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Identifying native plants for coordinated habitat management of arthropod pollinators, herbivores and natural enemies

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Abstract

1. Providing non-crop flowering resources in agricultural landscapes is widely promoted as a strategy to support arthropods that deliver pollination and pest control services. However, management options have largely been developed separately for pollinators and natural enemies, whereas possible effects on insect herbivores, such as crop pests, have often been overlooked. A first critical step for design and implementation of multifunctional plantings that promote beneficial arthropods while controlling insect pests is to identify suitable plant species to use.

2. We aimed to identify California native plants and, more generally, plant traits suitable for the coordinated management of pollinators (wild bees and honey bees), insect herbivores and arthropod natural enemies (predators and parasitic wasps). We established 43 plant species in a common garden experiment and sampled arthropods by weekly netting (wild bees), observations (honey bees) or vacuum sampling (insect herbivores, arthropod predators and parasitic wasps) during peak bloom of each plant species over two years.

3. Plant species differed in attractiveness for each arthropod functional group. Floral area of the focal plant species positively affected honey bee, predator and parasitic wasp attractiveness. Later bloom period was associated with lower numbers of parasitic wasps. Flower type (actinomorphic, composite or zygomorphic) predicted attractiveness for honey bees, which preferred actinomorphic over composite flowers and for parasitic wasps, which preferred composite flowers over actinomorphic flowers.

4. Across plant species, herbivore, predator and parasitic wasp abundances were positively correlated, and honey bee abundance correlated negatively to herbivore abundance.

5. *Synthesis and applications*. We use data from our common garden experiment to inform evidence-based selection of plants that support pollinators and natural enemies without enhancing potential pests. We recommend selecting plant species with a high floral area per ground area unit, as this metric predicts the abundances of several groups of beneficial arthropods. Multiple correlations

between functionally important arthropod groups across plant species stress the importance of a multifunctional approach to arthropod habitat management.

Keywords: biological control, honey bee, multifunctionality, native bee, natural enemy, parasitic wasp, pollinator, wild bee

Introduction

Integration of functionally important biodiversity and associated ecosystem services into crop production is important for the long term sustainability of agricultural systems (Cardinale *et al.* 2012; Kremen & Miles 2012). Crop pollinators and natural enemies to crop pests are two primary examples of such functional biodiversity that have received particular attention (Losey & Vaughan 2006; Klein *et al.* 2007). Increased use of these supporting ecosystem services has the potential to reduce anthropogenic inputs to agriculture such as pesticides and intensive honey bee keeping practices, and thereby contribute to sustainable agriculture (Bommarco, Kleijn & Potts2013). Despite great potential, the ability to integrate supporting ecosystem services into crop production is constrained by limited guidance on how this can be achieved in practice. The challenge is magnified when multiple services are sought simultaneously, as potential trade-offs, marginal gains and losses must be considered (Bennett, Peterson & Gordon 2009; Tamburini *et al.* 2016).

Crop pollination and pest control are mobile-agent-based ecosystem services (Kremen et al. 2007), and in the case of pest damage - disservices (Zhang *et al.* 2007), and as such the organisms responsible for delivering them can be affected by similar environmental drivers (Shackelford *et al.* 2013). Natural and semi-natural habitats in the agricultural landscape, for example, promote both pollinators (Ricketts *et al.* 2008) and natural enemies to crop pests (Chaplin-Kramer *et al.* 2011). Managing for crop pollination and pest control provided by arthropods in agriculture often entails actions that provide food, nesting or overwintering habitat, and protection from agricultural disturbance for the target service providers (Landis, Wratten & Gurr 2000; Garibaldi *et al.* 2014). Management actions to promote pollinators and natural enemies have, however, largely been

developed separately and the possible effects on insect herbivores, such as crop pests, have often been overlooked. Habitats with flowering resources, for example, are typically established either for pollinators or for natural enemies, although each of these planting types may affect both organism groups (Fiedler, Landis & Wratten 2008; Wratten *et al.* 2012). There has been limited effort to integrate provision of flowering resources for pollination and pest control (but see Grab *et al.* 2018; Sutter *et al.* 2018). This is surprising, given that for growers it is important that plantings for pollinators do not increase pest pressure, and desirable that they provide biological pest control services (Sidhu & Joshi 2016). Considering pollination and pest control services in tandem also has great potential to make habitat plantings more cost effective and increase the likelihood of adoption (Morandin, Long & Kremen 2016; Garbach & Long 2017). A first critical step towards design and implementation of multifunctional plantings is identification of suitable plant species to use that support pollinators and natural enemies, but not pests.

