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Floral resources shape parasite and pathogen dynamics in bees facing urbanization

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Abstract

Urbanization is associated with increases in impervious land cover, which alters the distribution of resources available to wildlife and concentrates activity in unbuilt spaces such as parks and gardens. How resource shifts alter the dynamics of parasite and pathogen transmission has not been addressed for many important species in urban systems. We focus on urban gardens, resource-rich "islands" within the urban matrix, to examine how the availability of floral resources at local and landscape scales influences the prevalence of six RNA viruses and three parasites in honey bees and bumble bees. Because parasites and pathogens are transmitted at flowers between visitors, we expected that floral abundance would concentrate bees within gardens, amplifying infection rates in pollinators, unless increases in floral resources would enhance bee diversity enough to dilute transmission. We found that garden size and flowering perennial plant abundance had a positive, direct effect on parasite and pathogen richness in bumble bees, suggesting that resource provisioning amplifies transmission. We also found that parasitism rates in honey bees were positively associated with parasites and pathogens in bumble bees, suggesting spillover between species. Encouragingly, we found evidence that management may mitigate parasitism through indirect effects: garden size had a positive impact on bee diversity, which in turn was negatively associated with parasite and pathogen richness in bumble bees. Unexpectedly, we observed that that parasite and pathogen richness in honey bees had no significant predictors, highlighting the complexity of comparing transmission dynamics between species. Although floral resources provide bees with food, we suggest more research on the tradeoffs between resource provisioning and disease transmission to implement conservation plantings in changing landscapes.

KEYWORDS
bee conservation, bee-parasite interactions, landscape epidemiology, RNA viruses, urban gardens, urbanization

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1 | INTRODUCTION

Urbanization is characterized by habitat degradation, conversion, and fragmentation and has therefore been implicated in species declines (Alberti, 2010; Fahrig, 2003; Knop, 2016; Magura et al., 2010; McKinney, 2002). With urban expansion (Seto et al., 2012), spaces like gardens and parks have been described as isolated green "islands" within a sea of impervious land cover (e.g., Davis & Glick, 1978; Faeth & Kane, 1978; Piano et al., 2020; Szlavecz et al., 2011). These spatially constrained habitats exhibit a high biodiversity of arthropods (e.g., Clucas et al., 2018; Egerer et al., 2017; Magura et al., 2010), birds (e.g., Carbó-Ramírez & Zuria, 2011; Mayorga et al., 2020), bats (e.g., Baker & Harris, 2007), and other mobile organisms that traverse between urban and open spaces (e.g., Angold et al., 2006; Magle et al., 2010; Withey & Marzluff, 2005). In recent years, urban gardens have also been identified as refugia that provide resources for threatened species (Colla et al., 2009; Goddard et al., 2010; Hernandez et al., 2009; Quistberg et al., 2016), but there may be unintended consequences when species artificially concentrate at isolated habitat resources that might render gardens as population "sinks." Urban gardens are thus natural laboratories for understanding how resource provisioning impacts urban biogeographic processes.

In disease ecology, theory predicts that resource provisioning may result in one of two outcomes for parasite and pathogen infection: dilution or amplification (Becker et al., 2015; Civitello et al., 2018). Amplification will occur if increases in resources result in host aggregation, increasing exposure rates and transmission between individuals (Becker & Hall, 2014). In contrast, dilution will occur if species vary in their parasite and pathogen transmission rates, such that higher species richness and diversity leads to lower infection prevalence (Johnson et al., 2013). Dilution will also occur if increases in the quality or quantity of resources for a host impart higher immunity or defence. In this study, we examine how urban landscapes impacts parasites and pathogens through resource-driven dynamics in bees, a species group that is often targeted for conservation in urban landscapes (e.g., Frey & LeBuhn, 2016; Matteson & Langellotto, 2011; Pawelek et al., 2009; Turo & Gardiner, 2019).

Bees (Anthophila) exhibit tremendous variation in their dispersal and plant visitation behaviors across ecosystems (Burkle & Alarcón, 2011), making them ideal for examining ecological patterns of parasitism. Bees are an exceptionally diverse group with some 20,000 species worldwide (Michener, 2007). Bees are also susceptible to a broad range of parasites and pathogens, including >20 RNA viruses (Dolezal et al., 2016), microsporidians, trypanosomatids (Paxton et al., 2007; Plischuk et al., 2009; Schwarz et al., 2015), neogregarines (Ravoet et al., 2014), and arthropod parasitoids (Core et al., 2012). In urban environments, gardeners often manage the honey bee (*Apis mellifera)*, a species introduced to North America from Europe and Western Asia. Honey bee colonies are experiencing high annual losses in temperate regions (Lee et al., 2015; vanEngelsdorp & Meixner, 2010) and honey bee management has been linked with parasite spillover to wild bees (Graystock et al., 2016; Tehel et al., 2016). Understanding whether urban landscapes can sustain managed and wild bee populations is critical because several bee species are thought to be in decline globally (Potts et al., 2016; Potts, Roberts, et al., 2010; Vanbergen, 2013).

Although the transmission mechanism of each parasite and pathogen varies, transmission at floral resources plays a role. Bees rely on flowers for pollen and nectar, but the transmission of parasites and pathogens occurs at flowers via direct bee-to-bee contact or exposure to infected faeces, pollen, or nectar (Durrer & Schmid-Hempel, 1994; Singh et al., 2010). Because multiple pathogens traditionally associated with honey bees have been found in sympatric wild bee populations (Fürst et al., 2014; McMahon et al., 2015; Ravoet et al., 2014; Zhang et al., 2012), and because viruses (Singh et al., 2010) and parasites (Graystock et al., 2015) have been found to disperse through shared flower visits, flowers in urban gardens probably facilitate transmission between bee species. In garden "islands" embedded in resource-poor landscapes, flowers may attract an aggregation of infected bees, amplifying parasitism. Alternatively, flowers may confer immune and reproductive benefits to bees (Di Pasquale et al., 2013), diluting parasitism. Epidemiology is further complicated by landscape-level features: habitat composition may indirectly impact host or pathogen physiology, behaviour, and community structure (Kilpatrick & Altizer, 2010). Indeed, both local and landscape-level resources have been shown to shape bee community composition (e.g., Matteson & Langellotto, 2010; Potts et al., 2003, 2005), which may result in amplification if parasites and pathogens have more hosts to colonize (Johnson et al., 2013; Kamiya et al., 2014; Rottstock et al., 2014), or dilution if bee species vary in competence or if transmission is greater within species than between species (Johnson et al., 2013).

