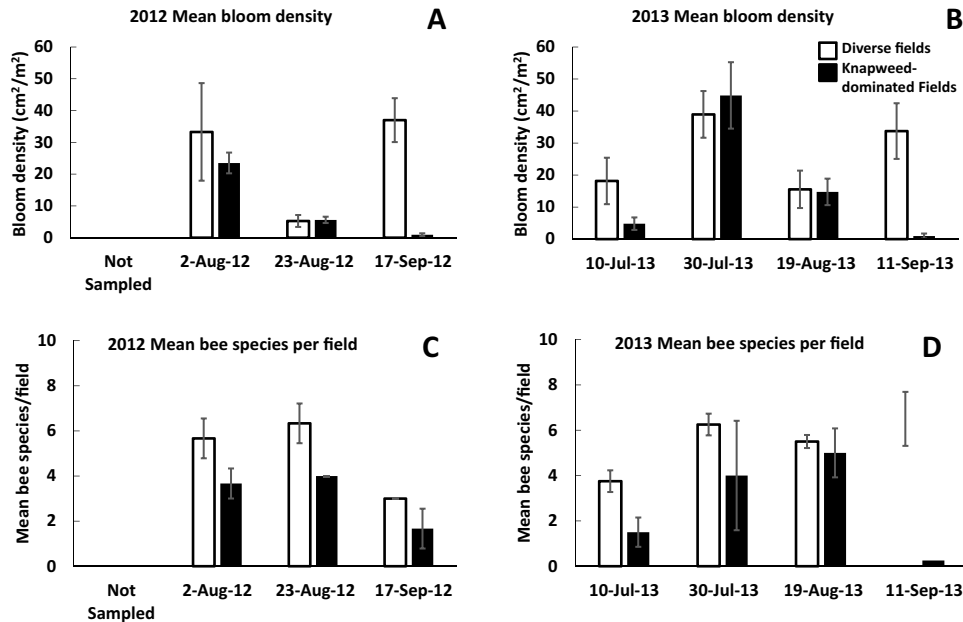
**Fig. 2.** The mean floral density (cm$^2$/m$^2$) ±SE in diverse and knapweed-dominated fields by sampling date in 2012 (A) and 2013 (B), and the mean bee species richness by sampling date in 2012 (C) and 2013 (D) ±SE (Oakland Co, Michigan).

visits, far more than the second most visited plant, *Berteroa incana*. In diverse fields, *C. stoebe* also had more bee visitors than any other plant species, with 125 total observed visits. However, in diverse fields other plant species were also heavily visited. *Monarda fistulosa*, *S. speciosa*, and *S. nemoralis* received 106, 96, and 48 bee visits, respectively. Notably, *M. fistulosa* flowers before and during the beginning of *C. stoebe*'s peak bloom period, while *S. speciosa* and *S. nemoralis* both flower after *C. stoebe* has ceased blooming.

There was also a significant difference in total bee visits across sampling years (diverse field mean = 42 ± 9 observed visits per field per sampling date; knapweed-dominated field mean = 23 ± 5 observed visits per field per sampling date; deviance = 66.281, df = 42, $p = 0.027$) (Fig. 3). There was a significant interaction between field type and sampling date (deviance = 59.943, df = 42, $p = 0.002$), indicating that bees' relative use of diverse and knapweed-dominated fields changed throughout the season. In post hoc pairwise *t*-tests comparing field type by sampling date, there were significantly more visits in diverse fields on September 17, 2012 ($p < .001$) and September 11, 2013 ($p < .001$). On July 10, 2013 there were strong numerical differences between diverse and knapweed-dominated fields, but these were not found to be significant in a conservative post hoc pairwise analysis. Solitary bees (diverse field mean = 6.5 ± 0.8 observed visits per field per sampling date; Knapweed-dominated field mean = 4.2 ± 0.9 observed visits per field per sampling date; deviance = 13,131, df = 42, $p = 0.042$) and honey bees (diverse field mean = 24 ± 9 observed visits per field per sampling date; knapweed-dominated field mean = 6 ± 3 observed visits per field per sampling date; deviance = 131.079, df = 42, $p < 0.001$) were significantly more abundant in

diverse fields across sampling years. Bumblebees showed no significant trends across years.

