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Mass-flowering monoculture attracts bees, amplifying parasite prevalence

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As the global agricultural footprint expands, it is increasingly important to address the link between the resource pulses characteristic of monoculture farming and wildlife epidemiology. To understand how mass-flowering crops impact host communities and subsequently amplify or dilute parasitism, we surveyed wild and managed bees in a monoculture landscape with varying degrees of floral diversification. We screened 1509 bees from 16 genera in sunflower fields and in non-crop flowering habitat across 200 km^2 of the California Central Valley. We found that mass-flowering crops increase bee abundance. Wild bee abundance was subsequently associated with higher parasite presence, but only in sites with a low abundance of non-crop flowers. Bee traits related to higher dispersal ability (body size) and diet breadth (pollen lecty) were also positively related to parasite presence. Our results highlight the importance of non-crop flowering habitat for supporting bee communities. We suggest monoculture alone cannot support healthy bees.

1. Introduction

Disease has been identified as a primary driver of biodiversity loss [1] and is exacerbated by habitat loss [2]. Although agriculture occupies half of the Earth's land [3], the spread of disease in agricultural landscapes is rarely considered. The expansion and intensification of cropping systems likely impacts disease dynamics through shifts in resource availability. Many economically important crops (including nut, fruit and oilseed crops) are grown in mass-flowering 'monocultures'—dense, single-species fields that are characterized by synchronized bloom events. These events provide a pulse of pollen and nectar [4,5] at high levels, but only for a short duration. Resource pulses may indirectly exacerbate parasite transmission by changing animal behaviour and population dynamics [6,7]. In agricultural systems, animals dependent on floral resources will spatially and temporally track bloom events [8]. Repeated mass-bloom events have been shown to increase animal population sizes and species richness [4,8–10]. This may result in host aggregation at a resource—increasing exposure between infected individuals and increasing parasitism (amplification) [11]. Alternatively, resource pulses may decrease parasitism (dilution) if they attract hosts that vary in their ability to transmit parasites and become infected or if resource availability is so high that host density at a resource is decreased [12].

Non-crop floral resources also impact parasite epidemiology. For example, strips of native plants along field edges, called 'hedgerows', can support higher richness and abundance of beneficial insects, mammals and birds [13–15]. Farms also feature unmanaged, weedy species along field margins that can attract biodiversity [16]. If non-crop resources from hedgerows and weeds attract and aggregate hosts, this may lead to parasite amplification. Piot *et al.* [17] found that wildflower resources were associated with parasite amplification

in bumblebees in simplified landscapes. Alternatively, non-crop resources may dilute parasitism if the presence of many flowers decreases the likelihood of interactions between infected and healthy individuals [18]. Non-crop habitat, by providing diverse and abundant resources, can also increase host species richness or immunity, reducing infection [19,20].

The ability of parasites to spread in response to a resource pulse may vary based on traits of their host, specifically resource specialization, movement ability, and sociality [21]. Because shared use of resources facilitates horizontal transmission of parasites, resource specialists may be at higher risk if they concentrate at resources that are associated with parasites [21–24]. In a meta-analysis, Becker *et al.* [21] found ectoparasite presence was highest in dietary specialists exposed to resource provisioning. In addition, movement ability increased infection risk, likely because individuals were able to disperse to where resource pulses were occurring—promoting dense aggregations that increased exposure to parasites [21]. Social behaviours may also mediate parasitism [25]. For wild bees, higher parasite presence was detected when social species were dominant in the local community [26].

We assessed whether mass-flowering crops and non-crop floral resources affect disease dynamics through impacts to host communities. We focused on bees—a species-rich group with variation in sociality, movement abilities and resource specialization. Bees are also known to respond to floral resource pulses [4]. Bees include managed species, which are seasonally introduced into the landscape at mass-bloom, and wild species, which must persist independently. Wild bees and managed honeybees (*Apis mellifera*) are both threatened by a suite of parasites that can be transmitted via shared flowers [27–29]. Horizontal parasite transmission between bee species occurs when parasites are deposited onto a plant or flower and then encountered by a new host. Bees are thus a model system to investigate the nexus between floral resources and parasitism. Furthermore, there is growing urgency to understand how inter-species variation influences epidemiology because multiple bee species are thought to be in decline globally [30].