Native plants, in particular, show promise for use in habitat management for pollinators and natural enemies, as they are adapted for growing under local conditions and are less likely to be invasive (Fiedler & Landis 2007a; Isaacs *et al.* 2009). Use of native plants, however, also complicates plant choice because plant species that are suitable for propagation and attractive for arthropods need to be identified in a region specific manner. The process of selecting plant species for multifunctionality is further complicated because the best species for supporting pollinators may or may not support natural enemies and vice versa, and furthermore trade-offs between benefiting beneficial arthropods and promoting pests must be considered. This selection process would be greatly facilitated if key plant traits could be identified that are associated with pollinator, herbivore and natural enemy attractiveness. Studies of plants native to Michigan (U.S.) showed that the timing of peak bloom and floral area were positively related to natural enemy abundance (Fiedler & Landis 2007a, b). Bloom period and floral area were also positively related to the abundance and diversity of wild bees visiting plants, whereas floral area was unrelated to the abundance of honey bees (Tuell *et al.* 2008). Apart from bloom period and floral area, the accessibility of resources (nectar and pollen) to arthropods is also likely to influence attractiveness. Resource accessibility is driven by several interacting factors,

including corolla width and depth, whether resources are offered in large versus many small flowers (eg., composite inflorescences in Asteraceae), and arthropod body and mouthpart size (Wäckers 2004; Carvalheiro *et al.* 2014; van Rijn & Wäckers 2016). Such multivariate interaction complicates selection of a single informative flower trait. It has not been tested whether flower type (actinomorphic, composite or zygomorphic flowers) could serve as a general proxy for a set of interacting factors affecting arthropod attractiveness. Actinomorphic and composite flowers generally present more accessible resources with less and more splitting of resources between flowers respectively, while zygomorphic flowers generally have less accessible resources due to deeper corollas or specific flower handling required to access resources.

The overall aim of our study was to identify California native plants, and more generally plant traits, suitable for coordinated habitat management of arthropod pollinators, herbivores and natural enemies and promote integrated ecosystem services in agricultural landscapes. More specifically we ask (i) which native plants among our candidate set attract the highest abundances of wild bees, honey bees, herbivores, predators and parasitic wasps, (ii) if the total abundances of arthropods within these functional groups across plant species are related to the peak flowering week, floral area or flower type of the focal plant species, and (iii) if the total abundances of arthropods within these functional groups are correlated to each other across plant species. In general we expected higher arthropod numbers on plant species with high floral area and actinomorphic flower type due to easy access to large resource amounts, and that arthropod numbers would be higher on plants with a later bloom period due to buildup of arthropod population sizes over the season. We also expected that the abundances of several groups of arthropods would be positively correlated across plant species due to shared responses to plant traits.

Materials and methods

Selection of plants. We tested a total of 43 plant species (Table 1). Selected species were forbs that were drought tolerant, native to California (one exception is listed below) and as a group, covered a range of flowering periods throughout the season. A further consideration for selection of most plant species was indications that they could be attractive to bees based on being listed as nectar and pollen plants for honey bees (Vansell 1941), being recommended as pollinator plants (Xerces Society 2018), being listed as associated with bees in Calflora (2017) or based on earlier collected data on bee attractiveness (Williams *et al.* 2015).). With the exception of one selected plant species, *Antirrhinum cornutum*, for which seed was hand collected, a further criteria that restricted selection was that plant material needed for propagation was commercially available either as seeds or plug plants. We also included *Achillea millefolium* and the shrub *Eriogonum fasciculatum* based on findings that these plants are attractive for locally abundant natural enemies (Morandin *et al.* 2011; Pisani-Gareau, Letourneau & Shennan 2013). Finally, we included *Fagopyrum esculentum*, which is an exotic species known to be attractive for natural enemies, and widely used in conservation biological control (Fiedler, Landis & Wratten 2008). No selected plants were major weeds of crops or pastures. However, *Amsinckia intermedia* and *Calandrinia menziesii* can, although they are desirable components of wildlands, become minor weeds in certain situations (UC IPM 2018).

