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RESEARCH ARTICLE

Agricultural specialisation increases the vulnerability of pollination services for smallholder farmers

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Abstract

1. Smallholder farms make up 84% of all farms worldwide and feed 2 billion people. These farms are heavily reliant on ecosystem services and vulnerable to environmental change, yet under-represented in the ecological literature. The high diversity of crops in these systems makes it challenging to identify and manage the best providers of an ecosystem service, such as the best pollinators to meet the needs of multiple crops. It is also unclear whether ecosystem service requirements change as smallholders transition towards more specialised commercial farming—an increasing trend worldwide.
2. Here, we present a new metric for predicting the species providing ecosystem services in diverse multi-crop farming systems. Working in 10 smallholder villages in rural Nepal, we use this metric to test whether key pollinators, and the management actions that support them, differ based on a farmers' agricultural priority (producing nutritious food to feed the family vs. generating income from cash crops). We also test whether the resilience of pollination services changes as farmers specialise on cash crops.
3. We show that a farmers' agricultural priority can determine the community of pollinators they rely upon. Wild insects including bumblebees, solitary bees and flies provided the majority of the pollination service underpinning nutrient production, while income generation was much more dependent on a single species—the domesticated honeybee *Apis cerana*. The significantly lower diversity of pollinators supporting income generation leaves cash crop farmers more vulnerable to pollinator declines.
4. Regardless of a farmers' agricultural priority, the same collection of wild plant species (mostly herbaceous weeds and shrubs) were important for supporting crop pollinators with floral resources. Promoting these wild plants is likely to enhance pollination services for all farmers in the region.

T. P. Timberlake and A. R. Cirtwill contributed equally to this manuscript.

5. *Synthesis and applications*. We highlight the increased vulnerability of pollination services when smallholders transition to specialised cash crop farming and emphasise the role of crop, pollinator and wild plant diversity in mitigating this risk. The method we present could be readily applied to other smallholder settings across the world to help characterise and manage the ecosystem services underpinning the livelihoods and nutritional health of smallholder families.

KEYWORDS
cash crop, ecological intensification, ecosystem service, Nature's Contributions to People, Nepal, nutrition, smallholder farming

1 | INTRODUCTION

Smallholder farms provide food and livelihoods for over 2 billion people (Lowder et al., 2021), but smallholder families are among the poorest and most food-insecure people on Earth (FAO, 2018). On these farms, alternative food sources (e.g. markets) and economic safety nets (e.g. savings or insurance schemes) are typically limited, as are agricultural resources such as chemicals and advanced technologies. Without these manufactured resources, smallholders depend heavily on local ecosystem services such as pollination, biological pest control and nutrient cycling (Steward et al., 2014; Timberlake et al., 2022). Such direct reliance on the local environment makes smallholder farmers vulnerable to environmental change and degradation (Harvey et al., 2014). However, it also enables them to sustainably enhance their livelihoods and food security through management of local ecosystem services—an approach known as ecological intensification (Bommarco et al., 2013; Pretty, 2018). Ecological intensification is highly effective in smallholder farms (Garibaldi et al., 2016); yet these systems remain understudied in the ecological literature as they are mostly located in low and middle income countries with limited research funding and commercial incentives (Lowder et al., 2021; Steward et al., 2014). This lack of scientific understanding is a major constraint on the path to sustainable global food security.

Pollination services play a major role in supporting global agricultural production (Klein et al., 2007), especially in smallholder farming regions (Garibaldi et al., 2016) where they support livelihoods (Tibesigwa et al., 2019), nutritional health (Eilers et al., 2011; Smith et al., 2015, 2022) and stability of yields (Bishop et al., 2022). Because of these strong impacts, the risks from future pollinator declines are thought to be most acute for smallholders (Millard et al., 2023) and management of pollination services should therefore be a high priority. However, managing pollination services on smallholder farms presents two important challenges. Firstly, unlike industrialised farms with large monoculture fields, smallholders typically cultivate numerous pollinator-dependent crops with different morphologies and phenologies in a small area of land. Hence, while an industrialised farmer may be able to identify and promote one or two insects which meet the pollination needs of their specific crop (e.g. honeybees for an almond crop), this single-crop approach does not work on a smallholder farm where many different crops are grown in the same small area. Instead, it is important to identify the set of insects that will pollinate *all* the crops on the farm. The second challenge is that smallholder farmers vary greatly in their agricultural priorities, making it difficult to assess the value of ecosystem services and the species providing them. Broadly speaking, smallholder farmers have two main agricultural priorities: one is to produce nutritious food to feed the family, and the other is to generate income. Some farmers are purely subsistence-based, meaning their primary goal is to feed the family and very little produce is sold for income. This situation is common in isolated regions of the world with limited access to regional or global markets. However, market access has increased substantially across the world, enabling the transition of many smallholders towards small-scale commercial production where the economic income from cash crops is prioritised over food production (Giller et al., 2021; Holmelin, 2021). This change typically involves a shift away from diversified systems, where a range of food crops are grown to meet the nutritional needs of the family, towards simplified systems where a few high-value cash crops are grown to generate income (Giller et al., 2021; Holmelin, 2021). Such a move provides new economic opportunities for impoverished communities but carries the risk of high dependence on a narrow range of crops, each of which could fail as a result of unsuitable environmental, economic or ecological conditions (Abson, 2019), including pollinator loss. To adapt to this new farming context and minimise risk, specialised cash crop farmers may need to manage their ecosystem services differently from diversified subsistence farmers whose risk is spread across multiple crops.

In this study, we present a novel metric for identifying the key species underpinning ecosystem service delivery in diverse multi-crop farming systems, such as smallholder farms. Our metric draws upon theory from the network cascade framework which links the ecosystem services demanded by people to the networks of interacting species that underpin them (Bianco et al., 2024; Stanworth et al., 2024). Using pollination service as an example, we apply this metric to identify insects with an empirically established role in crop pollination, as well as the wild plant species that support these insects. The metric we present—termed the Multi-Crop Pollinator

Importance (MCPI) metric—represents the total contribution of each insect taxon to all of the pollinator-dependent crops grown on a farm. It therefore distils the complexity of the system into one single value for each pollinator, reflecting its total contribution to pollination service provision. When calculating this metric, crops can be weighted by their relative value to the household, making it adaptable to whichever output a farmer chooses to prioritise. For example, crops could be weighted by their relative nutritional value, reflecting their importance to a subsistence farmer aiming to feed the family. Alternatively, they could be weighted by their relative economic value, reflecting their importance to a cash crop farmer aiming to generate income. Therefore, not only does the metric enable us to identify species providing ecosystem services on a smallholder farm, it also allows us to investigate differences in ecosystem service requirements between farmers with distinct agricultural priorities.

Working in replicate smallholder villages in Nepal, we apply the MCPI metric to predict the best crop pollinators and test whether these 'best' pollinators and management recommendations for them differ based on a farmers' agricultural priority. We explore two contrasting priorities: pure subsistence farming (prioritising crops that feed the family), and cash crop farming (prioritising crops that generate income). Although most smallholders lie somewhere on a continuum between these two strategies, our approach highlights the broad patterns of change a farmer is likely to experience as they transition from primarily subsistence-based agriculture to commercial farming—a common trend in our study region, and worldwide. Following this approach, we ask three specific questions: (1) Are the pollinators underpinning the production of nutritious food the same as those underpinning income generation on a smallholder farm?; (2) Do the wild plants supporting key pollinators differ for farmers focusing on nutrient production versus income generation?; and (3) Does the resilience of pollination services change as farmers specialise on cash crops?

