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Non-native honey bees disproportionately dominate the most abundant floral resources in a biodiversity hotspot

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Most plant–pollinator mutualisms are generalized. As such, they are susceptible to perturbation by abundant, generalist, non-native pollinators such as the western honey bee (*Apis mellifera*), which can reach high abundances and visit flowers of many plant species in their expansive introduced range. Despite the prevalence of non-native honey bees, their effects on pollination mutualisms in natural ecosystems remain incompletely understood. Here, we contrast community-level patterns of floral visitation by honey bees with that of the diverse native pollinator fauna of southern California, USA. We show that the number of honey bees visiting plant species increases much more rapidly with flower abundance than does that of non-honey bee insects, such that the percentage of all visitors represented by honey bees increases with flower abundance. Thus, honey bees could disproportionately impact the most abundantly blooming plant species and the large numbers of both specialized and generalized pollinator species that they sustain. Honey bees may preferentially exploit high-abundance floral resources because of their ability to recruit nest-mates; these foraging patterns may cause native insect species to forage on lower-abundance resources to avoid competition. Our results illustrate the importance of understanding foraging patterns of introduced pollinators in order to reveal their ecological impacts.

1. Introduction

Given that interactions between plants and pollinators are often highly generalized, they are susceptible to perturbation by generalist, non-native pollinators [1,2]. As with invasions in general [3], the non-native species most likely to disrupt interactions between plants and pollinators include those that achieve high levels of abundance or that have a large *per capita* ecological effect. For example, non-native plant species that reach high abundance can depress reproduction of native plants through competition for pollinators (e.g. [4,5]). On the other hand, factors influencing *per capita* ecological effect reflect not only invader traits but also how those traits compare to those of native species [6]. For instance, eusocial yellowjacket wasps introduced to the Hawaiian Islands fundamentally differ from the solitary native insects that visit flowers in this region and negatively impact plant reproduction [7,8].

In this study, we examine how the foraging behaviour of the non-native western honey bee (*Apis mellifera* L.) differs from that of native insects foraging in natural ecosystems. Native to parts of Europe, the Middle East and Africa, the western honey bee (hereafter ‘honey bee’) now occurs widely throughout the New World, Asia and Oceania, where it has been intentionally introduced for honey production and crop pollination [9]. Honey bees often establish feral populations throughout their large introduced range (e.g. [10,11]). Despite the status of *A. mellifera* as a geographically widespread and locally abundant introduced species, the ecological effects of honey bee introductions remain

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incompletely understood [11,12], in part owing to the difficulty in assessing the effects of honey bees on populations of native pollinating insects. However, recent acknowledgement of the potential for negative ecological impacts of honey bee introductions (e.g. [13,14]), and an improved empirical understanding of the ability of honey bees to depress reproduction or population sizes of native pollinating insects [15–18] and to affect plant reproductive success [19,20], demonstrate the clear need for further work evaluating the impacts of this widespread species in natural habitats.

Here, we examine how patterns of visitation between honey bees and other insects vary as a function of flower abundance in coastal sage scrub ecosystems of San Diego County, southern California, USA. Honey bees account for approximately 75% of all floral visitors in coastal sage scrub habitats, one of the highest levels of numerical dominance by honey bees in plant–pollinator interaction networks from natural habitats worldwide [21]. Thus the San Diego region should be instructive with regards to how non-native honey bees impact pollination mutualisms. The San Diego region is also part of a global hotspot of plant and pollinator diversity. San Diego County alone supports over 600 species of native bees [22], a diversity of other pollinating insects, and the highest plant species richness of any county in the United States [23] with insects serving as pollinators of many of these plant species. It thus seems important to clarify how non-native honey bees affect pollination mutualisms in this system.

Besides attaining high local abundance, honey bees differ from most native insect pollinators in coastal sage scrub ecosystems because of their ability to form populous, long-lived colonies and to communicate information about the quality and location of food to nest-mates. These behavioural attributes presumably enable non-native honey bees to differentially exploit high density, or locally abundant resources. By contrast, the great majority of native floral visitors in this region are solitary insects that are unlikely to communicate resource locations to others.

We quantified differences in floral visitation patterns of honey bees and other insects at replicate coastal sage scrub sites across a typical flowering season to address two questions. (i) At the level of the local community of plants and floral visitors, do the numbers of visiting honey bees and non-honey bee insects increase with flower abundance? (ii) At the level of the individual plant species, do the numbers of honey bees and native insect visitors increase with flower abundance? These questions are aimed at discerning the foraging habits of non-native honey bees and how they may differ from those of native insects. Evaluating differences in floral visitation by honey bees and native insects as a function of flower abundance sheds light on the impact of honey bees across the gradient of floral resource availability in space and time, and enables identification of the plant taxa (and their associated pollinators) that may be disproportionately influenced by these impacts.