We conducted this study in hybrid sunflower (*Helianthus annuus*), a mass-flowering oilseed. We first examined how mass-blooming crops affected host communities within and between years. We then evaluated whether local wild bee abundance and richness amplified or diluted parasite presence in both wild bees and managed honeybees, and if non-crop flowering resources mitigated or intensified this effect. Lastly, we tested whether bee traits-related movement, diet breadth and sociality were associated with parasite presence in wild bees.

2. Methods

(a) Study system and collection methods

We conducted the study in hybrid sunflower (*Helianthus annuus*) fields in the California northern Central Valley in Yolo County (electronic supplementary material, figure S1). Sunflower is a fully pollinator-dependent, mass-flowering crop that is visited by a diverse community of bees, including pollen specialists (oligolectic) and pollen generalists (polylectic). The breeding system of sunflower grown for hybrid seed is gynodioecious, with separate 'male' plants (nectar and pollen producing) and 'female' plants (nectar-only producing). In the field, rows of male plants are interspersed across rows of female plants. Hybrid sunflower is on a 3-year rotation and is commonly rotated with tomato and winter wheat [31]—plants that are unattractive to most bees.

Non-crop floral resources include intentionally managed hedgerows and unmanaged weedy margins. Hedgerows are rows of perennial shrubs located along field edges that often include drought-tolerant natives found in nearby oak woodland and chaparral communities. Hedgerows occupy less than 1% of this landscape (electronic supplementary material, figure S1). Because the location of sunflower rotates across the landscape, hedgerows can be found adjacent to sunflower, fallow fields, or other crops. The hedgerows in this region include native flowering plants such as *Rosa californica*, *Ceanothus lemmonii* and *Sambucus mexicana*. Weedy margins in fields without hedgerows often include non-native flowering species such as *Carduus pycnocephalus*, *Lactuca serriola* and *Malva parviflora*. Beyond hedgerows, the broader landscape is characterized by very little remnant natural habitat [32].

In 2019, we surveyed wild and managed bees at 12 sites. We selected sites that featured different combinations of sunflower, hedgerows and weedy margin transects. In sunflower farms without hedgerows ($n = 3$), we collected bees from the sunflower crop and from the weedy margins. In sunflower farms with hedgerows ($n = 3$), we collected bees from the sunflower crop and hedgerow. We also collected at sites composed of hedgerows or weedy margins next to non-sunflower, non-mass blooming fields ($n = 3$ each); at these sites we sampled along the hedgerow or weedy margin. Collections from weedy margins and hedgerows occurred along two 50 m transects along the edge of the habitat. Collections from sunflower occurred along two 50 m transects into the field. The mean distance between sites was 13.53 km, the minimum distance between sites sampled in the same year was 1.26 km, and the maximum was 24.00 km. The distance between sites was greater than the foraging distance of all the wild bees in our community (except *Xylocopa* spp. [33]). The entire area surveyed spanned almost 200 km^2.

We surveyed bee communities to capture parasite dynamics before, during and after the mass-bloom event. Because bloom peaks in July, we surveyed six times between early June and early August. Survey periods were approximately 7 days apart. Sites were only sampled under sunny conditions between 17°C and 32°C, and when wind speeds were below 2.5 m s^{-1}. We netted wild insects visiting plants for 1.5 h of active search time, noting the plant visited and collecting into sterile 1.5 ml microcentrifuge tubes. At sunflower transects we spent an additional 30 min collecting infrequent species to increase the sample size for parasite screenings (these samples were not included in our calculations of bee richness or abundance). Honeybees are stocked in this system at an average rate of 1.5 hives per acre and are ubiquitous. We therefore additionally collected five *A. mellifera* bees during each sampling event and at each transect type. Samples were stored on dry ice in the field and then at −80°C.

(b) Site characterization

(i) Non-crop floral resources

We identified flowering plants at each site in fifty 1 m vegetative quadrants at equally distanced 5 m intervals along the length of the hedgerow and weedy margin transects. Floral surveys were conducted within 0–2 days of the bee collections. We identified plants to species or morphospecies. We estimated the abundance of non-crop floral abundance across quadrants. We measured non-crop floral richness as the number of blooming species across the quadrants.

