# Which insects are the most important pollinators on Nepali smallholder farms, and how can we tell?

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# Abstract

Nowhere are ecosystem services more concrete than on subsistence farms, where the majority of food consumed on the farm is derived from the local agroecosystem. This direct coupling of ecosystem service and recipient means that local management actions to increase ecosystem services can yield direct rewards by improving farmers' food and nutrition security. Subsistence farm ecosystems are, however, severely understudied, making evidence-based management difficult. Here we begin to address this knowledge gap by describing the plant-pollinator network– the source of pollination services for crops –of ten smallholder farming villages in rural Nepal. To dissect the overall service, we ask: which insects are the key pollinators of individual food crops, how much does the importance of pollinators vary between crops, villages, and different parts of the growing season, and what plants are most important to crop pollinators? Together, the answers to these questions should indicate plant and pollinator taxa that are useful management targets for enhancing the provision of pollination services and boosting the local supply of pollinator-dependent foods. From the perspective of the pollinators' importance to plants, we find that the native Asian honeybee (*Apis cerana*) is the most important pollinator across crops, but that other highly-important taxa include bees (*Hylaeus*, *Bombus*, and other genera), flies (*Eristalis* and *Lucilia*), beetles (*Popillia*), and butterflies (*Celastrina* and *Pieris*). Different crops had different sets of important pollinators and pollinator importance was highly variable between villages and over time, highlighting the importance of maintaining a diverse pollinator community. From the perspective of plants' importance to pollinators, we find that many of the most important plants are actually crops, including

taxa originating in the Americas. The high importance of crops and weedy plants for pollinators suggests that floral resources may generally be in short supply. To remedy this shortfall, we suggest that farm managers protect wildflowers close to their farms, e.g., by preventing grazing of some areas. These findings show how insights from community and network ecology may be used to trace ecosystem services to specific taxa, and how management actions may be guided by these insights.

# Introduction

Climate and land use changes are causing rampant changes in natural communities and the ecosystem services they provide (Bongaarts, 2019). Developing strategies to protect services by understanding and managing the communities they depend upon is thus a critical task for ecology. Managing ecosystem services is especially pressing, but also most feasible, in smallholder farm systems. Smallholder farming supports over two billion people (**??**) but the families that run them are often highly food-insecure (**?**).

Unlike industrial agricultural production systems which depend on diffuse links to ecosystem services solicited across the globe (Silva *et al.*, 2021; **?**), smallholder farmers largely rely on local ecosystem services for pollination, soil fertility, etc. (Timberlake *et al.*, 2021). This dependence on the local ecological community makes smallholder farms particularly amenable to studies linking ecosystem services to the structure of local communities and biotic interactions (**?**). Meanwhile, the dependence of smallholder farmers on the integrity of local ecosystem services makes them especially vulnerable to disruptions in these services as a result of climate or land-use change (**??**).

A necessary first step to managing ecosystem services is understanding which taxa provide them, yet despite their ubiquitous nature and the unique scope for using them as a window to studying communities vs services, smallholder farms remain massively ecologically under-studied (?). Here we focus on pollination, an especially important ecosystem service for human nutrition and food security in the smallholder farm context. While many staple grains are wind-pollinated (), highly nutrient-dense fruits and vegetables commonly rely on insect pollination (?Klein *et al.*, 2007). In smallholder farms, where seed is saved between years rather than being purchased commercially, the pollinator dependence of many crops will extend to their non-reproductive parts such as roots (e.g. carrot and radish) and leaves (e.g. spinach and cabbage), as the production of seeds for ongoing cultivation is dependent on insect pollination. As smallholder farms typically include multiple crop species (as opposed to the monocultures typical of industrialised agriculture), considering crop pollination as the outcome of a network of plant-insect interactions offers unique opportunities to understand pollination service to the whole farm as well as to each crop separately. Given limited resources available for pollinator management, farmers may then wish to target taxa that are important across a variety of crops rather than focusing on an insect that may be very important to a single crop.

Moreover, taking a network perspective also allows us to consider how insects rely upon plants for resources (usually food () but occasionally heat or other benefits ()). As most pollinators typically interact with a wide range of plant taxa and may not be able to meet their nutritional needs with crops alone (Pocock *et al.*, 2012; ?), pollination services may thus depend on pollinator access to non-crop plants. As managing plant populations will often be easier than the direct management of insect populations, identifying and favouring important non-crop plants will thus provide a useful tool for any farmer seeking to boost crop pollinator populations (Timberlake *et al.*, 2022).

When estimating taxa' importance as service providers, it is vital to remember that ecological networks are not constant over space and time (**?**Cirtwill *et al.*, ????; **?**). Rather, both the taxa and interactions in a network may show substantial spatiotemporal turnover (Pellissier *et al.*, 2018; Rasmussen *et al.*, 2013; MacLeod *et al.*, 2020). Thus, the importances of pollinators and their food plants should be assessed against this dynamic background. In particular, some taxa may have low overall importance but fill a major gap in pollination service during a particular part of the growing season, while others may be much more important at one village than another.

Here we introduce a multi-crop importance index based on insects' visitation patterns and the amount of pollen carried. Studies of plant-pollinator networks from an ecological perspective, however, more commonly define taxa as 'important' if they play particular roles in the structure of the network. For example, highly *central* taxa (broadly, those that can affect many others) are often identified as important (Koski *et al.*, 2015; Martín González *et al.*, 2010; Gómez & Perfectti, 2012; Kaiser-Bunbury *et al.*, 2010; Arceo-Gómez *et al.*, 2020; Lázaro *et al.*, 2020). Central taxa cause many secondary extinctions when removed (Kaiser-Bunbury *et al.*, 2010), and can transmit the effects of a disturbance throughout the network (Delmas *et al.*, 2019). As such, changes in the abundance of highly central taxa have the potential to control the abundances of other taxa (Cagua *et al.*, 2019) and such taxa are usually listed as conservation and reintroduction priorities (Devoto *et al.*, 2012; Pires *et al.*, 2017). However, when considering pollination networks from an ecosystem service perspective, an insect's interactions with crops are much more important than interactions with non-crop plants. It is therefore possible that recommendations to protect highly-central species (e.g., generalist insects) may neglect highly important crop pollinators and therefore have little effect on food security. Before using network structure as a guide for managing a particular ecosystem service, it is thus important to understand how structural measures may differ from measures which directly relate to service provision.

