Article

BEE DIVERSITY IN APPLE ORCHARDS OF THE LOWER HIMALAYA: RESEARCH SYNTHESIS, A NEW FIELD STUDY, AND FUTURE NEEDS

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Abstract—In northern India and surrounding countries of the Lower Himalaya, apple is an important cash crop that contributes significantly to state economies and farmer livelihoods. Apple cultivation is shifting to higher elevations to counter declining fruit yields associated with climate change. Pollinator scarcity is another factor linked to declines in fruit yield and quality. To advance understanding of bee diversity and pollination ecology in apples for this region, we compiled a taxonomically updated list of bee taxa associated with apple orchards using records from existing literature and a new field study. Our list includes 25 bee genera, 75 named species, and numerous morphospecies. Common genera also feature prominently in apple studies elsewhere in the world. *Apis cerana* and *A. mellifera* were the most frequently reported visitors to apple flowers; *Bombus*, *Ceratina*, *Lasioglossum*, and Syrphidae flies were the most common non-*Apis* floral visitors. Bee species richness was inversely correlated with elevation and pollination deficit whereas bee abundance was not. Therefore, apples grown at higher elevations may experience more favourable growing conditions but also incur greater pollination deficits that are linked to reduced bee richness. This underscores the importance of conserving bee diversity to safeguard pollination services and farmer livelihoods in the region. Our literature review further highlights the need for more tools to identify the regional bee fauna, more thoroughly documented and standardised study methods to build capacity within the research community and aid comparative studies, and more expansive cataloguing and monitoring of pollinator communities to better understand the diversity, roles, and status of bees throughout this under-studied region.

Keywords—Bees, diversity, abundance, apple, pollination deficit, elevation

INTRODUCTION

Pollinators are critical to plant reproduction in natural ecosystems and food production in agricultural systems (Klein et al. 2007). The diversity and abundance of pollinators directly influences the efficiency and success of pollination, which in turn affects crop yields and quality (Garibaldi et al. 2013, 2014; Reilly et al. 2020; Vasiliev & Greenwood 2020; Katumo et al. 2022). Declines in wild and managed pollinator populations – driven by factors such as habitat loss, pesticide use, and climate change (Kremen et al. 2007; Potts et al. 2010; Tylianakis 2013; Goulson et al. 2015; Wagner 2020) – threaten human food security and livelihoods (Bauer & Sue Wing 2010; Garibaldi et al. 2013; Cely-Santos & Lu 2019). Knowledge of the diversity, status, and roles of pollinators in food systems is important for

understanding the resilience of pollination interactions in the face of changing environmental conditions.

Apple (*Malus domestica*) is one of the most widely cultivated and consumed fruits worldwide (Worldostats 2025). For most apple varieties, crop production is highly pollinator-dependent (Ohlnuud et al. 2022; classified as 'great' by Klein et al. 2007) and bees are their primary pollinators (Pardo & Borges 2020). Pollination success is correlated with bee diversity and abundance; any decrease in these factors can increase pollination deficit and decrease crop yield and quality (Garibaldi et al. 2013; Garratt et al. 2014; Mallinger & Gratton 2015; Martins et al. 2015; Blitzer et al. 2016). There is evidence of widespread declines in wild and domesticated bee populations, although most data come from Europe and North America (Potts et al. 2010; Wagner 2020). There remains a pressing need for baseline pollinator data and pollination research in other areas of the globe, including Asia as a whole (Warrit et al. 2023) and India specifically (Adit et al. 2024).

Asia ranks first worldwide in apple production and India is fifth among nations (Pardo & Borges 2020; USDA Foreign Agricultural Service 2025). Both of these regions lag well behind North America and Europe in terms of understanding the pollinator communities associated with apples and the factors that affect services they provide (Pardo & Borges 2020). The prime area for apple cultivation in India and surrounding countries lies along the southern slopes of the Lower Himalaya between 1,500 and 3,500 m elevation (Sahu et al. 2020). Most farms in this region belong to smallholder farmers and apple growing is an important contributor to state economies and farmer livelihoods (Vedwan 2008; Joshi & Sarkar 2017; Bhat et al. 2021). Most smallholder farmers rely primarily on wild insects (mostly bees) for crop pollination services (Partap & Partap 2002; Rather et al. 2017; Dorji, Marshall, et al. 2022). Apple production has been declining in recent decades, however, and increasing pollinator scarcity has been cited as an important contributing factor (Partap & Partap 2002; Gautam et al. 2004; Partap & Partap 2004; Dorji, Marshall, et al. 2022). Although multiple insect surveys in the region have documented insect communities associated with agricultural lands or specific plant species (Joshi & Joshi 2010; Kapkoti, Joshi, et al. 2016a, 2016b; Kapkoti, Rawal, et al. 2016; Chauhan et al. 2021; Arya et al. 2022), few studies have focused specifically on bees. Moreover, methods used to sample general insect diversity may not be the most effective for sampling bee communities (Prendergast et al. 2020; Thompson et al. 2021; Klaus et al. 2024). These limitations in taxonomic focus and sampling methodology have likely under-documented the bee fauna.

Alongside the need for more information on bee communities associated with apple orchards in the Lower Himalaya, our understanding of how elevation impacts wild bee richness and abundance in this mountainous landscape is incomplete. Addressing this gap is important because apple cultivation in this region has been shifting upward due to climate change to take advantage of cooler temperatures needed for apple cultivation (Rana et al. 2011; Singh et al. 2016; Rahimzadeh 2017; Sahu et al. 2020; Khan et al. 2023). However, bee species richness and abundance generally decrease with increasing elevation (Hoiss et al. 2012; Jugran et al. 2019) and several studies from the Himalayan region support these findings (Joshi et al. 2008; Jugran et al. 2019; but see Kapkoti, Rawal, et al. 2016). Previously for this region we showed that, in apples, pollination deficit (a shortfall in crop output due to a lack of pollination; Webber et al. 2020) increased with elevation (Fraser et al. 2024). We did not test for connections between these measures and bee richness or abundance, however. Here, we address this gap.

To consolidate knowledge about bee communities associated with apples in the Lower Himalaya and better understand their relationships with elevation and pollination deficit, we sought to (1) compile a comprehensive and taxonomically updated catalogue of bee taxa associated with apple-production sites using records from the published literature and a new field survey; (2) assess relationships between elevation and bee richness, abundance, and community composition; and (3) assess relationships between pollination deficit and bee richness and abundance. With respect to the latter two goals, we predicted that bee species richness and abundance would decrease with increasing elevation, and that pollination deficit would

increase with decreasing bee richness and abundance. Within our field survey, we also explored whether pan trap colour influenced bee captures.

MATERIALS AND METHODS

REVIEW OF APPLE POLLINATOR DIVERSITY SURVEYS IN THE LOWER HIMALAYA

To compile a comprehensive list of bee taxa associated with apple-production sites in the Lower Himalaya, we began by conducting a Boolean search in Google Scholar using the keywords "insects", "pollinators", and "Himalaya" to locate potentially relevant studies that included records of bee taxa. We included only those studies conducted in the south-facing slopes of India and adjacent countries (Pakistan, Nepal, Bhutan) that included bee data. Information on taxa other than bees that was included in sources was not used as a selection criterion. We then checked the references cited in each study to identify other potentially relevant sources that were not located by our Google Scholar keyword search. In total, we generated a preliminary list of 63 sources for review.

From this list, we narrowed the scope to include only those studies (or portions thereof) that were conducted at elevations from 1,100 to 4,000 m a.s.l. (the elevational range for apple production in the region), that included sampling within apple orchards, that focused on more than a single bee genus (e.g. more than just *Bombus* or *Apis*), and that attempted to identify at least some specimens to species or morphospecies level. Based on these criteria, we excluded 36 studies from our preliminary list. Two more studies that met selection criteria contained previously published results from apples rather than original data (Raj & Mattu 2014; Joshi et al. 2016) and were not counted as new studies; instead, data from these studies were merged with data from the original studies (Joshi & Joshi 2010; Raj et al. 2012) to avoid duplication of information.

In the end, 25 studies were included in our review. For each study, we extracted information on study site location, elevation range, sampling dates, fruit types from which data were extracted (apples exclusively or apples and other fruit types combined when data were not disaggregated in the original study), stated or inferred sampling methodology, names of all bee taxa recorded in each study, whether the study contained data on floral visitors, and order or family name of predominant non-bee floral visitors. Bee names as originally reported in each study were checked against valid names listed in Discover Life (https://www.discoverlife.org/), Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/), and the Integrated Taxonomic Information System (ITIS) (https://www.itis.gov/). Misspelled and invalid taxon names were updated to reflect current taxonomy; names as they appeared in the original studies were preserved in a comments column. We also used information contained in the ITIS database and inferred from occurrence maps on Discover Life and GBIF to record the documented geographic distribution of each taxon.

In addition to compiling a list of bee taxa associated with apples, we used data from studies to summarize patterns in the geographic distribution and taxonomic focus of studies, methods used to survey insects, and predominant bee genera found visiting or in close proximity to apple flowers.