2. Material and methods

(a) Study system

Floral visitor and flower abundance data were collected in 2016 at 12 different study sites in coastal sage scrub habitat in San Diego County, CA, from late February to July, the peak blooming season [24]. Details about study sites are presented in electronic supplementary material S1 and S2, table S1-1 and figure S2-1, respectively. Coastal sage scrub supports a rich assemblage of largely insect-pollinated plant species, dominated by relatively short-statured drought-deciduous perennial shrubs intermixed with annual forbs and (largely non-native) grasses [24]. Among the 45 insect-pollinated plant species on which we observed floral visitors, the most abundant species vary with time of season and across plots, but often include *Salvia mellifera* Greene, *S. apiana* Jeps., *Eriogonum fasiculatum* Benth., *Malosma laurina* (Nutt.) Nutt. ex Abrams and *Deinandra fasciculata* (DC.) Greene (see electronic supplementary material S1, table S1-2). Including honey bees, we recorded 269 insect taxa (species or morphogroups) with body lengths greater than or equal to 2 mm (the minimum size we could reliably detect) visiting flowers in this study: 167 Hymenoptera (of which 113 were bees), 77 Diptera, 15 Lepidoptera and 10 Coleoptera (see electronic supplementary material S1, table S1-3). For our analyses, visitors were classified as either honey bees or non-honey bee insects. The vast majority of non-honey bee visitors were native insects (see electronic supplementary material S1, table S1-3). Floral visitor surveys were always conducted on warm (greater than 19°C), sunny days (less than 30% cloud cover) to capture the peak activity of flower-visiting insects. Previous work in this region documented that most honey bee foragers in non-agricultural habitats originate from feral, Africanized colonies rather than managed hives [10].

(b) Sampling methods

We employed two approaches to quantify patterns of floral visitation. These differed with respect to the frequency of survey visits, the level of replication, and whether the number of floral visitors was quantified using timed transects or timed observations of a fixed number of flowers of each flowering species. ‘Approach 1’ involved 16 surveys conducted every 4–5 days at a single site to examine patterns of flower abundance and visitation with high temporal resolution. At this site, we established five transects (50 m × 2 m) that were separated from one another by 30–50 m. During each survey, we spent 10–15 min walking the length of each transect and counted all floral visitors observed and what plant species they visited. On each survey day, data were collected for each transect once in the morning (10.00 h–11.30 h) and once in the afternoon (12.30 h–14.30 h) in order to account for diel variation in the activity of different floral visitor taxa. In this approach, the allocation of effort across plant species is proportional to the frequency of plant–pollinator interactions, enabling a direct comparison of the numbers of visiting honey bees and non-honey bee insects across plant species and sampling dates.

‘Approach 2’ involved six surveys conducted approximately every two weeks in 1 ha study plots at 11 additional study sites. In Approach 2, each site visit consisted of 15 repetitions of 1 min timed observations on each insect-pollinated plant species in bloom, and pollinated by insects at least 2 mm in length, within the study plot. Between 09.00 h and 15.00 h, we observed a single patch of conspecific plants for 60 s, counting all floral visitors present as well as those that arrived within this observation period. After 60 s, we moved on to the next patch. Patch sizes were determined by our ability to count floral visitors in our field of view, and thus ranged from a portion of the inflorescences present on a single large shrub (e.g. *Malosma laurina*) to over a hundred individuals for small, annual forbs (e.g. *Deinandra fasciculata*). For each plant species at each study site during a given survey, the same number of flowers were observed in each observation patch. The surveys in Approach 2 were performed as part of a separate study to examine the structure of plant–pollinator interaction networks in our study system, and used equal observation effort for each plant species, the preferred method for constructing empirical pollination networks (see [25]). Nevertheless, data collected using this approach can be used to estimate the relationships between visitor numbers and flower abundances when combined with data on total flower abundances within each site (see below) and are used here to assess the generality of the patterns observed using Approach 1.

For both sampling approaches, we estimated total flower abundance of individual plant species at each site using the same methods. During each survey, we estimated the abundance of all open flowers of each insect-pollinated plant species in transects (Approach 1) or 1 ha study plots (Approach 2). Owing to variation in the floral architectures and abundances of plant species [24], we estimated flower abundance for different plant species using a variety of strategies (see electronic supplementary material S1, table S1-2). Briefly, we counted increasingly larger components of flower abundance (e.g. number of flowers on a branch, number of branches on an individual plant) and then multiplied across all components to obtain estimates of flower abundance at the level of transects (Approach 1) or study plots (Approach 2). We counted 3–6 replicates per component to obtain averages, except for the largest component (for instance, the number of patches of a plant at the transect or plot level), which was counted once.

(c) Statistical analysis

All analyses were conducted in program R (v. 3.5.0 [26]), using packages *lme4* [27], *lmerTest* [28], *psychometric* [29], *reshape2* [30] and *plyr* [31]. For the dataset collected using Approach 1, we constructed a linear mixed model (LMM) to test how the number of visiting honey bees and non-honey bee insects responded to variation in flower abundance. The response variable in this model is the number of individuals of a particular floral visitor type (honey bees or non-honey bee insects) recorded for each plant species during each survey round, summed across all five transects and both morning and afternoon observations. Independent variables treated as fixed factors were floral visitor type (honey bees or non-honey bee insects), the daily flower abundance of each plant species, and the interaction between floral visitor type and flower abundance. Plant species identity and survey round were included as random effects. To determine whether or not plant species identity affected patterns of visitation, we constructed an alternate model without the inclusion of plant species identity as a random effect, and performed a likelihood ratio test to evaluate the significance of plant species identity.