Both local and landscape resources are important determinants of amplification and dilution in disease systems. For bees, it is important to examine the direct effects of local and landscape resources on disease dynamics, and their indirect effects via impacts to host community composition, to elucidate how heterogenous landscapes might influence epidemiology. We address this goal in urban garden "islands" across >125 km of the California Central Coast. We first assess if a wild bee (the yellow-faced bumble bee, *Bombus vosnesenskii*) and a managed bee (the honey bee, *Apis mellifera*) are infected with similar parasite and pathogen communities and if those communities vary across garden sites. We then evaluate the direct and indirect factors responsible for parasites and pathogens (Figure 1). We ask whether resource availability directly amplifies or dilutes parasite and pathogen prevalence in each host species. To examine if bee community composition exerts an indirect effect, we test for a relationship between resource availability and bee abundance and diversity. We then examine if bee abundance and diversity are, in turn, associated with amplification or dilution of parasite and pathogen prevalence. Because spillover between managed and wild species is a concern, we evaluate if parasite and pathogen prevalence in one host species is associated with parasite and pathogen prevalence in the other (Figure 1).

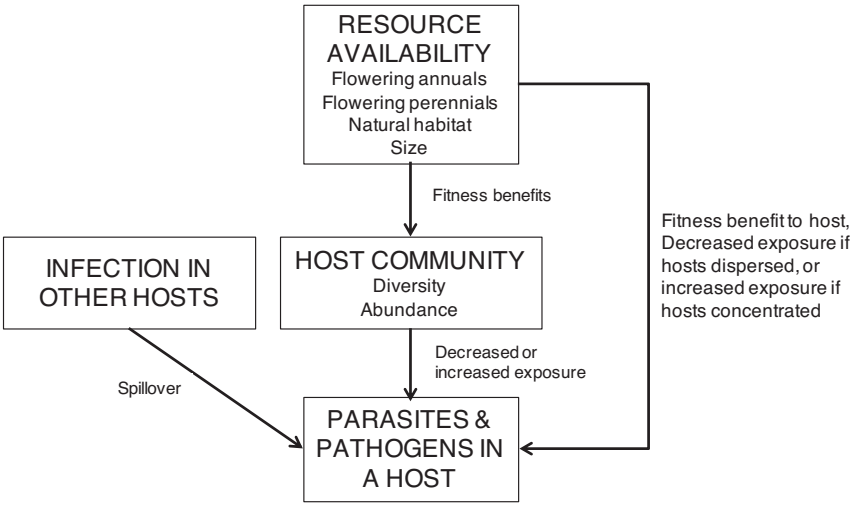

FIGURE 1 Conceptual diagram of the landscape epidemiology of flower-vectored parasites and pathogens. To simplify the representation of this complex system, both indirect and direct relationships are represented by a solid line, though it should be noted that these interactions may occur through both direct and indirect mechanisms

2 | MATERIALS AND METHODS

2.1 | Characterization of study sites

Our study system is comprised of urban gardens located across three counties (Monterey, Santa Clara, Santa Cruz) on the California central coast that are embedded in heterogenous urban habitat. Within this region, we examined characteristics of 18 urban gardens (444 m^2–15,525 m^2), each separated by 2 km or more. To quantify resource availability, we measured local characteristics within a 20 × 20 m plot at the centre of each garden between two sampling periods in June and July 2015. We counted and identified all flowering perennials (trees and shrubs in flower) to obtain abundance and richness estimates of flowering perennial species (Table S1). In each garden we selected four 1 × 1 m plots using a stratified random sampling approach. We selected one plot within each of four 5 × 20 m strips inside the sampling area. To obtain abundance estimates of annual flowers, we counted the number of flowers in the 1 × 1 m plots. We counted all flowers on composite flowers as individual flowers. We also measured total garden size (acres) to account for local habitat area in our analyses. Values for all variables were averaged across the two sampling periods.

To quantify resources availability at the landscape scale, we quantified natural habitat from the 2015 National Land Cover Database. Natural habitat was the total percentage of land cover identified as deciduous, evergreen, mixed forests, dwarf scrub, shrub/scrub, and grassland/herbaceous land cover. We excluded land cover that was identified as impervious urban development, agriculture, or commercial land-use (such as golf courses). We selected a 1 km buffer around each site, as this scale has been previously recognized as biologically relevant for bee foraging behaviors (Kremen et al., 2004).

2.2 | Bee community surveys

To examine the effect of bee community composition on disease transmission, we sampled bee diversity and bee abundance at each site using elevated pan traps and aerial nets across two sampling periods between mid-June and early July 2015 (Grundel et al., 2011). In each sampling period, we placed three 1 m PVC pipes 5 m apart in a triangle within the 20 × 20 m experimental plot at each site, and placed one bowl (yellow, white, blue) atop the pipes (Tuell & Isaacs, 2009). Pan traps were filled with 300 ml water and 4 ml dish soap, placed at each site between 8–9 AM, and collected between 3–5 PM on the same day. Contents were stored in 70% ethanol solution for identification.

We sampled bees using aerial netting once per sampling period. We searched for bees for 30 min at each site between 9:30 AM and 4:30 PM, and only when wind speed was below 2.5 m/s. A collector walked each of four 5 × 20 m strips at the center of the garden and bees were collected at random, as they were encountered in flight or visiting flowers. Collection was paused for handling time. We used dichotomous keys (Michener et al., 1994; Discover Life) to identify bees to species (or morphotaxon for certain genera such as Lasioglossum (*Dialictus*) where species identification is not feasible). Bee community data includes honey bees and bumble bees and ƒ is provided in Table S2.

2.3 | Collecting bees for parasite and pathogen detection

For three sampling periods within a 15-day span between late June and early July, we conducted an additional, targeted collection of the honey bee *Apis mellifera* (Hymenoptera: Apidae) and the yellow-faced bumble bee *Bombus vosnesenskii* (Hymenoptera: Apidae) from each site for parasite and pathogen detection. The honey bees we collected probably originated from both feral and domesticated colonies. At each sampling period, we used nets to collect foraging bees for 30 min. Each bee was placed into a sterile 2 ml vial, held in dry ice, and stored at −80°C. We sterilized equipment and gloves between handling specimens in the field. In total across all sites, we collected an additional 1,578 honey bees and 291 bumble bees from which we selected a random subsample for parasite and pathogen screening.