FIELD STUDY

Study area and farm selection

This study was conducted between early February and late April 2023 on apple-producing farms that ranged in elevation from 1,680 to 2,360 m in the Mukteshwar region of Uttarakhand state in northern India (79.60°N – 79.64°N and 29.43°E – 29.48°E; Fig. S1). Fifteen farms were selected for inclusion based on farm acreage, number of apple trees in the orchard, farming practices, elevation, and willingness of farmers to participate in the study (Table S1). Sampling was conducted on all fifteen farms but the number of statistically independent farms was subsequently reduced to 13 because two pairs of adjacent farms (H and J, and P and Q) were each located within 50 m of one another. We merged data collected from adjacent pairs and adjusted for the greater sampling effort on these merged farms (HJ and PQ) prior to data analyses by using per trap abundances across all farms and mean species richness values for the two merged farms. The distances between other farms ranged from between 100 to 350 m (farms in clusters D, E, F and K, L, M, N) to over 500 m (all remaining farms; Fig. S1).

The land cover in the region is a mosaic of mixed-use farms, fodder slopes, forests of varying composition (e.g. pine- or oak-dominated) and disturbance level, abandoned lands, and urban or built environments. The terrain is mountainous with many farms located on terraced slopes 500 m or more from the nearest road and accessible only by walking path. This made repeated visits to farms challenging. To make periodic insect collections over a ten-week period more feasible, we engaged farmers as community scientists and trained them to use passive collecting methods (pan traps and vane traps) to collect samples within apple orchards. Multiple apple varieties are cultivated in the study area, of which Brown Delicious (also known as 'DK') and Fenny (another Delicious variety) predominate (see Table S1). Fraser et al. (2024) demonstrated high pollinator dependence among these varieties, with over 75% higher fruit set across the elevational gradient under open pollination conditions compared to under pollinator exclusion conditions. All chosen farms use conventional methods to manage pests. We did not survey farmers about spray frequency but farmers acknowledged using pesticides on peach trees just before apple bloom typically begins. This likely has an impact on pollinator abundance during apple bloom season. All chosen farms practice polyculture and plant various annual crops (e.g. peas, onions, potatoes) beneath and around rows of apple trees. Vegetable crops were in their early (preflowering) stages of growth during the first half of the study period; some pea and mustard plants flowered at the same time as apple but the number of vegetable crop blossoms relative to apple blossoms was low. Most farms relied on wild bees for pollination; three farms kept one or more (maximum seven) managed hives of *Apis cerana*, the indigenous honey bee species.

Bee sampling

We used two passive collection methods, pan traps and vane traps, to sample the bee fauna within orchards. A total of six samples were collected on each farm with one exception (Farm B, five samples only) at roughly biweekly intervals, beginning mid-February and ending late-April (Table S2). Samples for farms HJ and PQ were composed of two merged samples from their respective farm pairs (farms H and J, and farms P and Q). We trained farmers in collection methods during the first round of sampling; thereafter farmers collected samples independently. All farmers were remunerated for their work on the project. Farmers recorded the date and time of trap placement and collection, along with the number of traps damaged or lost during each sampling instance. One farm's vane trap (Farm K) was irreparably damaged during the first sampling instance and some other farms were unable to collect a vane trap sample at each sampling date (Table S2).

For pan trap sampling, we used 3.25 oz plastic cups (Solo Cup Company, Urbana, IL) that were opaque white in colour and left unpainted, or translucent and painted on the inner surface with a silica flat base colour mixed with either fluorescent blue or fluorescent yellow pigment (Guerra Paint and Pigment Corp., New York, NY). We set out 30 cups per site (ten of each colour) on each sampling date. Cups of alternating colours were placed on bare ground at 5 m intervals between two tree rows and arranged along two parallel transects containing 15 cups each. Parallel transects were 10 m apart. The distance between the ground and the lower branches of the apple tree canopy varied with tree size but was less than 1.5 m. On terraced slopes, pan traps placed at ground level on one terrace reached the lower to mid canopy height of trees on the adjacent downhill terrace. As a result, both ground-and canopy-foraging insect species likely encountered the coloured cups when foraging. Each cup was partially filled with a solution of soapy water to break the surface tension. Sampling was conducted on days when the weather was forecast to be sun/part sun, seasonably warm temperatures (> 14°C), and light winds. Cups were set out by 0900 h on one day and collected 24 h later. At each site, the contents of all intact cups of the same colour (up to 10 in total) were poured through a tea strainer and then transferred to a labeled Whirl-Pak® bag to which a small amount of 70% ethanol preservative was added. This was repeated for each cup colour. Samples were stored at ambient temperature until they were processed. The number of damaged or missing cups of each colour were recorded to adjust for sampling effort prior to data analysis.

For vane trap sampling we used a single blue vane trap (SpringStar Inc., Woodinville, WA). The upper portion of the trap consisted of two blue plastic vanes inserted into a blue funnel lid. This screwed onto a 32 oz. clear plastic container (Ziploc® Twist 'n Loc®). The vane trap was partially filled with soapy water and hung from a bare branch within the orchard, at least 5 m from the pan traps. The vane trap was to be deployed and collected at the same time as were pan traps. Specimens were extracted and preserved as described above and damaged or missing vane traps were recorded. For unknown reasons, vane traps were not deployed in a consistent manner across farms. For this reason, vane trap data were used for descriptive purposes only.

Specimen processing and identification

Two bee biologists (AMF and PSV) examined each sample bag and separated bees from other bycatch specimens. For the first few samples, all bycatch was discarded. As processing progressed, we began saving syrphid flies and recording the number of Lepidoptera present as well. Bees and many syrphid fly specimens were washed, dried, pinned and labeled with a unique identification number according to procedures described in Droege et al. (2016). All bees were identified to genus by AMF and PSV using a dichotomous key for Indian bees (Batra 1977). We did not have the expertise to determine syrphid fly specimens to genus or species and have not included them in this study. We used taxonomic keys to identify *Apis* (Burrows et al. 2021) and *Bombus* (Williams 2022) specimens to species. We could not locate species keys for other bee taxa. Consequently, specimens from remaining genera were sorted by sex and assigned morphospecies designations by PSV based on discernible differences in morphological features among specimens (Table S5). Within a genus, female and male bees were assigned morphospecies numbers independently of one another; therefore, identical morphospecies numbers for male and female specimens does not imply that these specimens are the same biological species. Information recorded in the specimen record database includes each specimen's unique identification number, collection date, location, elevation, collection method, pan trap colour, taxonomic determinations, and intertegular distance (Table S4). Preserved specimens are currently housed in PSV's personal collection.

Taxonomic richness, abundance and occurrence

To describe the bee community present during the sampling period (mid-February and ending late-April) we used all bee records from both trap types to calculate bee richness (total number of taxa) at the family, genus, and species levels; abundance (total number of individuals) at family and genus levels; and occurrence (total number of farms on which a taxon occurred) at the genus level. We calculated species-level abundance separately for females and males and did not pool abundance data across sexes because we could not confidently match female morphospecies to male counterparts. We used the raw data—unadjusted for sampling effort—for reporting totals when describing general patterns in bee community richness, abundance, and occurrence. For later analyses involving abundance data at the species-level, we used female data only and adjusted for sampling effort prior to analysis (described under applicable sections below).

Trap capture comparisons

To explore whether the type of trap (pan vs. vane trap) in which bees were captured was related to bee body size, we first constructed a pie chart for each genus that depicted the proportion of specimens captured by each trap type (unadjusted for sampling effort). We next determined the mean intertegular distance (the shortest distance between the inner margins of the wing tegulae) for each bee genus and used this as a proxy for bee body size (Cane 1987; Kendall et al. 2019). We measured ITD on each specimen using a dissecting stereomicroscope fitted with an ocular micrometer. For genera with fewer than 5 specimens, ITD was measured for all individuals; for genera with 10 or more specimens, a subsample of 8-49 specimens, representing the range of body lengths present in our collection for that genus, were selected for measurement. For genera in which males accounted for 25 to 75% of genus captures, approximately equal numbers of females and males were used; otherwise only female specimens were selected for measurement. Once ITD measurements were obtained, we arranged bee genera names along an x-axis in increasing order of mean ITD and then plotted corresponding mean ITD values on the y-axis while using the

respective relative trap capture pie charts as pictorial data points. This provided a visual means for qualitatively assessing the body size-trap bias relationship.

To assess whether pan trap colour (blue, white, yellow) affected the abundance of bees captured, we first calculated the effort-adjusted abundance per cup for each cup colour on each farm by dividing the total number of individuals captured by the number of intact cups retrieved across all sampling dates. For farms HJ and PQ, we summed abundance and cup number values for the two merged farms (H and J, P and Q) when calculating effort-adjusted abundances. We normalized the mean effort-adjusted abundance data by taking the natural log to meet distributional assumptions of the ANOVA test and compared resulting abundances among cup colours using ANOVA with Tukey HSD *post hoc* pairwise comparisons. To assess whether cup colour affected the number of species captured, we determined total species richness per farm and compared species richness among cup colours using ANOVA with Tukey HSD *post hoc* pairwise comparisons. For farms HJ and PQ, species richness values were averaged between the two adjacent farms (H and J, P and Q) before analysis. Pan trap capture bias was also visualized by constructing ternary plots (TernaryPlot.com).

We did not compare bee richness and abundance between pan and vane traps statistically because vane traps were not deployed consistently on farms and because sampling effort (30 pan traps vs. 1 vane trap) could not be equalized between methods.