For the dataset collected using Approach 2, the raw numbers of floral visitors do not directly reflect visitation rates because the number of flowers observed per observation patch varied across plant species, study plots, and survey days and because the raw values do not consider the total number of flowers of each species in a plot on a given survey day. Thus, we estimated plot-level numbers of floral visitors for each plant species and floral visitor type on each day as the mean number of visitors of that type counted during a 1 min observation of a focal patch of a plant species, multiplied by the total number of flowers of that species on that day in the plot, and then divided by the number of flowers of that species in a focal patch.

To test for relationships among floral visitor type, the number of floral visitors and flower abundance using these plot-level estimates of the numbers of floral visitors, we constructed an LMM structured similarly to the model described for Approach 1, with the exception that study plot identity was included as an additional random effect. As in Approach 1, we evaluated the effect of plant species identity using a likelihood ratio test. We also used the dataset of Approach 2 to test for differences among taxonomic orders of native insects in their responses to variation in flower abundance (see electronic supplementary material, S3).

In order to examine how the relative numerical dominance of honey bees varies across the range of documented flower abundances, we constructed a generalized linear mixed model with a binomial distribution (link = logit). In short, the outcome of a binomial regression model is based on a binomial distribution of 'successes' versus 'failures' [32], which enables the modelling of proportion data drawn from a population of discrete, binary outcomes. In our case, the response variable is the number of honey bees (successes) versus the number of non-honey bee visitors (failures) recorded for each plant species during each survey round. The independent variable is the daily flower abundance of each plant species (fixed factor; $\log_{10}$-transformed). As with the previous models, random factors included plant species identity, survey round, and study plot identity (for data from Approach 2), and we again evaluated the effect of plant species identity using a likelihood ratio test.

The analyses described thus far quantify patterns of visitation by honey bees and non-honey bee visitors across all plant species present at each study site. To examine the degree to which honey bees and other insect visitors differ in their response to variation in flower abundance within individual plant species, we estimated the slope of the relationship between the number of floral visitors of each type and flower abundance for every plant species individually. These comparisons provide a test of the hypothesis that the number of honey bees visiting a given species will increase with flower abundance at a higher rate compared to that of non-honey bee insects. To compare slopes across a wide range of flower abundances, slope estimates were standardized for each plant species by scaling flower abundances to a mean of zero and standard deviation of one, across all sampling rounds and all study sites. Visitation data for honey bee and non-honey bee visitors were scaled to a common, pooled, mean and standard deviation for each plant species. In order to examine whether plant- and floral visitor-specific slope estimates differed between plants of low versus high flower abundance, standardized slope estimates were used as the response variable in a multiple regression with visitor type (honey bee or non-honey bee), maximum recorded flower abundance ($\log_{10}$ transformed), and their interaction as independent variables. For this analysis, we excluded all plant species for which there were fewer than five data points (one species in Approach 1, 21 species in Approach 2), as well as all plant species for which we recorded zero honey bee or non-honey bee insect visits in at least 80% of data points (four species in Approach 2), since the sign and magnitude of the slope cannot be reliably estimated when there are few non-zero data points.

3. Results

For the data obtained using Approach 1, employed at a single study site, honey bees represented 73% of the 2539 recorded insects visiting 10 plant species. The number of floral visitors increased with overall flower abundance (table 1), but the significant interaction between flower abundance and floral visitor type indicates that the number of visiting honey bees increased with flower abundance to a greater degree than did the number of other visiting insects, which exhibited little variation across the observed range of flower abundances (figure 1*a* and table 1).

The pattern depicted in figure 1*a* was also evident across larger spatial scales. In the dataset obtained using Approach 2, employed at 11 study sites, honey bees made up 73% of the 13 785 recorded insects visiting 45 plant species. Here, as with results from Approach 1, a significant interaction between

Table 1. Significance levels of variables used to evaluate the effects of flower abundance, and where appropriate, visitor type and the interaction between visitor type and flower abundance on the number of floral visitors. Where indicated, plant species identity was included in models as a random variable. Model numbers correspond to figures.

variable	test statistic	*p*-value
Model 1a		
flower abundance	$F_{1,172} = 285.41$	<0.0001
visitor type	$F_{1,160} = 2.20$	0.14
flower abundance × visitor type interaction	$F_{1,160} = 195.36$	<0.0001
plant species identity (random)	$\chi^2_1 = 0$	1
Model 1b		
flower abundance	$F_{1,292} = 420.20$	<0.0001
visitor type	$F_{1,662} = 5.07$	0.025
flower abundance × visitor type interaction	$F_{1,662} = 422.05$	<0.0001
plant species identity (random)	$\chi^2_1 = 2.31$	0.13
Model 2a		
$\log_{10}$(flower abundance)	$z = 10.41$	<0.0001
plant species identity (random)	$\chi^2_1 = 88.59$	<0.0001
Model 2b		
$\log_{10}$(flower abundance)	$z = 16.60$	<0.0001
plant species identity (random)	$\chi^2_1 = 1706.9$	<0.0001
Model 3a	$F_{3,14} = 3.96$	0.031
$\log_{10}$(max flower abundance)	$t = 2.50$	0.025
visitor type	$t = 2.82$	0.014
$\log_{10}$(max flower abundance) × visitor type interaction	$t = 3.13$	0.0074
Model 3b	$F_{3,36} = 6.86$	0.0009
$\log_{10}$(max flower abundance)	$t = 2.13$	0.04
visitor type	$t = 2.04$	0.049
$\log_{10}$(max flower abundance) × visitor type interaction	$t = 3.13$	0.0034

flower abundance and floral visitor identity indicates that honey bees increased in abundance at a higher rate than did non-honey bee insects in response to increasing flower abundance (figure 1*b* and table 1). In both datasets, plant species identity was not a significant predictor of the number of floral visitors (table 1). While the numbers of both visitor types increased significantly with flower abundance, honey bees are estimated to have increased around 12–13 times as fast as non-honey bee visitors (see electronic supplementary material S1, table S1-4). The responses of non-honey bee visitors to flower abundance did not differ across taxonomic orders of insects (see electronic supplementary material, S3).