Here we investigate which insects provide pollination service, which plants they rely on, and whether these highly-important species are also highly central in the remote Jumla district of Nepal. The high altitude, steep slopes, and challenging climate (cold and relatively dry) means that agricultural productivity is lower here than in many other regions, resulting in high rates of poverty, food insecurity and malnutrition (of Nepal & United Nations Children's Fund, 2019). Like many smallholder farming regions, this area is ecologically under-studied and the diversity and composition of the insect community in farming villages has not been previously described. In this region, we use a network framework to describe the relationship between crop plants, pollinators and the semi-natural vegetation surrounding ten smallholder farming villages. We combine visitation data with measurements of pollen transport by different insects to identify the insects which are likely to be important crop pollinators. More specifically, we ask: 1) Which insects are the key pollinators of individual food crops, and does pollinator importance differ among crop taxa and/or over space and time? 2) Which plant taxa are most important to crop pollinators? and 3) Would centrality provide a reliable guide to highly-important crop pollinators in this system?

# Methods

## Study site and sampling methods

The study was conducted in 10 smallholder farming villages in Patarasi Rural Municipality, Jumla District, Nepal (2400-3000 m altitude; *Appendix S1*). Each study village included 100-400 closely-spaced households (80-100% of which identify as subsistence farmers). The houses are surrounded by small vegetable gardens (see Fig. **??** for a list of crops) and livestock paddocks, embedded in a larger area of small arable fields, apple orchards, and large areas of steep, heavily-grazed grassland pasture and native coniferous forest (Fig. **??**).

In each of the 10 study villages, a 600 x 600 metre sampling area was established around the centre point of the village and the landscape inside this study area was divided into three different landcover categories (village, crop, and semi-natural; Fig. **??**) using QGIS (Version 3.16.8-Hanover). In each of the three habitat types, three fixed survey plots of 60 x 60 metres were randomly located, giving 9 plots in total for each village and 90 plots across all 10 villages. A 40-minute survey was conducted every two weeks from 18 April to 4 November 2021 to record the visitation of insect pollinators to crop and non-crop plants inside each plot. Surveys were conducted between the hours of 09.00 and 17.00 when temperatures exceeded 15°C and when rain was absent or light. During each survey, data collectors walked haphazardly between flowering patches and captured and killed any insect they observed visiting a flower. On each sampling day, data collectors also recorded the percentage flower cover of each plant taxa inside or directly above 15 replicate 1 $m^2$ quadrats within the plot, enabling the phenology of floral abundance to be determined. See *Appendix S1* for further details and acknowledgements for details of taxa identification.

## Pollen quantification

## Network description

As a first step to describe the pollination networks, we counted the numbers of plants, insects, and links (interactions) in each village and in total. For insects and links, we then calculated sampling coverage. Not to be confused with the area covered by a plant, sampling coverage estimates the proportion of the total number of individuals (observations) belonging to taxa (links) included in the sample (Chao & Jost, 2012). A high sampling coverage indicates that most common species have been sampled and, in our case, any undetected (rare) insects are unlikely to be important crop pollinators. We calculated sampling coverage as in Chao & Jost (2012) for each village network and the metaweb including all villages. As we did not observe specific plant individuals (rather, only those visited by insects), we cannot calculate sampling coverage of plants. We also calculated the connectance (proportion of possible links that were observed) of each network and the Jaccard similarity in the communities of plants and insects between villages as well as investigating potential drivers of this turnover (*Appendix S2*).

## Estimating pollinator importance

In mixed-cropping systems such as Nepali smallholder farms, it may be easiest for managers to make decisions based on which pollinators are most important over the whole system rather than on a crop-by-crop basis. We therefore modify the single-crop pollinator importance estimate in Gibson (2012) to give an aggregate estimate over many crops. This revised index combines estimates of the amount of pollen an average individual carries, the probability that deposited pollen will include conspecific pollen grains for the crop plant, and the number of visits made by the taxa.

For a single crop $j$, we estimate the importance $I$ of each pollinator $i$ as:

$$I_{ij} = \frac{P_i \times F_{ij} \times V_{ij}}{\sum_i P_i \times F_{ij} \times V_{ij}} \tag{1}$$

where $P_i$ is the average number of pollen grains carried per individual of pollinator taxon $i$, $F_{ij}$ is the proportion of pollinator $i$'s observed visits that were made to plant $j$, and $V_{ij}$ is the total number of visits pollinator $i$ made to plant $j$.

$P_i$ describes the pollen transport capacity of insect $i$. Large and/or hairy insects tend to carry more pollen than small and smooth insects, and are therefore likely to deposit larger amounts of pollen on the flowers they visit (Cullen *et al.*, 2021). $F_{ij}$ is the visitor fidelity of insect $i$ to crop $j$. An insect which mainly visits the focal crop will likely have a more homogeneous pollen load and deposit a higher proportion of pollen grains than an insect which rarely visits the focal crop. Finally, $V_{ij}$ indicates the frequency with which insect $i$ visits plant $j$ and likely incorporates the influence of both abundance (abundant insects will tend to make more visits overall than rare ones) and insect preferences (abundant insects may not visit plants with incompatible floral morphology, unsuitable nectar, etc.). Because this index includes a measure of pollen transport capacity, we included only insects where the number of pollen grains per individual were counted for at least one individual. This restricted our estimated importance to 92 insect taxa. As our selection of insects for pollen swabbing targeted the most common visitors for four major food crops (apple, Jumli bean, pumpkin, and slipper gourd) and the insects swabbed participate in a majority of the observed interactions (74%), we do not expect to have neglected any highly important pollinators.

Although this index neglects several components of pollination (e.g., insect taxa may differ in the proportion of pollen load deposited per visit), the numerator of equation 1 provides an approximation of the amount of conspecific pollen deposited on plant $j$ by pollinator $i$. The denominator is the the sum of numerator values over all pollinator taxa, such that $I_i j$ is a proxy for the proportion of total conspecific pollen grains of crop $j$ expected to be carried by pollinator $i$. This index will range between 0 and 1 for each $ij$ and will sum to 1 for each plant $j$, ensuring that all crops are weighted equally. If some crops are more important than others based on nutrient composition, monetary value, etc., $I_{ij}$ can be weighted accordingly.

To estimate a pollinator's importance over all crop plants, we can sum $I_{ij}$ over all crops $j$ as follows:

$$I_i = \sum_j \frac{P_i \times F_{ij} \times V_{ij}}{\sum_i P_i \times F_{ij} \times V_{ij}} \tag{2}$$

This is the sum of the proportions of conspecific pollen insect $i$ is expected to contribute to all crops $j$. We calculated two versions of this sum: one including all crops that are at least partially insect-pollinated (including root and leaf crops grown from insect-pollinated seed) with equal weight and one weighting the sum by the estimated proportion of yield depneding on pollinators (taken from the literature; Table S2, *Appendix S2*). As these sums gave qualitatively similar results, we focus on the simpler equal-weighted sum below. To identify crops with similar sets of important pollinators, we calculated Euclidean distance between vectors of importance for pairs of crops in order to identify crops visited by very similar, or very different, sets of pollinators.