Relationships with elevation and pollination deficit

Before assessing whether species richness, abundance, and community composition exhibited relationships with elevation and pollination deficit, we first pruned the full dataset down to one containing only pan-trapped females (90% of all pan-trapped individuals) of non-parasitic species (98% of all pan-trapped females). Our reasons for doing so were that (1) pan traps were employed more consistently than vane traps and could easily be adjusted for sampling effort; (2) the lack of species keys for most taxa meant that specimens could only be identified to morphospecies and this had to be done separately for females and males. Consequently, abundance data for females and males could not be merged before analysis. Females provide the bulk of pollination services and are the more relevant sex to use in these analyses; (3) parasitic species were only 1% of all individuals captured and are not adapted for collecting pollen; therefore, their contributions to pollination services are likely small. For each farm, data were pooled across relevant sampling dates and abundance data were adjusted for sampling effort prior to analysis.

To explore the relationship between elevation and bee richness and abundance, we used regression analysis to fit species richness data (total number of species on each farm) and effort-adjusted abundance data (mean number of individuals collected per cup on each farm) to farm elevation and compared the fit of linear and non-linear models for each variable separately using ANOVA.

While assessing the relationship between elevation and bee abundance, we also wondered whether apple flowers might compete with pan traps for bee attraction. To explore this, we first estimated floral resource abundance by counting the number of open flowers per inflorescence on two inflorescences from each of 10 trees per farm during one visit to each farm in late March. We then used regression analysis to fit percentage of open flowers per cluster to corresponding effort-adjusted bee abundance and species richness using data from the bloom period between mid-March and early-April (combined sampling periods four and five except for farms B, D, E, and F that had data for sampling date four only; Table S2). Finally, we used regression analysis to fit the percentage of open flowers to farm elevation and compared the fit of linear and non-linear models using ANOVA.

To assess dissimilarities in pollinator communities between farms, we calculated Bray-Curtis distances using effort-adjusted abundance data. We assessed the relationship between elevation difference between farm pairs and their corresponding compositional dissimilarities using linear regression.

To examine the relationship between pollination deficit and bee richness and abundance, we fit linear regressions separately for species richness, effort-adjusted abundance across all sampling dates (n = 6 samples per farm), and

effort-adjusted abundance during bloom-time only (combined sampling periods four and five, except for farms B, D, E, and F that collected samples during period four only; Table S2). We calculated pollination deficit using predicted fruit set values derived from models built in previous analyses (Fraser et al. 2024) that were based on field measured fruit set under open pollinated (OP) and open plus supplemental hand pollination (OH) conditions. Proportional fruit set was predicted for each farm based on model-derived relationships with elevation (Fraser et al. 2024). We took those values and calculated pollination deficit as:

$$Pollination\ deficit\ (PD) = 1 - X_{OP}/X_{OH}$$

where X represents predicted fruit set in a flower cluster for the indicated treatment.

RESULTS

LITERATURE REVIEW FINDINGS

There were disparities in where apple pollinator surveys have been conducted in the Lower Himalaya. Nearly all studies were conducted in India (India = 23 of 25, Bhutan = 1, Pakistan = 1, Nepal = 0). Within India, over half (13 of 23) of the studies were conducted in the state of Himachal Pradesh and the remainder were distributed equally between the Jammu and Kashmir (N = 5) and Uttarakhand (N = 5) (Table 1).

The taxonomic scope of pollinator surveys ranged from broad to focused (Table 1). Over half of all studies (15 of 25) consisted of general diversity surveys that sought to record a broad range of insect orders in association with apples. The remaining studies were more focused, targeting bees only (2 studies); Hymenoptera only (1 study); or some combination of Hymenoptera, Diptera, and Lepidoptera (7 studies).

Owing to different study aims, methods used to survey pollinators varied among studies (Table 1). Among the 23 studies for which sampling methodology was clearly stated or could be inferred, two studies (9%) appeared to use observation alone (no specimens collected) when cataloguing diversity; 20 studies (87%) collected specimens using at least one form of active sampling, and 7 studies (30%) collected specimens using at least one form of passive sampling. Aerial netting (N = 14 studies) and sweep netting (N = 12) were the most frequently employed forms of active sampling. For sweep netting, method descriptions were not always clear about whether "sweep netting" involved aerial or ground sweeping. Pan trapping (N = 5) was the predominant form of passive sampling. Six studies (26%) used a combination of active and passive sampling methods.

The number of bee genera and species reported by authors ranged widely, from 1 to 15 genera (mean = 7 genera, median = 6), and from 3 to 33 species (mean = 11.6 species, median = 9.5; Tables 1, S3). Across all studies, *Apis* and *Bombus* were the two most frequently recorded genera (N = 22 studies for each), followed by *Xylocopa* (N = 20 studies). *Andrena*, *Lasioglossum*, and *Halictus* were each reported from over half of all studies. In terms of abundance, most published studies found *Apis* species, and specifically *A. cerana* and *A. mellifera*, to be the most abundant taxa at farm sites (Table S3). In a few studies, non-*Apis* bees from the genera *Bombus*, *Ceratina*, *Lasioglossum* or *Osmia* predominated.

The taxonomic level to which specimens were identified varied within and among studies (Tables 2, S3). All studies identified *Apis* specimens to species level and 82% identified at least some *Bombus* to species level. For other genera, species level identifications ranged from 0% to 73% of all studies. Details on taxonomic resources used for identifying specimens were usually not stated and a number of reported species names were misspelled, no longer valid, or dubious for other reasons (Tables 2, S3).

After applying taxonomic updates and other corrections to reported taxa, the list of bees associated with apples in the Lower Himalaya comprised 6 families, 25 genera, 76 named species and numerous morphospecies (Table S3). We reduced this to 22 genera, 72 named species, and numerous morphospecies (Table 2) after removing questionable records for *Euglossa*, *Melissodes*, *Bombus ternarius*, and *Ceratina calcarata* (Table S3, highlighted taxa) because these are New World taxa whose known distributions fall well outside of Southern Asia. Another species, *Jetraponica trinctano* (listed under Halictidae) (Chauhan et al. 2021) was excluded because the name could not be

Table 1. Summary of study characteristics and richness findings for 25 pollinator diversity studies from the Lower Himalaya that involved bee sampling in apple orchards exclusively or in combination with other fruit crops. Only studies conducted at the main apple growing elevations, between 1,100 and 4,000 m a.s.l., were included. Details on the genera and species found in each study are provided in Table S3.

					Sampling method										
						Active					Passive				
Reference	Location (Country | State | Districts)	Elevation (m asl)	Sampling time	Taxonomic focus	Unspecified	Observation/ scan	Sweep	Aerial/ handpick	Beat	Aspirator	Pan	Malaise	Vane	No. genera	No. species
Abrol (1993)	India | Jammu and Kashmir | District unspecified	300 - 4200	Unspecified	Hymenoptera, Diptera, Lepidoptera	x									5	15
Arya and Badoni (2023)	India | Uttarakhand | Nainital	1900 - 2305	Feb - May 2019	General insect diversity		x		x						3	7
Arya et al. (2022)	India | Uttarakhand | Nainital	2044	Mar 2019 - Feb 2020	General insect diversity			x							3	6
Batra (1997)	India | Uttarakhand | Tehri Garwhal, Pauri Garwhal, Uttarkashi	1500 - 3100	Mar - May 1995	Bees		x		x						15	17
Chauhan et al. (2021)	India | Himachal Pradesh | Lahaul and Spiti	2500 - 4000	Unspecified	Hymenoptera, Lepidoptera	x									14	33
Dashad and Sharma (1993)	India | Himachal Pradesh | Solan	1300	Mar - Apr 1988; Mar - Apr 1989	Apis and Diptera		x								1	3
Devi et al. (2024)	India | Himachal Pradesh | Mandi	2000	Mar - Apr 2023	General insect diversity		x	x							8	11
Dorji et al. (2022)	Bhutan | Haa, Paro, and Thimphu |	2288 - 2712	Apr - May 2020	Hymenoptera, Diptera, Lepidoptera				x			x			6	14
Ganie et al. (2014)	India | Jammu and Kashmir | Pulwama and Shopian	1900	Mar - Apr; year unspecified	Hymenoptera, Diptera, Lepidoptera				x			x			3	4

Table 1 continued.

Hussain et al. (2012)	Pakistan | Gilgit Baltistan | Skardu	1500 - 3000	2009; months unspecified	Hymenoptera		x	x					x		6	9
Joshi and Joshi (2010); Joshi et al. (2016)	India | Uttarakhand | Nainital	2000 - 2292	Oct 2007 - Feb 2010 (8 sites); Nov 2009 - Oct 2011 (4 sites)	General insect diversity			x	x	x					3	7
Kapkoti et al. (2016a)	India | Uttarakhand | Nainital	1770 - 2250	Apr, Aug, and Dec; year unspecified	General insect diversity							x			5	6
Kaundil and Thakur (2020)	India | Himachal Pradesh | Solan, Shimla and Kullu	1300 - 2150	Mar - Apr 2018; Mar - Apr 2019	General insect diversity			x	x			x			5	8
Kaundil et al. (2022)	India | Himachal Pradesh | Solan	1260	Mar - Apr 2019; Mar - April 2021	General insect diversity		x	x				x			10	22
Kumar (1988)	India | Himachal Pradesh | Solan	1260	Mar - Apr 1985; Mar - Apr 1987	Bees			x							11	15
Mattu and Bhagat (2015)	India | Himachal Pradesh | Kullu	Unspecified	Apr-13	General insect diversity		x	x	x	x	x				9	14
Mattu and Nirala (2016)	India | Himachal Pradesh | Shimla	2000 - 2648	Mar - Apr; year unspecified	General insect diversity		x	x	x	x	x				6	8
Mushtaq, Bilal and Aziz (2018)	India | Jammu and Kashmir | Anantnag, Baramulla and Srinagar	Unspecified	Apr - May 2010; Apr - May 2011	General insect diversity		x								14	16
Paray et al. (2014)	India | Jammu and Kashmir | Shopian, Baramulla and Pulwama	Unspecified	2012 - 2013; months unspecified	Hymenoptera and Diptera				x						5	10
Raj et al. (2012); Raj and Mattu (2014)	India | Himachal Pradesh | Solan and Shimla	1104 - 2648	2007 - 2009; months unspecified	General insect diversity			x	x	x	x				6	9
Saharan and Abrol (2023)	India | Jammu and Kashmir | Doda	1600	Apr 2020	General insect diversity			x					x		11	15
Sharma and Gupta (2010)	India | Himachal Pradesh | Kullu	Unspecified	2010; apple bloom	Hymenoptera, Diptera, Lepidoptera		x		x						3	4
Sharma and Mitra (2012)	India | Himachal Pradesh | District unspecified	Unspecified	2004 - 2006; apple bloom	General insect diversity		x		x						6	9
Thakur and Mattu (2014)	India | Himachal Pradesh | Shimla	1575 - 2250	Mar - May 2004	General insect diversity			x	x	x	x				6	9
Verma and Chauhan (1985)	India | Himachal Pradesh | Shimla	1800 - 2720	Apr - May 1983	General insect diversity		x		x						7	11