A total of 59 species of bees were collected across both years of the study; 19 in 2012, and 42 in 2013. During our more intensive collection effort in 2013, a total of 33 bee species were found in diverse fields and 27 in knapweed-dominated fields (Appendix A. Table 2). In 2013, 82% of bee species collected in knapweed-dominated fields were observed on *C. stoebe*, while only 42% of bee species in diverse fields were observed on *C. stoebe*. Also in 2013, a site-wide total of 20 bee species were observed using *C. stoebe*, and 23 species were never observed using *C. stoebe*. Four species (all generalists) were only collected on July 10, before *C. stoebe* flowers were readily available, and seven species (two generalists and five specialists) were only collected on September 11, after *C. stoebe* had ceased flowering. Thus, of the 23 bee species that did not use *C. stoebe* in 2013, 13 were not observed within the *C. stoebe* bloom period, and their presence at the site may have been facilitated by an extended period of floral resource availability in the diverse fields (Fig. 2).

The mean bee species richness of diverse fields was greater than that of knapweed-dominated fields across both sampling years (diverse field mean = 4.6 ± 0.3 captured species per field per sampling date; knapweed-dominated field mean = 2.4 ± 0.5 captured species per field per sampling date; deviance = 63.592, df = 42, $p < 0.001$). The season-long mean bee diversity as measured by Shannon's H' was also higher in diverse fields than in knapweed-dominated fields across both sampling years (diverse field mean = 1.04 ± 0.09; knapweed-dominated field mean = 0.37 ± 0.08 (SEM); deviance = 7.490, df = 42, $p < 0.001$).
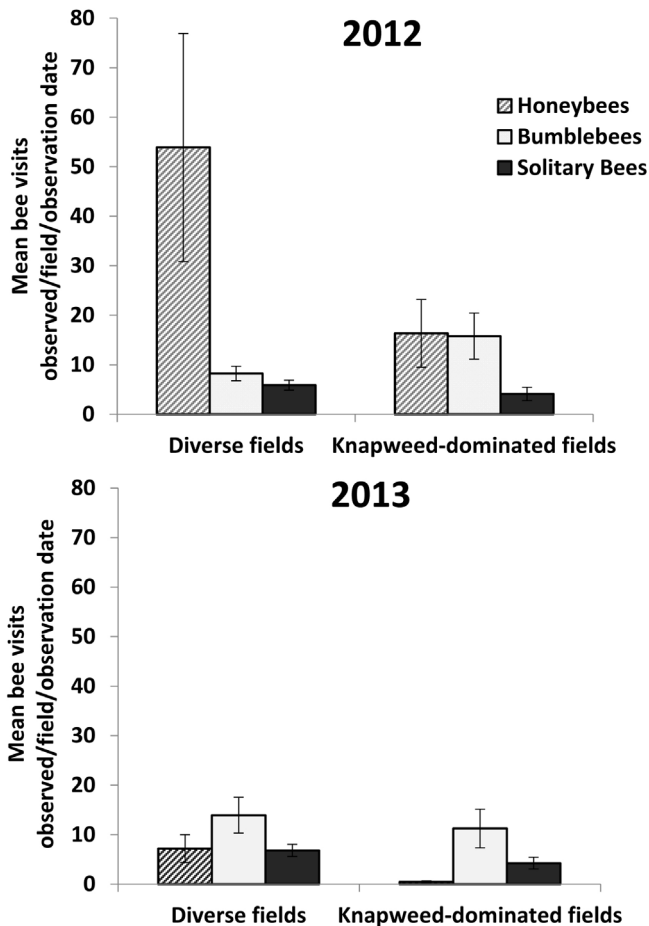
**Fig. 3.** The mean number ±SE of bee visits observed per field per observation date in 2012 and 2013. Total bees are subdivided into solitary bees, bumble bees, and honey bees of each group (Oakland Co, Michigan).