(ii) Sunflower cultivation

To measure the effect of mass-blooming crops on parasite dynamics, we estimated the amount of sunflower in cultivation

in the landscape with the USDA CropScape Data Layer [31]. As central-place foragers, bees are limited by their maximum foraging distance [34], which has been found in sunflower [35]. Because sunflower located closer to the study sites may have greater influence on biological responses than sunflower further away, we weighted the sunflower area within the landscape by distance to each site, following Ponisio *et al.* [32]. We quantified the amount of sunflower in concentric rings (radii from 50 m to entire study landscape on a log scale). We used a Gaussian decay function to assign weights to the sunflower within each ring. The sunflower in more distant rings was assigned a lower weight than sunflower in closer rings [36,37]. We used both steep and gradual decay rates to specify how quickly weightings decrease with distance ($\alpha = 350$, $\alpha = 1000$). A decay rate in which $\alpha = 350$ represents that 95% of weight is within 575 m, whereas $\alpha = 1000$ represents that 95% of weight is within approximately 1600 m. Beyond this scale, the influence of sunflower in the landscape is likely negligible because it is far outside the foraging distance of all but the largest bees in our landscape [33]. We then calculated the logarithm of the weighted sum of the area of sunflower by summing the area of sunflower, then multiplying by that ring's weight across all of the rings. We refer to this variable as *sunflower area weighted proximity*. This was calculated for both the current year and previous year because we hypothesized that (1) mass-blooming crops within a year may redistribute individuals spatially, and (2) annual bee population sizes may be positively associated with the amount of sunflower resources available to reproductive females in the previous year, when they provision for their young. For transects within sunflower fields or for hedgerows/weedy margins adjacent to sunflower fields, the area of these sunflower fields is included in the estimate of the sunflower area weighted proximity.

(c) Bee species characterization

We identified specimens to species (or morpho species for some bee specimens in the genera *Lasioglossum* and *Hyleaus*) with the assistance of expert taxonomist Doug Yanega (University of California, Riverside (UCR)) and the UCR Entomology Museum bee collection. We characterized each species in terms of its traits: sociality, diet breadth and body size. Species were categorized as either social or solitary based on published literature. Primitively eusocial species in the genera *Bombus*, *Lasioglossum* and *Halictus* were categorized as social. To categorize diet breadth, we classified bees as oligolectic or polylectic, again based on published literature [34]. We quantified body size using intertegular distance (mm), taken as the mean value from five randomly selected female specimens. We saw little evidence for high levels of intraspecific variation in body size in the species in our community.

(d) Parasite screening

We randomly screened five individuals of each species from each site and survey period (a maximum of 30 individuals of a species per site). When there were fewer than five individuals of a species in a sampling period, we screened all individuals that were available. We removed the gut of each specimen using flame-sterilized tools. We extracted DNA from each bee gut with the Qiagen DNeasy blood and tissue kit. To lyse samples, we added 180 µl Buffer ATL to each sample, two sterile 5 mm stainless steel beads, and approximately 100 µl of 0.1 mm zirconia beads in a Qiagen Tissue Lyser II for 4 min. We included one negative control for every plate of 94 samples.

We screened each bee for parasites that vary by taxonomy, symptoms and transmission. Wild bees and honeybees share parasites such as microsporidians, trypanosomatids and neogregarines [38]. We therefore screened for the presence of *Apicystis* spp. and *Ascosphaera* spp. using parasite-specific primers for genus-level identification. We used a multiplex protocol to screen bees for *Nosema bombi* and *Nosema ceranae* [26]. We also screened bees for *Crithidia* spp., *Crithidia expoeki* and *Crithidia bombi* [26]. All primer references and conditions are given in electronic supplementary material, table S1. An individual was assigned a positive prevalence for *Crithidia* spp. only if it was positive for *Crithidia* spp. and negative for *C. expoeki* and *C. bombi*. If an individual was assigned a positive prevalence of *C. expoeki* or *C. bombi*, it was not assigned a positive prevalence of *Crithidia* spp. Each assay included a negative and positive control. We confirmed that each sample contained bee DNA by amplifying an EF–1α gene sequence associated with bees [39]. We resolved amplicons with electrophoresis on a 1% agarose gel. We confirmed positive calls by submitting a subset of positive samples for Sanger sequencing.