Study site and design. We collected data over two consecutive seasons 2015-2016 at the Harry H. Laidlaw Jr. Honey Bee Research Facility (38°32'11"N, 121°47'18"W) at University of California Davis, CA, USA. Davis has a Mediterranean climate with dry, hot summers and cool, rainy, winters. Soil type on the site is a Yolo silt loam (USDA NRCS 2017). Land use within 1 km of the study site is dominated by agricultural lands, with a range of field and orchard crops in small fields. Twenty to 40 honey bee *Apis mellifera* L. colonies were kept at the site within 100 m from our experiment. In addition, eight managed research colonies of the yellow-faced bumble bee *Bombus vosnesenskii* Radoszkowski were on site in 2015, and thus both wild and managed individuals of this species are included among the group henceforth referred to as wild bees in our analyses. The study used a randomized complete block design, with each plant species growing in a monospecific one by one

meter plot in each of four replicate blocks. Plots within blocks were separated by one meter alleys, and blocks were separated by five meters or more. Details of plant establishment and maintenance are given in Appendix S1 in the supporting information.

Plant traits affecting arthropod attractiveness. We determined three plant characteristics, floral area, peak flowering week and flower type, which we expected would influence arthropod attractiveness. To determine flora area, we recorded the number of floral units containing open flowers in each plot weekly. A floral unit was equal to an individual flower in most cases, but for Asteraceae species a floral unit was an inflorescence (composite flower). Flower counts were always done within one day of sampling arthropods (see below). We also measured the diameter (actinomorphic or composite flowers) or length and width (zygomorphic flowers) of five to ten floral units per plant species, and calculated from these data the average floral area per floral unit for each plant species (Williams *et al.* 2015). This average floral area per floral unit was multiplied by the number of open floral units in each plot each week in order to calculate the floral area per plot. We defined the peak flowering week for each plant species as the week number of the year that was centered on the three consecutive weeks having the highest floral area. Plant species were also placed into three flower types: actinomorphic, composite or zygomorphic flowers. Plant species in the families Fabaceae, Lamiaceae, Plantaginaceae and Scrophulariaceae had zygomorphic flowers (n=11) that either had deep corollas or required flower handling to access resources. Plant species within Asteraceae had composite flowers (n=11) with short corollas, resulting in accessible resources split between many small flowers. Remaining plant species had actinomorphic flowers, which generally offered accessible resources with a lower degree of resource splitting compared to the composite flowers. Common names, flowering phenologies, families and traits for each plant species are listed in Tables S1-S2.

Wild bees and honey bees. To determine wild bee and honey bee attractiveness we sampled all plots with open flowers weekly between 0600-1730 hours when temperatures were at least 15 degrees Celsius, wind was low (3.5 m/s or less) and the sky was at least partly sunny or brightly overcast. To

control for potential diurnal patterns in bee visitation to flowers, each flowering plot was sampled twice each week with the first 30 s generally being in the morning and the second 30 s generally being in the afternoon of the same day. However, this sometimes varied depending on the season and focal plant species. For example, both weekly 30 s observations for *Madia elegans* and *Oenothera elata* were conducted early in the same day, because flowers close in the late morning. During each 30 s observation, the number of honey bees visiting flowers were counted. We caught any wild bees visiting flowers with a hand net during the same 30 s. We paused the observation time for handling specimens caught. Any wild bees escaping the net were noted and are included in analyses as undetermined wild bees. Each bee present or entering and visiting flowers within the plot was counted as a new individual. Any honey bees that left the plot, or wild bees that escaped the net, and then returned to the plot again during the observation might therefore have been counted twice. Our sampling time per plot was limited due to the large total number of plots sampled. Because managed bumble bees that were part of another experiment were present at the study site in 2015 (see above), bumble bees were not collected in 2015. Instead they were identified directly in the field, either to genus or species depending on observer. Netted wild bee specimens were determined to species, or the lowest taxonomic level possible, in the laboratory. In analyses, we only use honey bee observation data and wild bee netted specimen data from the three-week peak flowering period (defined above) of each plant species. This resulted in a standardised sampling effort for each plant species that also matched the coverage for herbivore, predator and parasitic wasp data (see below). Data from the two 30 s observations each week in each plot and the three weekly observations per plot in each year were summed before analysis.

Herbivores, predators and parasitic wasps. To determine herbivore, predator and parasitic wasp attractiveness we vacuum sampled all plots with open flowers weekly for 30 s between 0730-1700 hours using a modified leaf vacuum (Stihl, Norfolk, VA, USA). Vacuuming targeted flowers, but included upper vegetative parts of the plants close to flowers. Arthropods were collected in one-gallon fine mesh paint strainer bags (Trimaco, Morrisville, NC, USA) placed over the intake of the vacuum.