2.4 | DNA and RNA extraction

We extracted DNA and RNA from each specimen (de Miranda et al., 2013) with a modified protocol combining procedures from Qiagen DNeasy Blood and Tissue kit and Qiagen QIAamp Viral RNA mini kit. We homogenized each bee in cold PBS (320 µl for honey bees, 345 µl for honey bees) with bead-beating for 6 min at 30 Hz with sterile stainless-steel beads and 0.1 mm glass beads in a Qiagen Tissue Lyser II (Qiagen). We briefly centrifuged the homogenate, then transferred 180 µl into a microcentrifuge tube for DNA extraction. We centrifuged the remaining homogenate at 1,500 *g* for 10 min, then removed 140 µl of solution for RNA extraction. We hydrolysed DNA extract with 20 µl proteinase K in 200 µl buffer AL without added ethanol. After 12 h. incubation at 56°C, we followed standard spin column protocols. We pulse-vortexed each RNA extract with 560 µl of Buffer RNA-AVE/AVL to isolate RNA; after incubation at room temperature for 10 min, we followed standard spin column protocols.

2.5 | Species identification

Because *B. vosnesenskii* is nearly morphologically identical to *B. caliginosus*, we confirmed the identity of all *Bombus* specimens collected for parasite and pathogen screening by sequencing the protein-coding elongation factor −1 alpha gene using primer pair F2-ForH/F2-RevH2 (Hines et al., 2006; Kawakita et al., 2004). The forward strand of each DNA product was sequenced using Sanger Sequencing (Applied Biosystems 3730xl DNA Analyser, Retrogen), then aligned (Maddison & Maddison, 2015) and queried against the National Centre for Biotechnology Information (NCBI) nucleotide data with BLAST.

2.6 | Parasite and pathogen detection

We tested each bee for parasites and pathogens that vary by symptoms and transmission (Table S3). We refer to RNA viruses as pathogens as they are capable of causing disease symptoms in bees (e.g., deformed wing virus is associated with wing deformities). We refer to *Crithidia*, and *Apicystis*, and *A. borealis* as parasites because they benefit at the expense of their host. We tested 499 honey bees and 254 bumble bees for parasites. We screened DNA for the presence of *Apicystis*, *Crithidia*, and *A. borealis* using parasite specific primers and conditions for genus-level identification (Table S4). The primers used for *Crithidia* also detect *Lotmaria passim* (Schwarz et al., 2015). Each assay included a negative and positive control.

We screened a subset of specimens for RNA viruses (N = 292 honey bees and 242 bumble bees) using a multiplex reverse transcription PCR protocol, multiplex ligation-dependent probe amplification (MLPA), developed to simultaneously detect chronic bee paralysis virus (CBPV), deformed wing virus (DWV) and relatives, the acute bee paralysis virus (ABPV) complex, black queen cell virus (BQCV), slow bee paralysis virus (SBPV), and Sacbrood virus (SBV) and a positive control gene β-actin (De Smet et al., 2012). We used an MLPA kit (RT EK5, unlabeled primers) from MRC-Holland. Amplicons were resolved with a fragment analyser (Applied Biosystems 3130XL Genetic Analyser) with a DNF-905 reagent kit (Advanced Analytical Technologies Inc). We used a detection limit of 75 RFU (relative fluorescent units) for interpretation of fragments to obtain yes/no prevalence data for each virus.

2.7 | Data analysis

We conducted a principal coordinate analyses (PCoA) to test whether parasite and pathogen community composition differed between bee species and sites (using the vegan package in R, Oksanen et al., 2013). Parasite and pathogen community dissimilarly were calculated using the Jaccard index. To test the null hypothesis that the centroids were random in respect to species and in respect to site, we first ensured homogenous group dispersion using the betadisper function. We then used a permutational analysis of variance (PERMANOVA) with 999 permutations using the adonis function.

To determine which factors directly and indirectly influence bee health (Figure 1), we quantified parasite and pathogen prevalence by calculating mean parasite richness pathogen richness across all honey bees at a site and across all bumble bees at a site. We calculated parasite and pathogen richness because multiple infections are a stronger predictor of mortality and population decline than infections in bees (Arismendi et al., 2020). We included only specimens that were screened for all parasites and pathogens.

To address spillover between species, a possible predictor effect, we calculated parasite and pathogen infection rates in honey bees: for each individual honey bee we divided parasite and pathogen richness by the maximum number of parasites and pathogens possibly detected, then averaged these values at each site across sampling periods. We repeated this calculation for bumble bees. To quantify bee community composition, we calculated bee abundance as the mean number of individual bees found at each site across sampling periods, and quantified bee diversity as a Shannon's diversity index, taken as a mean at each site across sampling periods. Local floral resources were categorized as the abundance of flowering perennials and the abundance of flowering annuals. Because gardens varied in size, we additionally selected garden size as a covariate. Landscape floral resources was defined as natural habitat within 1 km.

We constructed a hierarchical analysis using Bayesian multilevel, multivariate models (Figure 1). We fit models to the data with a Markov Chain Monte Carlo method using the programming language Stan within R (v.4.1.1) (brms package, Bürkner, 2017). We first modelled the effect of local and landscape resource availability (garden size, abundance of flowering perennials, abundance of flowering annuals, and natural habitat within 1 km) on bee community abundance and on bee community diversity. We then tested whether parasite and pathogen richness is directly influenced by resource availability or is mediated by bee community diversity and abundance. To account for spillover effects between hosts, we included honey bee parasite and pathogen infection rate as an indirect effect on parasite and pathogen

richness in bumble bees. For honey bees, we included bumble bee parasite and pathogen infection rate as an indirect effect. We used a binomial response distribution for parasite and pathogen richness and included a random effect of site. We then constructed the same analyses with the prevalence of each individual parasite and pathogen as the response variables, for both honey bees and bumble bees.