3. Analyses

We fitted linear and generalized linear mixed models (LMMs and GLMMs) that represented our hypotheses on how mass flowering and non-crop resources shape bee richness and abundance. We then asked how bee abundance, richness, bee traits and non-crop floral resources contribute to the dilution or amplification of parasite presence, again using GLMMs. Analyses were conducted in R 4.0 (r-project.org).

(a) Wild bee abundance and richness

We first tested the response of bee abundance and richness to mass-bloom events. To test the hypothesis that mass-flowering crop bloom will concentrate individuals and increase local population sizes, we initially included the following explanatory variables in our models: transect type (sunflower, weedy margin, hedgerow), sunflower weighted proximity in the current year, and sunflower weighted proximity in the prior year. To account for changes in bee phenology and sunflower bloom across the season, we included day of year and its squared term as variables to fit model assumptions. To examine whether non-crop flowering habitat from hedgerows and weedy margins augment abundance, we included non-crop floral abundance and richness as explanatory variables. We included site as a random effect. To model bee abundance, we fitted a negative binomial error model, and to model richness we fitted a Gaussian error model [40,41]. We calculated variance inflation factors (VIF) using the car package [42] to look for colinearity between variables in the models. VIF scores >2 indicate colinearilty. We subsequently dropped non-crop floral richness from the model because it was colinear with floral abundance, and the corrected Akaike information criterion (AICc) indicated a marginally better model fit using floral abundance over richness (AICc = 1.77).

We then ran the model twice, once with sunflower weighted proximity $\alpha = 350$ and once with sunflower weighted proximity $\alpha = 1000$, and selected the former model based on AICc score. After this model refinement process, our final model (electronic supplementary material, formula S1) included: transect type, the sunflower weighted proximity in the current year ($\alpha = 350$), the sunflower weighted proximity in the prior year ($\alpha = 350$), floral abundance, day of year and its squared term, and site as a random effect. In the negative-binominal GLMM, an exponential link function was employed. All explanatory variables were centred. We used standard model assessment techniques to determine whether the top model met all the assumptions of a GLMM/LMM. We computed the conditional pseudo-R^2 value as a goodness-of-fit metric using the r.squaredGLMM function in the MuMIn package [43].

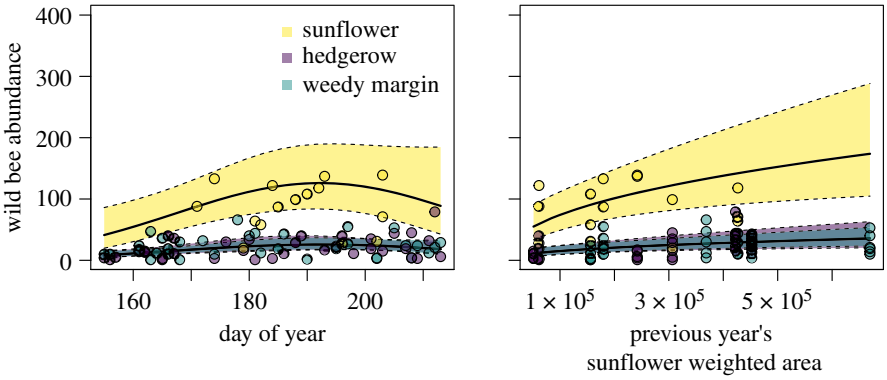

Figure 1. The variables significantly associated with wild bee abundance. Day of year and sunflower proximity in the previous year were positively related to abundance. Points represent wild bee abundance at a site at each survey period. The solid line indicates the slope estimate and the dashed lines are the 95% confidence intervals around the estimate.

Table 1. The estimates, adjusted standard errors, test statistics and *p*-values for wild bee abundance, wild bee richness, parasite prevalence in wild bees and parasite richness in wild bees.