Table 2. List of bee taxa compiled from studies at apple growing sites in the Lower Himalaya. Data include records from 25 published studies and our present field study. Values in rows indicate the number of studies reporting that taxon. See Table S3 for a detailed breakdown by study of taxa shown below and excluded taxa. Bee names as reported in original studies were checked against valid taxon names listed in Discover Life (https://www.discoverlife.org/), Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/), and the Integrated Taxonomic Information System (ITIS) (https://www.itis.gov/). Misspelled and invalid taxon names noted in the Comments column were updated to reflect current taxonomy (see Table S3 for relevant studies).

Updated taxon name	Comments (name as recorded in at least one literature review source when it differs from updated taxon name, and other notes)	# reviewed studies reporting taxon	Field study (X = present)	Total # studies reporting taxon
Andrenidae				
Andrena anonyma Cameron, 1897	*recorded incorrectly as *Osmia anonyma* in source Table 2 but correctly as *Andrena anonyma* in source Fig. 1 and text of source	1		1
Andrena cineraria (Linnaeus, 1758)		1		1
Andrena flavipes Panzer, 1799	*recorded as *Andrena flaviceps;* no *Andrena* species by this name, assumed spelling error	2		2
Andrena gravida Imhoff, 1832		1		1
Andrena induta Morawitz, 1894	*recorded as synonym *Andrena patella*	1		1
Andrena leaena Cameron, 1907		1		1
Andrena savignyi Spinola, 1838	*recorded as synonym *Andrena ilerda*	1		1
Andrena sp.		10	X	11
Apidae				
Amegilla binghami (Schulz)	*recorded as synonym *Anthophora crocea*	1		1
Amegilla confusa (Smith)	*recorded as synonym *Anthophora confusa; **Anthophora confuse* [*sic*] Smith	2		2
Amegilla himalajensis (Radoszkowski, 1882)	*recorded as synonym *Anthophora himalayensis*	1		1
Amegilla niveocincta (Smith, 1854)	*recorded as synonym *Anthophora niveo-cincta* [sic]	1		1
Amegilla sp.		3	X	4
Anthophora sp.		5		5
Apis cerana Fabricius, 1793	* includes *Apis cerana indica*	21	X	22
Apis dorsata Fabricius, 1793		9		9
Apis florea Fabricius, 1787		2		2
Apis laboriosa Smith, 1871		3		3
Apis mellifica Linnaeus, 1758		20	X	21

Table 2 continued.

Bombus albopleuralis Friese, 1916 / *Bombus montivagus* Smith, 1878	Williams (2022) notes that these two species are difficult to distinguish without COI barcodes.		X	1
Bombus asiaticus Morawitz, 1875		2		2
Bombus breviceps Smith, 1852			X	1
Bombus flavescens Smith, 1852			X	1
Bombus funerarius Smith, 1852		1		1
Bombus haemorrhoidalis Smith, 1852	**recorded as Bombus haemorrhidalis* [*sic*]; ***Bombus haemorridalis* [*sic*]	12	X	13
Bombus hypnorum (Linnaeus, 1758)		1		1
Bombus pascuorum (Scopoli, 1763)	*recorded as synonym *Bombus agrorum*	1		1
Bombus rufofasciatus Smith, 1852		1		1
Bombus simillimus Smith, 1852	*recorded as *Bombus simillmus* [*sic*]	2		2
Bombus subtypicus (Skorikov, 1914)		1		1
Bombus trifasciatus Smith, 1852		1		1
Bombus tunicatus Smith, 1852		9		9
Bombus sp.	*recorded as synonym *Bremus spp.* for one of two species entries	9		9
Braunsapis sp.	*recorded as genus *Allodape sp* but likely synonym *Braunsapis* because *Allodape* is restricted to Africa	2	X	3
Ceratina binghami Cockerell, 1908		1		1
Ceratina hieroglyphica Smith, 1854		3		3
Ceratina simillima Smith, 1854		1		1
Ceratina smaragdula (Fabricius, 1787)	*recorded as *Ceratina smaragdina* [*sic*]; recorded as synonyms ***Pithitis smaragdula* and *Ceratina sexmaculata* Sm.	3		3
Ceratina sp.		6	X	7
Cubitalia parvicornis Mocsáry, 1879	*recorded as synonym *Eucera parvicornis*	1		1
Eucera clypeata Erichson, 1835	*recorded as *Eucera clypeta* [*sic*]	1		1
Eucera hungarica Friese, 1895	*recorded as synonym *Tetralonia hungarica*	1		1
Eucera vernalis (Morawitz, 1875)		1		1
Nomada sp.	*recorded as *Nomodo*[*sic*] *sp.*	3	X	4
Thyreus nitidulus (Fabricius, 1804)		1		1
Thyreus ramosus (Lepeletier, 1841)	*recorded as synonym *Crocisa ramosus*	1		1
Xylocopa aestuans (Linnaeus, 1758)		1		1

Table 2 continued.

Xylocopa amethystina (Fabricius, 1793)	*recorded as *Xylocopa amethystine* [*sic*]	2		2
Xylocopa bentoni Cockerell, 1919		1		1
Xylocopa fenestrata (Fabricius, 1798)	*recorded as *Xylocopa fenestrate* [*sic*]	8		8
Xylocopa nasalis Westwood, 1842	*recorded as *Xylocopa dissimilis* [*sic*]	1		1
Xylocopa pubescens Spinola, 1838		1		1
Xylocopa tranquebarica (Fabricius, 1804)	*recorded as synonym *Xylocopa rufescens* Smith	1		1
Xylocopa valga Gerstäcker, 1872		2		2
Xylocopa violacea (Linnaeus, 1758)		3		3
Xylocopa sp.		9	X	10
Colletidae				
Colletes eous Morice, 1904		1		1
Hylaeus sp.		1	X	2
Halictidae				
Halictus confusus Smith, 1853	*recorded as *Halictus confuses* [*sic*] Smith	1		1
Halictus kessleri Bramson, 1879	*recorded as *Halictus kessaleri* [*sic*]	1		1
Halictus lucidipennis Smith, 1853		1		1
Halictus propinquus Smith, 1853		1		1
Halictus scabiosae (Rossi, 1790)	*recorded as *Halictus scaliosa* [*sic*] but may closest name match is *Halictus scabiosae* (Rossi, 1790)	1		1
Halictus sp.		13	X	14
Lasioglossum dasygaster (Vachal, 1895)	*recorded as synonym *Halictus dasygaster*	6		6
Lasioglossum himalayense (Bingham, 1898)	*recorded as *Lasioglossuma* [*sic*] *himalayense*	2		2
Lasioglossum malachurum (Kirby, 1802)	*recorded as *Halictus mulachurus* [*sic*]; synonym of *Lasioglossum malachurum* (Kirby, 1802)	1		1
Lasioglossum marginatum (Brullé, 1832)		1		1
Lasioglossum matianense (Blüthgen, 1926)		1		1
Lasioglossum morio (Fabricius, 1793)		1		1
Lasioglossum nursei (Blüthgen, 1926)	*recorded as *Lasioglossumanursie* [*sic*]	2		2
Lasioglossum pallens (Brullé, 1832)	*recorded as synonym *Halictus pallens*	1		1
Lasioglossum sp.		4	X	5
Nomia elliotii Smith, 1875		1		1
Nomia westwoodi Gribodo, 1894		1		1

Table 2 continued.

Nomia sp.		2		2
Nomioides feai Vachal, 1895	*recorded as synonym *Halictus vachalii*	1		1
Sphecodes albifrons Smith, 1879		1		1
Sphecodes lasimensis Blüthgen, 1927		1		1
Sphecodes rubicundus von Hagens, 1875		1		1
Sphecodes tantalus Nurse, 1903		1		1
Sphecodes sp.		3	X	4
Megachilidae				
Coelioxys sp.			X	1
Heriades sp.			X	1
Lithurgus sp.			X	1
Megachile lanata (Fabricius, 1775)	*recorded as *Megachile lenata* [*sic*]	1		1
Megachile maritima (Kirby, 1802)		1		1
Megachile umbripennis Smith, 1853	*Megachile umbripan	1		1
Megachile sp.		8		8
Osmia adae Bingham, 1897		1		1
Osmia cornifrons (Radoszkowski, 1887)		1		1
Osmia sp.		4	X	5
Melittidae				
Melitta harrietae (Bingham, 1897)	*recorded as synonym *Andrena harriete* [*sic*] and *Andrena harrietae*	1		1

reconciled with any taxonomic entity in the GBIF or Discover Life databases.

