

Bees in disturbed habitats use, but do not prefer, alien plants

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Abstract

Alien plants form important interactions with flower visitors across many systems and are especially likely to dominate these interactions in disturbed habitats where native plants are rare. Most studies of alien plant–pollinator interactions have focused on the effects of alien plants on native plant reproduction; however, these alien plants may also be important food resources for native bees especially if they dominate the “floral market”. Dominance of alien species in the diet of bees could occur due to high relative density and abundance of alien plants and flowers, and/or to bee preference for alien plants when they are present. We investigated bees’ use of and preference for alien plants using two data sets from distinct regions of North America, central California and southern New Jersey. In each system, we sampled bees and flowering plants in multiple habitat types that differ in level of disturbance and in the relative abundance of alien plant species. Alien plants as a group dominated interactions with bee communities in more disturbed habitats. Importance, however, varied among plant species such that a subset of highly used plant species drove the overall pattern of use within the community. Despite higher use of alien plants in more disturbed sites, alien plants as a group were not more preferred. Rather, bees’ use of individual alien plants correlated with plant abundance in the community. Consistent with the interpretation that bees use, but do not prefer, alien plants, we found no effect of alien plant abundance or richness on bee abundance or richness.

Zusammenfassung

Gebietsfremde Pflanzen interagieren mit Blütenbesuchern in vielen Systemen, und es ist wahrscheinlich, dass sie diese Interaktionen in gestörten Habitaten, in denen einheimische Pflanzen selten sind, dominieren. Die meisten Untersuchungen zu Interaktionen zwischen gebietsfremden Pflanzen und Bestäubern konzentrierten sich auf die Auswirkungen der fremden Pflanzen auf die Reproduktion der einheimischen Pflanzen. Indessen können fremde Pflanzen auch eine wichtige Nahrungsressource für einheimische Bienen darstellen, insbesondere wenn sie den “Blütenmarkt” beherrschen. Eine solche Dominanz von fremden Pflanzen in der Nahrung von Bienen könnte entstehen als Ergebnis einer hohen Dominanz und Abundanz der fremden Pflanzen und Blüten und/oder wenn die Bienen vorhandene fremde Pflanzen bevorzugen.

Wir untersuchten die Nutzung von und die Präferenz für gebietsfremde Pflanzen durch Bienen anhand von zwei Datensätzen aus unterschiedlichen Regionen Nordamerikas: Zentralkalifornien und Süd-New Jersey. In beiden Systemen erhoben wir Daten zu den Bienen und Blütenpflanzen in mehreren Habitaten, die sich hinsichtlich der Störungsintensität und der Abundanz gebietsfremder Pflanzen unterschieden.

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Fremde Pflanzen dominierten die Interaktionen mit den Bienengemeinschaften in den stärker gestörten Habitaten. Die Bedeutung einzelner Pflanzenarten variierte indessen dergestalt, dass eine kleine Anzahl stark genutzter Arten das Gesamtbild der Nutzung in der Gemeinschaft bestimmte. Auch wenn fremde Pflanzen stärker in mehr gestörten Habitaten genutzt wurden, wurden fremde Pflanzen als Gruppe nicht stärker präferiert. Vielmehr korrelierte die Nutzung fremder Pflanzen durch Bienen mit der Abundanz der Pflanzen in der Gemeinschaft. In Übereinstimmung mit der Interpretation, dass Bienen gebietsfremde Pflanzen nutzen aber nicht präferieren, fanden wir keinen Effekt von Abundanz oder Artenreichtum der fremden Pflanzen auf die Abundanz oder den Artenreichtum der Bienen.

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Introduction

Human-induced land use changes are often accompanied by a loss of native plant diversity and abundance (Hensen 2005; McKinney 2002) as well as shifts in the composition of plant communities toward an increasing proportion and abundance of alien species (Lonsdale 1999). Such changes in composition may be associated with changes in the effects that alien plants have on native plant and animal communities. In addition to direct competitive effects on native plants (Busch & Smith 1995; Dantonio & Mahall 1991; Schmidt, Hickman, Channell, Harmony & Stark 2008), alien plants interact with native and alien floral visitors and thus potentially affect pollinator populations and communities (Moron et al. 2009; Stout & Morales 2009). Considerable attention has been paid to the potential impacts of invasive aliens on native plant reproduction and evolution through competition or facilitation of pollination (Aizen, Morales & Morales 2008; Bjerknes, Totland, Hegland & Nielsen 2007; Morales & Traveset 2009); less is known about the functional importance of alien plant species as food resources for bees or other visitors (Stout & Morales 2009; but see Tepedino, Bradley & Griswold 2008). We explore bees' use of alien and native plant species and test whether the importance of alien plants as resources for pollinators might change with land use.