## Estimating plant importance to pollinators

When estimating the importance of wild plants to pollinators, we use a similar logic to that outlined in equation 2. However, as we do not know the amount or nutritional composition of nectar and pollen provided by wild plants, we consider only the proportion of an insect's total visits made to each plant (ignoring fidelity and potential differences in plant quality). As we are most interested in wild plants which are heavily used by crop pollinators, we weight the proportion of visits by the insect's overall importance. Note that insects which never visit crop plants have an importance score of 0 and do not contribute to wild plant importance scores. Thus, for a wild plant $W_j$, our estimate of importance is:

$$W_j = \sum_i I_i \times \frac{V_{ij}}{V_i} \tag{3}$$

where $I_j$ and $V_{ij}$ are as above and $V_i$ is the total number of visits made by insect $i$ to all plants.

## Relating estimated importance to pollinators' network roles

While here we identify important crop pollinators based on their visitation patterns and pollen capacity, ecological network studies often define important species as those that are highly central within the network structure (i.e., how much the focal taxon is able to affect the rest of the network). When using information from ecological network studies to guide management, it is vital to know whether these different approaches to identifying key species will give similar results. We therefore calculated two measures of centrality for each insect on their positions in the metaweb and relate each to our estimate of pollinators' importance as crop pollinators. Degree centrality is the number of interaction partners for a focal taxa (Freeman, 1977), while closeness centrality is a measure of the average path length between the focal taxa and other taxa in the network (Freeman, 1979; Delmas *et al.*, 2019); both were calculated using the R (R Core Team, 2016) function 'specieslevel' from the package *bipartite* (Paul & Held, 2011). We then used Kendall's rank correlation analysis to measure the association between centrality measures and the estimated importance. In addition, to test whether centrality and our importance estimate would suggest the same management targets, we calculated the percentage of the 10 and 20 most-important pollinator taxa that were also among the top 10 and 20 most-central taxa using each centrality measure. We preformed all centrality analyses using overall importance and importance to each crop calculated separately.

# Results

## Community summary

Combining all villages, there were 237 plants from 57 families (not counting 50 plant morphospecies which have not been taxonomically identified, involved in 257 interactions). Of these, 56 taxa of plants from 20 families were cultivated as crops or ornamental plants (23.6% of identified plant taxa). The 46 food crops were particularly diverse, coming from

16 families (Fig. S3, *Appendix S1*). Many of these crops originated in the Americas (e.g., corn, pumpkin, tomato, chilli, potato).

The same all-village metaweb included 306 insect taxa from 66 families (excluding 596 individuals not identified at least to family; 5.4% of all individuals). 174 insects from 45 families (60.4% of all taxa observed) visited cultivated plants. Only one insect, the native Asian honeybee (*Apis cerana*) is semi-domesticated, living in both managed hives and as wild swarms. No other insect taxa is domesticated in these villages.

Plants and insects that were not identified at least to family were omitted from the interaction networks. This left 11,051 observations producing 2,774 unique links, represented by 1-557 individual observations. Over half of the links (1629) were represented by a single observation. Sampling coverage (the estimated proportion of individuals belonging to sampled species) was high for insects (>95% in all villages) but lower for links (66.5-85.3%). In the metaweb, connectance was quite low (C=0.038).

## Variation in network composition in space and time

Networks for a single village had far fewer taxa than the metaweb (54-89 plants and 73-131 insects) but a greater proportion of possible links between these taxa were observed (Table S3, *Appendix S3*). This suggests that many of the potential interactions which were not observed in the metaweb related to taxa which were never observed co-occurring in any village. Most taxa were found in only one or two villages, but domesticated plants and insects that visit at least one domesticated plant tended to be found in more villages than wild plants and insects visiting only wild plants (Fig. 1A-B,D-E; $t_{76.85}$=2.53, $p$=0.014 for plants and $t_{225.58}$=13.3, $p$<0.001. for insects). Since most taxa were observed in few villages (means of 3.31 and 3.04 for domesticated and wild plants and 3.96 and 2.75 for insects visiting domesticated or only wild plants), it is not surprising that turnover in the plant and insect communities was high between any pair of villages (Fig. 1C).

Similarly, networks describing interactions occurring in a single week included fewer taxa (1-79 plants and 1-101 insects) than the full-year metaweb. These networks were also more fully-connected than the annual metaweb, emphasising the importance of spatial and temporal coexistence before a plant and pollinator can interact. Many domesticated and wild plants had flower visitors in only one or two weeks, and the majority of insects visiting