	variable	estimate ± s.e.	*z*-value	*p*-value
bee abundance	transect type hedgerow	−1.690 ± 0.256	−6.593	24.32×10^{-11}***
	transect type weedy	−1.593 ± 0.256	−6.204	5.52×10^{-10}***
	day of year	4.70 ± 2.142	2.195	0.028*
	day of year squared	−4.463 ± 2.136	−2.090	0.037*
	floral abundance	0.027 ± 0.105	0.266	0.790
	sunflower current year ($\alpha = 350$)	−0.188 ± 0.107	−1.767	0.077
	sunflower last year ($\alpha = 350$)	0.338 ± 0.104	3.255	0.0011**
bee richness	transect type hedgerow	−0.102 ± 0.172	−0.594	0.553
	transect type weedy	−0.312 ± 0.178	−1.751	0.0799
	day of year	1.026 ± 0.665	1.543	0.123
	day of year squared	−0.918 ± 0.661	−1.388	0.165
	floral abundance	0.082 ± 0.065	1.264	0.2061
	sunflower current year ($\alpha = 350$)	$-1.257 \times 10^{-5} \pm 0.067$	0.00	0.999
	sunflower last year ($\alpha = 350$)	0.123 ± 0.067	1.836	0.066
parasite prevalence	bee abundance	0.243 ± 0.108	2.242	0.025*
	floral abundance	−0.3.08 ± 0.083	−3.725	0.0002***
	sociality (solitary)	−0.662 ± 0.574	−1.153	0.250
	lecty (polylectic)	−1.617 ± 0.711	−2.275	0.023*
	body size	0.506 ± 0.228	2.221	0.026*
	wild bee abundance × floral abundance	−0.219 ± 0.092	−2.380	0.017*
parasite richness	bee abundance	0.010 ± 0.029	0.343	0.757
	floral abundance	−0.040 ± 0.030	−1.332	0.183
	sociality (solitary)	−0.379 ± 0.237	−1.598	0.110
	lecty (polylectic)	−0.629 ± 0.228	−2.768	0.006**
	body size	0.111 ± 0.060	1.848	0.065
	total abundance × floral abundance	−0.002 ± 0.029	−0.0561	0.954

Note: *, ** and *** indicate significance at the 0.05, 0.01 and 0.001 levels, respectively.

(b) Parasitism in wild bees and honeybees

We fitted a binomial GLMM with parasite presence or parasite richness as a response variable. We represented parasite presence as a binary value (0,1), with a 1 indicating that an individual had at least one parasite, and a 0 indicating that an individual had no parasites detected. We calculated parasite richness as the number of distinct parasites found in each individual. Because we screened for seven different parasites, the possible values for parasite richness within an individual ranged from 0 (no parasites

detected) to 7 (all parasites detected). We modelled this response variable at the individual level using a binomial GLMM with the number of trials fixed at 7 (total possible parasites) and number of parasites detected in an individual as the number of successes. An assumption of this approach to modelling parasite richness is that each individual parasite has an independent, equal probability of colonizing the host. However, no other discrete distributions or data transformations led to model fits that met the assumptions of linear models.

To test whether host abundance amplifies parasitism we included bee abundance as an explanatory variable. We could not include bee richness in the same model because it was colinear with bee abundance, and AICc indicated a better model fit using bee abundance than richness (AICc 9.54). To test whether non-crop flowers mitigate or enhance the effect of bee aggregation on parasitism, we included an interaction between bee abundance and non-crop floral abundance. To test whether bee traits influence parasite presence and richness, we included body size, lecty and eusociality as explanatory variables. We included random effects of site and bee species. The effect of transect type was not included in this model because we assumed that transect type affects parasitism through its influence on bee abundance. A logit link function was employed.

All explanatory variables were centred. The model for parasite presence and richness can be found in electronic supplementary material, formula S2.

We also tested this model for *A. mellifera* parasite richness and presence, using a separate model because honeybees are actively managed by beekeepers.

4. Results

(a) Wild bee abundance and richness

We collected 3376 wild bees comprising 35 species from 15 genera (including males and females, which we analysed together because we did not observe significant differences in parasitism between the sexes). Body size, lecty and sociality varied across bees in our system (electronic supplementary material, table S2). We found evidence of the positive influence of mass-blooming crops on bee abundance, both within and across seasons. Sunflower area weighted proximity in the previous year, when females provision for their offspring, had a positive effect on bee abundance, suggesting sunflower resource proximity increases interannual bee population sizes locally. Sunflower proximity in the current year had a slight negative effect on bee abundance (significance was marginal, table 1). Within a year, bee abundance also followed a phenological curve with a unimodal peak during peak sunflower bloom (figure 1 and table 1). In addition, hedgerow and weedy margin transects had fewer bees than the sunflower transects (figure 1 and table 1). Together these results suggest that sunflower aggregates individuals within crop fields during bloom at a higher density than in other flowering habitat. The R^2 for the model of bee abundance was 0.567.