Recent studies investigating the pattern of interactions between pollinator and plant communities show that alien plants can vary in importance from relatively under-visited components of the community (Memmott & Waser 2002) to fully-integrated core species within plant–pollinator networks (Bartomeus, Vila & Santamaria 2008; Morales & Aizen 2006; Valdovinos, Ramos-Jiliberto, Flores, Espinoza & Lopez 2009; Vila et al. 2009). Some of this variation in the importance of alien species might be because studies have explored interactions at sites differing in the level of human disturbance. Because disturbance favours increased abundance and diversity of alien plants, their importance is likely to be greater in more disturbed habitats (Aizen et al. 2008). In addition, many studies have focused on one or a few abundant invasive species rather than exploring all aliens within a given plant community, which may bias interpretation of how important alien species are for pollinators. Finally, studies on the integration of alien plant species into

plant–pollinator webs have generally recorded bee visits to alien versus native plants in the community, but have not simultaneously considered how plant abundance may affect the use of alien versus native plant species (Aizen et al. 2008; Morales & Aizen 2006; Olesen, Eskildsen & Venkatasamy 2002). Floral density and abundance are known to affect use of different plant species within a community (Potts et al. 2003; Stang, Klinkhamer & van der Meijden 2006). Here we explicitly consider the effect of plant abundance on differential visitation of alien versus native plants. Alien plants could potentially dominate pollinators' use of flowers in the community either due to their greater floral abundance (Vila et al. 2009), or through greater attraction and rewards offered per plant (e.g., Brown, Mitchell & Graham 2002; Chittka & Schurkens 2001; Morales & Traveset 2009). Greater rewards are likely to lead to preference by pollinators for a particular plant species or group. Preference is here defined as use of a plant species or group in excess of its relative abundance in the community. Whether the pattern of flower use by pollinators is driven primarily by plant abundance or by pollinator preference will determine how alien plants influence pollinator populations. If alien plants are preferred by pollinators over native plants, then their presence should positively affect pollinator communities across a variety of contexts. If pollinators show no such preference, then alien plants will exert strong effects on pollinator populations only at sites where they dominate numerically.

The disturbed habitats of agricultural landscapes, where alien plants are likely to be relatively more abundant, represent one case where alien plant species might affect bee abundance and diversity. Agricultural intensification and the loss of natural habitat are associated with reduced abundance and diversity of native bees (Kremen, Williams & Thorp 2002; Ricketts et al. 2008; Winfree, Aguilar, Vázquez, LeBuhn & Aizen 2009). Several authors have suggested that such declines in bees are due, at least in part, to the loss of floral resources on which bees rely (e.g., Kremen et al. 2002; Steffan-Dewenter & Tschardtke 1999). However, in some cases agricultural landscapes support more diverse and abundant bee communities than do the natural habitats they replaced (Hoehn, Tschardtke, Tylianakis & Steffan-Dewenter 2008; Klein 2009; Tylianakis, Klein & Tschardtke 2005; Winfree, Griswold & Kremen 2007). If native plant abundance and diversity are reduced in these disturbed landscapes,

alien plants might maintain bee populations that would otherwise be diminished.

In this paper, we examine the importance of alien plants for native bees using two data sets on bee–plant interactions across habitat types differing in disturbance and the extent of alien plant invasion. Specifically, we investigated the following questions. (1) Does the use of alien as compared to native plants for bees vary among habitat types within the same landscape, and do alien plants dominate interactions between plants and bees most strongly in disturbed habitats? (2) Do bees use alien plants in proportion to their floral abundance in the habitat, or are alien plants avoided or preferred? (3) Are alien plant abundance and diversity associated with bee abundance and diversity at a site? The answers to these questions will elucidate the mechanisms by which alien plants influence bee communities.

Methods

Study sites and sampling

Our first dataset was collected in the California central valley grasslands and interior chaparral/woodlands ecoregion (Ricketts et al. 1999) in two drainages within Yolo and Solano counties CA, USA. We sampled a total of 21 sites in four habitat types: conventional farms (orchards, flowering row crops; 4 sites), organic farms (diverse vegetable farms; 5 sites), semi-natural near to agriculture (riparian/chaparral/oak savannah within 20–500 m of farmland; 7 sites; see (Williams & Kremen 2007) for more details), and semi-natural far from agriculture (chaparral/oak savannah-woodland > 4.8 km from crop fields; 5 sites). The last two site types were categorized as semi-natural rather than natural, because all have been impacted by grazing in recent history and host alien plants. Sites were a maximum of 62.5 km and a minimum of 1.4 km apart. Sampling areas averaged 1.8 ± 0.04 ha within a habitat type and each habitat type contained a consistent mixture of microhabitats. On farms these microhabitats included fields, borders and small fallow areas and in natural areas they included chaparral, oak savannah, and riparian areas.