We separated the models for honey bees and bumble bees. Before analysis we calculated variance inflation factors (VIF) using the car package (Fox et al., 2007) to check for collinearity between all variables in the models. All VIF scores were less than 2. All variables were scaled to a mean of zero and variance of 1. For each model, we ran four chains of 10^5 iterations each. Model fit and successful convergence was assessed with R-hat estimates (<1.00), trace plots, and posterior-predictive checks. We estimated model predictive power via Watanabe-Akaike information criterion (Watanabe & Opper, 2010). We also ran the models with richness of perennial plants rather than abundance of perennial plants. Because significant results were the same, we report here results from models with abundance of perennial plants. Host density can influence parasitism, but bee community abundance was colinear with both bumble bee abundance and honey bee abundance, and models run with these variables instead of bee abundance and diversity yielded the same significant results, reported in the supplement (Table S5).

3 | RESULTS

3.1 | Parasites and pathogens in urban bees

In our bee diversity survey we captured 1,670 bees (Table S2). This included 39 unique bee species and morphospecies and an average of 10.5 bee species per site. Both honey bee and bumble bee individuals were infected with parasites and pathogens (Figure 2, Table 1 for parasitism rates). Only a small subset of bees were entirely free of parasites and pathogens (1.03% of honey bee and 1.25% of bumble bees). The majority were infected with four parasites and pathogens (20.34% of honey bee and 19.09% of bumble bees). No bees had all RNA viruses and parasites, but a few had 8 parasite and pathogens (1.03% honey bees, 1.24% of bumble bees).

At the species level, honey bees and bumble bees hosted significantly different parasite and pathogen communities ($p < .001$, $F = 62.01$, df = 1; Figure S1a). At the site level, parasite and pathogen composition across all bees differed significantly between sites ($p < .001$, $F = 2.81$, df = 17; Figure S1b), suggesting that variation at both the site and species-level influences the composition of parasites and pathogens within bees.

3.2 | Resource availability and parasite and pathogen richness

We found evidence that garden size as positively associated with both bee abundance and bee diversity. We found additional evidence that natural habitat was associated with bee abundance, and the abundance of flowering perennials was negatively associated with bee diversity (Table 2, Figure 3).

We found evidence of parasite amplification due to local resource availability, but only for bumble bees (Table 3, Figure 4). For bumbles bees, garden size and flowering perennials were positively associated with parasite pathogen richness. Furthermore, parasitism in honey bees was positively associated with parasite and pathogen richness in bumble bees. Interestingly, we also found that bee diversity was negatively associated with parasite and pathogen richness in bumble bees, suggesting that bee

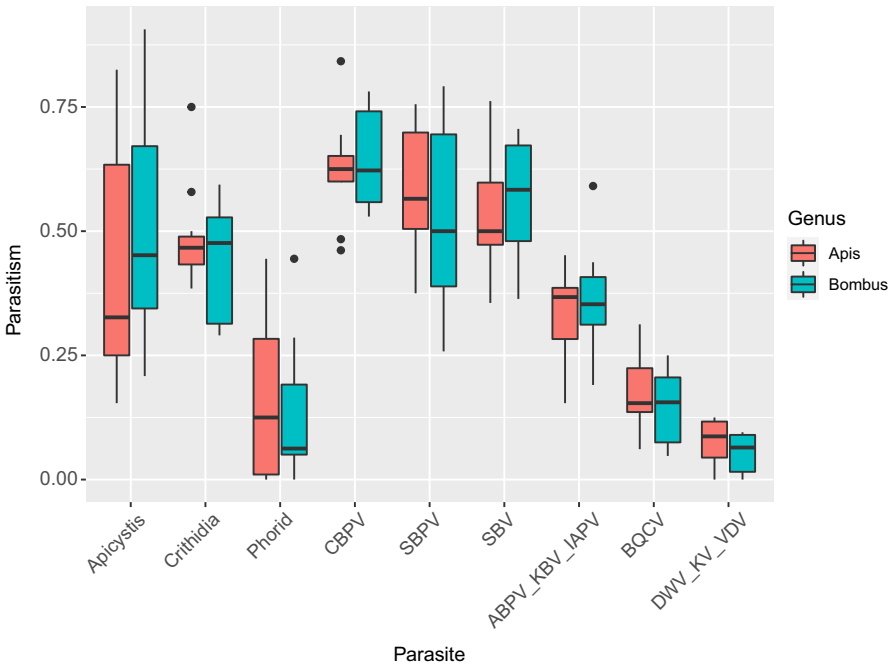

FIGURE 2 Mean parasitism rates for individuals within a species [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Infection prevalence rates for each parasite and pathogen. Standard error (SE) calculated as the standard deviation divided by square root of the sample size

	A. mellifera				*B. vosnesenskii*			
	# infected, all sites	*n*, all sites	% infected	SE (+/-)	# Infected, all sites	*n*, all sites	% Infected	SE (+/-)
Crithidia spp.	224	499	44.89	0.022	124	254	48.82	0.031
Apicystis spp.	199	499	39.87	0.022	134	254	52.76	0.031
A. borealis	50	499	10.02	0.013	84	254	33.07	0.029
DWV complex	30	292	10.27	0.018	9	241	3.73	0.012
ABPV complex	108	292	36.99	0.028	87	241	35.95	0.031
BQCV	62	292	21.23	0.024	21	241	8.67	0.018
SBPV	177	292	60.62	0.029	124	241	51.24	0.031
SBV	121	292	41.43	0.029	183	241	75.62	0.032
CBPV	148	292	50.68	0.029	194	242	80.17	0.025

diversity dilutes pathogen richness for bumble bees (Table 2). We found no significant predictors of parasite and pathogen richness in honey bees.

3.3 | Resource availability and the prevalence of each parasite and pathogen

The impact of bee diversity and bee abundance on the prevalence rate of each individual parasite and pathogen varied (Table 3, Table S6). Bee diversity was positively associated with ABPV CBPV in honey bees and with *Apicystis* in bumble bees. Bee diversity was negatively associated with DWV in honey bees and with CBPV in bumble bees. Bee abundance was positively associated with SBPV in honey bees and with *Crithidia* and SBV in bumble bees. Bee abundance was negatively associated with Crithidia in honey bees.