None of the variables we explored had a statistically significant effect on wild bee richness ($R^2 = 0.072$), but there was marginal significance for a negative effect of weedy margins and for a positive effect of sunflower cultivation in the previous year.

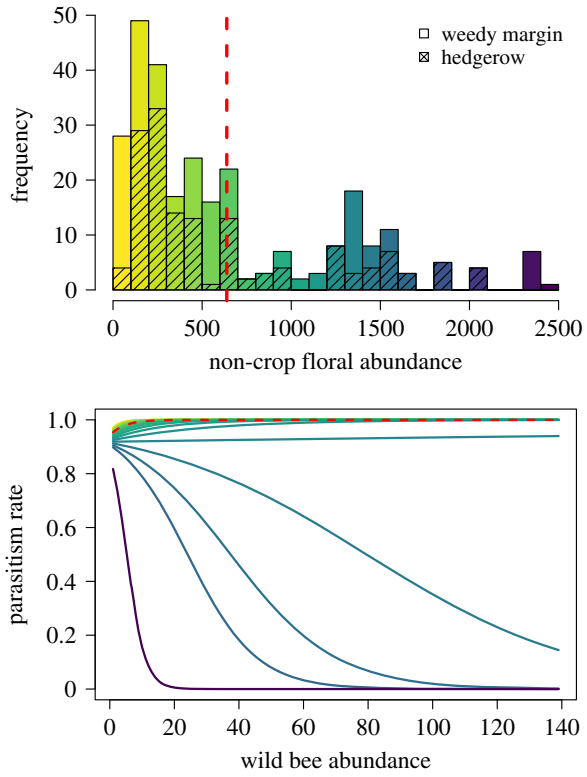

Figure 2. Interaction between non-crop floral richness and bee abundance was significantly related to parasite prevalence. The top histogram depicts the frequency distribution of floral richness across the surveys (site, date combinations). Different levels of non-crop floral richness are represented by a suite of colours in the histogram, which are matched to the lower panel in order to illustrate the interaction between wild bee abundance and floral richness in determining parasite prevalence. Low floral richness is yellow–green, and high floral richness is blue–purple. The striped fill reflects the proportion of floral abundance provided by hedgerows; the remaining floral abundance comes from weedy margins. The mean floral abundance is indicated by a red dashed line in the histogram and bottom panel. When non-crop floral abundance is low, the relationship between wild bee abundance and parasitism is positive. As non-crop floral abundance becomes higher (blue–purple), the slope of the relationship between wild bee abundance and parasitism becomes less steep. At very high non-crop floral abundance, the relationship between bee abundance and parasitism is negative.

(b) Parasitism in wild bees and honeybees

We screened 1509 wild bees for parasites, of which 292 (19.35%) had no parasites, 684 (45.32%) had one parasite, and 533 (35.3%) had two or more parasites. The maximum number of parasite types within a single bee was three. For each specific parasite, we found a range of prevalence rates. For wild bee individuals, 38.04% harboured *Ascosphaera* spp. *Apicystis* was found in 54.80% of the wild bee individuals. We found *N. ceranae* in 6.16% of bees and *N. bombi* in 6.10% of wild bees. We found that 8.61% of individuals we collected had *C. expoeki*, 4.17% had *C. bombi*, and 6.49% had a different species of *Crithidia*. We also found that the rate of parasitism prevalence for each bee species varied by parasite and whether there was sunflower found adjacent to the transect (electronic supplementary material, figures S2 and S3).

Parasite presence in wild bees, measured as bee individuals with at least one parasite, was significantly positively related to bee abundance (figure 2 and table 1). Parasite presence was also significantly negatively related to non-crop floral abundance. There was a significant interaction between bee