All sites were sampled eight times between March and mid-August 2002, with samples organized into discrete rounds separated by 3–4 weeks. Sites were only sampled on days with full sun and wind of less than 2 m/s. On each sampling day we collected three types of data. First, we netted bees from all flowering plants within the site during one hour in the morning (08:30–11:30 h) and one hour in the afternoon (12:30–15:00 h). Collectors moved systematically throughout the study plot collecting all bees observed. Thus sampling effort was in proportion to the abundance of a plant species at the site. Second, we collected bees by pan trap placing 10 clusters of three traps (Solo brand 178-mL plastic bowls of white, fluorescent blue and fluorescent yellow in each cluster) spaced 15 m between clusters across the cen-

ter of the site and leaving them in place for 8 h. Third, we counted the number of open flowers of each species within 1 m² quadrats spaced at 5 m intervals along stratified transects throughout the site. For species with tightly clustered inflorescences (e.g., the capitula of Asteraceae) we scored single inflorescences as flowers because individual flowers could not be efficiently/reliably measured. All flowers from ground-level up were included in counts.

Crops, although generally alien species, were considered separately from other aliens because they are cultivated in large, regular arrays and represent a different type of plant in the landscape. Mass flowering crops can impact native bee populations (Diekötter, Kadoya, Peter, Wolters & Jauker 2010; Westphal, Steffan-Dewenter & Tschamtko 2003); therefore, we included crop flower abundance as an additional covariate in our analysis of bee abundance.

Our second data set was collected in the Atlantic coastal pinelands ecoregion (Ricketts et al. 1999) of southern New Jersey, in Burlington, Camden and Atlantic counties. A total of 27 sites were selected in three habitat types: native vegetation (pine-oak ericaceous heath; 14 sites), suburban development (7 sites), and conventional agriculture (6 sites). Farms within these agriculture sites grew a diverse mixture of vegetable crops and a lesser amount of orchard crops. Sites were a maximum of 49 km and a minimum of 1.4 km apart.

At each site, all data were collected within one 110 m × 3 m transect located within habitat type, such as trails within woodland or internal field margins between adjacent fields within farm sites. Sites were sampled four times between April and mid-August 2003, with sampling organized into rounds such that sites were sampled in the same order in each round. Bee data were only collected on sunny or partly cloudy days (see Winfree et al. 2007 for further details). In each sampling event, we collected three forms of data. First, we netted bees from all flowering plants within the transect for 30 min in the morning (09:00–12:00 h) and 30 minutes in the afternoon (12:00–15:00 h). Second, we collected bees by pan trap placing 12 traps (alternating white, fluorescent blue, and fluorescent yellow) evenly spaced along the transect and leaving them in place for 8 h. Third, we counted all open flowers in 1.6-m³ quadrats placed every 5 m, for a total of 23 quadrats per transect. Cubic quadrats were used to adequately measure flowering shrubs. As was done in California, inflorescences were counted rather than flowers for species with tightly clustered inflorescences. Sampling for the three forms of data was done on separate days to avoid interference among methods. The mean time elapsed between the bee netting and the floral abundance sampling, which is relevant to the preference analysis, was 3.7 days (SD = 3.4 days, maximum = 8 days).

Analysis

To test the importance of alien plant species to the bee community and how their importance differed among habi-

tat types we compared the total number of individuals and species richness of bees collected from alien and native plants among habitat types using general linear mixed models (SAS Proc Mixed, v9.2 SAS Institute). The outcome variables, bee abundance and richness, were log transformed for analysis. For the analysis of the California data set, plant type (native versus alien) and habitat type and their interaction were included as fixed effects and sampling date was included as a repeated factor at the level of site. Site nested within habitat type was a random factor, and sampling area was included as a covariate. For the analysis of the smaller New Jersey data set, we pooled visits within a site across all seasonal samples at each site and ran the analysis without the repeated factor. Because sampling areas were equal, sampling area was not included in the models. Both of these analyses consider overall use of different plant types rather than considering species separately.

For our larger California data set, we did an additional species-based analysis to determine whether particular alien plant species were especially important resources for bees and thus drove the trends observed for the alien plant group as a whole. Here we measured bee abundance and richness separately for each plant species within each sampling event, and averaged each metric among all sites separately by habitat type and season. We then compared averages between alien and native plant species for each habitat type and across the landscape as a whole using a general linear mixed model (SAS Proc Mixed, v9.2 SAS Institute). We used only plant species that were recorded in at least five sampling events. Season was included as a fixed effect in the analysis because the availability of individual plant species shifted over the season. Plant species was included as a random factor.