Fifteen studies included floral observations or netting at apple flowers (Table S3). Of these, 12 reported *A. cerana* and 8 reported *A. mellifera* as, or among, the most frequent bee floral visitor. Other bee genera reported as frequent floral visitors were *Lasioglossum* (4 studies), *Ceratina* (2 studies) and *Bombus* (2 studies). Nearly all studies also reported Syrphidae flies as frequent floral visitors, sometimes more so than bees, and four studies noted Muscidae flies in abundance at flowers (Table S3).

FIELD STUDY FINDINGS

Taxonomic richness, abundance and occurrence

We documented a diverse bee community associated with apple orchards at our study area in Uttarakhand. We captured a total of 2,592 bees (Table S4) representing 57 species/morphospecies from 16 genera and five bee families (Tables 3, S5). Fourteen morphospecies from three genera (*Nomada*, *Sphecodes* and *Coelioxys;* Table S5) were parasites of other bee species.

Compared with findings from studies in our literature review, we captured three genera – *Coelioxys*, *Heriades*, and *Lithurgus* – not reported in earlier studies. Conversely, previous studies reported nine genera – *Anthophora, Colletes, Cubitalia, Eucera, Megachile, Melitta, Nomia, Nomioides,* and *Thyreus* – not captured in our study (Tables 2, S3). Combining bee records from the literature review with those from our field study produced a combined list of six bee families, 25 bee genera, 75 named species, and numerous morphospecies associated with apple orchards in the Lower Himalaya (Table 2).

Table 3. Summary of richness, abundance, capture method, and occurrence data for all bees collected from 13 apple orchards between February and April, 2023. All values represent combined totals from pan trap (P) and vane trap (V) sampling methods.

Taxon	No. genera	No. (%) morphospecies	No. (%) individuals	No. (%) female	Capture method	No. (%) farm occurrences
Andrenidae	1	11 (19.3%)	448 (17.3%)	320 (71.4%)		
Andrena		11 (19.3%)	448 (17.3%)	320 (71.4%)	P/V	13 (100%)
Apidae	7	27 (47.4%)	442 (17.1%)	351 (79.4%)		
Amegilla		1 (1.8%)	1 (<0.1%)	1 (100%)	V	1 (7.7%)
Apis		2 (3.5%)	159 (6.1%)	159 (100%)	P/V	11 (84.6%)
Bombus		4 (7.0%)	37 (1.4%)	36 (97.3%)	P/V	10 (76.9%)
Braunsapis		2 (3.5%)	10 (0.4%)	4 (40.0%)	P	3 (23.1%
Ceratina		7 (12.3%)	210 (8.1%)	139 (66.2%)	P/V	13 (100%)
Nomada		10 (17.5%)	23 (0.9%)	11 (47.8%)	P	11 (84.6%)
Xylocopa		1 (1.8%)	2 (0.1%)	1 (50.0%)	P/V	2 (15.4%)
Colletidae	1	1 (1.8%)	1 (<0.1%)	1 (100%)		
Hylaeus		1 (1.8%)	1 (<0.1%)	1 (100%)	P	1 (7.7%)
Halictidae	3	13 (22.8%)	1683 (64.9%)	1679 (99.8%)		
Halictus		4 (7.0%)	287 (11.1%)	287 (100%)	P/V	13 (100%)
Lasioglossum		6 (10.5%)	1373 (53.0%)	1369 (99.7%)	P/V	13 (100%)
Sphecodes		3 (5.3%)	23 (0.9%)	23 (100%)	P	12 (92.3%)
Megachilidae	4	5 (8.8%)	18 (0.7%)	9 (50.0%)		
Coelioxys		1 (1.8%)	1 (<0.1%)	1 (100%)	P	1 (7.7%)
Heriades		1 (1.8%)	2 (0.1%)	2 (100%)	P	2 (15.4%)
Lithurgus		1 (1.8%)	2 (0.1%)	2 (100%)	P	1 (7.7%)
Osmia		2 (3.5%)	13 (0.5%)	4 (30.8%)	P	6 (46.2%)
Grand Total	16	57 (100%)	2592 (100%)	2360 (91.0%)		13 (100%)

Apidae contained the most genera (7) and morphospecies (27), followed by Halictidae (3 genera, 13 morphospecies) and Andrenidae (1 genus, 11 morphospecies). Halictidae was the most abundant family (64.9% of all captured specimens; Table 3), within which *Lasioglossum* predominated (81.6% of Halictidae). Andrenidae (17.3% of all bee captures) and Apidae (17.1% of all specimens) were intermediate in abundance (Table 3). Megachilidae (5 morphospecies and 0.7% of all specimens) and Colletidae (1 species and <0.1% of all specimens) were the least species-rich and least abundant families in our collections (Table 3).

The vast majority (91.0%) of captured specimens were female and most genera were represented exclusively or nearly exclusively by females (Table 3). Exceptions to this pattern, when considering only genera from which at least 10 individuals were captured, were *Andrena* (71.4% female), *Ceratina* (66.2% female), *Braunsapis* (40.0% female), *Nomada* (47.8% female), and *Osmia* (30.8% female).

Lasioglossum was the most commonly captured bee genus, representing 53.0% of all individuals, followed by *Andrena* (17.3%) and *Halictus* (11.1%) (Table 3). The most species-rich genera were *Andrena* (11 spp.), *Nomada* (10 spp.), *Ceratina* (7 spp.), and *Lasioglossum* (6 spp).

A number of bee genera were widespread throughout the study area. *Andrena, Ceratina, Halictus* and *Lasioglossum* occurred on all 13 farms; *Apis, Bombus, Nomada* and *Sphecodes* occurred on at least 10 (77%) of the 13 farms (Table 3). At the species level (using a pruned dataset of females of non-parasitic genera only), we saw a positive relationship between species abundance and distribution across farms: the number of farms on which a species occurred was closely associated with its mean abundance at capture rates below 0.03 bees/cup (Fig. 1 inset). Above this threshold, a ceiling effect emerged because all remaining species but one (*Lasioglossum sp. 6*) were widespread – occurring on at least 10 of the 13 farms (Fig. 1). Eight species were collected on at least 12 of the 13 farms, of which five were

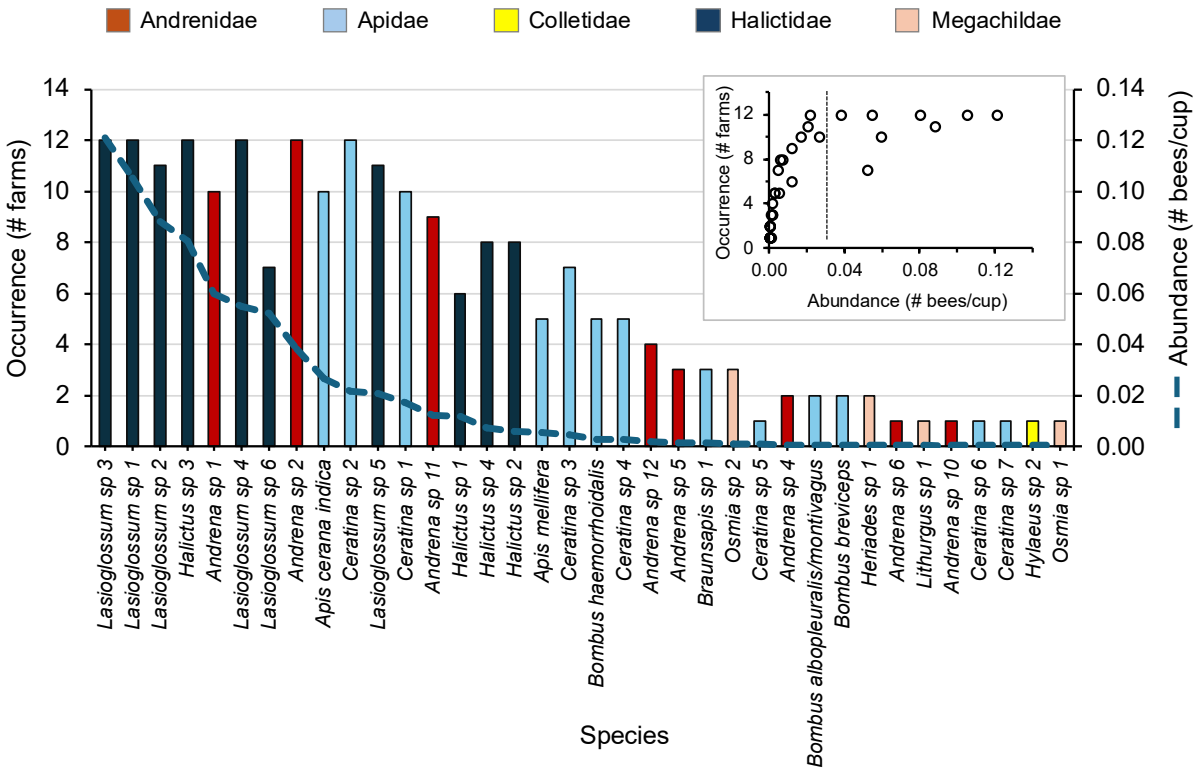

Figure 1. Bee abundance (number of bees/cup) and spatial distribution (occurrence on number of farms) across species. Data represent 1966 female specimens of non-parasitic species collected by pan trapping (N = 36 species). Bars represent occurrence data from farms (N = 13) and are colour coded by bee family. The dashed line shows bee abundance as mean captures per cup across all sampling dates. The panel inset shows the same data plotted with axes reversed and each dot representing a single bee species.