2 | MATERIALS AND METHODS

2.1 | Study sites

Fieldwork took place in 10 smallholder farming villages (2400–3000 m a.s.l.; temperate climate) in Patarasi Rural Municipality of Jumla District, Nepal (see Figure S1; Appendix S1). Each study village comprised a cluster of 100–400 closely spaced households interspersed with small vegetable gardens and livestock enclosures. Village surroundings include many small (0.01–0.3 ha) arable fields and apple orchards as well as large areas of steep, heavily grazed grassland pasture and native coniferous forest (Figures S2 and S3). A wide range of pollinator-dependent crops are grown in each village including apple, bean, pumpkin and mustard. Like many other parts of the world, improved market access and economic incentives have driven many subsistence farmers in Jumla towards more specialised cash crop farming, primarily of apples. In our study region, 37% of households remain as pure subsistence farms, 60% grow cash crops as well as food and 3% are specialised cash crop farmers, though this number is increasing (Sapkota et al., 2022). Survey permissions were provided by landowners the Nepal Ministry of Forest and Environment [Ref: 258].

2.2 | Recording plant–pollinator visitation

To characterise the plant–pollinator interaction network underpinning pollination service delivery, we conducted plant–pollinator visitation surveys every 2 weeks from 18 April to 4 November 2021 (spring to autumn) in a 600 × 600 m sampling area centred on the midpoint of each study village. This area was divided into three habitat categories: village, crop and semi-natural vegetation. In each of these habitats, we randomly located three replicate fixed survey plots of 60 × 60 m (nine plots per village; Figure S2). Every 2 weeks, a 40-min survey was conducted in each plot to record the interactions between plants (both crop and non-crop species) and flower-visiting insects. Insects were captured, pinned and identified to species or morphospecies (see acknowledgements). For further details, see Appendix S2.

2.3 | Estimating the effectiveness of insect taxa as crop pollinators

Without detailed studies on the behaviour and morphology of each insect taxon, and on the seed set of plants exposed to different pollinators, we cannot know which flower visitors are truly pollinators (King et al., 2013). Here, we make the assumption that any insect which visits a flower is a potential pollinator and estimate pollinator importance (PI) based on two aspects of relatively accessible information: visitation frequencies and the total amount of pollen an insect carries. Thus, we define the potential importance of an insect as a pollinator (hereafter, 'pollinator importance') as the visitation frequency of an insect to a specific crop multiplied by the mean number of pollen grains carried on its body (hereafter: pollen carrying capacity). This makes the assumption that insects which visit a focal crop frequently and carry large amounts of pollen on their bodies are likely to be better pollinators than insects which visit less frequently and carry little pollen (consistent with Földesi et al., 2021; Howlett et al., 2011). Pollen carrying capacity was estimated by swabbing individuals of each insect taxon and calculating the mean number of pollen grains carried on their body and available for pollination (i.e. not corbicula pollen; more details in Appendix S3). For each insect, the metric estimates its proportional contribution to the total pollen transport for a given crop species, based on the following equation:

$$\text{Pollinator Importance (PI)}_{ic} = \frac{V_{ic} \times P_i}{\sum_i \left(V_{ic} \times P_i\right)},$$

where V_{ic} is the visitation frequency of insect *i* to crop *c* and P_i is the pollen carrying capacity of insect *i*. Thus, insects which carry lots of pollen and make up a high proportion of all visits to a crop will receive a high importance score. This metric could be extended to include other proxies for pollinator effectiveness (e.g. morphological or behavioural matching between plants and insects) where these are known.

2.4 | Quantifying the relative agricultural value of different crops

We aimed to quantify the relative value of each crop plant based on two contrasting scenarios of farming priority. The first scenario (nutrient production) assumed that a farmers' priority was to produce sufficient nutrients to feed the family. The second scenario (income generation) assumed that a farmers' priority was to maximise income from the sale of cash crops. In the nutrient production scenario, we quantify the value of each crop based on its relative nutritional value across 12 essential dietary nutrients. We used a modified version of the approach of Darmon et al. (2005) and ranked crops in ascending order of nutrient density for each of the 12 nutrients. We then took a mean rank value for each crop across all nutrients (values in Table S1). In the income generation scenario, we quantified the value of each crop by its contribution to household income. This was assessed through a survey of 200 farming households (20 from each study village), representing approximately 10% of the total population of households (Appendix S4; Table S2). Ethical approval for the surveys was provided by the Nepal Health Research Council [Ref: 1709] and informed consent (signature or thumb print) was obtained from each participant. Households reported their total annual income from each pollinator-dependent crop, and the mean value across all households growing the crop was used as a proxy for the crop's economic value (values in Table S1). To ensure comparability between the two scenarios, we normalised each value metric (economic or nutritional) so that all scores fell between 0 and 1 (values in Table S3).

2.5 | Estimating PI at the multi-crop level

In dense multi-crop systems, managers need to make decisions based on which pollinators are important over the whole range of crops, rather than any one crop individually. We therefore extend the single-crop PI score (outlined above) to provide an aggregate estimate of each insect's importance to multiple crops in each of the 10 villages. To account for differences in pollinator dependence among crops, the PI scores for each crop were multiplied by the percentage pollinator dependence of the crop defined as the reduction in yield recorded when flower visitors are excluded (values taken from the literature and our own pollinator exclusion experiments; see Table S3; Appendix S5). Finally, to reflect the agricultural priority of the farmer, each crop is weighted by its relative value to the farmer (see section above) so that the pollinators of important crops are given more value than those of less important crops. Thus, for a given insect (*i*), its importance score is calculated as:

$$\text{Multi Crop Pollinator Importance (MCPI)}_i = \sum_{ic} \left(\text{PI}_{ic} \times D_c \times C_c \right),$$

where PI_{ic} is the PI score of insect *i* for crop *c* (see the PI equation above), D_c is the pollinator dependence of crop *c* and C_c is the relative value of crop *c* to farmers. Thus, an insect which carries lots of pollen, and which frequently visits pollinator-dependent crops with a high value to farmers, will receive a high MCPI score.

2.6 | Question 1: Are the pollinators underpinning nutrient production the same as those underpinning income generation on a smallholder farm?

Our goal was to investigate whether the pollinators that are most important (as defined above) for a subsistence farmer (prioritising nutrient production) are the same as those which are most important for a cash crop farmer (prioritising income generation). We tested this by calculating MCPI scores separately for these two scenarios, weighting crops by either their nutritional or economic value, as described above (parameter C_c in the MCPI Equation above). We tested for correlations between the economic and nutritional value of crops using linear models fitted in base R (R Core Team, 2023).

2.7 | Question 2: Do the wild plants supporting key pollinators differ for farmers focusing on nutrient production versus income generation?