To determine whether bees preferred alien plants, or simply used them because they were abundant, we used both California and New Jersey data to compare bee preference for alien versus native plants. Preference in general assesses use of a resource adjusted for its availability. We measured preference using a simple ranks-based index (Johnson 1980). This index is calculated by first ranking use among different items (for our data, the number of bee specimens collected from each plant species) and then ranking availability of the same items (for our data, the number of flowers of the same plant species). Preference for each item is calculated as the difference between rank use and rank availability. Negative values indicate a preference for the particular item. One advantage of a ranks-based index over calculating preference by simply dividing plant use by plant abundance is that it is less sensitive to incidental collection from very rare plant species, which produces highly inflated values and thus increases the variance in the data set.

We first calculated preferences for alien plants as a group and native plants as a group at each sampling event in each region. We used a Wilcoxon signed-rank test (JMP v8, SAS Institute) to determine whether bee preference for alien plants differed from zero. With our larger California data set,

we also calculated average preference separately for each plant species among all sites within a habitat type. We then used these species averages to compare preference between native and alien species using a general linear mixed model. In this model, habitat and plant type (alien versus native) were included as fixed effects and plant species as a random effect. Preference index values met assumptions of normality and equal variances between native and alien species. Only species that were found in at least five sampling events were included in the analysis. To quantify the role of plant abundance on bees' use of aliens more directly, we calculated the correlation between visits a plant species received and its floral abundance within a sampling event. If use is driven by plant abundance we would expect these variables to be positively correlated among species. A positive correlation does not, however, rule out an added effect of attraction on bees' use of plants. All variables were log transformed prior to analysis.

We used general linear models (Proc GLM, v9.2 SAS Institute) to test whether the floral abundance of alien plants at a site affected the total abundance of bees, and whether alien plant species richness affected bee species richness, at each site. Plant species richness was used as the predictor of bee richness because floral phenotype is known to affect bee species' use of flowers (Stang et al. 2006), thus more diverse floral communities might support more species of flower visitors. All variables were sums over the season. We also used a separate model to test whether bee abundance and species richness were related to total floral abundance and floral species richness at the site. For all of these analyses, we supplemented the net data with pan trap and aerial net records collected in the same study to generate total bee abundance and species richness for each sampling event. At agricultural sites the abundance and richness of bees might be affected by flowering crops in addition to non-crop species (Westphal et al. 2003). We therefore included crop abundance at the site as a covariate. In New Jersey crop plants did not appear in our transects and so were not included in the analysis.

Results

In California we collected 219 bee species from 140 plant species, 89 of which were native and 51 of which were alien. We recorded a total of 6769 bee–plant interactions, with each interaction representing a bee specimen netted while visiting a flower. In New Jersey we collected 61 bee species from 37 plant species, 14 of which were native and 23 of which were alien. We recorded a total of 318 bee–plant interactions. For the analysis of bee communities, we used an additional 20571 specimens and 14 additional species from California collected in pan traps and an additional 1164 specimens and 21 additional species from New Jersey collected in pan traps or by aerial netting; both provide information about the bee species present in a habitat, but do not indicate floral associations.

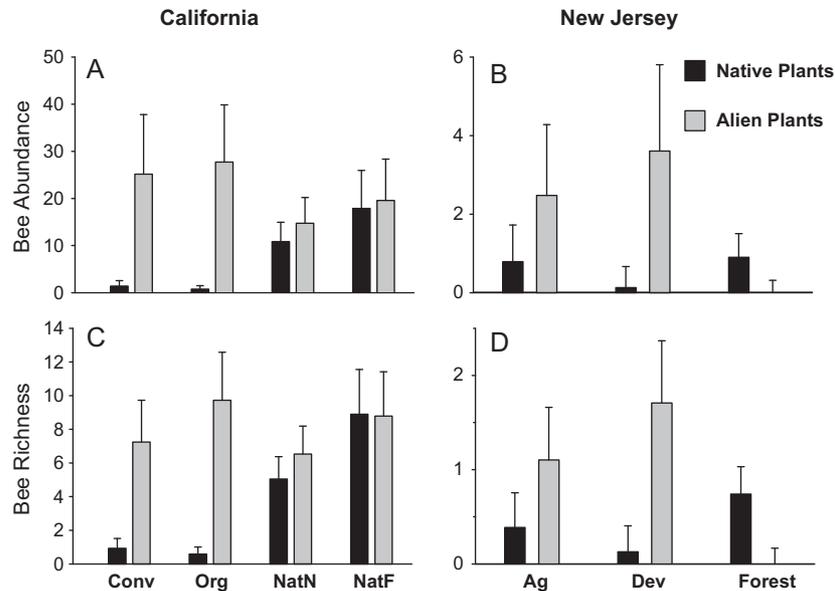


Fig. 1. Bee visitor measures across habitat types in California and New Jersey. All values are means per site \pm 95% CL: (A and B) number of specimens collected from alien versus native plants and (C and D) number of bee species collected from alien versus native plants in each habitat type. Black bars indicate native plants and shaded bars represent alien plants. Conv = Conventional Agriculture, Org = Organic Agriculture, NatN = semi-natural Near Agriculture, NatF = semi-natural Far from Agriculture; Ag = Agriculture, Dev = Suburban Development, and Forest = Forested sites.