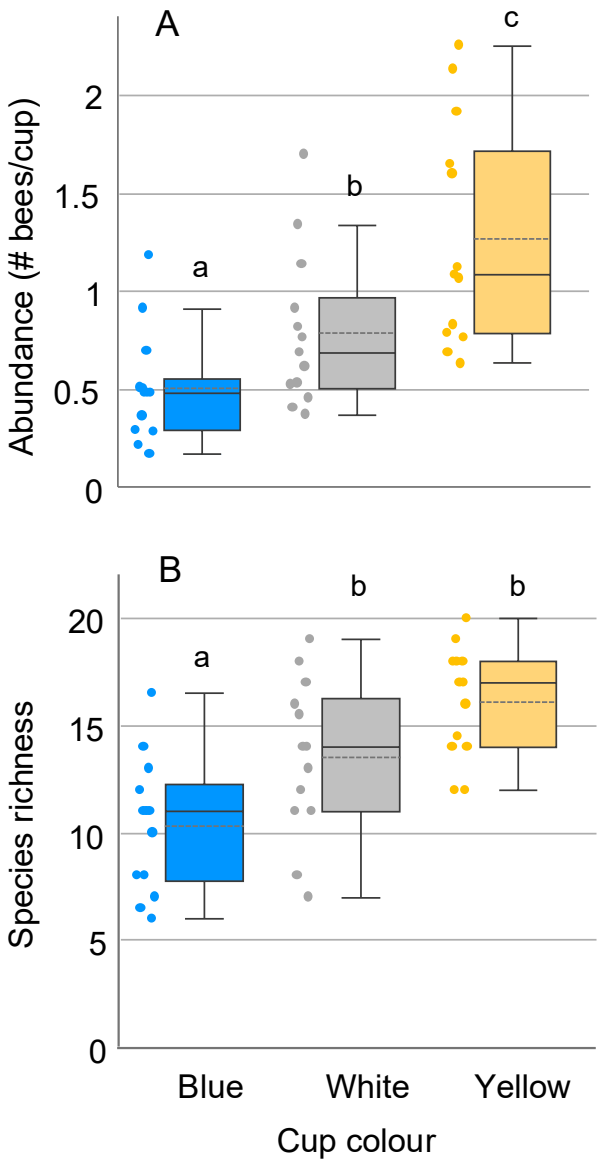

Figure 2. Comparison of trap captures by cup colour for (A) bee abundance and (B) species richness. Abundance data were adjusted for sampling effort and natural log transformed prior to analysis. Each data point represents a single farm (N = 13); solid lines within boxplots represent median; dashed lines represent mean. Boxplot means that do not share the same letter are significantly different (Tukey HSD, P < 0.05).

Lasioglossum species. One *Andrena* species was found on all farms and a second *Andrena* species occurred on over 75% of all farms. *Ceratina sp. 1* and *sp. 2* and *Apis cerana* were the most widespread species within the Apidae, each occurring on over 75% of all farms. No members of Colletidae or Megachilidae were widespread or abundant (Fig. 1).

Sampling Method Comparisons

More genera and individuals were captured in pan traps than in vane traps (Table 3; Fig. S2), but values are not directly comparable between sampling methods because sampling effort could not be normalized. Using unadjusted abundances, smaller-bodied bees were captured exclusively or in much greater proportion in pan traps than in vane traps (Fig. S3). Larger-bodied bees (*Apis, Bombus, Xylocopa* and *Amegilla*) were captured at near equal or greater frequency in vane traps compared to in pan traps (Fig. S3).

Pan trap colour influenced both the number of individuals captured per cup ($F = 12.73$, df= 2,36; $P < 0.0001$; Fig. 2A) and the number of species captured per cup ($F = 10.99$, df= 2,36; $P < 0.001$; Fig. 2B). Yellow cups captured the most bees, white cups were intermediate in capture rate, and blue cups captured the fewest bees (Tukey HSD pairwise comparisons: $P < 0.05$; Fig. 2A). With respect to species richness, yellow and white cups captured similar numbers of species and both captured more species than did blue cups (Tukey HSD, blue vs yellow $P < 0.01$, blue vs white $P < 0.05$; Fig. 2B). Most genera tended to be caught more often in yellow traps than in white or blue cups (Figs. S2, S4B). One notable exception to this trend was the genus *Apis*, which was caught most frequently in white cups.

Relationships with elevation and pollination deficit

Species richness decreased as elevation increased ($R^2 = 0.39$, $F = 6.99$, DF = 1,11, $P = 0.02$; Fig. 3A) whereas abundance was greatest at the lowest and highest elevation sites, resulting in a relationship best described by a convex quadratic model (Fig. 3B; Table S6). Bee abundance was inversely related to floral resource availability on apple trees: as the percentage of open flowers increased, bee abundance in cups decreased ($R^2 = 0.55$, $F = 13.35$, DF = 1,11, $P = 0.004$; Fig. 3C). Fitting percentage of open flowers to elevation produced a relationship that was best represented by a concave quadratic model (Fig. 3D; Table S7), a relationship that is opposite to that for bee abundance and elevation (Fig. 3B). We did not find a significant relationship between the percentage of open apple flowers and species richness ($F = 0.61$, DF = 1,11, $P = 0.449$).

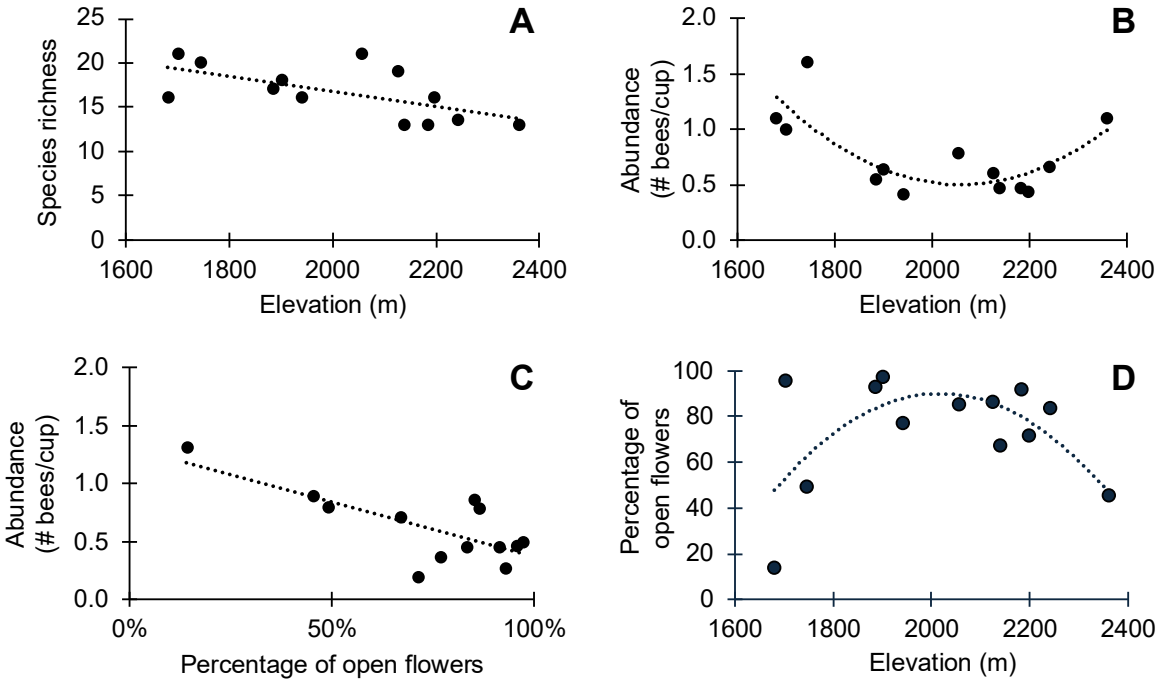

Figure 3. Relationship between (A) elevation and cumulative species richness (R^2 = 0.39, F = 6.99, DF = 1,11, P = 0.02; y = -0.008x + 33.737); (B) elevation and mean bee abundance over the entire sampling period; (C) percentage of open flowers in late March and bee abundance in mid-March to early-April (R^2 = 0.55, F = 13.35, DF = 1,11, P = 0.004; y = -0.941x + 1.312); and (D) elevation and percentage of open flowers in late March. Each data point represents a single farm (N = 13).