Several local and landscape factors mediated parasite and pathogen outcomes (Table 3 for summary and Table S6 for full model statistics). For honey bee parasites, *Crithidia* was positively associated with garden size. Phorid prevalence was negatively associated with phorid parasitism in bumble bees. *Apicystis* was positively associated with the abundance of flowering perennials. For honey bee viruses, BQCV was positively associated with natural habitat (1 km), CBPV was negatively associated with garden size, and DWV was positively associated with DWV parasitism in bumble bees. SBPV was negatively associated with garden size. ABPV and SBV had no associations with local or landscape variables.

For bumble bee parasites, *Crithidia* was negatively associated with garden size. Phorid prevalence had no association. *Apicystis* was positively associated with *Apicystis* prevalence in honey bees. For bumble bee viruses, BQCV was positively associated with the abundance of flowering perennials, and CBPV and DWV were positively associated with garden size. SBPV was positively associated with the abundance of flowering perennials. SBV was positively associated with the abundance of flowering annuals. ABPV had no associations with local or landscape variables.

4 | DISCUSSION

4.1 | Bee species share parasites and pathogens and have high infection rates

We corroborate that bee species share parasites and pathogens (Evison et al., 2012; Gamboa et al., 2015; Goulson et al., 2008; McMahon et al., 2015; Ravoet et al., 2014), but report that the *composition* of parasite and pathogen communities significantly differs between honey bee and bumble bee hosts. The use of managed honey bees has been implicated in the spillover of parasites and pathogen to wild species (Graystock, Blane, et al., 2016), and we here confirm that parasite and pathogen prevalence in honey bees was significantly correlated with parasite and pathogen richness in bumble bees. This relationship was not reciprocal, as honey bee parasite and pathogen richness did not respond to bumble bee prevalence. Our study additionally found that parasite and pathogen prevalence in honey bees and in bumble bees responds to different environmental variables. We suggest that morphological and physiological differences in traits between host species may drive parasite and pathogen colonization and persistence in this system. There is little literature on the role of bee host traits in epidemiology, but traits such as body size and diet breadth have been found to play a role in pathogen exposure (Cohen et al., 2021; Figueroa et al., 2019, 2020), probably by mediating bee behaviour at flowers harbouring parasites and pathogens. For example, bees with a broader diet breadth may visit more plant species and therefore risk exposure to a diversity of parasites and pathogens.

We found high infection rates in both *Apis mellifera* and *Bombus vosnesenskii*. While *Apicystis* has previously been considered a minimal threat, it was recently reported in 30%–50% of sampled honey bee and bumble bee colonies and has both lethal and sublethal effects for bumble bees (Graystock et al., 2013, 2014, 2016). Our study found high *Apicystis* rates at 52.76% prevalence in bumble bees and 41.77% in honey bees. It is important

TABLE 2 The results of analyses illustrating relationships between resource availability and bee abundance/diversity, and bee abundance/diversity and infection prevalence. Table includes the parameter estimates, upper and lower credible 95% intervals, bulk effective sample size, and proportion of the posterior samples greater or less than zero. a and b indicate that 95% (strong support), or 85% (support) of the posterior is either greater than or less than zero, respectively. Variables with support are additionally bolded

Model	WAIC ± SE	Response	Explanatory variable	Est.	Error	l−95% CI	u−95% CI	Bulk_ESS	Tail_ESS	$p > .0$	$p < .0$	Support
Honey bees	1131.6 ± 30.9	Bee abundance	**Natural habitat 1 km**	0.58	0.22	0.14	1.02	204660.25	137023.97	.99	.01	a
			Abundance perennials	0.07	0.23	−0.38	0.53	209696.09	138127.79	.62	.38	
			Abundance annuals	0.04	0.16	−0.28	0.36	221565.75	136393.62	.61	.39	
			Garden size	0.36	0.24	−0.13	0.84	217626.13	132679.17	.93	.07	b
		Bee diversity	Natural habitat 1 km	−0.21	0.27	−0.74	0.33	211925.42	142057.32	.21	.79	
			Abundance perennials	−0.42	0.28	−0.98	0.14	220472.62	143681.96	.06	.94	b
			Abundance annuals	−0.15	0.2	−0.54	0.25	224990.91	134255.35	.22	.78	
			Garden size	0.35	0.3	−0.25	0.93	225934.26	141089.69	.88	.12	b
		Parasite/pathogen richness	Bee diversity	0.11	0.13	−0.15	0.37	89787.88	110434.41	.82	.18	
			Bee abundance	0.03	0.19	−0.36	0.41	71641.17	95089.28	.56	.44	
			Natural habitat 1 km	−0.04	0.18	−0.39	0.31	75742.36	100038.21	.4	.6	
			Abundance perennials	0.04	0.13	−0.21	0.3	108573.36	119665.11	.63	.37	
			Abundance annuals	−0.01	0.09	−0.18	0.17	108922.91	118712.8	.47	.53	
			Garden size	−0.06	0.15	−0.36	0.23	91706.65	110408.36	.33	.67	
			Bumble bee parasitism rate	0.08	0.09	−0.1	0.27	89581.48	110697.29	.83	.17	
Bumble bees	961.2 ± 31.9	Bee abundance	**Natural habitat 1 km**	0.64	0.21	0.22	1.06	207863.96	134052.51	1	0	a
			Abundance perennials	0	0.22	−0.44	0.44	204517.5	138919.72	.49	.51	
			Abundance annuals	0.08	0.15	−0.23	0.38	229227.77	134654.18	.71	.29	
			Garden size	0.45	0.23	−0.03	0.91	203754.97	136992.61	.97	.03	a
		Bee diversity	Natural habitat 1 km	−0.2	0.28	−0.77	0.36	214637.8	139652.49	.23	.77	
			Abundance perennials	−0.43	0.3	−1.01	0.18	208617.38	143786.1	.08	.92	b
			Abundance annuals	−0.14	0.21	−0.56	0.27	222891.35	137429.15	.23	.77	
			Garden size	0.35	0.32	−0.29	0.97	211018.57	134084.39	.87	.13	b
		Parasite/pathogen richness	**Bee diversity**	−0.14	0.15	−0.45	0.16	78038.03	89449.45	.15	.85	b
			Bee abundance	0.12	0.18	−0.25	0.48	72915.37	90576.38	.77	.23	
			Natural habitat 1 km	−0.08	0.19	−0.44	0.31	66464.45	82341.05	.3	.7	
			Abundance perennials	0.21	0.11	−0.01	0.45	117070.41	110293.86	.97	.03	a
			Abundance annuals	−0.03	0.09	−0.21	0.16	91125.4	102809.89	.36	.64	
			Garden size	0.14	0.13	−0.12	0.41	103093.28	107052.18	.88	.12	b
			Honey bee parasitism rate	0.2	0.15	−0.12	0.48	76762.66	91171.37	.91	.09	b