We vacuum sampled either directly after bee observations were completed, or on the following day using the same weather criteria as for the bee observations. Vacuum samples were frozen for later processing in the laboratory. We only processed samples from the three-week peak flowering period (defined above) of each plant species. Taxonomic identification of arthropods in vacuum samples was focused on identifying three broad functional groups: herbivores, predators and parasitic wasps. The taxonomic rank to which specimens were identified was typically to family. This varied, however, from the order to species level, depending on the variation of feeding habits within taxa, and our capacity to identify specimens from multiple arthropod orders. We classified arthropods in clades with mainly plant feeding habits as herbivores, and arthropods in clades with mainly predatory feeding habits as predators. The most common arthropods not classified into any of our functional groups were taxa with omnivorous, scavenging or unknown feeding habits within Diptera, Coleoptera, Miridae and Berytidae (for specification of which taxa within these orders and families we considered, see results). Parasitic wasps were only identified to a single taxonomic unit: Hymenoptera (Parasitica). Life stages considered for each taxa are specified in the results section. The three weekly samples per plot in each year were summed before analysis.

Statistical analyses. We analyzed data in SAS 9.4 for Windows (SAS Institute Inc., Cary, NC, USA). Data transformations described were performed to achieve approximately normal distribution of model residuals, which was verified by inspections of residual plots.

Attractiveness across plant species. We analysed the number of wild bees, honey bees, herbivores, predators and parasitic wasps summed per plot and year in generalised linear mixed models (PROC GLIMMIX) with plant species and year as fixed factors, and block as a random factor. The ln-transformed number of weekly samples was included as an offset so that the unit of the response variable became number of individuals per 60 s of observation for wild bees and honey bees, and per 30 s of vacuum sampling for herbivores, predators and parasitic wasps. Adaptive quadrature was used as estimation method to facilitate model convergence. Means and standard errors on the scale of data were derived using the ilink option. We did not follow up overall significant effects of plant species

with any post hoc pairwise comparisons. This was because our dataset had a high number of potential pairwise comparisons between plant species that each had limited statistical power.

Predictors of plant species attractiveness. We ran general linear models (PROC GLM) with the mean number of wild bees and honey bees (log10 [x+0.05] transformed), and herbivores, predators and parasitic wasps (log10 transformed) per plant species as estimated from the mixed model described above as response variables. By using model estimated means as the response variables, we focus our analyses on variation between and not within plant species in the predictors (van de Pol & Wright 2009), and account for unbalanced sampling effort, e.g., that not all plant species were sampled in both years. Predictor variables were floral area (log10-transformed), peak flowering week and flower type for each plant species. A single estimated mean floral area and peak flowering week per plant species was obtained by adding these as response variables in the mixed model described in the previous paragraph, assuming normal distribution. However, because peak flowering week was determined at the plant species level each year, and not individually for each block, the model that predicted peak flowering week used data summarized per plant and year and did not have any block effect. A quadratic effect of bloom period was also tested and was retained in final models if significant. Floral area and peak flowering week were not collinear (Pearson correlation; r=0.16, p=0.30, variance inflation factor = 1.03), but flower types differed in bloom period (ANOVA; $F_{2,40}$=5.71, p=0.0066) with composite species blooming later than species with actinomorphic flowers (Fig S1). Flower types also differed in floral area (ANOVA; $F_{2,40}$=5.04, p=0.011), with species with zygomorphic flowers having a lower floral area than species with composite flowers (Fig. S1). We therefore always tested the effect of flower type with floral area and peak flowering week included in the model.

Covariation across arthropod functional groups. To test if arthropod functional group abundances co-varied across plant species we ran pairwise correlation tests (PROC CORR). Input data were the model estimated mean number of wild bees, honey bees, herbivores, predators and parasitic wasps for each plant species.

Results

In total we sampled 908 wild bees, 5,209 honey bees, 25,804 herbivores, 8,009 predators and 2,827 parasitic wasps. *Halictus ligatus* Say and *Bombus vosnesenskii* were the most common wild bees (Table S3), aphids (Aphididae), hoppers (Auchenorrhyncha) and seed bugs (Lygaeidae) were the most common herbivores, and minute pirate bugs (Anthocoridae) and spiders (Araneae) were the most common predators (Table S4). All arthropod functional groups were sampled in higher numbers in 2015 compared to in 2016 (wild bees: $F_{1, 241}$=55.17, p<0.00010; honey bees: $F_{1, 241}$=13.83, p<0.0010; herbivores: $F_{1, 240}$=19.76, p<0.00010; predators: $F_{1, 240}$=207.74, p<0.00010; parasitic wasps: $F_{1, 240}$=41.59, p<0.00010). Total floral area across all plant species in the experiment over the sampling seasons is shown in Figure S2.