One of the most widely practised pollination management strategies is the addition of wild flowering plants to farmland to provide food for pollinators. Focusing our attention on this common pollination-management approach, we identify the most important non-crop plants for supporting the key crop pollinators at our field sites. We assess the 'Crop Pollinator Resource Importance' (CPRI) of each wild flowering plant by calculating its visitation by insects and weighting the visitation of each insect by its MCPI score. This means that plants which are utilised by important crop pollinators are assigned a higher CPRI score than those which are utilised by less important crop pollinators. Thus, for a wild plant *p*, our estimate of its CPRI is:

$$\text{Crop Pollinator Resource Importance (CPRI)}_p = \sum_{ip} \left(\text{MCPI}_i \times V_{ip} \right),$$

where MCPI is derived from the MCPI Equation above and V_{ip} is the visitation frequency of each Insect *i* to Plant *p*.

To evaluate whether plant recommendations differ depending on the farmer's agricultural priority (nutrient production or income generation), we calculate CPRI scores separately for the two scenarios, weighting pollinators by their nutritional or economic MCPI scores in each case.

2.8 | Question 3: Does the resilience of pollination services change as farmers specialise on cash crops?

As well as identifying the most important crop pollinators and the plant resources that support them, we were interested in assessing how resilient the pollination service is likely to be over time.

rop pollination is more resilient to environmental stressors if the service is provided by a diverse community of insects which respond in different ways to environmental change and can, to some extent, substitute for each other in the event that some species decline (Kühsel & Blüthgen, 2015; Lemanski et al., 2022; Senapathi et al., 2021). As a baseline, we therefore calculated the Shannon diversity of interactions for the observed crop–pollinator network, with interaction weights defined as visitation frequency multiplied by pollen-transport capacity, as outlined in the sections above. Using this baseline, we asked two related questions: (1) are the crop–pollinator interactions underpinning nutrient production more or less diverse than those underpinning income generation? (2) Does the diversity of crop–pollinator interactions change as farmers specialise on a narrower range of crops? For the first question, the Shannon diversity of crop–pollinator interactions (no wild plants included) was calculated at the network-level, with crops in the network (and therefore crop–pollinator link weights) alternately weighted by their nutritional or economic value. Networks were constructed separately for each of the 10 villages and diversity scores were compared between nutrition-weighted and economic-weighted networks using one-way analysis of variance (ANOVA). To address the second question, we simulated farmers' increasing agricultural specialisation on cash crops by sequentially removing crops from the network (in order of lowest to highest economic value) and recalculating diversity. In all cases, the Shannon diversity of interactions was calculated using the function 'networklevel' from the package bipartite (Dormann et al., 2008) in R (R Core Team, 2023).

3 | RESULTS

We recorded a total of 10,975 plant–insect interactions during 1146 separate surveys. This represented 3339 unique interactions between 240 plant species from 59 families, and 503 insect taxa from 66 families, predominately Apidae (40% of all interactions), Syrphidae (21%), Lycaenidae (7%), Calliphoridae (5%), Andrenidae (4%) and Halictidae (4%). Of the 10,975 insect specimens, 5871 (54%) were identified to species level (76 species), 3827 (35%) to genus level (though still grouped into morphospecies), 339 (3%) to family level and 569 (5%) to order level. Only one of these insects, the native Asian honeybee (*Apis cerana* Fabricius, 1793), is semi-domesticated (defined as living in both managed hives and as wild colonies). Of the 240 plant species, 50 were cultivated as crops (21%; Table S4), whilst the rest were wild (75%) or ornamental (4%). Of these 50 crop plants, 21 are considered pollinator-dependent (Table S3).

3.1 | Characterising crops and their pollinators

The relative nutritional value of crop plants differed substantially from their economic value (Figure 1), suggesting crops prioritised by subsistence farmers would likely differ from those prioritised by cash crop farmers. There was no correlation between the economic and nutritional value of crops ($F_{1,19}=0.17$, Adj.$R^2=-0.04$, $p=0.68$; Figure 1b). The nutritional value of crops was much more even than their economic value (Figure 1a), reflecting the fact that different crops provide different nutrients, whereas income depends mainly on one or two high-value crops (in this case, apples and beans).

Crops differed greatly in the identity and diversity of insects that were predicted to be their best pollinators. Some were heavily reliant on the semi-domesticated *A. cerana* whilst others were primarily reliant on wild insects (Figure 2a). For example, 73% of all apple pollen and 52% of cucumber pollen was estimated to be moved by *A. cerana*, compared to only 20% of Jumli bean pollen and 25% of sunflower and buckwheat pollen (Figure 2a; Table S5). Although *A. cerana* was the most important single pollinator species across most crops, wild pollinators (primarily bumblebees, solitary bees and flies) collectively accounted for 62% of all visits to pollinator-dependent crops. Flies (mainly *Lucilia* spp. and *Eristalis tenax* L.) were particularly important for buckwheat, mustard and slipper gourd. Butterflies showed high visitation rates to many crops, but transported little pollen and thus had lower PI scores than bees, flies and beetles (Figure 2a). Crops differed substantially in the diversity of pollinators supporting their production (Figure 2b). Buckwheat exhibited the most diverse pollinator community, with 67 different species from 22 families. Apple was one of the most frequently visited crops, but 67% of these visits (73% of pollen transport) were performed by *A. cerana*.

3.2 | Question 1: Are the pollinators underpinning nutrient production the same as those underpinning income generation on a smallholder farm?

The native semi-domesticated honeybee *A. cerana* had the highest MCPI score for both nutrient production and income generation, and was therefore important to all farmers in the region, regardless of their agricultural priority (Figures 3 and 4). This was particularly true for cash crop farmers, where 53% of the estimated pollination service was provided by *A. cerana*. In contrast, nutrient production relied on a more diverse community of wild insects which collectively provided 59% of the estimated pollination service. The most important wild insect species (based on MCPI scores) were: *Bombus tunicatus* Smith, 1852, *Andrena* sp.02, *Lasioglossum* sp.02, *Eristalis tenax* and *Bombus asiaticus* Morawitz, 1875 (Figure 3; Table S6). The most important taxa generally remained similar across villages, as did the order of PI (Figure 4; Figure S4). Overall, flies (mainly *Lucilia* spp. and *Eristalis* spp.) and bumblebees were more important for supporting nutrient production than income generation (Figure 4),