Although honey bees constituted 73% of recorded floral visitors overall, their proportional representation significantly differed across the range of flower abundances in datasets from both approaches (table 1). The percentage of visitors represented by honey bees tended to be low when plant species were not blooming abundantly, but was generally high on plant species that reached the highest estimated flower abundances (figure 2*a*,*b*). The proportional representation of honey bees differed significantly across plant species in datasets from both approaches (table 1).

The pattern of increasing numerical dominance by honey bees with increasing flower abundance was broadly consistent across individual plant species for data collected using both approaches (figure 3). For plants that never achieved high flower abundance (maximum recorded abundance less than 10^4), there was little pattern as to whether or not honey bees or non-honey bee insects increased faster with flower abundance (figure 3). But for plants that attained higher flower abundances (greater than 10^4), honey bee visitors usually increased at greater rates than did non-honey bee visitors. The one exception to this trend (see arrows, figure 3) was *Cryptantha intermedia* (A. Gray) Greene, for which visits by non-honey bee insects sharply increased with flower abundance while honey bee visitation was uniformly low and did not increase with flower abundance. Despite this exception, multiple regression analyses of plant-specific standardized slope estimates for both datasets revealed that the slope of the relationship between the number of visitors and flower abundance was overall higher for honey bees than for non-honey bee insects (table 1), and that a significant interaction was evident between visitor type (honey bees and non-honey bee insects) and maximum recorded flower abundance (table 1). Across plant species, maximum flower abundance is strongly and positively related to the range of flower abundance (i.e. the difference between maximum and minimum recorded flower abundance), such that plant species with the highest maximum flower abundance also spanned the largest range in flower abundance ($R^2 > 0.99$ for linear regression between $\log_{10}$-transformed maximum and range of flower abundance for both approaches).

4. Discussion

To our knowledge, this study describes the first community-level analysis that relates visitation by non-native honey bees and native insects to variation in flower abundance across space and time. The number of visiting honey bees strongly increased with flower abundance, while the number of other insects exhibited little variation across the same six order of magnitude span of flower abundances. Honey bees were thus not only frequent visitors to plants in coastal sage scrub ecosystems (73% of all visitors), but their numerical dominance reached its highest levels on plant species that produced the most flowers. Flower abundance clearly drives patterns of differential resource use by honey bees versus native floral visitors. Using two different methodological approaches (table 1, Model 1a–b), plant species identity was a not a significant predictor of the number of floral visitors recorded once flower abundance was accounted for. For the proportion of visitors represented by honey bees, plant species identity was a highly significant factor alongside flower abundance (table 1, Model 2a–b), suggesting that

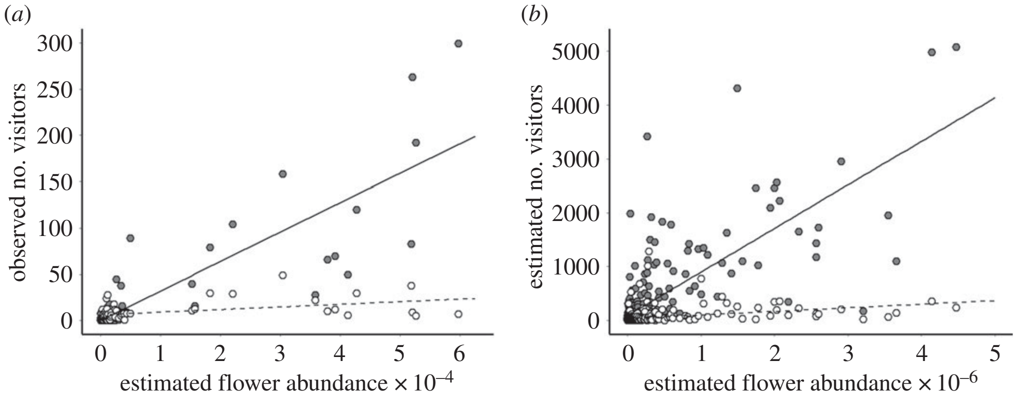

Figure 1. Number of floral visitors versus estimated flower abundance for honey bees (filled symbols; solid regression lines) and non-honey bee insects (open symbols; dashed regression lines). Panels show (*a*) numbers of floral visitors observed in standardized transects in Approach 1, and (*b*) estimated numbers of floral visitors observed in 1 ha study plots in Approach 2. Each data point indicates the number of floral visitors of a given type (honey bees or non-honey bee insects) observed on flowers of a particular plant species during a single day of observation at each site. See table 1 (Model 1a, Model 1b) for significance of independent variables used in this analysis.