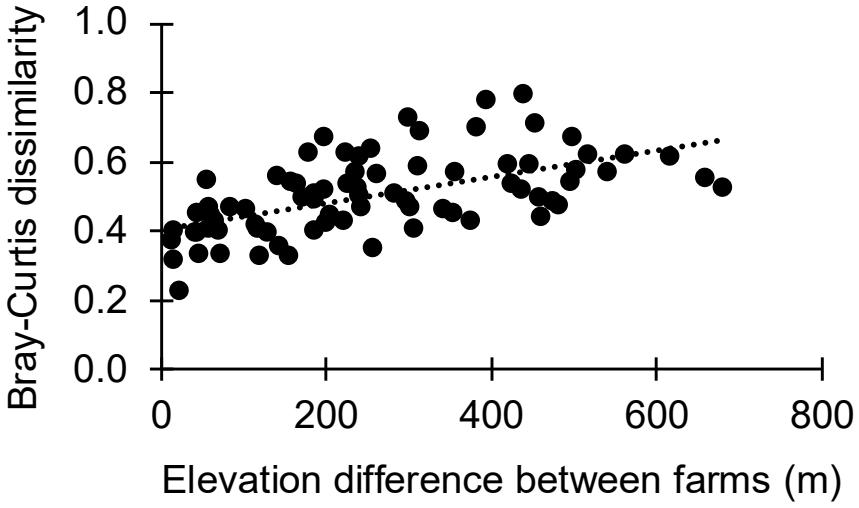

Figure 4. Relationship between difference in elevation and dissimilarity in bee community composition as represented by Bray-Curtis distance (R^2 = 0.32, F = 35.14, DF = 1,76, P < 0.0001; y = 0.0004x + 0.4072). Each point represents a single comparison between two farms (N = 13).

Community dissimilarity increased with elevation difference between farms (R^2 = 0.32, F = 35.14, DF = 1,76, P < 0.0001; Fig. 4).

Pollination deficit was significantly negatively correlated with bee species richness (R^2 = 0.41, F = 7.50, DF = 1,11, P = 0.02; Fig. 5). We did not find any significant relationship between pollination deficit and either of our measures of bee abundance (Table S8).

Discussion

Bee diversity and abundance

Using data from existing literature and our present field study, we compiled a comprehensive and taxonomically updated list of bee taxa found in association with apple-growing sites in the Lower Himalaya. The combined list comprised six

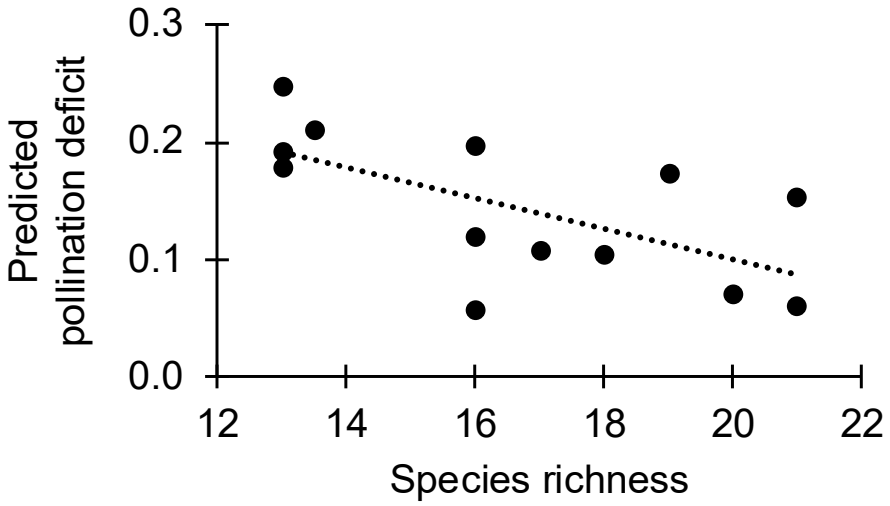

Figure 5. Relationship between cumulative species richness and predicted pollination deficit (R^2 = 0.41, F = 7.50, DF = 1,11, P = 0.02; y = -0.013x + 0.363). Each data point represents a single farm (N = 13).

bee families, 25 genera, and 75 named species (excluding unnamed morphospecies). Study aim, sampling methodology, and sampling effort varied among studies, resulting in a range of richness totals from individual studies. Upper richness values of 15 genera and 33 species from reviewed studies, and 16 genera and 57 morphospecies for our field study, are in line with results from diversity studies in some North American orchards (Mallinger & Gratton 2015; Joshi et al. 2015; Blitzer et al. 2016; Gibbs et al. 2017). *Apis*, *Bombus,* and *Xylocopa* were recorded in over 80% of all reviewed studies, while *Andrena, Lasioglossum*, and *Halictus* were recorded in over half of all studies. These genera, along with *Ceratina* and *Osmia*, were all captured in our field study and are commonly associated with apples in other parts of the globe (Pardo & Borges 2020; Leclercq et al. 2023). The broad geographical overlap in bee genera that associate with apples suggests that population status changes detected in more well-studied regions such as North America and Europe (Goulson et al. 2008; Cameron et al. 2011) could inform monitoring needs for related taxa in less-studied regions like the Himalaya.

Prominent pollinator taxa

Our literature review revealed that *A. cerana* was the most common bee visitor to apple flowers in the Himalaya, followed closely by *A. mellifera*. Leclerc et al. (2023) reported similar results for northern India in their global study. In our field study, *A. cerana* was nearly ten times more abundant and occurred on nearly twice as many farms compared to *A. mellifera*. We observed *A. mellifera* hives at only one large commercial operation > 5 km from the farms we surveyed, and, of the three farms in our study that kept managed bees, all were *A. cerana* hives. While *Apis* bees may be common visitors to apple flowers if managed hives or feral colonies are present in the area, most farms in our study area did not keep *Apis* hives. Like most smallholder farmers in Western Himalaya, farmers in our study area depend on wild bees, including wild *Apis*, for pollination. Interestingly, a study in the United States by Mallinger & Gratton (2015) found that species richness of wild bees, rather than the use of managed honey bees (*A. mellifera*), was an important determinant of fruit set in apples. More research is needed to determine if this is also true in the Himalayan region.

Among non-*Apis* bees captured in our field study, *Andrena, Bombus, Ceratina, Xylocopa, Colletes, Lasioglossum, Halictus,* and *Osmia* have been noted as key pollinators of apples in other areas of the globe (Pardo & Borges 2020). In our literature review, non-*Apis* genera that were most frequently recorded at apple flowers were *Bombus*, *Ceratina,* and *Lasioglossum.* These three genera were widely distributed across farms in our study area and *Ceratina* and *Lasioglossum* were captured in high numbers in traps. Interestingly, *Andrena* – the most species-rich and second most abundant genus in our survey, was not recorded as a prominent pollinator of apples in the literature review. This contrasts with *Andrena*'s dominance among wild bees at apple flowers in temperate North America

(Russo et al. 2015; Blitzer et al. 2016; Gibbs et al. 2017) and may reflect differences in regional species' functional traits or landscape features that affect bee foraging behaviour (Goulson 2009; Jha & Kremen 2013).

Contributions of non-bee insects to apple pollination should also be considered in future pollinator surveys. A range of non-bee taxa were present in our samples, including flies (Diptera), butterflies and moths (Lepidoptera), wasps (Hymenoptera), and beetles (Coleoptera). Unfortunately, we did not systematically record or preserve all bycatch but we observed that syrphid and muscoid flies, along with butterflies, were the most abundant bycatch taxa. A meta-analysis of bee-fly pollinator communities from locations around the globe showed that flies become a more dominant part of the pollinator community relative to bees as elevation increases (Hodkinson 2005; McCabe & Cobb 2021). Among studies in our literature review that sampled insects at apple flowers, a majority also noted that syrphid flies, and to a lesser extent muscid flies, were abundant floral visitors. The role of nocturnal pollinators (especially moths) in apple pollination is also understudied (Chatterjee & Singh 2025). For a more complete picture of the apple pollinator community, future studies in the Himalaya should be expanded beyond bees to include the broader pollinator community where possible.

Field methods

The pan traps and blue vane traps we used to survey the bee fauna are easy to operate and require little time investment on the part of the collector, making them well suited to our purpose of engaging farmers as community scientists to collect bee samples. Both methods efficiently attract and capture a range of bee species (Klaus et al. 2024) but also possess taxonomic biases. Pan traps tend to capture smaller-bodied, low-flying bees, especially members of the family Halictidae and solitary parasitic species (Roulston et al. 2007; Portman et al. 2020; Prendergast et al. 2020). This likely explains the large number of *Lasioglossum* specimens in our collections – over half of all specimens we sampled. Parasitic species were caught in low numbers, but all were captured in pan traps. Placement of pan traps at ground level, rather than at the level of flowering branches, may have also undersampled the community of bees that actively forage at crop blossoms (Tuell and Isaacs 2009), although this bias was likely reduced when traps were placed on terraced rows. Blue vane traps were also used to sample pollinators foraging at canopy height.

In comparison with pan traps, blue vane traps accumulate more bee species per number of specimens captured (Joshi et al. 2015) and are more efficient at capturing larger-bodied taxa (Bell et al. 2023). Our data supported this latter point: despite deploying only one vane trap on each farm, near equal or greater numbers of the larger-bodied genera (*Apis, Bombus, Xylocopa, Amegilla*) were caught in vane traps. We anticipated this and purposefully limited the number of blue vane traps we deployed because early spring is the time when queens of many social *Bombus* species are active and some evidence suggests that vane traps can deplete populations of certain species when large numbers of reproductive individuals are captured (Gibbs et al. 2017).

Pan trap colour influenced the number of individuals and species captured in our samples: yellow cups captured the most individuals, whereas yellow and white cups captured more species than did blue cups. Some other studies also report differences in capture rates among trap colours, but patterns vary among studies and across seasons (Joshi et al. 2015; Kapkoti, Joshi, et al. 2016a; Sircom et al. 2018; Westerberg et al. 2021; Dorji, Tashi, et al. 2022). Bowl captures are influenced by the reflectance properties and age of trap materials (Joshi et al. 2015; Sircom et al. 2018), by floral resource availability (O'Connor et al. 2019; Kuhlman et al. 2021; Chamorro et al. 2023), and by sensory biases of taxa (Joshi et al. 2015; Sircom et al. 2018). To achieve fuller taxonomic representation using pan traps, a mixture of blue, white, and yellow traps are typically used. Vane trap colour similarly influences capture rates and blue vane traps have become the standard for bee surveys because of their greater efficacy compared to yellow traps at attracting and capturing bees (Joshi et al. 2015; Hall 2018).