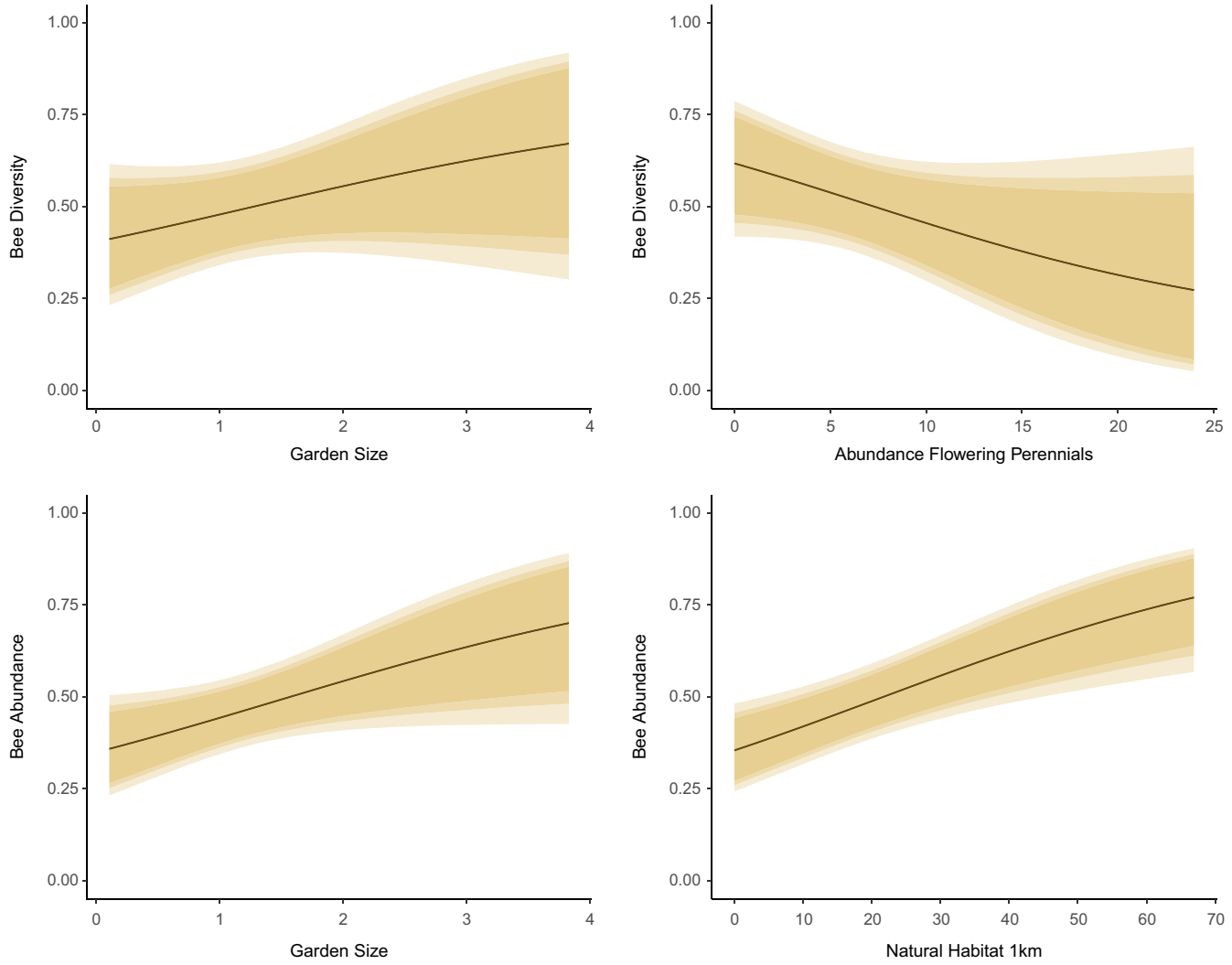

FIGURE 3 Bee diversity and bee abundance were positively associated with garden size (acres). Bee diversity was additionally negatively related to flowering perennials, and bee abundance positively related to natural habitat (1 km). The solid black indicates the slope estimate (mean of the posterior) and the colored regions from dark to light purple are the 95%, 90%, and 85% credible intervals around the estimate [Colour figure can be viewed at wileyonlinelibrary.com]

to note that we did not surface sterilize each specimen, and therefore testing positive for parasite or pathogen presence does not necessarily indicate that a parasite or pathogen is replicating in the host gut. The impact of parasites and pathogens may vary by habitat; for example, condition-dependent pathogens can appear asymptomatic under good, resource abundant conditions, and negative impacts on host fitness may only become apparent under resource-limited conditions (Brown et al., 2003; Manley et al., 2017). High infection rates may reflect low resistance to infection or high tolerance to infection (Goulson et al., 2012). However, even individuals passively carrying a parasite or pathogen might still be infectious to others (Graystock et al., 2013). We also observed that many bee individuals hosted multiple parasites and pathogens, calling for further work to determine if there are interactive and cumulative effects of hosting multiple parasites and pathogens.