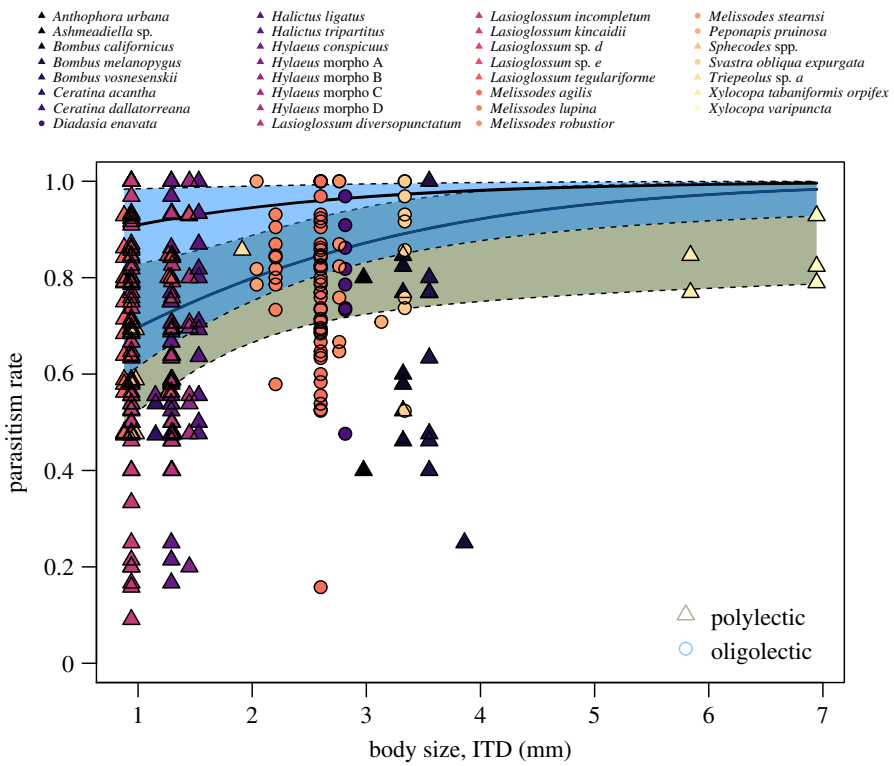

Figure 3. The relationship between body size (measured as intertegular distance, ITD) and parasitism prevalence rate for each species for a site and survey period. The solid lines indicate the slope estimate for the relationship between body size and parasitism and the dashed lines are the 95% confidence intervals around the estimate. Because oligolectic species (pollen specialists, blue fill) had higher average parasitism rates, the intercept for the slope of body size and parasitism is higher than that of polylectic species (pollen generalists, green fill). Species are represented by coloured points with shapes that reflect their diet breadth (polylecty = triangles; oligolecty = circles).

abundance and non-crop floral abundance. Specifically, bee abundance was positively associated with parasitism at sites with average or low floral abundance, and negatively associated with parasitism when floral abundance was far above average (figure 2). We also found that larger bees, which have longer dispersal ranges [33], had higher rates of parasitism (figure 3). Polylectic (generalized) species had lower rates of parasitism than oligolectic (specialized) species (table 1). The R^2 for the model of bee parasite presence was 0.363.

Parasite richness was significantly negatively related to lecty, with oligolectic species hosting higher parasite richness than polylectic species. Parasite richness marginally increased with bee body size (table 1). No other variables were significantly related to parasite richness. The R^2 for the model was 0.189 (table 1).

We screened 145 honeybees, of which 23 (15.86%) had no parasites, 38 (26.21%) had one parasite and 84 (57.93%) had two or more parasites. We found 21.38% of honeybees with *Ascosphaera* spp., 59.31% with *Apicystis*, 5.72% with *N. ceranae*, 5.55% with *N. bombi*, 9.65% with *C. expoeki*, 3.45% with *C. bombi* and 11.72% with a different species of *Crithidia*. None of the variables considered had statistically significant effects on parasite presence ($R^2 = 0.039$) or richness ($R^2 = 0.012$) in honeybees.

5. Discussion

We show that, through indirect effects, mass-flowering crops have a strong effect on wildlife epidemiology. Specifically, sunflower monoculture increased the abundance of hosts in an intensively managed agricultural landscape with limited natural habitat. Within a year, bee abundance was highest in July, tracking peak sunflower bloom, and was higher in sunflower fields than other flowering habitat types. In addition, the cultivation of sunflower in the previous year, when females provision for next year's offspring, positively influenced bee abundance. Our results suggest that repeated annual mass-bloom events can increase bee population sizes across years. Increases in host abundance were subsequently associated with amplification of parasite prevalence, possibly by increasing exposure and transmission between susceptible individuals. Supplementary resources provided by humans have repeatedly been linked with parasite transmission in wildlife [44–46], but monoculture farming is rarely viewed as a form of resource provisioning. Here we show that monoculture agriculture contributes to wildlife parasitism.