Bee use of alien versus native plants

In both California and New Jersey, bees' use of alien plants was greater in disturbed habitats than in semi-natural habitats (plant type \times habitat interaction: California $F_{3,17} = 53.1$, $p < 0.01$, New Jersey $F_{2,24} = 33.0$, $p < 0.01$). In agricultural habitats, alien plants received significantly more bee visits and were visited by more bee species, as compared to native plants (Fig. 1A–D; California, bee abundance on alien versus native plants at conventional farms $t_{17} = 10.95$, $p < 0.001$, at organic farms $t_{17} = 14.34$, $p < 0.001$ California, richness at conventional farms $t_{17} = 9.43$, $p < 0.001$, at organic farms $t_{17} = 13.88$, $p < 0.001$; New Jersey abundance at agricultural sites $t_{24} = 2.71$, $p = 0.012$, richness $t_{24} = 2.85$, $p = 0.009$). The same pattern was observed in suburban habitats in New Jersey (abundance $t_{24} = 5.79$, $p < 0.001$, richness $t_{24} = 5.89$, $p < 0.001$). Natural and semi-natural habitats showed different patterns. In California, the abundance and richness of bee species visiting alien versus native plant species differed only marginally (sites near to agriculture: abundance $t_{17} = 1.72$, $p = 0.11$; richness $t_{17} = 1.89$, $p = 0.08$) or not at all (sites far from agriculture: abundance $t_{17} = 0.43$, $p = 0.67$; richness $t_{17} = 0.08$, $p = 0.98$; Fig. 1A and C). In natural habitats in New Jersey alien species received fewer visits and had fewer bee species than native plants (abundance $t_{24} = -5.05$, $p < 0.001$; richness $t_{24} = -6.53$, $p < 0.001$; Fig. 1B and D).

The abundance and richness of bee species visiting each type of plant mirrored the floral abundance of each plant type in the same habitat. Floral abundance of alien plants was significantly greater than that of native plants at

farm sites (Fig. 2A and B; California: conventional farms $t_{17} = 3.79$, $p < 0.01$, organic farms $t_{17} = 3.01$, $p < 0.01$; New Jersey, $t_{24} = 3.90$, $p = 0.001$) and in suburban areas in New Jersey ($t_{24} = 5.97$, $p < 0.001$). Richness of flowering alien plants was also significantly higher than that of native plants (Fig. 2C and D; California: conventional farms $t_{17} = 6.7$, $p < 0.01$, organic farms $t_{17} = 7.76$, $p < 0.01$; New Jersey farms $t_{24} = 5.87$, $p = 0.001$, suburban areas: $t_{24} = 5.87$, $p = 0.001$). In semi-natural habitats in California, alien species did not differ in abundance from natives (semi-natural near to agriculture, $t_{17} = 1.61$, $p = 0.13$; semi-natural far from agriculture, $t_{17} = 1.37$, $p = 0.19$) although native plants were more speciose than aliens (semi-natural near to agriculture, $t_{17} = 2.58$, $p = 0.02$; semi-natural far, $t_{17} = 7.88$, $p \leq 0.01$). In New Jersey, alien plants were nearly absent from natural sites.

Results based on individual alien plant species in California matched those based on alien plants as a group. On average, bees used alien plant species more than native plant species ($F_{1,1028} = 8.32$, $p = 0.004$) and their use of aliens was greater in agricultural habitats than in semi-natural habitats, although only marginally so (plant type \times habitat type interaction, $F_{3,1028} = 2.24$, $p = 0.08$). Bees' use of alien plants, however, was unevenly distributed among species. A few alien plant species received most of the visits within their communities, whereas the majority of species received relatively few visits (Fig. 3A). Indeed over 78% of visits to alien species as a group on average were to just four plant species. The majority of alien plant species also were visited by relatively few bee species although approximately 10% of alien plant species received 25% or more of the bee visitors within their communities (Fig. 3B). The distributions of bee