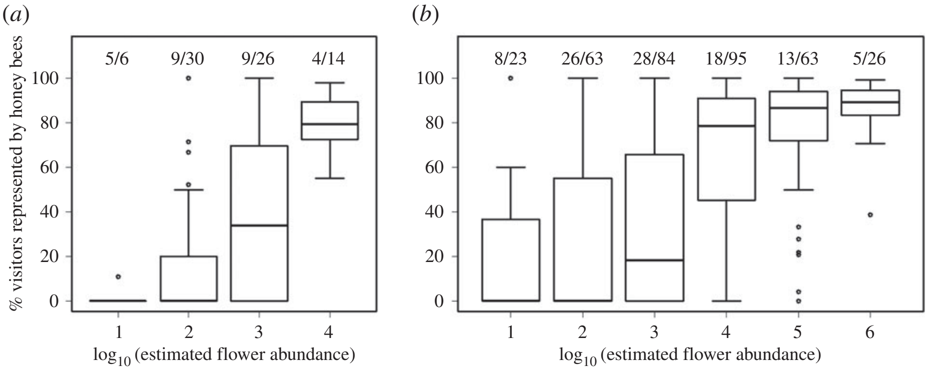

Figure 2. The percentage of observed floral visitors represented by honey bees across orders of magnitude of estimated flower abundance for data collected using (*a*) Approach 1 and (*b*) Approach 2. To aid visualization, plants that have estimated daily recorded flower abundances within the same order of magnitude are binned together into a single boxplot. Numbers above each boxplot indicate the number of plant species represented, followed by the number of data points in each bin. Data points in this analysis represent visitors documented on flowers of a given plant species during a single day of observation at each site; thus some plant species are represented in multiple bins. Boxes show central 50% of data and bold horizontal lines represent the median; whiskers extend from the quartiles to 1.5 × the interquartile range (or most extreme values of data, whichever is closest to median); circles depict outliers, if any. See table 1 (Model 2a, Model 2b) for patterns of significance of independent variables used in this analysis.

species-specific traits may play some role in determining floral visitor preferences, particularly for low-abundance plant species (figure 3). For individual plant species, those that produced the most flowers generally exhibited visitation patterns that mirrored those of the community as a whole: honey bees generally increased faster with increasing flower abundance than did non-honey bee insects (figure 3).

Methods used to estimate flower abundances varied among plant species (see electronic supplementary material S1, table S1-2), and we did not attempt to quantify interspecific variation in the quality or quantity of pollen or nectar per flower. Despite these limitations, estimated flower abundances strongly predicted variation in the number of visiting honey bees, implying that our methods captured ecologically relevant variation in floral resource availability. One reason that our estimates of flower abundance appear meaningful may be that many of the plant species in coastal sage scrub produce large clusters of small flowers that attract numerous insect taxa [33]. For example, *Deinandra fasciculata*, a common annual composite forb in this system, attracts 70 different taxa of floral visitors [34]. The preponderance of generalist plant species in coastal sage scrub may help to explain why flower abundance, rather than plant species identity, emerged as the strongest predictor of variation in floral visitors.

The near absence of a response by non-honey bee visitors to increasing flower abundance requires explanation. Given that honey bees have been present in California since the 1850s [35], no baseline data exist bearing on patterns of floral visitation or abundances of native insects prior to the introduction of honey bees. Currently, most non-honey bee floral visitors in this system are solitary insects, while bumble bees and yellowjacket wasps, the only native floral visitors thought to coordinate long-distance foraging via recruiting nest-mates [36–38], make up only 0.2% of floral visitors (see electronic supplementary material S1, table S1-3). Perhaps assemblages consisting of primarily solitary insects, each operating independently within a limited foraging range, lack the ability to collectively respond within a season to fluctuations in flower abundances.

At least some studies that focused on single plant species, however, find that visitation by non-honey bee insects increases strongly either with the size of the patch [39,40] or the size of the floral display [41]. In the present study, we obtained evidence that the number of non-honey bee visitors increased strongly with flower abundance for some low-

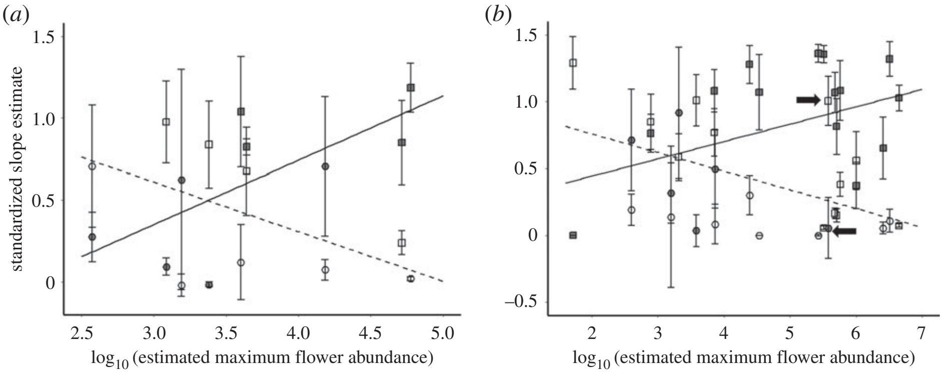

Figure 3. Standardized slope estimates from regressions of numbers of floral visitors versus flower abundance for individual plant species. Slopes for each pollinator type on each plant species are then plotted and regressed on estimated maximum recorded flower abundance of each plant species for data collected using (*a*) Approach 1 and (*b*) Approach 2. Data for honey bees are depicted as filled symbols and solid regression lines; data for non-honey bee insects are depicted as open symbols and dotted regression lines. Slopes significantly different from zero are depicted as squares; slopes not different from zero are depicted as circles. Error bars show 1 standard error. Data pertaining to *Cryptantha intermedia* are identified with arrows. See table 1 (Model 3a, Model 3b) for patterns of significance of independent variables used in the regression analysis.