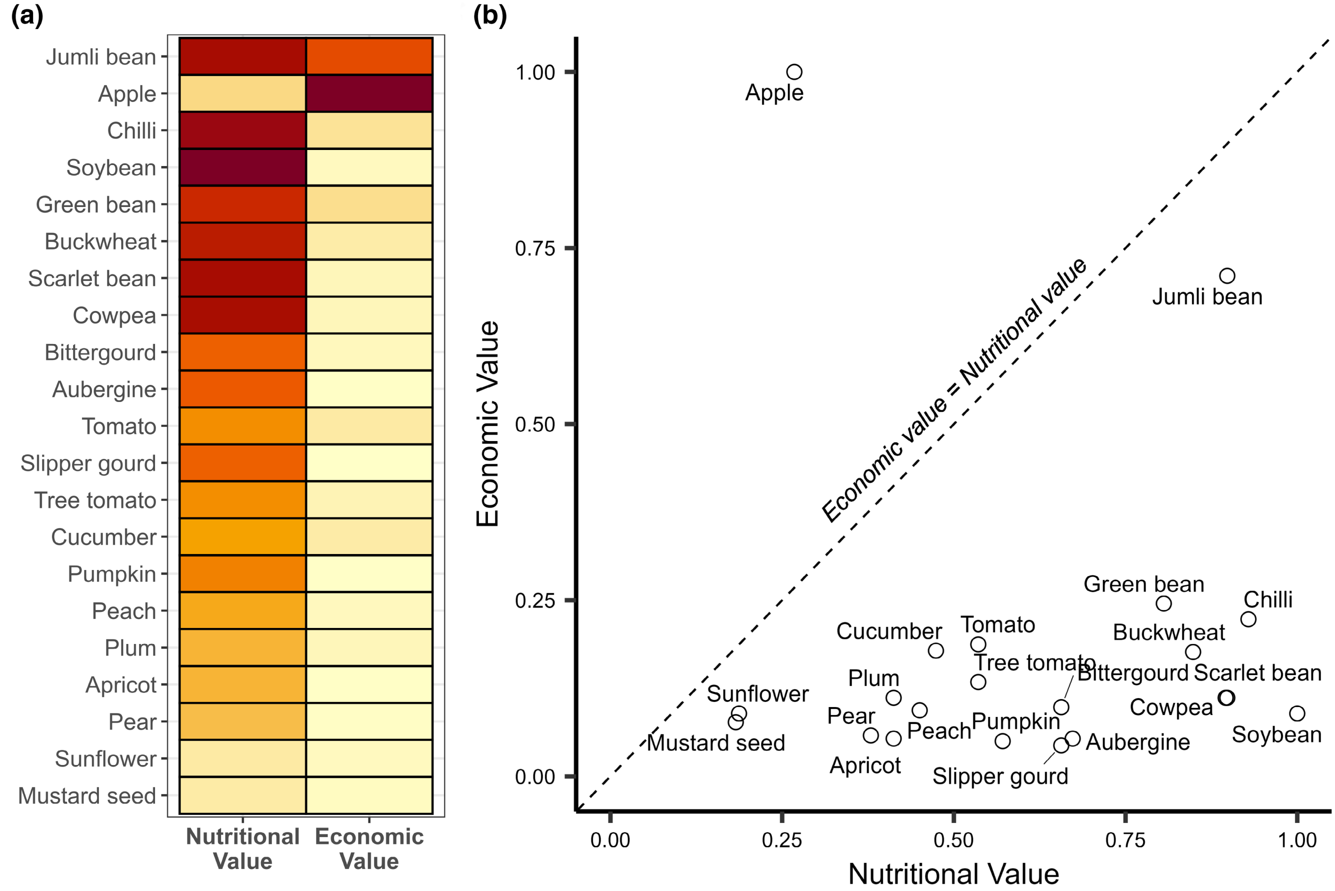

FIGURE 1 Crops differ in their relative value to farming households, depending on the farmers' agricultural priority. These plots visualise the value of each pollinator-dependent crop to smallholder farmers in the study region, based on their nutritional or economic value. Values are shown: a) separately as a heatmap (darker red = more important) as well as b) together as a scatter plot which demonstrates no relationship between the economic and nutritional value of each crop ($F_{1,19}=0.17$, Adj.$R^2=-0.04$, $p=0.68$). The nutritional value of each crop was based upon its contribution to 12 essential dietary nutrients while the economic value was based upon its contribution to household income.

largely due to their role in the pollination of nutritionally important buckwheat, pumpkin and beans (Figure 2).

3.3 | Question 2: Do the wild plants supporting key pollinators differ for farmers focusing on nutrient production versus income generation?

The best wild plants for supporting crop pollinators differed very little regardless of whether nutrient production or income generation was prioritised, as evidenced by a strong positive correlation in the nutrition-weighted and economic-weighted CPRI scores of each plant species ($F_{1,186}=1.11^{e+6}$, Adj.$R^2=0.99$, $p<0.001$). The plants with highest CPRI scores were mostly wild-growing shrubs such as *Cotoneaster microphyllus* Wall, *Rosa sericea* Lindl and *Spiraea canescens* Rydb.; agricultural weeds such as *Persicaria nepalensis* Meisn. and *Galinsoga ciliata* Raf.; and wildflower herbs such as *Thymus linearis* Benth. and *Cynoglosum zeylanium* Lehm (Table S7). However, some ornamental plants such as marigold (*Tagetes erecta* L.) scored highly too. The most important plants generally remained similar across all villages, as did the order of plant importance (Figure S5).

3.4 | Question 3: Does the resilience of pollination services change as farmers specialise on cash crops?

The community of insect pollinators underpinning income generation was significantly less diverse than that underpinning nutrient production, suggesting a lower resilience to environmental stressors. Shannon interaction diversity scores across the 10 replicate crop–pollinator networks were significantly lower when crops were weighted by their economic value than when crops were weighted by their nutritional value ($F_{1,18}=14.16$, $p=0.001$; Figures 3 and 5). Moreover, the Shannon diversity of interactions for the overall crop–pollinator network declined markedly as crops with low economic value were removed, leaving a small number of high-value cash crops remaining (Figure 6).

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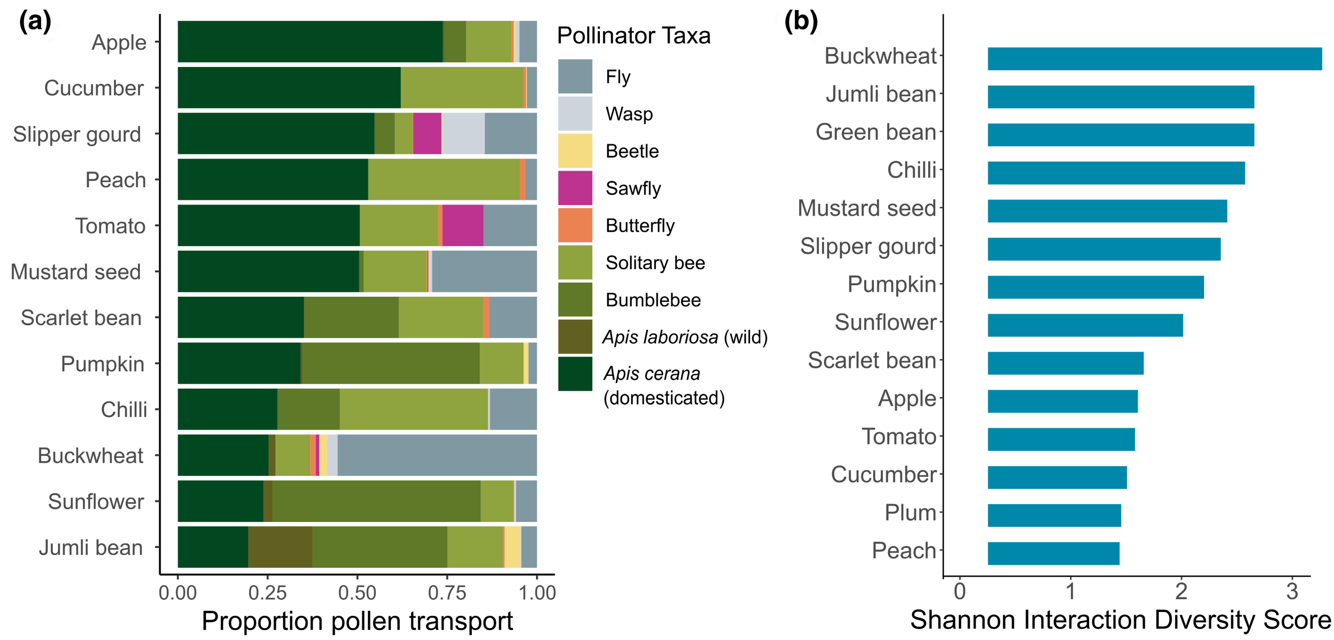