Attractiveness across plant species. Attractiveness varied across plant species for all arthropod functional groups (wild bees: $F_{42, 241}$=5.23, p<0.00010; honey bees: $F_{42, 241}$=10.03, p<0.00010; herbivores: $F_{42, 240}$=7.41, p<0.00010; predators: $F_{42, 240}$=16.16, p<0.00010; parasitic wasps: $F_{42, 240}$=6.97, p<0.00010). Attractiveness of all plant species for each arthropod functional group is presented in Table 1 and Figure S3.

Predictors of plant species attractiveness. The abundances of honey bees, predators and parasitic wasps were all positively affected by floral area, with a nonsignificant trend in the same direction for wild bees (Fig. 1f, 1g, 1i, 1j, Table 2). Later bloom period was associated with fewer parasitic wasps (Fig 1e, Table 2). Herbivores were not affected by either floral area or bloom period (Fig. 1c, 1h, Table 2).

Actinomorphic flowers were more attractive than composite flowers to honey bees, while composite flowers were more attractive than actinomorphic flowers to parasitic wasps (Fig. 2b, 2e, Table 2). Other arthropod groups showed no significant attraction to either flower type (Fig. 2, Table 2)

Covariation across arthropod functional groups. Herbivore, predator and parasitic wasp abundances were all positively correlated across plant species (Fig. 3). Honey bee abundance was negatively correlated to herbivore abundance (Fig. 3).

Discussion

Recommendations of which plant species to use to support beneficial arthropods are often based on personal experience and opinion rather than empirical data (Garbuzov & Ratnieks 2014), resulting in an unclear evidence base for the recommendations. Here we address this gap with a data-driven approach that assessed the attractiveness of plants native to California to several functionally important arthropod groups. We expand the list of California native plants that previously have been assessed for wild bee and honey bee attractiveness (Frankie *et al.* 2005), and add information regarding arthropod groups which are of importance for pest management. Detailed recommendations of which plant species to use to support functionally important arthropods based on data presented here will depend on the crop targeted (e.g., spring flowering versus summer flowering) and the relative importance of supporting different groups of functionally important arthropods. Recently, tools for selecting plants native to California to use in pollinator restoration mixes have been developed (M'Gonigle *et al.* 2017; Williams & Lonsdorf 2018). With the data presented here such selection tools can be extended to also consider arthropod natural enemies and herbivores.

Plant species with a higher floral area attracted greater numbers of honey bees, predators and parasitic wasps, and there was a nonsignificant trend in the same direction for wild bee abundance. Thus, floral area, measured here as the combination of flower number and flower size within a fixed plot area (i.e., floral display density), emerges as a simple metric that can be used for plant selection as it predicts the abundances of several groups of beneficial arthropods. Although these results in part are similar to those of Fiedler and Landis (2007b) and Tuell *et al.* (2008), they also differ in several aspects. First, we found that floral area predicted honey bee abundance more strongly than wild bee abundance, whereas Tuell *et al.* (2008) found that floral area predicted wild bee but not honey bee abundance.

This discrepancy may be due to the fact that our bee community was more strongly dominated by honey bees, and to a lesser extent by wild bumble bees, which might have shifted interspecific competition and floral choice (Roubik & Villanueva-Gutierrez 2009) between the two groups of bees. Second, we found that attractiveness to parasitic wasps generally was highest for plant species flowering early in the season and then declined on later flowering species, whereas Fiedler and Landis (2007b) found the opposite for chalcid parasitic wasps. Our result might have been driven by parasitic wasp flower visitation peaking in late spring (Fig. 2e), when total flower abundance reaches its maximum in natural habitats in California's Mediterranean climate (e.g., Williams, Regetz & Kremen 2012).

Honey bees preferred actinomorphic over composite flowers. The dispersed resources of multi-flowered composites might be more energetically demanding to harvest compared to larger single flowers (Carvalheiro *et al.* 2014), especially for a generalist and relatively large species like the honey bee. Composite flowers attracted higher numbers of parasitic wasps compared to actinomorphic flowers. High attraction of parasitic wasps to Asteraceae has been previously reported (Fiedler & Landis 2007a, b), despite their narrow and, from the perspective of parasitic wasps, relatively deep corollas that can restrict their access to nectar (e.g., Wäckers 2004). It has been suggested that nectar pooling may explain this pattern (Fiedler & Landis 2007b); however, we did not measure standing nectar levels within Asteraceae florets. Flower type did not explain wild bee attractiveness. We recommend that additional floral traits, such as quantity and quality of nectar and pollen (Vaudo *et al.* 2015), be included in future studies as they may better explain floral visitation patterns by wild bees, which often are more specialized flower visitors that also can harvest less accessible nectar and pollen. Furthermore, the honey bee is a single species, but our wild bee category consisted of a large set of species with diverse morphologies and life histories. This means that the overall lack of response to floral traits found here for all wild bees combined, does not preclude floral area or flower type as important predictors of plant attractiveness for individual bee species or species groups. Herbivores did not respond to any of the traits tested. Many herbivores in the most common groups, like aphids (Aphididae) and hoppers (Auchenorrhyncha), were probably vacuumed from underneath

or vegetative parts around flowers rather than directly from flowers, and this likely explains why the flower characteristics tested not were important predictors of their abundance.