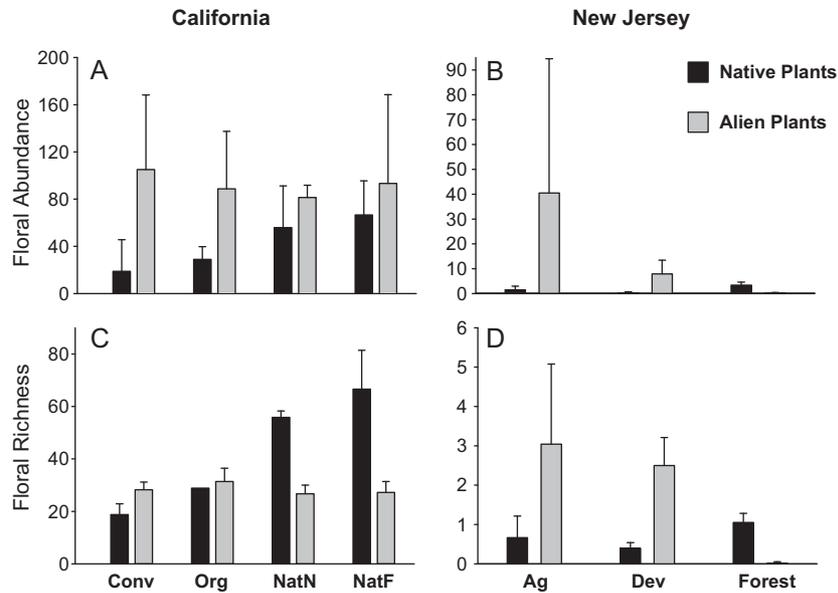


Fig. 2. Floral measures across habitat types in California and New Jersey. All values are means per site \pm 95% CL: (A and B) flower density (m^2) and (C and D) species richness of each plant type in each habitat type. Black bars indicate native plants and shaded bars represent alien plants. Conv = Conventional Agriculture, Org = Organic Agriculture, NatN = semi-natural Near Agriculture, NatF = semi-natural Far from Agriculture; Ag = Agriculture, Dev = Suburban Development, and Forest = Forested sites.

use or among plant species were generally similar for native plants and indeed did not differ significantly between native and alien plant species (Kolmogorov–Smirnov; abundance

$D = 0.28, p = 0.23$; richness $D = 0.23, p = 0.44$). The greatest differences between alien and native plant species were that fewer alien species received no visits and more alien species received the highest proportions of visits and visitor species. Like for the pooled use of aliens, use of individual alien plant species correlated with their floral density within the community ($r = 0.30, p < 0.001$). The same pattern was true of native plants ($r = 0.18, p < 0.001$) albeit with a weaker relationship.

Bee preference for alien versus native plants

Bees did not prefer alien plants as a group over native plants at any habitat in either study system (Table 1). Results based on individual plant species in California were consistent with those based on pooled alien versus native plants. There was no significant preference for alien plants compared to native species ($F_{1,237} = 0.01, p = 0.93$) and no significant interaction between habitat type and plant type ($F_{3,237} = 1.30, p = 0.28$).

Effect of alien versus native plants on bee communities

Neither alien floral abundance, native floral abundance, nor species richness affected bee abundance or richness at sites in either region (Table 2). The effect of alien flowers on native bee populations also did not differ among habitat types (Table 2). Inclusion of on-farm crop abundance or species richness did not help to explain bee abundance or species richness (crop effect on bee abundance, $F_{1,8} = 0.21, p = 0.66$; richness $F_{1,8} = 0.17, p = 0.69$). Bee abundance and richness

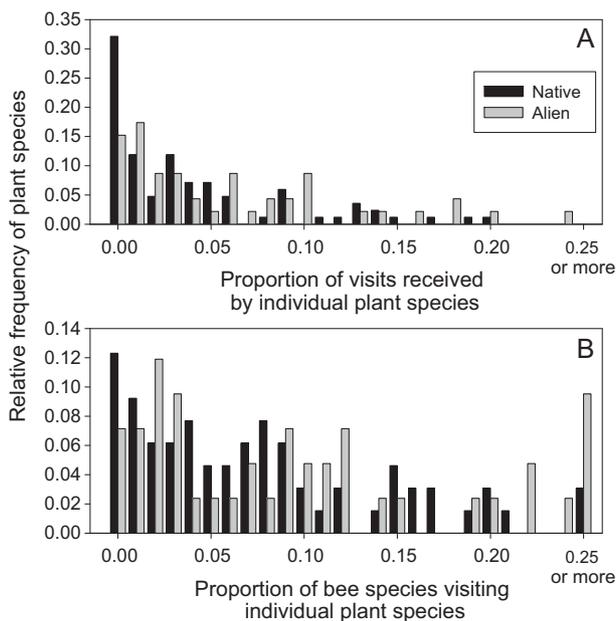


Fig. 3. Distribution of (A) bee visits and (B) bee species visiting individual alien and native plant species within a community. Values along the X-axis are proportion of visits (A) or visitor species (B) to individual alien or native plant species within their communities. The frequencies were standardized by total number of species of each plant type ($n = 42$ alien, $n = 65$ native plants) such that bars within each plant type sum to 1. Data are for California only.

Table 1. Mean preferences for alien plants for each habitat type in California and overall for New Jersey. Negative values indicate preference.