## Common garden experiment

Twenty-five hours of bee observations were completed in 2012, and 23.5 h were completed in 2013. In total, we collected 37 bee species, 18 in 2012, and 31 in 2013 (Appendix A. Table 3). *Centaurea stoebe* was visited by 23 bee species, more than any other plant in our experiment. *Rudbeckia hirta* was visited by ten bee species, *Helianthus occidentalis* was visited by eight species, and *Penstemon hirsutus* was visited by six species. The majority of bee species (62%) visited *C. stoebe* at least once.

Combining data from 2012 and 2013, *Penstemon hirsutus* and *Coreopsis lanceolata* were the only species which bloomed in June and attracted bee visits. Of these, *P. hirsutus* was more attractive, with a mean of 2 ± 1 bees/plant in bloom/6 min observation. In July, 12 plant species flowered (Fig. 4). Of these, *C. stoebe* had the highest visitation rate (1.9 ± 0.3 bees/plant in bloom/6 min observation), closely followed by *P. hirsutus*, *Co. lanceolata*, and *Monarda fistulosa* L. Eight species flowered in August, of which *C. stoebe* had the highest visitation rate, with a mean of 1.6 ± 0.4

bees/plant in bloom/6 min observation. Ten plant species were in bloom in September, with *Solidago speciosa* Nutt. having the highest visitation rate (2.1 ± 0.6 bee visits/plant in bloom/6 min observation).

In 2012, *C. stoebe* had the greatest visitation to floral area ratio (0.02 ± 0.02 bees/cm$^2$). In 2013, *P. hirsutus* had the highest mean ratio of visits to floral area (0.009 ± 0.002 bees/cm$^2$). It was closely followed by *C. stoebe* (0.007 ± 0.001 bees/cm$^2$), *Co. lanceolata* (0.007 ± 0.002 bees/cm$^2$) and *Symphyotrichum laeve* (0.005 ± 0.001 bees/cm$^2$).

## Discussion

The common garden and field level floral diversity studies both showed that *C. stoebe* is inherently attractive to many bee species. In the common garden, *C. stoebe* received a high number of total bee visits per plant in bloom, and a high number of visits per unit of floral area, indicating that each flower is individually attractive. The attractiveness of each individual flower and an abundance of flowers per plant led to a high number of visits to *C. stoebe* in both years in the common garden. In the field level floral diversity study, these factors combined with a high density of *C. stoebe* plants and resulted in more bee visits to *C. stoebe* than any other plant species. Because the common garden experiment was conducted in a landscape largely devoid of *C. stoebe*, we know that bees did not target it only because of its local abundance and familiarity.

In both years and studies, *C. stoebe* was visited by a greater number of bee species than any other plant species, indicating its attractiveness to a wide variety of bee species. Most of the species visiting *C. stoebe* were generalists, but also included two bee species (*Melissodes subillatus* LaBerge and *Megachile pugnata* Say) that specialize on plants in the family Asteraceae (LaBerge 1961; Tepedino & Frohlich 1982). Furthermore, many generalist bee species were only observed visiting *C. stoebe*.