The positively correlated abundances of herbivores, predators and parasitic wasps across plant species might have been caused by shared mechanisms of attraction to plants, or by attraction of predators and parasitic wasps to plant species that hosted the largest numbers of their herbivore prey. The two explanations are not mutually exclusive. The fact that predator and parasitic wasp abundances were positively correlated to both floral area and herbivore abundance (which in itself was unrelated to floral area) suggests that both plant and herbivore cues are important for natural enemy attraction to plants. Our results suggest that resource plantings for natural enemies need to consider the risk of herbivore attraction, especially for generalist herbivores that also may damage crops (e.g., McCabe, Loeb & Grab 2017). More unexpectedly, the sets of plant species that supported the highest abundances of herbivores also showed lower honey bee attractiveness. As the most common herbivore groups were sap-sucking insects like aphids and leafhoppers that do not directly damage flowers, the negative correlation between insect herbivore and honey bee abundances might instead have been driven by indirect negative effects on floral resources through decreased overall plant quality.

We acknowledge some important limitations of the approach used here. First, it is not straightforward to classify arthropods into groups that either are functionally 'desirable' (e.g. pollinators) or 'undesirable' (e.g., herbivores) in agroecosystems (see Saunders *et al.* 2016). The most important pest species among the herbivores will vary heavily depending on what crops are targeted. For example, the high herbivore score for narrowleaf milkweed *A. fascicularis* was driven by oleander aphids (*Aphis nerii* Boyer de Fonscolombe), which are not known as crop pests in California. Limitations of this type can to some extent be addressed by considering species-specific interactions between plant visitors and candidate resource plants (e.g., Russo *et al.* 2013), which was something that was beyond the scope of our study. A second limitation is that performance of individual plant species might have been affected by the local environment, such as the soil type and arthropod species pool, at our study site. Most promising plant species identified here should, therefore, ideally be further tested in

multiple locations, both in monospecific plots (see Rowe et al. *in press*) as well as in plant mixes across a variety of local environments. However, the analyses which explored plant traits that explain arthropod attractiveness and arthropod correlations in attractiveness used the 43 plant species as replicates, and are thus more robust against lack of replication at the site level. Finally, it is important to test plants that are found to be attractive to beneficial arthropods with the screening approach used here with additional on-farm trials, in order to assess whether high attractiveness also translates into higher pollination and pest control services delivered to nearby crops.

Our screening of the attractiveness of native plants for five functionally important groups of arthropods indicates that research on habitat plantings for arthropods benefits from considering multiple potential ecosystem services and disservices. This multifunctional approach is especially valuable for the case of pollination, biological pest control and pest damage, which are delivered by closely related or even partially overlapping groups of arthropods. Habitat management directed at one of these functional groups may, as we illustrate, also affect other functional groups. Multifunctional habitat management, therefore, must further explore how synergies between pollination and pest control delivery can be maximized while tradeoffs are minimized.

Data accessibility

Data available via the Dryad Digital Repository https://doi:10.5061/dryad.c92k731 (Lundin, Ward, & Williams, 2018).

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Supporting Information

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

Appendix S1. Plant establishment and maintenance.

Figure S1. Peak flowering week and floral area in relation to flower types.

Figure S2. Total floral area in the experiment across the season.

Figure S3. Attractiveness of all plant species for each arthropod functional group.

Table S1. Plant common names and flowering phenologies.

Table S2. Additional plant characteristics.

Table S3. Wild bee and honey bee taxa.

Table S4. Herbivore, predator and parasitic wasp taxa.

Figure 1. Influence of peak flowering week and floral area (cm² per m², log10-transformed) on attractiveness of 43 plant species to wild bees (a, f) honey bees (b, g), herbivores (c, h), predators (d, i) and parasitic wasps (e, j). The unit is number of individuals per 60 s of observation (log10 [x+0.05] transformed) for wild bees and honey bees, and number of individuals per 30 s of vacuum sampling (log10 transformed) for herbivores, predators and parasitic wasps. Solid lines indicate significant slopes and dashed lines indicate non-significant slopes. Note that the y-axes ranges vary by arthropod functional group.