Habitat type	Mean preference for alien plants	Wilcoxon signed-rank test <i>z</i> -value	# of sampling events	<i>p</i> -Value
California				
Conventional farm	0.016	1.5	31	1.0
Organic farm	−0.025	1.0	39	1.0
Semi-natural near	0.080	27.5	56	0.42
Semi-natural far	−0.090	−12.5	39	0.28
New Jersey				
Pooled habitats	−0.076	1.0	13	1.0

were also not associated with total floral abundance among sites in California (abundance $F_{1,13} = 0.21$, $p = 0.66$, richness $F_{1,13} = 0.00$, $p = 0.99$) or New Jersey (abundance $F_{1,21} = 0.73$, $p = 0.40$, richness $F_{1,21} = 0.12$, $p = 0.73$).

Discussion

Alien plant species were the dominant resources used by bees, particularly in habitats that were heavily impacted by humans. In agricultural sites the majority of individual bees (70% in California and 67% in New Jersey) and bee species (86% in California and 77% in New Jersey) were collected from the alien plant species. In New Jersey, 96% of all individual bees in suburban sites were collected from alien plants. These sites had few if any native plants. Use of alien species within natural habitats, however, differed dramatically between the California and New Jersey landscapes. In California, alien plant species were abundant and heavily used by bees in the semi-natural habitats. These areas included mosaics of different sub-habitats and some of these, such as oak savannah and riparian, are disturbed by grazing and invaded by alien plants. Alien plants were essentially absent from the natural habitat sites in New Jer-

sey. These sites were situated within an extensive protected area of pine-oak ericaceous heath and on a sandy, nutrient-poor soil (Dighton, Tuininga, Gray, Huskins & Belton 2004), an ecosystem type that is little invaded by alien species (Howard, Gurevitch, Hyatt, Carreiro & Lerdau 2004). The few other studies exploring the effect of disturbance on alien plant–pollinator interactions suggest that alien plant species receive high proportions of visits and are used by diverse pollinators especially at more disturbed sites (Morales & Aizen 2006; Vila et al. 2009), which is consistent with our findings.

The greater use of alien plants by bees in agricultural habitats appears to be primarily due to their greater abundance rather than to greater attractiveness to pollinators. Greater reliance of bees on alien plants in both study systems was limited to sites where alien flowers were more common and more diverse than those of native plant species. Alien plants as a group were no more preferred than natives in either region. Furthermore, relative use of individual alien species within plant communities strongly correlated with their relative abundance, a pattern that was also true for native species. Previous studies have found that alien plants are more used than natives in the same community or co-opt visits from natives even if they are not more abundant (Brown et al. 2002; Cariveau & Norton 2009; Chittka & Schurkens 2001;

Table 2. Fixed effect results from mixed model analysis of native bee abundance as a function of alien and native plant flower abundance and of bee richness as a function of alien and native plant richness in California and New Jersey landscapes. Table values are *F*-statistics (with associated *p*-values) from Type 3 testing.

	California		
	df	Abundance	Richness
Alien flower abundance	1, 9	0.22 (0.65)	0.14 (0.71)
Alien flower abundance × habitat	3, 9	0.13 (0.94)	1.36 (0.32)
Native flower abundance	1, 9	0.25 (0.63)	1.01 (0.34)
Native flower abundance × habitat	3, 9	0.14 (0.94)	0.24 (0.86)
	New Jersey		
	df	Abundance	Richness
Alien flower abundance	1, 18	1.64 (0.50)	0.50 (0.49)
Alien flower abundance × habitat	2, 18	0.71 (0.51)	0.43 (0.66)
Native flower abundance	1, 18	0.46 (0.50)	0.14 (0.71)
Native flower abundance × habitat	2, 18	0.75 (0.49)	0.03 (0.97)

Kandori, Hirao, Matsunaga & Kurosaki 2009; Muñoz & Cavieres 2008; Totland, Nielsen, Bjercknes & Ohlson 2006). However, these studies focused on one or a few invasive alien plant species known to be highly pollinator-attractive and/or rewarding. As a result these studies do not test whether alien species in general are preferred compared to natives. The few studies that have quantified species-specific patterns of use among all alien plants in the community (e.g., Morales & Aizen 2006; Olesen et al. 2002) find similar patterns to ours. Since these studies did not include measures of relative plant abundance, they could not elucidate whether abundance or attraction (preference) determined use of alien plants.