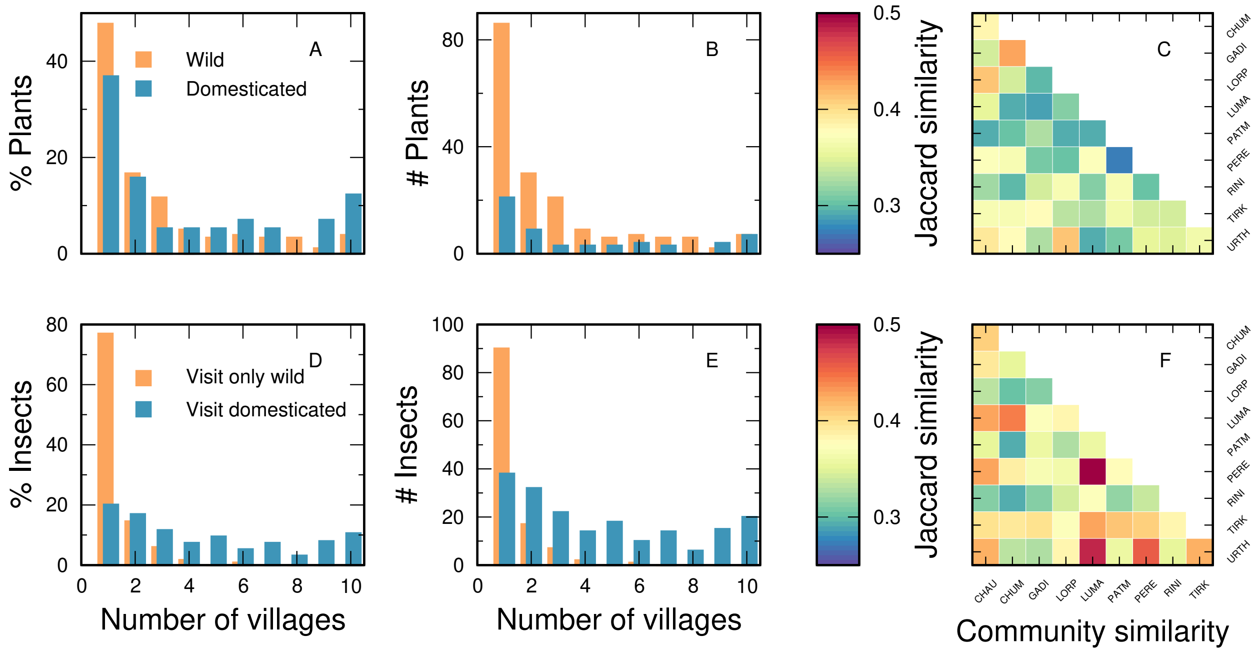



**Figure 1:** Most plants and insects were observed in few villages. **A-B)** We show a histogram of the percentage and absolute numbers of wild plants (yellow) and domesticated plants (blue) observed in varying numbers of villages. Domesticated plants were, on average, observed in slightly more villages than wild plants. **C)** Jaccard similarity of plant communities between villages was generally low. **D-E)** We show a histogram of the percentages and absolute values of insects visiting only wild plants (yellow) and visiting at least one domesticated plant (blue) observed in varying numbers of villages. Insects visiting at least one domesticated plant were, on average, seen in more villages than those visiting only wild plants. **F)** Jaccard similarity of insect communities between villages was higher than similarity of plant communities but still generally low.

wild plants were observed flying in only one week (Fig. 2A-B,D-E). Domesticated and wild plants received visitors for similar lengths of time on average while insects visiting crops tended to have longer active periods than insects visiting only wild plants ($t_{75.61}$=1.30, $p$=0.197 for plants and $t_{204.7}$=11.2, $p$<0.001. for insects). The brief active periods of many taxa creates large turnover in the plant and insect communities observed in different weeks (Fig. 2C,F).

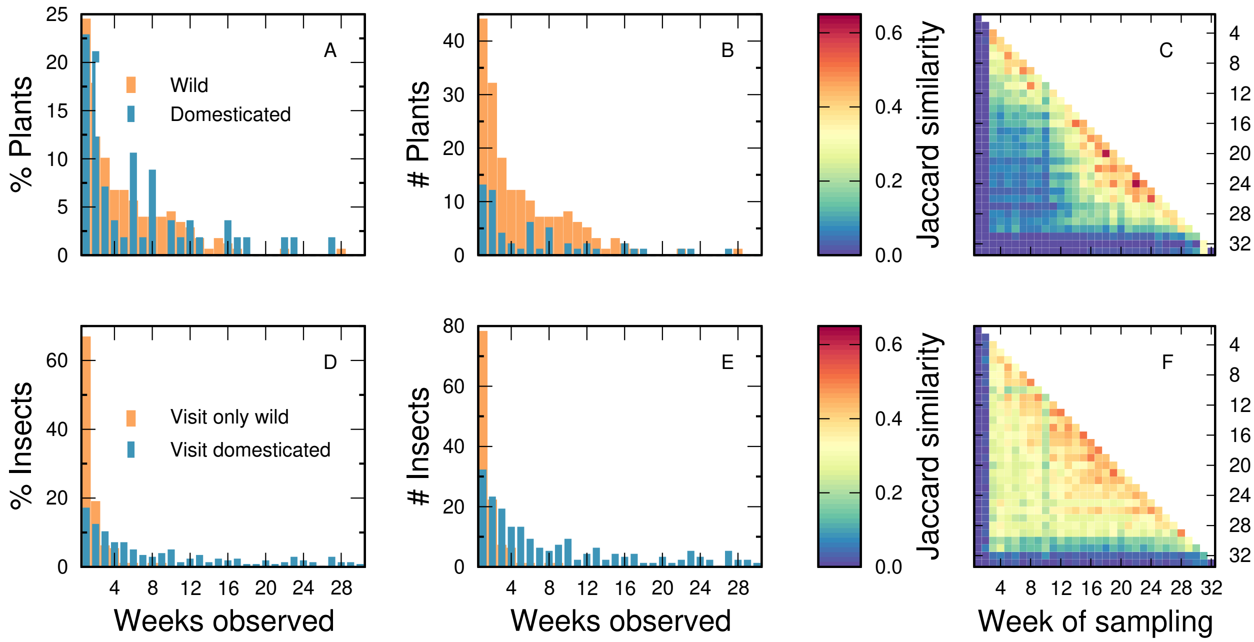


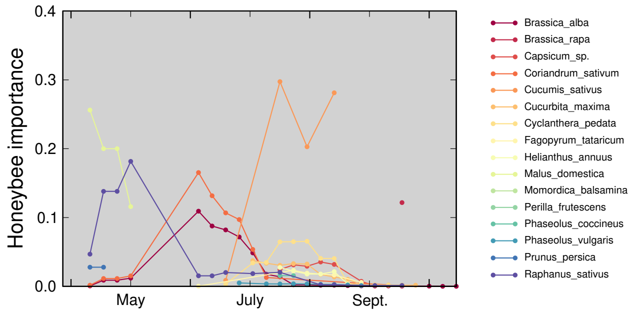

**Figure 2:** Most plants and insects were observed flowering or visiting flowers in few weeks, corresponding to brief active periods. **A-B)** We show a histogram of the percentage and absolute numbers of wild plants (yellow) and domesticated plants (blue) observed flowering in varying numbers of weeks. Domesticated plants had, on average, slightly longer active periods than wild plants. **D-E)** We show a histogram of the percentages and absolute values of insects visiting only wild plants (yellow) and visiting at least one domesticated plant (blue) observed visiting flowering in varying numbers of weeks. Insects visiting at least one domesticated plant had, on average, much longer active periods than those visiting only wild plants. **C, F**) Jaccard similarity in insect visitors was generally higher than in plants visited between weeks, but in both cases similarity was highest between samples that were close in time.