Figure 2. Influence of flower type (Acti = actinomorphic, Comp = composite or Zygo = zygomorphic) on wild bee (a), honey bee (b), insect herbivore (c), arthropod predator (d) and parasitic wasp (e) attractiveness. For definitions of flower types see main text. The unit is number of individuals per 60 s of observation (log10 [x+0.05] transformed) for wild bees and honey bees, and number of individuals per 30 s of vacuum sampling (log10 transformed) for herbivores, predators and parasitic wasps. Groups with different letters are significantly different (p<0.05) based on pairwise post-hoc comparisons with Tukey adjustment.

Figure 3. Correlation matrix with r and p values for pairwise correlations between arthropod functional groups on 43 plant species shown in the upper triangle, and correlation plots shown in the lower triangle. The unit is number of individuals per 60 s of observation (log10 [x+0.05] transformed)

for wild bees and honey bees, and number of individuals per 30 s of vacuum sampling (log10 transformed) for herbivores, predators and parasitic wasps. Solid lines indicate significant slopes and dashed lines indicate non-significant slopes.

Table 1. Attractiveness of 43 plant species for five functional groups of arthropods. For each group, the model estimated mean number of arthropods per 60 s of observation (wild bees and honey bees) or per 30 s of vacuum sampling (herbivores, predators and parasitic wasps) is presented along with the standard errors (SE) of the means. Plant species are sorted in order of peak bloom month, and then alphabetically within each month.

Plant species	Wild bees	SE	Honey bees	SE	Herbivores	SE	Predators	SE	Parasitic wasps	SE
Amsinckia intermedia	0.21	0.11	2.59	0.93	36.94	13.71	3.81	0.92	5.21	1.26
Calandrinia menziesii	0.62	0.26	0.19	0.12	63.79	24.82	1.55	0.45	2.81	0.77
Nemophila maculata	0.04	0.04	5.01	1.74	5.25	1.95	1.49	0.40	0.65	0.22
Nemophila menziesii	0.15	0.09	4.68	1.73	11.15	4.35	3.44	0.89	3.12	0.83
Phacelia ciliata	1.63	0.56	8.31	3.25	3.18	1.38	0.33	0.15	1.82	0.56
Achillea millefolium	0.60	0.21	0.34	0.17	76.73	27.88	38.93	8.67	16.81	3.87
Collinsia heterophylla	0.38	0.15	2.59	0.94	15.56	6.06	1.55	0.45	0.95	0.32
Fagopyrum esculentum	0.00	0.00	0.18	0.11	13.75	5.33	2.06	0.59	1.34	0.41
Lasthenia fremontii	0.72	0.26	0.51	0.22	40.01	14.52	3.30	0.82	4.96	1.20
Lasthenia glabrata	0.77	0.32	0.10	0.08	85.23	36.04	1.38	0.45	7.67	2.12
Limnanthes alba	0.50	0.19	6.08	2.12	34.38	12.60	2.15	0.56	2.44	0.63
Lupinus microcarpus densiflorus	1.40	0.44	1.21	0.49	18.59	7.21	13.37	3.25	4.29	1.12
Lupinus succulentus	0.80	0.35	0.31	0.20	16.57	8.50	12.66	4.05	1.04	0.42
Phacelia californica	1.77	0.59	16.31	6.44	13.08	5.62	1.63	0.52	1.32	0.45
Phacelia campanularia	0.07	0.07	6.01	3.36	2.21	1.36	0.28	0.16	0.98	0.46
Phacelia tanacetifolia	1.16	0.35	16.62	5.67	26.97	9.96	1.39	0.39	2.58	0.69
Salvia columbariae	0.05	0.05	7.82	3.08	6.41	2.75	4.07	1.15	1.70	0.55
Sphaeralcea ambigua	1.09	0.34	5.37	1.85	22.66	8.28	10.71	2.46	4.57	1.12
Trifolium fucatum	0.05	0.05	0.00	0.01	16.99	8.72	4.67	1.54	2.42	0.87
Trifolium gracilentum	0.00	0.00	0.15	0.11	34.40	14.35	3.87	1.09	4.46	1.27
Antirrhinum cornutum	1.19	0.56	1.59	0.94	1.45	0.92	0.34	0.19	0.81	0.39
Clarkia purpurea	0.04	0.04	4.93	1.71	12.89	4.73	8.04	1.88	3.64	0.91
Clarkia unguiculata	0.99	0.31	46.24	15.41	6.24	2.29	6.60	1.55	2.16	0.57
Clarkia williamsonii	0.23	0.11	16.27	5.46	9.32	3.41	26.16	5.87	3.15	0.80
Eriophyllum lanatum	2.26	0.64	0.85	0.34	37.48	13.70	22.24	5.01	8.42	1.98
Eschscholzia californica	0.36	0.15	7.93	2.71	12.94	4.73	3.16	0.80	4.55	1.11
Monardella villosa	0.74	0.25	4.84	1.70	9.15	3.37	6.69	1.60	1.13	0.34
Scrophularia californica	1.57	0.47	6.42	2.24	5.73	2.14	1.03	0.31	1.59	0.44
Asclepias eriocarpa	0.05	0.05	0.74	0.33	112.64	45.21	6.25	1.66	0.15	0.09