FIGURE 2 The Pollinator Importance (PI) of different insect taxa varies from crop to crop (panel a), as does the Shannon diversity of interactions with each crop (panel b). Some crops such as apple, cucumber and slipper gourd (shown towards the top of panel a) are highly visited by semi-domesticated honeybees (*A. cerana*; dark green), while others such as beans, sunflower, buckwheat and chilli are mostly visited by wild insects. Included here are crops for which yield is increased by insect pollination, and which received at least 10 visits from insects. Shannon interaction diversity scores were calculated at the network-level with link weights defined as the PI score of each insect.

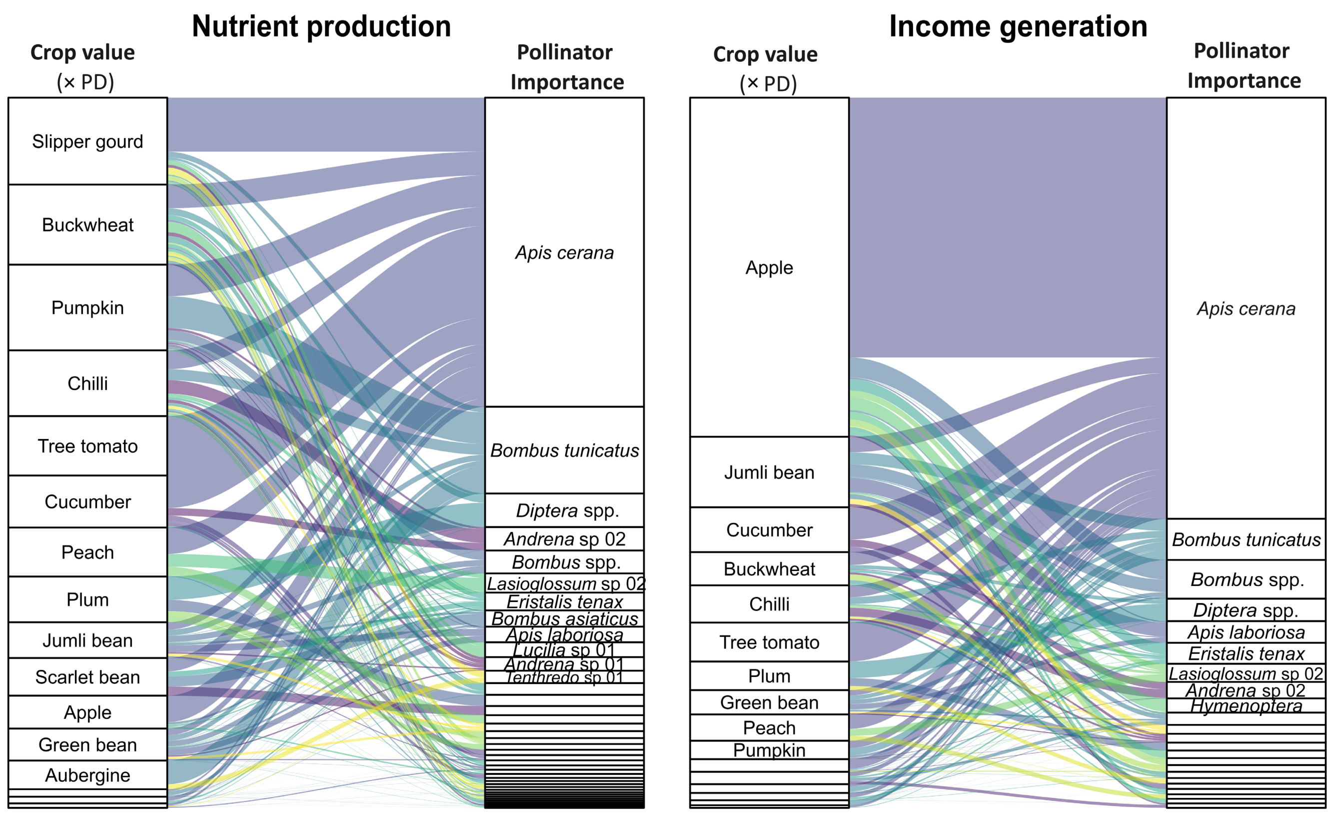

FIGURE 3 The crop–pollinator network underpinning nutrient production (left) differs in its structure from the network underpinning income generation (right), despite many of the same key pollinators. For the nutrient production scenario, crops are weighted (and ordered) by their nutritional value × pollinator dependence (PD), while for the income generation scenario, crops are weighted by their economic value × pollinator dependence. Insects are weighted by their Multi-Crop Pollinator Importance scores (total estimated contribution to the pollination service) and the links show their estimated contribution to the pollination of specific crops. The two networks are derived from the same interaction data and differ only in the value weightings placed on each crop.