4.2 | Bee diversity reduces parasite and pathogen risk for bumble bees

Several epidemiological models predict a relationship between species diversity and transmission (Keesing et al., 2006; Schmidt & Ostfeld, 2001). We found that bee community diversity was associated with lower parasite and pathogen richness in bumble bees. While bee diversity might drive infection if pathogens have more hosts to colonize, our findings suggest, for bumble bees, wild bee diversity dilutes risk, effectively "protecting" bees against pathogens. Our diversity index accounts for abundance and evenness of the species present. Therefore, it is possible that parasitism was reduced by mechanisms related to increased host abundance, such as encounter reduction (decreases in parasite contact between hosts) or host-host competition (reduction of host fitness due to competition, resulting in reduced parasite

TABLE 3 The parameter estimates and errors for the variables associated with each individual parasite and pathogen. a and b indicate that 95% (strong support) or 85% (support) of the posterior is either greater than or less than zero, respectively. Only significant variables are reported. For full model statistics, see Table S5

Host	Model	Bee diversity	Bee abundance	Natural habitat (1 km)	Abundance perennials	Abundance annuals	Garden size	Parasitism rate of other host species
Honey bees	Apicystis				0.42 ± 0.42 b			
	Crithidia		−0.57 ± 0.34 b				0.35 ± 0.27 b	
	Phorid							−1.12 ± 0.80 a
	ABPV	0.62 ± 0.23 a						
	BQCV			0.58 ± 0.29 a				
	CBPV	0.45 ± 0.25 a					−0.36 ± 0.27 b	
	DWV	−0.63 ± 0.37 a						0.55 ± 0.38 b
	SBPV		0.76 ± 0.45 a				−0.51 ± 0.38 b	
	SBV							
Bumble bees	Apicystis	0.42 ± 0.3 b						0.88 ± 0.29 a
	Crithidia		0.55 ± 0.48 b				−0.52 ± 0.41 b	
	Phorid							
	ABPV							
	BQCV				0.61 ± 0.46 b			
	CBPV	−0.39 ± 0.39 b					0.42 ± 0.37 b	
	DWV						1.08 ± 0.62 a	
	SBPV				0.49 ± 0.48 b			
	SBV		0.68 ± 0.34 a	−0.69 ± 0.32 a		0.92 ± 0.51 a		

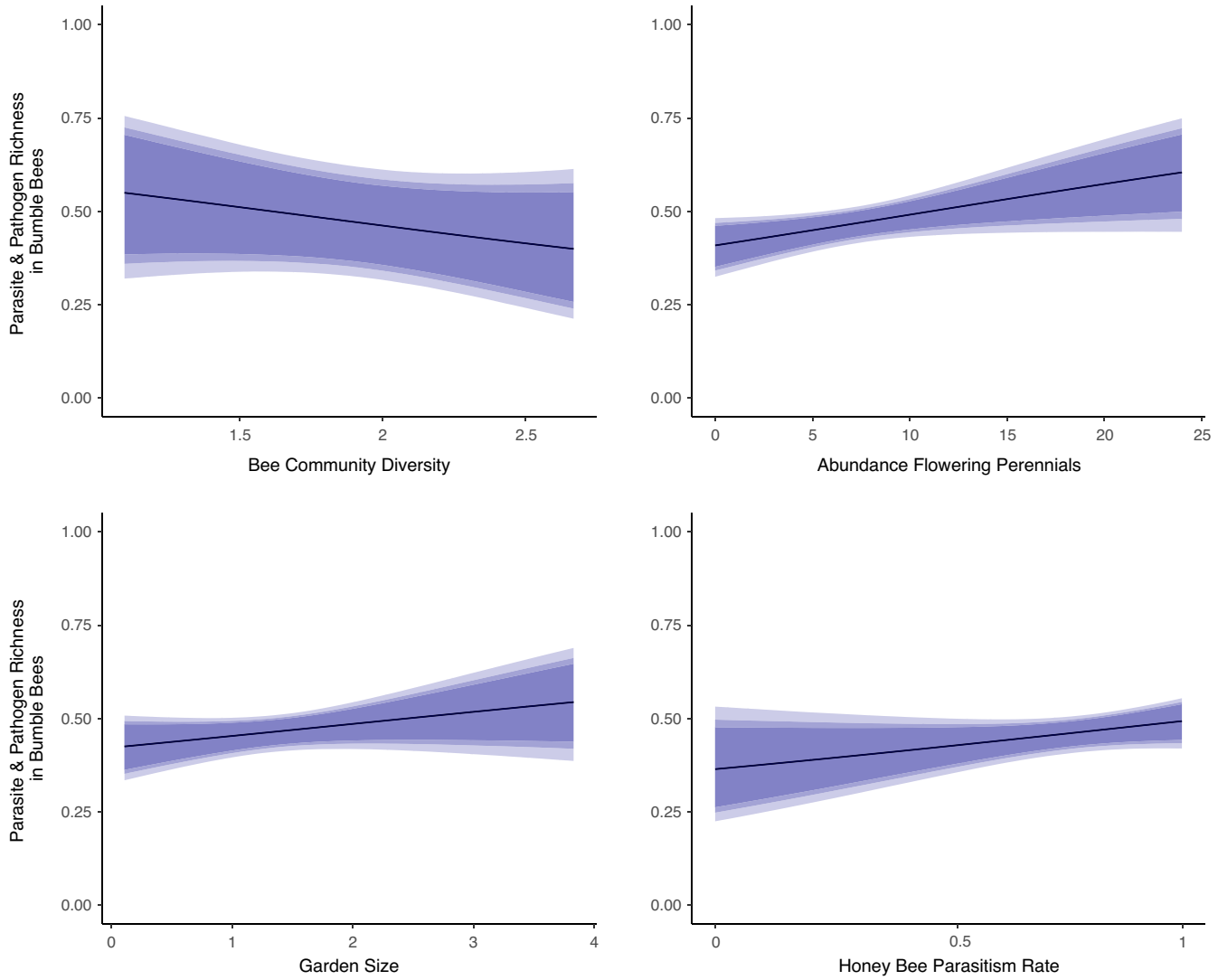

FIGURE 4 We found evidence that parasite and pathogen richness in bumble bees was negatively related to bee community diversity at garden sites and positively related to flowering perennials, garden size (acres), and parasitism in honey bees. The solid black indicates the slope estimate (mean of the posterior) and the colored regions from dark to light purple are the 95%, 90%, and 85% credible intervals around the estimate. No variables significantly predicted parasite and pathogen richness in honey bees [Colour figure can be viewed at wileyonlinelibrary.com]

success; Civitello et al., 2015; Keesing et al., 2006). However, bee abundance alone was a not a significant predictor, suggesting that increases to host abundance without increases to richness does not confer risk dilution.