A more detailed analysis from California revealed that greater use of the alien component of plant communities was also uneven among plant species such that some alien species were heavily visited by a large proportion of the bee fauna at a site and other species were unvisited. Thus, although alien plant species appear to be extensively integrated into bee–plant networks, the greater use of alien plants as a group was driven by a subset of highly visited and abundant species. Some of these species were unique to agricultural habitats (for example, *Convolvulus arvensis*, *Raphanus sativus*), while others were widespread among sites and abundant in both semi-natural and farm habitats (*Centaurea solstitialis*, *Brassica nigra*). In the lexicon of plant–pollinator networks, such species are abundant super-generalists that form links with large proportions of the native bee fauna (Olesen, Eskildsen & Venkatasamy 2002). Super-generalist plant species appear commonly in plant–pollinator interaction webs (Bascompte & Jordano 2007; Vázquez & Aizen 2004; Vázquez, Blüthgen, Cagnolo & Chacoff 2009) and highly linked alien plant species have been reported in disturbed habitats from other regions (Aizen et al. 2008; but see Olesen et al. 2002). Those studies found that super-generalist alien plants can affect visitation and pollination of native plants. Our data indicate that such generalist weedy alien plants also can provide important resources for bees in habitats with depauperate native plant communities, thus indicating a more positive role for these plants. It would be interesting to know whether these highly visited invasive aliens share ecological or morphological traits that separate them from less visited aliens and whether preferred alien plant species share traits with preferred native species (Morales & Aizen 2006). The same type of functional guild approach also could be considered for bee visitors to determine whether species groups differ in their use of alien plants (Olesen et al. 2002). Bee life history and ecological traits, such as nesting location and sociality, can affect habitat use and species responses to different disturbances (Williams et al., 2010; Weiner et al., 2011). Although, in the case of alien plant use it is not as clear which bee-specific traits would predispose them to use of alien plants as a group, degree of trophic generalization may be one (Olesen et al. 2002). As a caveat, it is important to recognize that individual bee species differ in their reliance on alien plants; some native bees do not visit aliens at all, but instead travel considerable distances to collect pollen from native plants (Williams

& Kremen 2007), suggesting that more detailed investigation of the mechanisms that structure bees' interactions with alien and native plants is warranted.

Although alien plants were the dominant resources used by bees in more disturbed habitats, sites with a higher density and richness of alien flowers did not support more bees. A possible reason for such a finding could have been that bees responded to total floral resources rather than to either native or alien species alone. This was not the case. Neither total floral abundance nor richness significantly affected bee abundance in any habitat. There are several possible reasons for a lack of relationship between floral abundance and bee abundance. First mass flowering crop resources might affect bee populations. We included crop abundance as an additional predictor of bee abundance and diversity for one of our data sets, but this did not help to explain the differences in bee abundance among sites. Second, bees use floral resources from multiple habitats throughout the landscape (Osborne et al. 2008; Williams & Kremen 2007) and populations respond to landscape structure and to crop and non-crop resources at scales beyond that of individual sites (Steffan-Dewenter, Münzenberg, Bürger, Thies & Tschardtke 2002; Westphal et al. 2003). Thus floral resources at a landscape scale, which we did not measure in this study, may have affected abundance and diversity of the bee community at the site (Kleijn & van Langevelde 2006). Third, it may be that in our study, floral abundance provided a poor assessment of the actual floral resources available to bees. Plant species differ in the amount and in the nutritional content of pollen and nectar resources they offer (Roulston, Cane & Buchmann 2000). Measurement of such resources across the 198 plant species in our studies, however, was beyond the scope of our investigation. Fourth, our single season assessment of floral resources and bee populations may not capture significant correlations that exist over longer time scales. Bee populations are highly dynamic among sites and years (Williams, Minckley & Silveira 2001). Finally, floral resources may not be limiting to bee populations in these landscapes. Bee populations are regulated not only by food resources, but also by nest availability (Steffan-Dewenter & Schiele 2008) as well as predators and parasites (Dukas 2001). A previous study of bees in New Jersey found that the best-fit model for bee abundance and richness included only habitat type and not floral abundance (Winfree et al. 2007). These findings suggest that bee communities are influenced by multiple variables associated with habitat type, rather than by floral resources alone.

Alien plant species have become dominant components of plant communities in natural and managed landscapes throughout the world and even more so in disturbed areas. Through their interactions with flower visiting insects, they can have functionally positive or negative impacts on natural communities. Patterns of pollinator visitation to alien plants will determine the degree to which aliens compete with or facilitate native plant reproduction. Alien plants and the quantity and quality of resources they provide might also affect

pollinator communities. The importance of aliens in our study systems derived from their greater floral abundance compared to native plant species, not pollinator preference for them over native plants. This result has important implications for native plant and pollinator conservation. First, because aliens are not consistently preferred over natives in either of our whole-web data sets, the potential for negative effects of aliens on native plants through the competition for pollinators may not be as ubiquitous as previous studies of focal alien species have suggested. Such effects may be more limited to areas where alien species dominate. Second, because bee communities heavily use alien plants, conservation programs that rapidly remove alien plants without restoring native plant populations could have deleterious impacts on native bees and subsequently native plant communities (Moragues & Traveset 2005; Zavaleta, Hobbs & Mooney 2001).

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