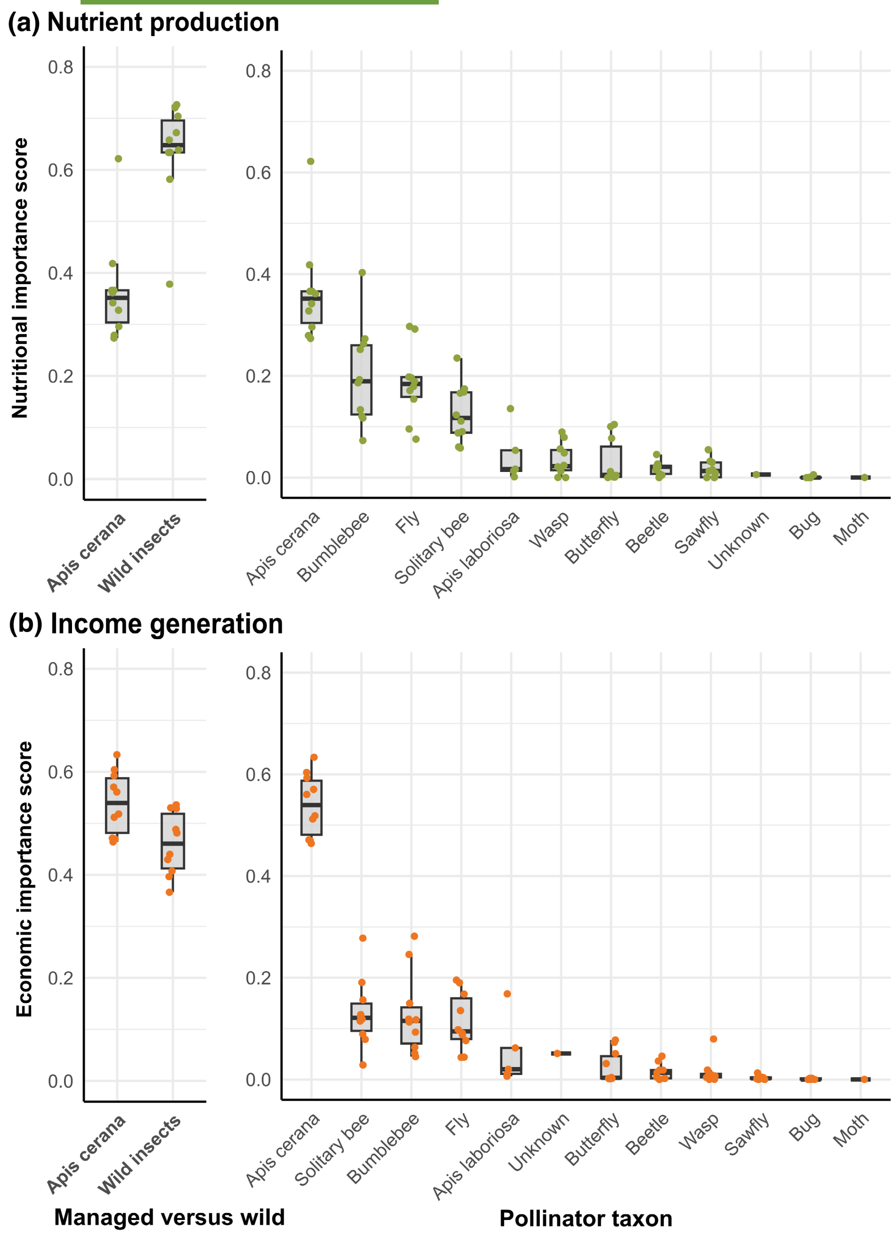

FIGURE 4 The Multi-Crop Pollinator Importance (MCPI) scores of pollinator guilds differ depending on which agricultural output a farmer prioritises: (a) nutrient production or (b) income generation. Semi-domestic honeybees (*A. cerana*) were more important for meeting economic goals (largely because of their major importance in apple pollination), while wild insects including bumblebees, flies and solitary bees played a more important role in meeting nutritional goals. The left-hand panels show the sum of MCPI scores for wild insects versus *A. cerana*, while the right-hand panel shows each guild separately (in order of highest to lowest importance). Each point represents the pollinator guild's MCPI score in an individual village.

4 | DISCUSSION

Our study presents a new approach for predicting the insects and wild plants which underpin pollination services in diverse multi-crop systems such as smallholder farms. This approach can be tailored to meet the specific priority of the farmer and investigate whether ecosystem service requirements change as farmers adapt to new agricultural contexts. We show that the structure of the pollinator community supporting nutrient production differs from that supporting income generation on a smallholder farm. Income generation from cash crops relied on a significantly lower diversity of pollinators (primarily *A. cerana* in this region), suggesting that cash crop farming is less resilient to environmental stressors affecting pollinators. The resilience of pollination services is likely to further decline as farmers specialise on a narrower range of high-value cash crops. Despite differences in the structure of the pollinator community supporting the two different agricultural priorities, the most important pollinators and the best wild plants for supporting these pollinators were similar, suggesting a single pollination management approach for all farmers in this region.

4.1 | Crop pollination requirements of smallholder farms

The native Asian honeybee, *A. cerana*, likely plays a crucial role in the provision of crop pollination services in this region and yet is known to be experiencing dramatic local declines, purportedly due to changing weather patterns and reduced flower availability (Kortsch et al., 2024). In the unlikely event of total honeybee loss, farmers stand to lose approximately 45% of all crop pollen transport (as much as 73% for apple). Wild pollinators provide insurance against these ongoing honeybee declines and often provide a more effective pollination service (Garibaldi et al., 2013). In Jumla, we estimate that wild pollinators collectively transport 55% of crop pollen and more than 75% for some nutritionally important crops including Jumli beans. As well as being effective pollinators in their own right, wild insects are known to complement honeybee pollination

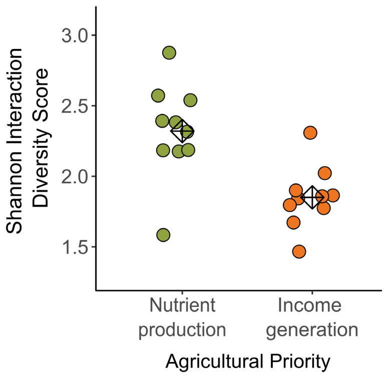

FIGURE 5 The crop–pollinator interactions underpinning nutrient production are significantly more diverse than those underpinning income generation ($F_{1,18}=14.16$, $p=0.001$). Each point represents the network-level Shannon diversity score of all crop–pollinator interactions in each of the 10 villages (mean values are marked by a cross). Interaction links were weighted by the pollinator importance score of each insect. The two scenarios are based on the same crop–pollinator interaction data, but with crops alternately weighted by their nutritional value (green points) or economic value (orange points). See Figure 3 for an example of these two alternately weighted networks.

by accessing different parts of the flower and visiting flowers at different times of the day and year (Rader et al., 2016). A diverse pollinator community will also respond in diverse ways to environmental stressors, ensuring a more resilient pollination service (Lemanski et al., 2022; Rader et al., 2016). Indeed, the most vulnerable crops in our study region were those in which the majority of pollen was transported by just one or two insect species (predominantly by *A. cerana*). These crops were characterised by a brief and early flowering phenology (e.g. apple and peach), when few pollinators except for honeybees had yet emerged. This makes them especially vulnerable to local honeybee declines or adverse weather conditions affecting honeybee foraging (Kortsch et al., 2024).

4.2 | The risks of agricultural specialisation

The economic outputs of our study farms (cash crops) were sustained by a less diverse community of pollinators than nutritional outputs (food crops), and this diversity will further decline as farmers specialise on a narrower range of crops. This has important implications for smallholder farmers transitioning to specialised cash crop systems as a low-diversity pollinator community is associated with reduced temporal stability and resilience of pollination services (Lemanski et al., 2022; Senapathi et al., 2021). Consequently, cash crop farmers may experience greater yield fluctuations and lower resilience to environmental stressors such habitat loss, extreme weather conditions or pesticide exposure. Farmers in our study region showed a very high economic reliance