abundance plant species (figure 3), as well as for *Cryptantha intermedia*, which flowered abundantly (nearly 10^6 ha^{-1}) in many plots (figure 3). On low-abundance plant species, there may be reduced competition with honey bees, which tend to ignore these plants. However, and perhaps instructively, non-honey bee visitors to *C. intermedia* strongly increased with increasing flower abundance, with a slope similar in magnitude to those exhibited by honey bees visiting other abundantly flowering plant species (figure 3). By contrast, *C. intermedia* was the only abundantly flowering plant species for which numbers of honey bees were uniformly low across the range of flower abundances, perhaps because honey bees struggle to access floral rewards through its extremely narrow floral tube.

Rather than being unable to respond to abundant floral resources, numbers of native insects may not increase in parallel with honey bees because they alter their foraging behaviour in response to the activities of abundant honey bees. For example, non-honey bee floral visitors have been known to switch from abundant and presumably high-quality food resources to alternative species when local densities of honey bee foragers increase [42,43]. In our system, it may be possible to examine changes in the foraging behaviours of non-honey bee insects through the use of targeted removals of honey bee foragers from focal patches of plant species [34,44].

In addition to the possibility that honey bees alter the foraging behaviour of non-honey bee insects, native floral visitor populations in our system may currently be reduced in size due to competition from honey bees. Honey bees harvest large amounts of pollen and nectar to support their large, long-lived colonies consisting of individuals that are themselves large by comparison to most native floral visitors [13]. Forces that currently limit population sizes of native floral visitors are largely unknown, though floral resource limitation appears to be among the best-documented factors [45], and there is evidence that non-honey bee abundance is negatively correlated with honey bee abundance in the previous year [46]. In particular, honey bees may exert especially strong competitive pressure on other highly eusocial species such as bumble bees [16,17], given their high niche overlap in terms of diet breadth, phenology, and foraging behaviour. The most useful experiments to evaluate the impact of honey bees on populations of native floral visitors would involve long-term, large-scale removals of non-native honey bees from non-agricultural areas. Such experiments are difficult, but warranted.

In addition to potential effects on native floral visitors, high rates of honey bee visitation, particularly on the most abundant plant species, could affect plant reproductive success. Honey bees may add pollination services and increase seed set in some species [20,34]. However, several authors suggest that too many visits, particularly by large, highly abundant and sometimes non-native floral visitors, can reduce plant reproductive success [19,42,47]. Mechanisms for this negative effect vary, but can include the effects of floral damage from over-visitation and clogging stigmas with too much pollen. In addition, honey bees often make more visits to flowers on the same plant before moving on to the next plant compared to other insect visitors [48,49]. We have preliminary data indicating a near twofold increase in same-plant visits by honey bees relative to native insects across several plant species in our system. This pattern of visitation could increase rates of self-fertilization [50] and reduce offspring fitness through inbreeding depression.

The results of this study document a previously underappreciated aspect of the foraging behaviour of honey bees. Honey bees are not only numerically dominant visitors in our system, but their level of dominance increases with flower abundance. As a result, they probably obtain the lion's share of floral resources removed from the most abundantly blooming plant species, which often form the stabilizing 'core' of local pollination networks [51]. This finding suggests that honey bees may have disproportionate impacts on the ecology and evolution of plant species that play a critical role in the structural integrity of pollination mutualisms. Additionally, since such 'core' plant species are instrumental in sustaining large numbers of both specialized and generalized floral visitors [52], honey bees may also have important impacts on native floral visitor assemblages. On the other hand, native insects often numerically dominate plants with lower flower abundances, which provide a partial refuge relatively free of honey bees (figure 3), although this pattern is also consistent with non-honey bee insects switching to alternative floral resources to minimize competition with honey bees [42,53]. To the extent that our findings are generalizable, they represent a notable divergence in the foraging patterns of honey bees versus those of other floral visitors. The observed patterns may shed light on which plant–pollinator interactions are particularly influenced by the presence of abundant, non-native, social pollinators and demonstrate the importance of considering the foraging behaviour of non-native pollinators when investigating their impacts on native plant–pollinator mutualisms.

Data accessibility. Raw data used in our analyses are available in electronic supplementary material S1, table S1-5.