## Estimated importance of pollinators

Across all crops and villages, the insects with highest estimated importance were mostly bees, although some fly and butterfly taxa also had high importances (Table 1). The five insects with the highest overall estimated importance as crop pollinators (Table 1) were among the insects with the highest degrees but did not have especially high closeness centralities. As these estimated importances are weighted by the amount of pollen an individual insect carries, only the 92 insect taxa where at least one individual was swabbed are included. However, as these insects were selected to include most taxa that visited crops, this means we are able to estimate pollen transport for 2,045 interactions (9,919 observations, 3,640 of which involved *Apis cerana*). We therefore expect that our sample covers most of the insects with high estimated importance. Despite the high overall importance of honeybees, crops differed in the sets of insects that were their most important pollinators (Figs. S6-8, *Appendix S4*). For example, honeybees were less important as pollinators of pumpkin (*Cucurbita maxima*) and slipper gourd (*Cyclanthera pedata*) which were more dependent on bumblebees and flies, respectively. Even crops within the same family could have substantially different sets of highly-important pollinators.

Importance of pollinators could vary widely between villages and over time Fig. 5; Fig. S6, *Appendix S4*). Honeybees (*Apis cerana*) had the highest overall importance through most of the season but had lower importance in late June-early July and October-November. Bumblebees tended to have the highest importance in late June-early July and in August, while hoverflies (*Eristalis*) were highly important late in the season

**Figure 3:** Importance of semi-domesticated honeybees *Apis cerana* varied between crops and over time. Honeybees were highly important as pollinators of apple (*Malus domestica*), cucumber (*Cucumis sativus*), radish (*Raphanus sativus*), and coriander (*Coriandrum sativum*).




(late August-late October). Most Lepidoptera and Coleoptera taxa likewise had low overall importance, except for *Celastrina* taxa which had high importance in July and August. *Celandrina* were important pollinators of dill, tomato, and Napa cabbage; their high importance in July and August may indicate that the other pollinators of cabbage and tomato (largely solitary bees and wasps in our dataset) have low abundance during this period. The varying importances of different groups of insects over time undoubtedly reflects the different flowering periods of crops but also suggests that these insects provide complementary pollination service to farms as a whole.

## Estimated importance of plants

The most important plants were generally found in many villages (Fig. S9 and Table S28, *Appendix S5*). As the plants with high importance within a village also generally had high overall importance, this is not likely to be simply an effect of summing importance across more villages for widely-distributed plants. Many of the highly-important plants were food crops and another is a common ornamental plant widely used in ceremonies (*Tagetes* *erecta*; marigold). Although crops which contributed large amounts of flower cover tended to have somewhat higher importance (Fig. S11, *Appendix S5*), there was no clear relationship between importance and flower cover considering all plants.

**Table 1:** The 20 insects with the highest all-crop estimated importance included Hymenoptera, Diptera, and Lepidoptera. Importance was estimated using visitation data weighted by the average number of pollen grains carried per individual as in 2. We first standardized importances for each crop to sum to 1 ($I_{EW}$) and then weighted importances by the extent of pollinator dependence ($I_{DW}$). This second overall importance estimate up-weights pollinators which are very important to highly pollinator-dependent crops. We also provide the ranks of each version of overall importance, as well as degree (number of plant taxa visited) and closeness centrality for each insect. The latter two metrics are commonly used to identify species with important structural roles in interaction networks.

| Pollinator | Order | $I_{EW}$ | $Rank_{EW}$ | $I_DW$ | $Rank_{DW}$ | Degree | Closeness |
|---|---|---|---|---|---|---|---|
| *Apis cerana* | Hymenoptera | 7.13 | 1 | 3.708 | 1 | 140 | $4.88\times10^{-3}$ |
| *Bombus tunicatus* | Hymenoptera | 2.21 | 2 | 0.941 | 2 | 39 | $4.27\times10^{-3}$ |
| *Eristalis* sp. | Diptera | 1.53 | 3 | 0.893 | 3 | 98 | $4.79\times10^{-3}$ |
| *Andrena* sp. | Hymenoptera | 1.34 | 4 | 0.336 | 7 | 86 | $4.78\times10^{-3}$ |
| *Bombus* sp. | Hymenoptera | 1.13 | 5 | 0.737 | 4 | 40 | $4.18\times10^{-3}$ |
| *Apidae* sp. | Hymenoptera | 1.03 | 6 | 0.277 | 10 | 9 | $3.39\times10^{-3}$ |
| *Anthophora* sp. | Hymenoptera | 0.977 | 7 | 0.286 | 9 | 59 | $4.59\times10^{-3}$ |
| *Celastrina* sp. | Lepidoptera | 0.965 | 8 | 0.240 | 13 | 39 | $4.54\times10^{-3}$ |
| *Apis laboriosa* | Hymenoptera | 0.874 | 9 | 0.225 | 15 | 5 | $3.31\times10^{-3}$ |
| *Bombus asiaticus* | Hymenoptera | 0.835 | 10 | 0.213 | 17 | 43 | $4.39\times10^{-3}$ |
| *Lucilia* sp. | Diptera | 0.720 | 11 | 0.518 | 5 | 53 | $4.47\times10^{-3}$ |
| *Diptera* sp. | Diptera | 0.706 | 12 | 0.459 | 6 | 71 | $4.74\times10^{-3}$ |
| *Tenthredo* sp. | Hymenoptera | 0.628 | 13 | 0.224 | 16 | 27 | $4.18\times10^{-3}$ |
| *Hylaeus* sp. | Hymenoptera | 0.461 | 14 | 0.246 | 12 | 45 | $4.37\times10^{-3}$ |
| *Calliphora* sp. | Diptera | 0.455 | 15 | 0.293 | 8 | 15 | $3.82\times10^{-3}$ |
| *Pieris brassicae* | Lepidoptera | 0.402 | 16 | 0.246 | 11 | 38 | $4.40\times10^{-3}$ |
| *Lasioglossum* sp. | Hymenoptera | 0.307 | 17 | 0.171 | 18 | 62 | $4.59\times10^{-3}$ |
| *Tetralonia* sp. | Hymenoptera | 0.272 | 18 | 0.026 | 28 | 10 | $3.33\times10^{-3}$ |
| *Polistes* sp. | Hymenoptera | 0.242 | 19 | 0.228 | 14 | 47 | $4.56\times10^{-3}$ |
| *Cerceris* sp. | Hymenoptera | 0.228 | 20 | 0.162 | 19 | 16 | $3.88\times10^{-3}$ |

## Relating centrality to importance

The overall estimated importance of a pollinator (across all crops; all insect-pollinated crops equally weighted) was significantly, but moderately strongly, correlated with both