Asclepias fascicularis	0.37	0.17	3.46	1.29	198.60	77.96	4.49	1.19	1.16	0.37
Camissoniopsis cheiranthifolia	0.20	0.14	3.84	2.18	28.47	16.76	9.12	3.38	5.77	2.23
Eriogonum fasciculatum	1.58	0.54	8.81	3.46	8.04	3.43	26.50	6.87	3.12	0.91
Gilia capitata	0.86	0.31	15.36	5.55	2.52	1.02	16.91	4.09	1.42	0.42
Grindelia camporum	4.98	1.46	3.55	1.33	29.93	11.57	13.90	3.42	4.89	1.26
Helianthus annuus	2.11	0.69	5.97	2.19	19.51	7.58	5.58	1.47	2.40	0.66
Lupinus formosus	0.34	0.15	0.27	0.15	3.88	1.56	4.75	1.26	0.82	0.31
Malacothrix saxatilis	0.71	0.29	3.80	1.53	6.98	2.99	1.90	0.60	1.28	0.43
Oenothera elata	0.27	0.17	1.25	0.76	31.87	19.15	1.30	0.54	1.06	0.49
Helianthus bolanderi	3.02	1.00	6.29	2.50	32.15	13.43	17.04	4.52	5.55	1.53
Helianthus californicus	0.65	0.23	0.26	0.13	2.43	0.94	0.78	0.25	0.81	0.25
Madia elegans	0.00	0.00	11.35	3.87	3.63	1.36	0.83	0.28	1.78	0.48
Trichostema lanceolatum	5.12	1.50	0.83	0.35	17.37	6.82	16.13	4.00	2.54	0.72
Heterotheca grandiflora	1.59	0.50	1.13	0.46	39.93	15.49	2.15	0.64	1.24	0.39

Table 2. Statistical test results from general linear models with F values, degrees of freedom (d.f.) and p-values for the effects of bloom period, bloom period squared, floral area and flower type on five arthropod groups (wild bees, honey bees, insect herbivores, arthropod predators and parasitic wasps). Statistically significant results (p<0.05) are indicated in bold.

	Bloom period			Bloom period squared			Floral area			Flower type		
	F	d.f.	p	F	d.f	p	F	d.f.	p	F	d.f.	p
Wild bees	2.96	1,38	0.093	0.20	1,37	0.65	3.85	1,38	0.057	0.81	2,38	0.45
Honey bees	2.55	1,38	0.12	1.39	1,37	0.25	8.10	1,38	**0.0071**	6.49	2,38	**0.0038**
Herbivores	0.15	1,38	0.70	0.29	1,37	0.59	1.02	1,38	0.32	1.91	2,38	0.16
Predators	0.83	1,38	0.37	2.38	1,37	0.13	5.60	1,38	**0.023**	0.67	2,38	0.52
Parasitic wasps	8.56	1,38	**0.0058**	0.09	1,37	0.77	5.62	1,38	**0.023**	3.74	2,38	**0.033**

Axis labels:

- a–e (left column): Peak flowering week (x-axis, 10 to 40)
- f–j (right column): Floral area (x-axis, 1 to 4)
- a, f: Wild bees (-1.6 to 0.8)
- b, g: Honey bees (-1.4 to 1.8)
- c, h: Herbivores (0 to 2.4)
- d, i: Predators (-0.6 to 1.0)
- e, j: Parasitic wasps (-1.0 to 0.6)

Wild bees   r=0.18 p=0.25   r=0.07 p=0.67   r=0.24 p=0.13   r=0.25 p=0.11

Honey bees   r=-0.34 **p=0.025**   r<0.01 p=0.99   r=-0.04 p=0.79

Herbivores   r=0.37 **p=0.016**   r=0.34 **p=0.024**

Predators   r=0.45 **p=0.0027**

Parasitic wasps