Bee diversity is an indirect link that mediates the relationship between garden size and pathogen outcomes in bumble bees because garden size was also associated with increased pathogen richness. The viral pathogens we tested have traditionally been considered honey bee diseases. One mechanistic possibility is that, while many species will host pathogens, some species are more competent hosts than others for the replication and reproduction of the virus. If transmission of pathogens is greater within species than between species, and if some species are more competent hosts than others, then the diversity of wild bees in a garden will reduce pathogen reproduction, persistence, and transmission.

4.3 | Bee diversity is promoted by garden size

Bee species diversity and abundance responded positively to garden size, confirming previous reports that garden size promotes bees (Pardee & Philpott, 2014). The importance of garden size probably reflects the life history requirements of bees. Bees are central place foragers, flying fixed distances from a nesting site (Michener, 2007). Several the bee species in this study exhibit limited foraging ranges (<500 m), suggesting that they nest near gardens. Within an urban matrix, large garden area probably provides nesting habitat and promotes diversity. Garden size also probably corresponds with factors we did not measure, such as proportion of habitat edge to area or garden heterogeneity. For example, Loram et al. (2008) found that garden size is positively to within-garden heterogeneity of land-use types such as unmown grass, mature trees and shrubs,

and ponds. Garden size is potentially related to floral area, which has been linked to urban bee species richness (Matteson & Langellotto, 2010). Our study suggests that the species-area relationship is applicable at the scale of urban gardens and highlights the importance of promoting garden size to enhance bee diversity, which subsequently dilutes parasitism risk. Although promoting garden size is a matter of geographic, historical, cultural, and socioeconomic factors (Gaston & Gaston, 2010), our research suggests that enhancing garden size is an opportunity for pollinator conservation.

4.4 | Parasite and pathogen prevalence exhibit complex responses to resource availability

For bumble bees, parasite and pathogen richness was positively driven by garden size and perennial floral resources. This was also true for a subset of bumble parasites and pathogens; when floral resources were significant for parasitism in these models, the relationship was always positive, suggesting a broad pattern of resource-based amplification. Amplification may be due to increased bee aggregation at floral sites and thus increased transmission between individuals of parasites and pathogens with density-dependent transmission.

For honey bees, none of the variables we measured had an impact on parasite and pathogen richness, although bee diversity, abundance, and resource availability had mixed associations with the prevalence of some specific parasites and pathogens. It is difficult to tease apart these complex interactions, probably because dynamics depend on the life history, phenology, and behaviors of the bee hosts. For example, infection by varroa mite *Varroa destructor* is ubiquitous in honey bees and associated with increased viral coinfection (Martin et al., 2012), but varroa mite does not reproduce in bumble bees. Additionally, we know very little about the importance of intracolony transmission of parasites and pathogens and how this differs between honey bee and bumble bee species. Transmission is also impacted by the features of each parasite and pathogen and infection dynamics probably differ between phorids (an arthropod parasitoid) and RNA viruses, microsporidians, and protozoans. For example, bee survivorship in the face of *Crithidia* is enhanced by diet (Figueroa et al., 2021), whereas bees are unlikely to overcome phorid fly infection through nutrition or immunological defence, so it is unreasonable to expect that annual or perennial floral resources would dilute phorid parasitism. Further, we found that some parasites and pathogens did not respond to bee diversity, bee abundance, or resource availability. For these parasites and pathogens, it is possible we did not capture relevant factors in our measurements, such as agrochemical exposure, which has been shown to influence pathogen prevalence (McArt et al., 2017). Alternatively, vertical transmission may be a better predictor of prevalence for some parasites and pathogens.

We expected that natural cover at the landscape scale would be significant for parasite and pathogen dynamics because a few studies have documented a relationship between urbanization and increased pathogen prevalence in honey bees (Youngsteadt et al., 2015) and bumble bees (Goulson et al., 2012; Theodorou et al., 2016), although McArt et al. (2017) observed greater pathogen prevalence in bumble bees in less urban areas in comparison to those from more urban areas. We observed that natural cover had positive, negative, or no association with parasite or pathogen prevalence depending on the host species and particular parasite or pathogen. Because natural habitat also had no association with parasite or pathogen richness, we suggest that the relationship between natural landscape cover and disease epidemiology in urban systems may depend on the composition of the habitat matrix. Generally, our field sites included perennial fruit trees, ornamentals, annual crops, and weeds, whereas natural habitat around each site includes vegetation such as grassland, shrubs, and forest – resources that bees may or may not utilize, depending on the site.

Because many pollinator species have undergone range contractions and extinctions over recent decades (Goulson et al., 2008; Kosior et al., 2007; Williams & Osborne, 2009) and contribute to pollination (Aizen et al., 2008; Ollerton et al., 2011), our findings call for greater understanding of disease transmission in changing landscapes. Our study suggests that, in the face of resource-driven amplification of parasites and pathogens, the spread of disease may be mitigated by increases in bee species diversity, but not for all bee species. We suggest that conservation management approaches should be species-specific and tailored to geographic region. We also found evidence of spillover between honey bees and bumble bees, and suggest caution when promoting urban beekeeping. Because garden size and the abundance of floral resources had an amplification effect for parasites and pathogens in bumble bees, and because floral traits influence transmission (Adler et al., 2018; McArt et al., 2014), we echo other calls to design (Figueroa et al., 2020) conservation plantings that will promote bee diversity, offer pollen and nectar resources, and minimize disease spread.

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CONFLICT OF INTEREST

We have no competing interests.

AUTHOR CONTRIBUTIONS

Hamutahl Cohen led grant acquisition and management, study design, fieldwork, laboratory work, data analysis, and manuscript writing. Lauren C. Ponisio contributed to data analysis and the manuscript. Kaleigh A. Russell contributed to laboratory protocol design and laboratory work. Stacy M. Philpott led field site design and contributed to fieldwork logistics and manuscript writing. Quinn S. McFrederick contributed to field research protocols, provided physical and financial access to laboratory supplies, helped design laboratory methods, and contributed to the manuscript.

BENEFIT-SHARING

Benefits Generation: The results of the research have been shared with participating communities and data shared via data and code repositories. This research addresses conservation of endangered organisms, a priority concern in the region of study.

DATA AVAILABILITY STATEMENT

Code is deposited on Github (https://github.com/hamutahlc/urbanbeeparasites). Data has been deposited at Zenodo (https://doi.org/10.5281/zenodo.3609232). Supporting materials have been included as part of supplementary material.

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