Authors' contributions. K.-L.J.H., J.M.K., A.L., D.A.H. and J.R.K. conceived and designed the research. K.L.J.H., J.M.K. and A.L. performed the research. K.-L.J.H., D.A.H. and J.R.K. analysed the data. K.-L.J.H., J.M.K., D.A.H. and J.R.K. wrote the manuscript. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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References

1. Morales CL, Traveset A. 2009 A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecol. Lett.* **12**, 716–728. (doi:10.1111/j.1461-0248.2009.01319.x)
2. Traveset A, Richardson DM. 2014 Mutualistic interactions and biological invasions. *Annu. Rev. Ecol. Evol. Syst.* **45**, 89–113. (doi:10.1146/annurev-ecolsys-120213-091857)
3. Parker IM *et al.* 1999 Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions* **1**, 3–19. (doi:10.1023/A:1010034312781)
4. Dietzsch AC, Stanley DA, Stout JC. 2011 Relative abundance of an invasive alien plant affects native pollination processes. *Oecologia* **167**, 469–479. (doi:10.1007/s00442-011-1987-z)
5. Flanagan RJ, Mitchell RJ, Karron JD. 2010 Increased relative abundance of an invasive competitor for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. *Oecologia* **164**, 445–454. (doi:10.1007/s00442-010-1693-2)
6. Strauss SY, Webb CO, Salamin N. 2006 Exotic taxa less related to native species are more invasive. *Proc. Natl Acad. Sci. USA* **103**, 5841–5845. (doi:10.1073/pnas.0508073103)
7. Wilson EE, Holway DA. 2010 Multiple mechanisms underlie displacement of solitary Hawaiian Hymenoptera by an invasive social wasp. *Ecology* **91**, 3294–3302. (doi:10.1890/09-1187.1)
8. Hanna C, Foote D, Kremen C. 2013 Invasive species management restores a plant–pollinator mutualism in Hawaii. *J. Appl. Ecol.* **50**, 147–155. (doi:10.1111/1365-2664.12027)
9. Ruttner F. 1988 *Biogeography and taxonomy of honey bees*. Berlin, Germany: Springer.
10. Kono Y, Kohn JR. 2015 Range and frequency of Africanized honey bees in California (USA). *PLoS ONE* **10**, e0137407. (doi:10.1371/journal.pone.0137407)
11. Goulson D. 2003 Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **34**, 1–26. (doi:10.1146/annurev.ecolsys.34.011802.132355)
12. Aslan CE, Liang CT, Galindo B, Kimberly H, Topete W. 2016 The role of honey bees as pollinators in natural areas. *Nat. Areas J.* **36**, 478–488. (doi:10.3375/043.036.0413)
13. Cane JH, Tepedino VJ. 2017 Gauging the effect of honey bee pollen collection on native bee communities. *Conserv. Lett.* **10**, 205–210. (doi:10.1111/conl.12263)
14. Geldmann J, González-Varo JP. 2018 Conserving honey bees does not help wildlife. *Science* **359**, 392–393. (doi:10.1126/science.aar2269)
15. Geslin B *et al*. 2017 Massively introduced managed species and their consequences for plant–pollinator interactions. *Adv. Ecol. Res.* **57**, 147–199. (doi:10.1016/bs.aecr.2016.10.007)
16. Thomson D. 2004 Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* **85**, 458–470. (doi:10.1890/02-0626)
17. Thomson DM. 2016 Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecol. Lett.* **19**, 1247–1255. (doi:10.1111/ele.12659)
18. Mallinger RE, Gaines-Day HR, Gratton C. 2017 Do managed bees have negative effects on wild bees? A systematic review of the literature. *PLoS ONE* **12**, e0189268. (doi:10.1371/journal.pone.0189268)
19. Aizen MA, Morales CL, Vázquez DP, Garibaldi LA, Sáez A, Harder LD. 2014 When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. *New Phytol.* **204**, 322–328. (doi:10.1111/nph.12924)
20. Hermansen TD, Britton DR, Ayre DJ, Minchinton TE. 2014 Identifying the real pollinators? Exotic honey bees are the dominant flower visitors and only effective pollinators of *Avicennia marina* in Australian temperate mangroves. *Estuaries Coasts* **37**, 621–635. (doi:10.1007/s12237-013-9711-3)
21. Hung K-LJ, Kingston JM, Albrecht M, Holway DA, Kohn JR. 2018 The worldwide importance of honey bees as pollinators in natural habitats. *Proc. R. Soc. B* **285**, 20172140. (doi:10.1098/rspb.2017.2140)
22. Hung K-LJ, Rightmyer MG, Wall M, Berrian J, Ascher J, Yanega D, Davids JA, Holway DA. 2015 *An annotated checklist of the bees (Hymenoptera: Anthophila) of San Diego County, California*. La Jolla, CA: UC San Diego Library Digital Collections. (doi:10.6075/J0PN93HK)
23. Rebman JP, Simpson MG. 2014 *Checklist of the vascular plants of San Diego County*, 5th edn. San Diego, CA: San Diego Natural History Museum.
24. Cleland EE, Funk J, Allen EB. 2016 Coastal sage scrub. In *Ecosystems of california* (eds HA Mooney, E Zavaleta), pp. 429–448. Berkeley, CA: University of California Press.
25. Gibson RH, Knott B, Eberlein T, Memmott J. 2011 Sampling method influences the structure of plant-pollinator networks. *Oikos* **120**, 822–831. (doi:10.1111/j.1600-0706.2010.18927.x)
26. R Development Core Team. 2018 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org.
27. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
28. Kuznetsova A, Brockhoff PB, Christensen RHB. 2016 lmertest: tests in linear mixed effects models. See https://CRAN.R-project.org/package=lmertest
29. Fletcher TD. 2010 psychometric: applied psychometric theory. See https://CRAN.R-project.org/package=psychometric.
30. Wickham H. 2007 Reshaping data with the reshape package. *J. Stat. Softw.* **21**, 12. (doi:10.18637/jss.v021.i12)
31. Wickham H. 2011 The split-apply-combine strategy for data analysis. *J. Stat. Softw.* **40**, 1. (doi:10.18637/jss.v040.i01)
32. Weisberg S. 2005 *Applied linear regression*, 3rd edn. Hoboken, NJ: Wiley-Interscience.
33. Hung K-LJ, Cen HJ, Lee A, Holway DA. 2017 *Plant-pollinator interaction networks in coastal sage scrub*

reserves and fragments in San Diego. La Jolla, CA: UC San Diego Library Digital Collections. (doi:10.6075/J0DZ067F)