Encouragingly, non-crop floral resources mitigated parasite prevalence rates. As non-crop floral abundance at a site increased, the positive effect of bee abundance on parasitism diminished such that, at sites with the highest floral abundance, the relationship between bee abundance and parasite prevalence was negative. Interestingly, non-crop floral abundance was not associated with significant increases to bee abundance or bee richness. Other studies also suggest that increases in floral abundance, without accompanying increases in bee abundance, dilute transmission of parasites and pathogens [19,26]. When floral abundance is high, bees may disperse across resources, and an individual bee may have a reduced likelihood of encountering an infected individual [18]. Non-crop resources can also provide immunity and fitness benefits to bees because *H. annuus* pollen has low protein content [47]. In our study system, floral abundance and floral richness were colinear, and the effects between the two could not be disentangled.

Bees in floral-rich environments may collect more pollen types, and pollen diversity has been found to enhance nutrition and improve parasitism outcomes [48,49]. By contrast, supplemental resources have also been reported to enhance parasitism in bumblebees [50]. These relationships may be dependent on landscape-level resource availability; Piot *et al.* [17] found that bumblebee parasitism in wildflower strips was only amplified in landscapes with limited natural habitat. In our system, the broader landscape is homogeneous and characterized by very little habitat [32]. We suggest that diversification practices such as installing hedgerows may promote healthy wildlife populations in agriculture, particularly when employed across the landscape in high proportion to intensively managed areas.

We found that parasite prevalence in bee communities was associated with bee traits related to movement and diet breadth. Specifically, larger bee species and pollen specialists had higher parasite prevalence and richness. Larger bees forage over longer distances [33] and produce more faeces [51], which has been linked with parasite transmission [51]. In contrast to our findings, previous studies have found that smaller bee species [52] and smaller individuals [51] host more parasites than larger bees. More research is needed to examine how host traits related to movement ecology affect parasitism. Our findings that specialists had higher rates of parasite prevalence is in agreement with pollinator epidemiological models [22]. Simplified landscapes (such as the intensively managed agriculture in which our study took place) have been shown to favour generalists [53] and smaller bees [32,34], likely because these bees have less-specialized resource needs. Increased parasitism may explain the lower persistence of specialist and larger-bodied species in simplified landscapes.

We did not find a significant effect of sociality on wild bee pararasite prevalence. We found that managed honeybees, which have an advanced eusocial lifestyle, did have high rates of parasite prevalence, but no significant predictors. The honeybees in this system likely come from beekeepers who use standardized, active management strategies to control for parasites and overall health. As a species managed for crop pollination, honeybees were brought to this system during bloom. This may explain why they are less likely to reflect local-scale habitat conditions than wild bees, which persist in the system over their lifespan. Our study suggests that the management needs of managed and wild bees are fundamentally different, but that efforts to promote wild bee abundance and richness are unlikely to increase parasite prevalence or richness in honeybees.

Monoculture farming predominates in commercial agriculture [3]. Some studies have concluded that mass-flowering crops enhance bee densities [4]—but we find this appears to amplify parasite presence in wild bees. We therefore caution against conclusions that mass-flowering crops can promote healthy bee populations. It is unknown whether all mass-flowering crops amplify parasitism. We suggest that amplification may be a widespread phenomenon because we found this effect in sunflower, which has previously been linked to reduced parasite infection intensity in bees [54]. The relationship between floral resources and parasitism is important because parasitism may impact population persistence, individual foraging efficiency and pollination services [55]. While there are challenges to restoring and diversifying agricultural habitats, this study highlights the importance of these practices for mitigating the spread of disease.

Data accessibility. Analysis code is available on Github at https://github.com/lponisio/sunflowerParasites and data are available on Zenodo at https://zenodo.org/record/5539429#.YVSpeWZKhTY.

Authors' contributions. H.C. and L.C.P. led study design, field work, laboratory work, analyses and manuscript preparation. G.P.S. led field work; J.F.Z. conducted laboratory work. H.S., Q.S.M. and S.H.W. contributed to study design, field and laboratory work protocols and manuscript preparation.

Competing interests. We declare we have no competing interests.

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