While *C. stoebe* is a highly attractive plant that is providing significant pollen and nectar resources to bees, our results also point to an important temporal mechanism in the role that flowering plant diversity plays in supporting abundant and diverse bee communities. In the common garden experiment, *C. stoebe* received the greatest number of bees/plant in bloom/6 min observation during its main flowering period in July and August, but in June and September native plant species received more visitors. This temporal mechanism is further supported by the field component of our study: while knapweed-dominated fields had high levels of floral area during *C. stoebe* peak bloom, before and after this period these fields contained very few floral resources. In contrast, diverse fields had a number of flowering plant species that provided floral resources before, during, and after *C. stoebe*'s bloom period. Diverse fields contained greater season-total floral area in both 2012 and 2013, likely resulting in the
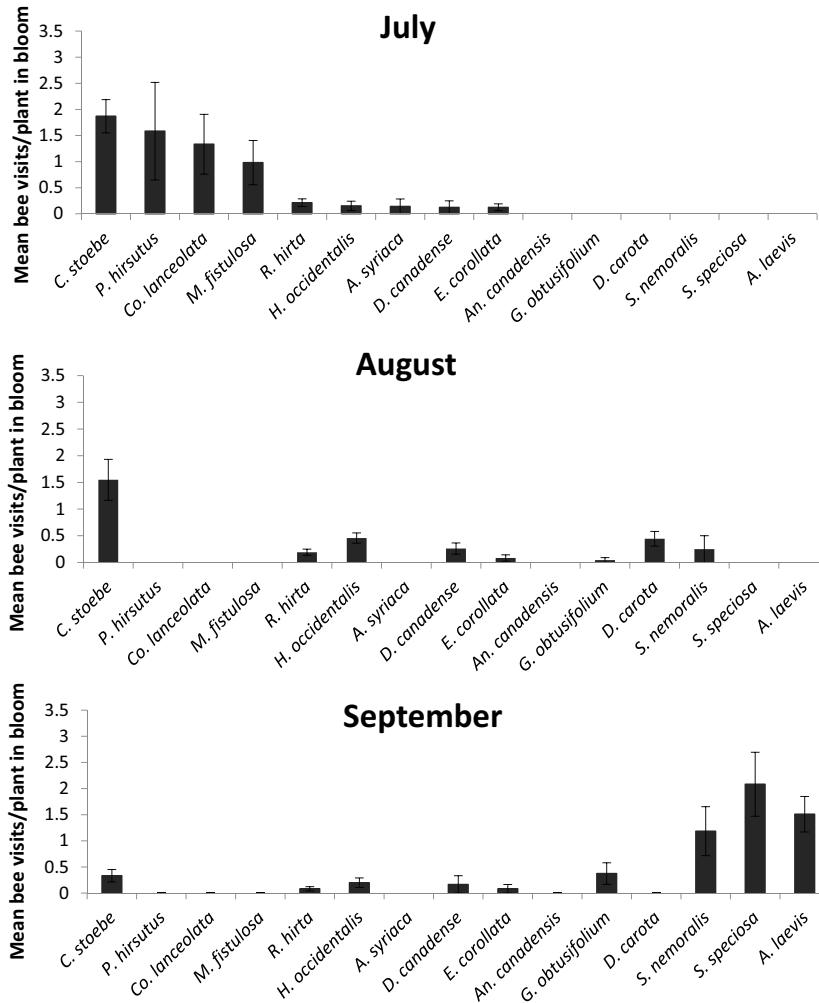
**Fig. 4.** The mean number of bees per plant in bloom (±SE) for each common garden species in July, August and September. 2012 and 2013 observations are combined (Ingham Co, Michigan).

higher season-total rate of bee foraging observed in these fields.

Diverse fields also had greater overall bee species richness and diversity, despite the fact that *C. stoebe* was visited by more bee species than any other plant in the study. While most of the bee species captured in the field study were generalists, several bee species (*Andrena hirticincta, Colletes americanus*, *C. compactus*, *C. simulans*) that specialize on fall blooming asteraceous plants such as *Solidago* and *Symphiotrichum* spp. were only observed in diverse fields. Thus, increased forb diversity can lead to more diverse bee communities via two mechanisms: Firstly, greater flowering plant diversity increases the likelihood that plants that support specialist bee species will be present. Late in the season *S. nemoralis* and *S. speciosa* made up a high proportion of the available floral resources, and these were visited by four species (listed above) specializing on *Solidago* spp. and other asteraceous plants. Secondly, the longer period of bloom availability may allow for temporal overlap of more generalist bees flight periods with nectar and pollen sources. Four generalist species were only observed in diverse fields

before *C. stoebe* reaches peak bloom, and two additional generalist species were observed in diverse fields after *C. stoebe* finished flowering. While the presence of these additional species hints that this mechanism is at play, it should be noted that several of these species were single observations. We believe that with further sampling, stronger evidence of this mechanism may be found.