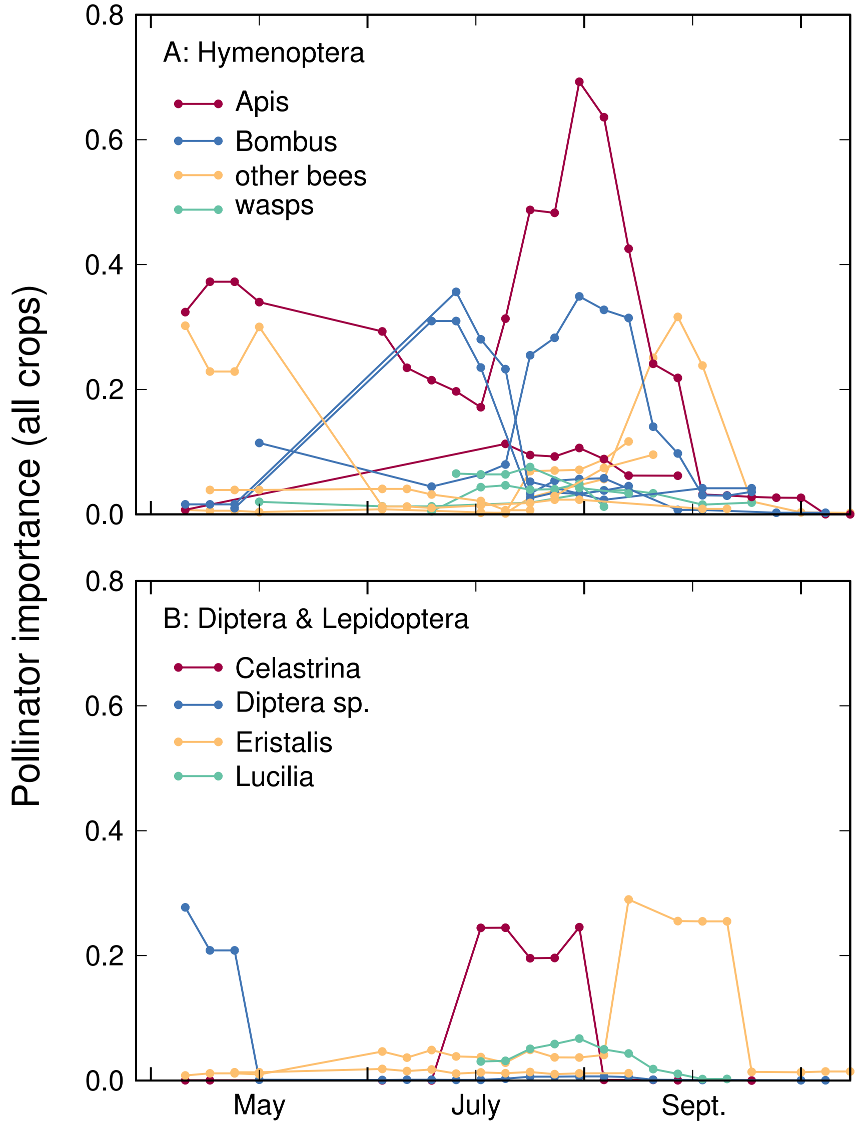



**Figure 4:** An insect taxon's importance summed over all crops and villages varied from week to week. Semi-domesticated and wild honeybees (*Apis cerana* and *A. laboriosa*, red, top panel) were highly important except during June-July and Spetember-November. During these periods, bumblebees (several *Bombus* species) and hoverflies (*Eristalis*) had the highest importance. We show five-week rolling averages of importance for the 20 taxa with the highest whole-year overall importances, with one line per taxon. Most were Hymenoptera but a few Diptera taxa (*Eristalis*, *Lucilia*, and unidentified Diptera) and a single Lepidopteran (*Celastrina* sp.) were also among the top 20. The importance of each insect to each crop in each week is scaled such that the importances of all insects to a crop over the whole season sum to one. Axis labels correspond to the middle of the month named.

closeness and degree centralities ($\tau$= 0.375, p< 0.001, z = 4.53 and $\tau$= 0.345, p< 0.001, z = 4.12, respectively; Fig. 6). However, using a list of the 10 or 20 insects with the highest centralities would capture only 60-70% of the insects with the highest overall importance