Overall, the passive sampling surveys we conducted provide a first approximation of the bee community associated with apples in our study area. We recognize, however, that these methods have limitations in the information they provide about bee communities. Because of taxon-specific

sensory biases and variation in foraging preferences of different bees, surveys using passive sampling can produce significantly different descriptions of the bee community compared to actively sampling using hand netting (Cane et al. 2000; Gibbs et al. 2017; O'Connor et al. 2019; Dorji, Tashi, et al. 2022). Passive sampling data also cannot inform us about plant-pollinator relationships unless pollen from specimens is analysed (Prendergast et al. 2020). Active sampling using non-lethal floral observations and aerial netting at flowers provides this information. In the future, we plan to add active sampling methods to our research to gain a more complete understanding of the bee community associated with apples and apple pollination. However, even if some bee taxa identified by passive trapping are not the main pollinators of apples, it is important to understand the broader pollinator community because farmers in the region practice polyculture and likely require a diverse bee community to support their livelihoods.

Relationships with elevation and pollination deficit

In a previous report from our study area, we showed that apples experienced pollination limitation, and that pollination deficit increased with elevation (Fraser et al. 2024). Here we explored two potential drivers of this relationship, bee richness and abundance. We found that bee species richness was negatively associated with elevation and pollination deficit, as expected, whereas abundance exhibited a more complex relationship with elevation and no relationship with pollination deficit. Decreases in bee richness with elevation have been reported from other regions of the globe (Perillo et al. 2017; Tronstad et al. 2022) and multiple studies have found that lower species richness is associated with lower pollination success and, by extension, greater pollination deficit (Mallinger & Gratton 2015; Földesi et al. 2016; Blitzer et al. 2016; Pardo & Borges 2020). Our results corroborate these findings.

Along with a decrease in bee richness with increasing elevation, we found that community dissimilarity increased with elevation. This suggests that there was greater turnover in the assemblage of species making up the bee community as elevation difference between sites increased. Therefore, a change in species composition, rather than in the number of species present, may underlie the change in pollination deficit with elevation. Whether changes in species composition impacts pollination services, however, will depend on whether the suite of functional traits influencing pollination (e.g. bee tongue length, body size, and elements of foraging behaviour; Martins et al. 2015) shift within the pollinator community. For example, even though the number of species in a community may decrease with elevation, the level of pollination that apples receive may not change unless functional diversity within the remaining community shifts, such that fewer members possess morphological or behavioural traits suited to pollinating apples (Martins et al. 2015; Roquer-Beni et al. 2022). Probing the relative contributions of bee richness (Földesi et al. 2016), community composition (Blitzer et al. 2016), and functional trait diversity (Hoehn et al. 2008) to apple pollination was beyond the scope of our study. Such investigations remain important for predicting plant-pollinator resilience (Bartomeus et al. 2013; Kammerer et al. 2021), especially as climate change and human activity change the environment of apple growing areas in the Himalaya.

Unlike with species richness, we found no significant relationship between bee abundance and pollination deficit. Bee abundance was inversely related to floral resource abundance on apple trees, however. Moreover, the complex curvilinear relationships between each of these variables and elevation were mirror opposites of one another. That is, whereas bee abundance was lowest at mid-elevations and highest on the two extremes, floral abundance was highest at mid-elevations and lowest on the two extremes. Collectively, these data suggest that pan traps competed with apple flowers for bee visits, and that apple flowers were more attractive than pan traps to bees. Effects of floral density may be context or system dependent, however. For example, pan trap captures of solitary bees have been found to be inversely related to floral density (O'Connor et al. 2019; Kuhlman et al. 2021; Chamorro et al. 2023), unaffected by floral density (Westerberg et al. 2021), and positively related to floral density (Kaundil et al. 2022). In their meta-analysis of pan trap studies focused on bee collection, Krahner et al. (2024) point out

numerous ways in which pan trap and floral survey methodologies vary among studies—making direct comparisons among studies difficult—and provide guidance for standardizing methodological practices moving forward.

Advancing knowledge of bee communities in the Lower Himalaya

Our literature review brought together many disparate sources documenting bee communities associated with apples in the Lower Himalaya. At the same time, this review highlights areas where more resources and baseline information are needed to better understand the diversity, roles, and status of bees throughout this apple-growing region. The paucity of taxonomic tools available to accurately identify species within most genera in this region, and Asia generally, is a major impediment to diversity, ecological, and comparative studies (Warrit et al. 2023). Given the limited supply of taxonomic experts and funding available for such taxonomic work (Orr et al. 2020), however, progress will be slow.

Authors of many studies in our review did not follow best practices for documenting taxonomic methodology (Packer et al. 2018). Details should be provided on the taxonomic sources used to identify specimens and who identified the specimens. Representative vouchers should be preserved and the location where they are housed should be provided so that other researchers can consult them if needed, to compare or verify identifications. Many journals also now invite or require researchers to make their study data accessible to the research community through deposition in a data repository such as Dryad (datadryad.org) or Zenodo (zenodo.org). Adherence to these best practices could help advance the state of bee knowledge in understudied regions.

With respect to sampling methodology, some studies in our review did not contain enough detail to permit others to repeat the study, In two cases (Abrol 1993; Chauhan et al. 2021), we could not discern the collection methodology that was used. We call on researchers to provide comprehensive descriptions of methodology, to permit replication of sampling protocols and adjustments for sampling effort when results are used in comparative studies. While the sampling methods used will depend on the study aims and research system, adopting standardized sampling protocols for diversity studies could help advance collaborative and comparative work across space and time (LeBuhn et al. 2003; O'Connor et al. 2019; Klaus et al. 2024).

Expanding the geographic range of bee surveys within apple growing areas of the Lower Himalaya is warranted. The distribution of studies in our review was highly skewed toward states in northwestern India, especially Himachal Pradesh. This distributional bias likely reflects the disparity among states in apple production and the resources available to support apple production. Western Himalaya produces 99% of India's apples (Joshi & Sarkar 2017; Bhat et al. 2021) and Himachal Pradesh receives significant state and grower association support to develop and promote apple growing (Vedwan 2008). Even in Western Himalaya, however, most of the area under cultivation is owned by farmers with land holdings of two hectares or less (Vedwan 2008; Rather et al. 2017). Apples are an important—if not the chief—source of livelihood for many thousands of smallholder farmers across the Lower Himalaya. Expanding the geographic range of pollinator studies will bring a fuller understanding of the status of wild pollinator populations throughout the Himalaya region.

In addition to the baseline information needed on pollinator communities, it is important to understand trends in pollinator populations and whether changes in population levels impact crop production. Growers in the Himalaya region have reported declines in apple yield and quality (Vedwan & Rhoades 2001; Pramanick et al. 2014; Bhat et al. 2021; Dorji, Marshall, et al. 2022) and declines in pollinator diversity and abundance have been cited as important contributing factors (Partap & Partap 2002, 2004). Data to support this latter claim mainly come from studies of managed bees or wild pollinators in other parts of the globe, however (Allen-Wardell et al. 1998; Potts et al. 2010; Cameron & Sadd 2020; Reilly et al. 2020). Robust longitudinal studies of wild pollinators (Lebuhn et al. 2013; O'Connor et al. 2019), coupled with tests for pollination deficits (Reilly et al. 2020; Olhnuud et al. 2022), can help address this knowledge gap.

The work presented here highlights the diversity of bees associated with apples in the

Himalaya but also points to several key areas of need for future research and capacity building. This includes more taxonomic tools to aid in species-level bee identifications, more comprehensive documentation and standardization of study methods to facilitate collaborative and comparative studies, and more expansive cataloguing and monitoring of pollinator communities to better understand the diversity, roles, and status of bees throughout this under-studied region. Knowledge gained through enhanced research will inform pollinator conservation strategies, and in turn help safeguard pollination services that sustain agricultural food production, farmer livelihoods, and natural ecosystems.

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AUTHOR CONTRIBUTION

GRHA, AMF, AL and PSV conceived the study design. All authors were involved in collecting the data and preparing bee specimens for identification; AMF and PSV identified bee specimens; GRHA, AMF and AL analysed the data and wrote the initial draft of the manuscript. All authors contributed critically to draft revisions and gave final approval for publication.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

Raw data file is available as an Excel file, Table S4, in the appendices.

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Field study farm characteristics table

Table S2. Table of trap collection dates and number of traps collected

Table S3. Summary table of bee taxa compiled from literature review and our present field study (extra file)

Table S4. Database of field study bee specimen records (extra file)

Table S5. Summary of field survey morphospecies, distinguishing characteristics, and abundances by trap method and sex.

Table S6. Linear and quadratic model output table for elevation vs bee abundance

Table S7. Linear and quadratic model output table for elevation vs floral abundance

Table S8. Linear model output table for pollination deficit vs species richness and abundance

Fig S1. Map of field study area

Fig S2. Graphical comparison of bees captures per genus by trap type

Fig S3. Graphical comparison of pan vs. vane trap captures according to bee body size

Fig S4. Ternary plot of relative attraction of pan trap colours for select bee genera

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