In addition to extending bloom phenology and facilitating the presence of specialist bee species, increases in flowering plant diversity can positively affect wild and managed bee communities in other ways. Many generalist bee species require pollen from several plant species to successfully develop through pupation (Sedivy, Muller, & Dorn 2011), and some generalists preferentially seek out the pollen of native plant species (Williams & Kremen 2007; Kleijn & Raemakers 2008). Thus, although many species visit *C. stoebe*, some might have additional obligate relationships with co-occurring native plant species. A diverse floral diet may also be important for maintaining health in bees. Alaux et al. (2010) found that honey bee larvae that were fed a diet of polyfloral pollen had increased levels of glucose

oxidase, leading to an increased baseline immuno-competence compared to larvae that were fed a monofloral pollen diet. Increases in floral diversity on a landscape scale could therefore increase the overall health of honey bees by increasing immuno-competence. It is likely that increased pollen diversity could similarly increase baseline immuno-competence in bumblebee and other native bee larvae.

The results of both our common garden and field study demonstrate that the invasive *C. stoebe* is a highly attractive plant that is used by many bee species during its bloom period. However, these results may not be generalizable to other invasive forbs, even when the species in question are known to be attractive to bees in their home range: Moroń et al. (2009) found that sites that were dominated by invasive goldenrods had drastically lower native bee abundance and diversity. While we observed reductions in both of these metrics in knapweed-dominated fields, they were not as pronounced as in the Moroń et al. (2009) study. The differences between knapweed-dominated fields and more diverse fields seemed to primarily be the result of a truncated period of floral resource availability in the knapweed-dominated fields. In an evaluation of bees' use of exotic and native plants in a landscape gradient ranging from "natural" to highly modified, Williams et al. (2011) found that native bees in disturbed habitats often use invasive plant species, but they do not usually exhibit preference for them. Instead, bees used them in proportion to their relative abundance in the plant community. In our common garden experiment, many native bees visited *C. stoebe* in the presence of flowering native plants, despite each species being present in similar abundances. We also observed use of *C. stoebe* by native bees in our field study, even when a diversity of native plant species were available. These findings indicate that the effects invasive flowering plant species have on bee communities are likely to vary based on traits the invasive plant exhibits, as well as the composition of the native plant and pollinator communities.

*Centaurea stoebe* is a major component of the forb community throughout old fields in the Midwestern United States, and it has been the focus of biological control efforts (Carson et al., 2015). The field portion of this study took advantage of relatively small pockets of diverse plant communities that resulted from active restoration of old fields within a landscape dominated by *C. stoebe*, and demonstrates the effect additional restoration could have on bee communities in the region. Because the flight radius of most bees is larger than any one of the field pairs in the study, this study reveals what floral resources are preferred by bees at any point in time, rather than measuring a direct effect of increasing floral diversity on bee populations. Despite the limited ability to scale-up the results of this study quantitatively, it is clear that the presence of these small pockets of early and late-blooming plant species allow bees to persist in old-field habitats for a longer period of time. It follows that increasing the amount of diverse old-field habitats in the landscape should lead to greater bee abundance, richness, and diversity.

In conclusion, *C. stoebe* is highly attractive to a wide diversity of native and managed bees found in Michigan old-fields. Efforts to manage *C. stoebe* at landscape scales should acknowledge the species and services that this invasive plant is supporting and seek to replace its function with native species. Our results suggest that when coupled with efforts to increase forb diversity, management of *C. stoebe* could enhance bee communities in old-field habitats.

## Acknowledgements

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2016.04.004.

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