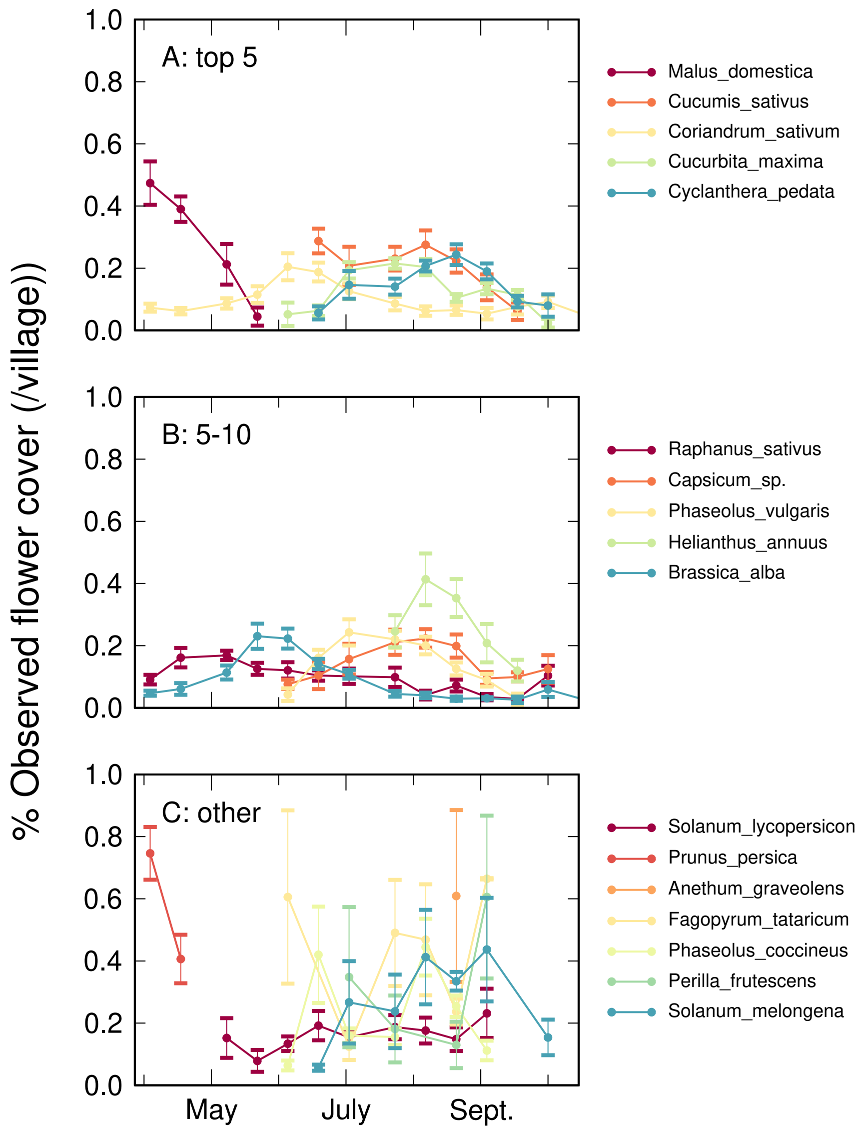



**Figure 5:** Crops had variable flowering times. Some, like apples, flowered relatively briefly at the beginning of the flowering season. Others, such as several Cucurbitaceae, had extended flowering periods later in the year. Some crops with very long flowering periods (e.g., *Coriandrum sativum*) may be re-sown several times during the growing season. We show the mean (across villages) proportion of a crop's total observed flower cover observed in each week. Error bars represent ±SE. We omit crop-week combinations that were not observed in more than one village. Crops are ordered based on their total observed flower cover, with *Malus domestica* having the most flowers in total.

(4/10 for degree, 5/10 for closeness, and 12/20 for both closeness and degree). This means that identifying key taxa based on ranks of centrality would neglect many of the most-important pollinators. When estimating pollinator importance separately for each insect-pollinated crop, centrality generally captured an even smaller proportion of the pollinators with the highest estimated importance (mean of 21.6-2.36% for the 10 most-important pollinators and 24.8-25.4% of the 20 most-important pollinators). *Capsicum* sp. was among the plants with the closest match between metrics, with centrality capturing 40-55% of the most-important pollinators. For other species, only one or two highly-important pollinators might be among the most-central insects (Tables *S29, Appendix S6*). The substantial mismatch between lists of 'key' taxa highlights the

**Table 2**

| Plant | Crop | Importance | Villages observed |
|---|---|---|---|
| *Brassica alba* | Food | 1.85 | 10 |
| *Phaseolus vulgaris* | Food | 1.70 | 10 |
| *Persicaria nepalensis* | Wild | 1.67 | 10 |
| *Cucurbita maxima* | Food | 1.39 | 10 |
| *Tagetes erecta* | Ornamental | 1.06 | 9 |
| *Cyclanthera pedata* | Food | 0.923 | 10 |
| *Cotoneaster microphylla* | Wild | 0.795 | 9 |
| *Malus domestica* | Food | 0.756 | 10 |
| *Anisomeles indica* | Wild | 0.685 | 5 |
| *Raphanus sativus* | Food | 0.612 | 10 |
| *Impatiens* sp. | Wild | 0.601 | 7 |
| *Coriandrum sativum* | Food | 0.589 | 10 |
| *Helianthus annuus* | Food | 0.567 | 7 |
| *Rosa sericea* | Wild | 0.554 | 6 |
| *Galinsoga ciliata* | Wild | 0.529 | 10 |
| *Cirsium wallichii* | Wild | 0.489 | 5 |
| *Cosmos bipinnatus* | Ornamental | 0.443 | 5 |
| *Origanum vulgare* | Food | 0.396 | 9 |
| *Fagopyrum tataricum* | Food | 0.391 | 9 |
| *Solanum tuberosum* | Food | 0.347 | 9 |

importance of choosing a measure that reflects management goals (i.e., preservation of biodiversity *per se* vs. protecting crop pollination).

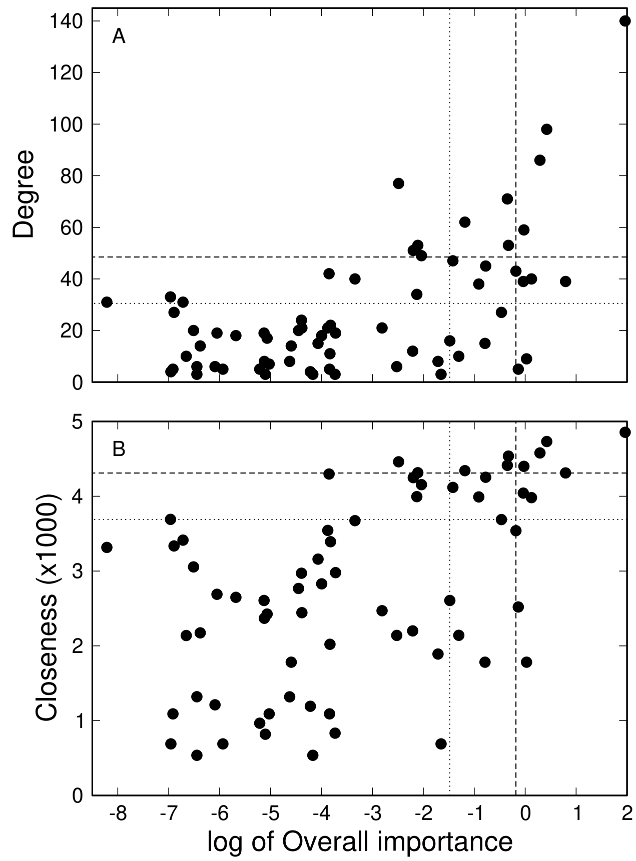



**Figure 6:** Rank of estimated pollinator importance was significantly but weakly correlated with ranks of degree (top) and closeness centrality (bottom). Here we show degree and weighted closeness (multiplied by 1000 for visibility) plotted against the log of overall importance for each insect. Importances were logged to make the differences among low-importance insects clearer. Insects to the right of the dashed (dotted) lines are among the 10 (20) with the highest importances and insects above the dashed (dotted) lines are among those with the 10 (20) highest centralities. Insects in the off-diagonal boxes would appear on a list of key species identified by one metric but not both.

# Discussion

In this study, we used ten Nepali villages to understand the underpinnings of local ecosystem services. We found a highly variable plant-pollinator community with a diverse set of important crop pollinators and substantial turnover in space and time. These pollinators largely depended upon crop plants, including plant taxa originating in the Americas. Estimates of importance for crop pollination, like community composition, varied over space and time and were not well predicted by measures of centrality. Together, these findings suggest concrete measures which may protect or improve pollination service while emphasising the need to consider measures of taxa importance that closely match the desired goal (e.g., obtaining crop pollination vs. maintaining biodiversity). Below, we will examine each finding in turn.