34. Nabors AJ, Cen HJ, Hung K-LJ, Kohn JR, Holway DA. 2018 The effect of removing numerically dominant, non-native honey bees on seed set of a native plant. *Oecologia* **186**, 281 – 289. (doi:10.1007/s00442-017-4009-y)
35. Watkins LH. 1969 John S. Harbison: California's first modern beekeeper. *Agric. Hist.* **43**, 239 – 248.
36. Lozada M, D' Adamo P, Buteler M, Kuperman MN. 2016 Social learning in *Vespula germanica* wasps: do they use collective foraging strategies? *PLoS ONE* **11**, e0152080. (doi:10.1371/journal.pone.0152080)
37. Dornhaus A, Chittka L. 2004 Information flow and regulation of foraging activity in bumble bees (*Bombus* spp.). *Apidologie* **35**, 183 – 192. (doi:10.1051/apido:2004002)
38. Wilson-Rankin EE. 2014 Social context influences cue-mediated recruitment in an invasive social wasp. *Behav. Ecol. Sociobiol.* **68**, 1151 – 1161. (doi:10.1007/s00265-014-1726-7)
39. Sih A, Baltus M-S. 1987 Patch size, pollinator behavior, and pollinator limitation in catnip. *Ecology* **68**, 1679 – 1690. (doi:10.2307/1939860)
40. Blaauw BR, Isaacs R. 2014 Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. *Basic Appl. Ecol.* **15**, 701 – 711. (doi:10.1016/j.baae.2014.10.001)
41. Chamberlain SA, Schlising RA. 2008 Role of honey bees (Hymenoptera: Apidae) in the pollination biology of a california native plant, *Triteleia laxa* (Asparagales: Themidaceae). *Environ. Entomol.* **37**, 808 – 816. (doi:10.1603/0046-225X(2008)37[808:ROHBHA]2.0.CO;2)
42. Magrach A, González-Varo JP, Boiffier M, Vilà M, Bartomeus I. 2017 Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nat. Ecol. Evol.* **1**, 1299 – 1307. (doi:10.1038/s41559-017-0249-9)
43. Lindström SAM, Herbertsson L, Rundlöf M, Bommarco R, Smith HG. 2016 Experimental evidence that honey bees depress wild insect densities in a flowering crop. *Proc. R. Soc. B* **283**, 20161641. (doi:10.1098/rspb.2016.1641)
44. Balfour NJ, Gandy S, Ratnieks FLW. 2015 Exploitative competition alters bee foraging and flower choice. *Behav. Ecol. Sociobiol.* **69**, 1731 – 1738. (doi:10.1007/s00265-015-1985-y)
45. Roulston TH, Goodell K. 2011 The Role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* **56**, 293 – 312. (doi:10.1146/annurev-ento-120709-144802)
46. Henry M, Rodet G. 2018 Controlling the impact of the managed honey bee on wild bees in protected areas. *Sci. Rep.* **8**, 9308. (doi:10.1038/s41598-018-27591-y)
47. Sáez A, Morales CL, Ramos LY, Aizen MA. 2014 Extremely frequent bee visits increase pollen deposition but reduce drupelet set in raspberry. *J. Appl. Ecol.* **51**, 1603 – 1612. (doi:10.1111/1365-2664.12325)
48. Ivey CT, Martinez P, Wyatt R. 2003 Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). *Am. J. Bot.* **90**, 214 – 225. (doi:10.3732/ajb.90.2.214)
49. Abe T, Wada K, Kato Y, Makino S, Okochi I. 2011 Alien pollinator promotes invasive mutualism in an insular pollination system. *Biol. Invasions* **13**, 957 – 967. (doi:10.1007/s10530-010-9882-9)
50. Karron JD, Holmquist KG, Flanagan RJ, Mitchell RJ. 2009 Pollinator visitation patterns strongly influence among-flower variation in selfing rate. *Ann. Bot.* **103**, 1379 – 1383. (doi:10.1093/aob/mcp030)
51. Bascompte J, Jordano P, Melián CJ, Olesen JM. 2003 The nested assembly of plant – animal mutualistic networks. *Proc. Natl Acad. Sci. USA* **100**, 9383 – 9387. (doi:10.1073/pnas.1633576100)
52. Bascompte J, Jordano P, Olesen JM. 2006 Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431 – 433. (doi:10.1126/science.1123412)
53. Roubik DW, Moreno JE, Vergara C, Wittmann D. 1986 Sporadic food competition with the African honey bee: projected impact on neotropical social bees. *J. Trop. Ecol.* **2**, 97 – 111. (doi:10.1017/S0266467400000699)