## Community composition was highly variable

The Nepali smallholder farm community is quite diverse, both in terms of the numbers of taxa and families included in the community overall, and in terms of differences in the local-scale networks in each village. The metaweb included 237 plant taxa identified at least to genus and 306 insect taxa identified at least to family, as well as many unidentified specimens. The true diversity of these communities is likely even higher as many of these taxa were only observed in one village, suggesting that sampling of other locations in the Jumla region might reveal additional taxa.

In evidence of the high diversity of the networks, less that five plants and less than 20 insects (about 10% of each group) were found in all villages. As sampling coverage for insects (% of individuals belonging to sampled taxa) was quite high, any taxa not observed in a given village are likely to be rare and relatively unimportant to food production on these farms. Domesticated plants (crops and ornamentals) and the insects that visit them were more widespread than wild plants and insects which only visited wild plants. Thus, despite the very high richness of locally cultivated crops, the cultivated part of vegetation is still more consistent than the non-cultivated part.

While the distribution of domesticated plants depends on human activity, the current distribution and flower use of insect taxa will partly reflect the history of the crops in this region. As most of the crop plants in this system are introduced (e.g., tomato, chilli pepper, and slipper gourd from the Americas), insects which already visited a wide variety of native plants may have been better able to take advantage of newly-introduced and highly abundant crop flower resources. These insects might be more widespread because they have followed the crops they visit or because their generalism allows them to persist in a wider variety of habitats.

## Highly-important pollinators are quite diverse

For provisioning of pollination services, insects are far from equal. The pollinators with high estimated importance included insects from several orders. Surprisingly, beetles (*Popillia* sp.) were among the frequent flower visitors with substantial pollen loads. These taxa are not generally considered effective pollinators in agricultural settings (). In Jumla smallholder farms, however, individual *Popillia* could carry a large number of pollen grains and are competent fliers. They may therefore contribute much more pollination service than beetles in other systems.

The most important pollinator across all crops was the native honeybee, *Apis cerana*. These insects are highly important as providers of honey (an important trade good as well as for local consumption) as well as pollinators. However, like the European honeybee (), local beekeepers report declines in Asian honeybee populations in Jumla (S. Kortsch, personal communication). It is currently not clear exactly what is driving these declines, though local beekeepers report changing weather patterns and reduced flower availability as the most important factors. Our results demonstrate the crucial importance of safeguarding *Apis cerana* populations, and emphasise the value of maintaining a diverse community of other important pollinator taxa which may respond differently to environmental changes, thereby buffering any impacts on crop pollination services (**?**).

## Crops, weeds, and shrubs are important to pollinators

Most of the plants with high estimated importance to crop pollinators were the crop plants themselves, including plants originating from the Americas (e.g., *Cucurbita maxima* and *Cyclanthera pedata*). As insects native to Nepal have had a relatively short exposure to these introduced crops (maximum hundreds of years), these high importances are likely to reflect the high abundance of crops, the richness of their floral rewards or their general flower morphology, rather than local evolution of strong preferences for these taxa. Among wild plants with high estimated importance, some were weedy taxa with small or low-quality flowers (e.g., *Persicaria nepalensis*, *Galinsoga ciliata*, and *Taraxacum*). Despite the small nectar and pollen rewards provided by these plants, they may nevertheless be valuable to insects because they are highly locally abundant, have very accessible floral resources and grow in dense patches in and immediately adjacent to crop fields. Other important wild plants (e.g., *Cotoneaster microphylla* and *Rosa sericea*) are shrubs with many flowers per plant which are frequently used in hedgerows to mark field boundaries. These plants may be particularly important to pollinators because they offer a spatially concentrated source of nectar and pollen and are situated in close proximity to crop fields.

The overwhelming importance of crop plants to native insects (including the semi-domesticated honeybee) suggests that the supply of wild floral resources in the Jumla region may be generally low. Much of the native grassland and shrubland surrounding villages is heavily grazed/browsed whilst many of the forested areas are coniferous, with a sparse herbaceous under-story. In semi-structured interviews, local beekeepers report declines in floral resources over time as one of the main drivers of their honeybee declines, citing over-grazing, changing weather patterns and habitat clearance as important drivers for the loss of flowers. In order to help protect pollinators from ongoing climate change and, ideally, increase pollinator populations in the villages studied, it might be useful to increase flowering plant populations. Assuming that the farmers already grow as many crop plants as is feasible, this could be done by setting aside small patches for wild plants to flower undisturbed near crop gardens (e.g., by limiting grazing in selected patches), increasing the number of flowers in field margins, and/or encouraging grazing-resistant plants such as shrubs. While such strategies may be challenging given high grazing pressure and low productivity, the pay-off may still be significant. We also recommend that large flowering shrubs be left in peace as these are likely to be very important pollinator food sources as individuals.

## Centrality does not closely match importance to crop production

Although centrality measures have commonly been used to identify keystone taxa, these methods neglect biologically-important information such as biomass (Delmas *et al.*, 2019). The correlation between centrality (both degree and closeness centralities) and pollinator importance was significant and moderately strong ($R^2$=0.46-0.48). Nonetheless, only a small fraction of taxa identified as highly-important crop pollinators (top 10 or top 20 taxa) were also highly central. This means that a farm manager relying on a shortlist of 'key insects' previously identified based on centrality-focused studies would neglect many highly-important pollinators. For example, while two highly-important insects, *Apis cerana* and *Eristalis* sp., had the highest degree centralities, *Eristalis* sp. had a lower estimated importance than the less-central *Hylaeus* sp. Conversely, focusing only on the most important crop pollinators may not be an effective approach for conservation of biodiversity (Klein *et al.*, 2007) as many pollinators which contribute to community stability are not major crop pollinators. It is therefore important to match the metric used to select key taxa to the focus of management efforts (e.g., improving crop pollination or preserving biodiversity).

## Conclusions

Our investigation of the plant-pollinator networks underlying pollination services on Nepali smallholder farms reveal high local diversity and large differences in community composition over small distances. Interactions between food crops and their pollinators are both embedded in the local ecology and show the impacts of globalisation. First, many crop plants and some of the most-visited wild plants (*Galinsoga*) have been introduced from the opposite side of the planet but are frequently visited by native insects. Second, important crop pollinators depend on both crop plants and surrounding wild flowers (native and introduced). These observations emphasize that no farm is an island, and that even in the most isolated setting, local ecosystem and services can only be understood with reference to large- and small-scale anthropogenic change. Overall, the variable importance of individual pollinator taxa for individual crops, and the large differences in importance over time and space emphasise the importance of sustaining local crop pollinator diversity in order to promote long-term stability and resilience in food production and nutrient availability in this region. We urgently await similar explorations of other smallholder farm ecosystems and their underlying ecosystem services in other regions and on other continents.

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