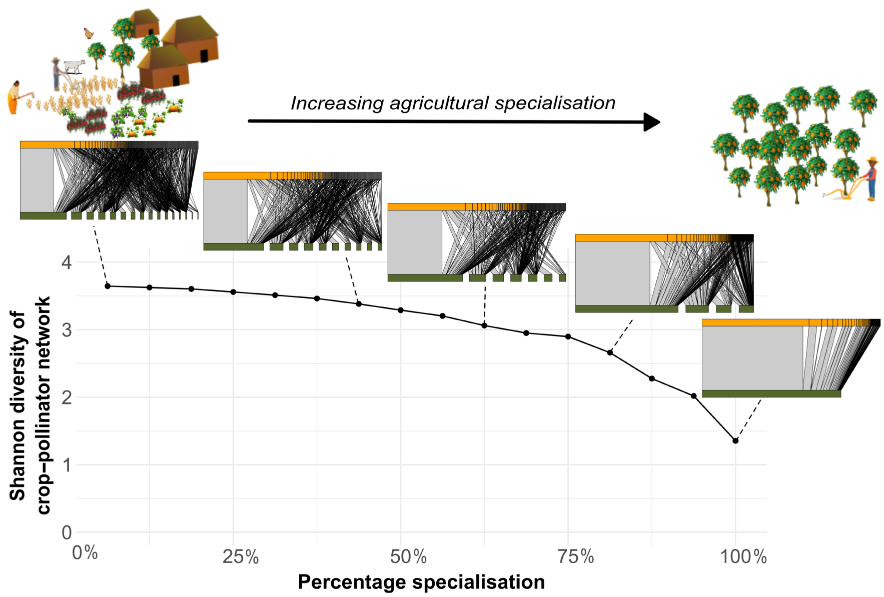

FIGURE 6 The Shannon diversity of the crop–pollinator interaction network declines as farmers specialise on fewer crops; this is likely to reduce the stability and resilience of pollination service provision. The crop–pollinator network at the top-left of the figure shows the interactions between all pollinator-dependent crops currently grown in the study system and all insects recorded visiting the crops. Crops (bottom green bars) are weighted by their relative contribution to household income, and insects (top yellow bars) are weighted by their Multi-Crop Pollinator Importance scores. Crops were incrementally removed from the network, in order of lowest to highest economic value, to simulate the changes in farming practices as farmers specialise on a narrow range of high-value cash crops. Following each crop removal, the Shannon diversity of interactions for the crop–pollinator network was recalculated and re-plotted.

on just two main crops: apples and beans. This exposes them to a high level of risk, particularly given the honeybee declines reported from this region (Kortsch et al., 2024; Theisen-Jones & Bienefeld, 2016) and the increasing rates of habitat loss, pesticide use and climatic changes reported in the wider Himalayan region (Partap et al., 2012). Indeed, declines in apple yield and quality have already been linked to local pollination deficits (Partap et al., 2012). These risks affect both individual households, and the region overall. For example, apple cultivation contributes c. 50% of local households' agricultural revenue (data from farmer questionnaires), and 20% of the local economy of Jumla (Sapkota et al., 2022). The impact of pollinator decline on human nutrition remains to be empirically quantified, but is an important avenue for further study. In regions where insurance systems are weak or absent, and vulnerability to environmental and ecological stressors is high, agricultural diversification is likely to be the most dependable strategy for a smallholder farmer.

4.3 | Management implications

Crop pollination services (and therefore yields) can be enhanced by adding plant species that provide a sufficient quantity and quality of food for pollinators (Blaauw & Isaacs, 2014). Our study provides an efficient method for identifying such plant species based on an empirically established role in supporting crop pollinators. We identify a range of important non-crop plants which include herbaceous species (e.g. *Persicaria nepalensis*, *Galinsoga ciliata* and *Thymus linearis*), shrubs (e.g. *Cotoneaster microphyllus*, *Rosa sericea* and *Spiraea canescens*) and ornamental plants (e.g. *Tagetes erecta*). Conveniently, these recommended plants remain the same regardless of the farmer's agricultural priority. Although the identity of important pollinators and wild plants will likely differ among regions, the close alignment in species supporting different farming outputs is likely to remain a consistent phenomenon due to the nested structure of most plant–pollinator communities, whereby a subset of common wild plants are visited by most generalist pollinators (Bascompte et al., 2003). Therefore, in the absence of highly resolved interaction data, it may still be possible for farmers to manage pollination services by promoting wild plants which they observe being visited by a wide variety of insects. However, it may also be necessary for farmers to provide less widely used plants which fill temporal or nutritional gaps in food supply; for example, early flowering species such as *Prinsepia utilis* Royle and *Taraxacum officinale* L. In addition to food resources, crop pollinators will also benefit from reduced pesticide exposure and provisioning of nesting sites including bare sloping earth for ground-nesting bees (e.g. *Andrena* spp.), cavities in walls, banks or trees for cavity-nesting bees (e.g. honeybees and bumblebees) and pools of nutrient-rich water for *Eristalis* spp. larvae. To be motivated to apply these management practices on their land, farmers must first be convinced of the value of pollination services (Osterman et al., 2021). Awareness of pollinators was low in our study region (Kortsch et al., 2024), perhaps because pollination services were not historically limited in this diversified system. However, as local pollinator populations decline Kortsch et al. (2024), there is an urgent need to raise awareness in schools, training colleges and agricultural extension services. Successful pollinator outreach projects in our region show this awareness can spread rapidly, resulting in the widespread uptake of pollinator-friendly management practices. However, the evidence-base to support such management recommendations is currently lacking in many smallholder farming regions of the world. Our study provides a widely applicable methodological toolkit for identifying key crop pollinators and pollination management practices in smallholder settings and we hope this facilitates further research to underpin farmer guidance and policy legislation across the world.

5 | CONCLUSION

Our study highlights the increasing vulnerability of pollination services when smallholder farmers transition from diversified food production systems towards more specialised cash cropping where the pollination service is provided by just a few dominant species. For these farmers in particular, we emphasise the importance of ecological insurance, whereby redundancy in ecosystem services is maintained through the promotion of on-farm biodiversity. In the face of rapid environmental change, this will help minimise the risk of pollination service disruption and resulting crop losses. Engaging with farmers to build their knowledge of key pollinators and the benefits they provide will also be essential for building resiliency in pollination services. Overall, we stress the value of sustaining the diversity of local crops, pollinators and wild plants in order to promote long-term stability and resilience in food security and livelihoods for smallholder farmers.

AUTHOR CONTRIBUTIONS

Thomas P. Timberlake, Jane Memmott, Alyssa R. Cirtwill, Sushil Baral and Tomas Roslin conceived the ideas and designed methodology; Sujan Sapkota, Thomas P. Timberlake, Naomi M. Saville, Kedar Devkota and Deepak Joshi coordinated the data collection; Daya-Ram Bhusal and Rashmina Karki led the specimen identification and pollen analysis; Thomas P. Timberlake, Alyssa R. Cirtwill and Susanne Kortsch analysed the data. All the authors contributed critically to drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad digital repository: https://doi.org/10.5061/dryad.0rxwdbs91 (Timberlake et al., 2024). R code available from Zenodo: https://doi.org/10.5281/zenodo.12609151 (Timberlake, 2024).

STATEMENT ON INCLUSION

Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out. All the authors and relevant local stakeholders were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset. Stakeholder engagement workshops were held with representatives from government, academia and the local community to ensure broad dissemination of our results.

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REFERENCES

Abson, D. J. (2019). The economic drivers and consequences of agricultural specialization. In G. Lemaire, P. C. D. F. Carvalho, S. Kronberg, & S. Recous (Eds.), *Agroecosystem diversity* (pp. 301–315). Elsevier.

Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 9383–9387.

Bianco, G., Manning, P., & Schleuning, M. (2024). A quantitative framework for identifying the role of individual species in Nature's Contributions to People. *Ecology Letters*, *27*(2), e14371.

Bishop, J., Garratt, M. P. D., & Nakagawa, S. (2022). Animal pollination increases stability of crop yield across spatial scales. *Ecology Letters*, *25*(9), 2034–2047.

Blaauw, B. R., & Isaacs, R. (2014). Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, *51*(4), 890–898.

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*, 230–238.

Darmon, N., Darmon, M., Maillot, M., & Drewnowski, A. (2005). A nutrient density standard for vegetables and fruits: Nutrients per calorie and nutrients per unit cost. *Journal of the American Dietetic Association*, *105*, 1881–1887.

Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite package: Analysing ecological networks. *Interactions*, *1*, 8–11.

Eilers, E. J., Kremen, C., Greenleaf, S. S., Garber, A. K., & Klein, A. M. (2011). Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS One*, *6*, e21363.

FAO. (2018). *Smallholder farmers' data portrait: What the numbers tell us about smallholder farms*. FAO.

Földesi, R., Howlett, B. G., Grass, I., & Batáry, P. (2021). Larger pollinators deposit more pollen on stigmas across multiple plant species—A meta-analysis. *Journal of Applied Ecology*, *58*, 699–707.

Garibaldi, L. A., Carvalheiro, L. G., Vaissière, B. E., Gemmill-Herren, B., Hipólito, J., Freitas, B. M., Ngo, H. T., Azzu, N., Sáez, A., Åström, J., An, J., Blochtein, B., Buchori, D., García, F. J. C., Oliveira da Silva, F., Devkota, K., Ribeiro, M. F., Freitas, L., Gaglianone, M. C., … Zhang, H. (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, *351*, 388–391.

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhöffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., … Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, *339*, 1608–1611.

Giller, K. E., Delaune, T., Silva, J. V., Descheemaeker, K., van de Ven, G., Schut, A. G. T., van Wijk, M., Hammond, J., Hochman, Z., Taulya, G., Chikowo, R., Narayanan, S., Kishore, A., Bresciani, F., Teixeira, H. M., Andersson, J. A., & van Ittersum, M. K. (2021). The future of farming: Who will produce our food? *Food Security*, *13*, 1073–1099.

Harvey, C. A., Rakotobe, Z. L., Rao, N. S., Dave, R., Razafimahatratra, H., Rabarijohn, R. H., Rajaofara, H., & MacKinnon, J. L. (2014). Extreme vulnerability of smallholder farmers to agricultural risks and climate change in Madagascar. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *369*, 20130089.

Holmelin, N. B. (2021). National specialization policy versus farmers' priorities: Balancing subsistence farming and cash cropping in Nepal. *Journal of Rural Studies*, *83*, 71–80.

Howlett, B., Walker, M., Rader, R., Butler, R., Newstrom-Lloyd, L., & Teulon, D. (2011). Can insect body pollen counts be used to estimate pollen deposition on pak choi stigmas. *New Zealand Plant Protection*, *64*, 25–31.

King, C., Ballantyne, G., & Willmer, P. G. (2013). Why flower visitation is a poor proxy for pollination: Measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution*, *4*, 811–818.

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 303–313.

Kortsch, S., Timberlake, T. P., Cirtwill, A. R., Sapkota, S., Rokoya, M., Devkota, K., Roslin, T., Memmott, J., & Saville, N. (2024). Decline in honeybees and its consequences for beekeepers and crop pollination in Western Nepal. *Insects*, *15*(4), 281.

Kühsel, S., & Blüthgen, N. (2015). High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. *Nature Communications*, *6*, 7989.

Lemanski, N. J., Williams, N. M., & Winfree, R. (2022). Greater bee diversity is needed to maintain crop pollination over time. *Nature Ecology & Evolution*, *6*(10), 1516–1523.

Lowder, S. K., Sánchez, M. V., & Bertini, R. (2021). Which farms feed the world and has farmland become more concentrated? *World Development*, *142*, 105455.

Millard, J., Outhwaite, C. L., Ceaușu, S., Carvalheiro, L. G., da Silva e Silva, F. D., Dicks, L. V., Ollerton, J., & Newbold, T. (2023). Key tropical crops at risk from pollinator loss due to climate change and land use. *Science Advances*, *9*(41), eadh0756.

Osterman, J., Landaverde-González, P., Garratt, M. P., Gee, M., Mandelik, Y., Langowska, A., Minarro, M., Cole, L. J., Eeraerts, M., Bevk, D., & Avrech, O. (2021). On-farm experiences shape farmer knowledge, perceptions of pollinators, and management practices. *Global Ecology and Conservation*, *32*, e01949.

Partap, U., Partap, T., Sharma, H. K., Phartiyal, P., Marma, A., Tamang, N. B., & Tan Ken, T. K. (2012). *Value of insect pollinators to Himalayan agricultural economies*. ICIMOD.

Pretty, J. (2018). Intensification for redesigned and sustainable agricultural systems. *Science*, *362*, eaav0294.

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., Cunningham, S. A., Mayfield, M. M., Arthur, A. D., Andersson, G. K. S., Bommarco, R., Brittain, C., Carvalheiro, L. G., Chacoff, N. P., Entling, M. H., Foully, B., Freitas, B. M., Gemmill-Herren, B., Ghazoul, J., … Woyciechowski, M. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 146–151.

Sapkota, D., Acharya, M., Gautam, S., & Kumar, P. (2022). Economics of apple production in Chandannath municipality, Jumla, Nepal. *Journal of Current Research in Food Science*, *3*, 27–31.

Senapathi, D., Fründ, J., Albrecht, M., Garratt, M. P., Kleijn, D., Pickles, B. J., Potts, S. G., An, J., Andersson, G. K. S., Bänsch, S., Basu, P., Benjamin, F., Bezerra, A. D. M., Bhattacharya, R., Biesmeijer, J. C., Blaauw, B., Blitzer, E. J., Brittain, C. A., Carvalheiro, L. G., … Klein, A. M. (2021). Wild insect diversity increases inter-annual stability in global crop pollinator communities. *Proceedings of the Royal Society B*, *288*(1947), 20210212.

Smith, M. R., Mueller, N. D., Springmann, M., Sulser, T. B., Garibaldi, L. A., Gerber, J., Wiebe, K., & Myers, S. S. (2022). Pollinator deficits, food consumption, and consequences for human health: A modeling study. *Environmental Health Perspectives*, *130*, 127003.

Smith, M. R., Singh, G. M., Arian, D. M., & Myers, S. S. (2015). Effects of decreases of animal pollinators on human nutrition and global health: A modelling analysis. *Lancet*, *386*, 1964–1972.

Stanworth, A., Peh, K. S. H., & Morris, R. J. (2024). Linking network ecology and ecosystem services to benefit people. *People and Nature*, *6*, 1048–1059.

Steward, P. R., Shackelford, G., Carvalheiro, L. G., Benton, T. G., Garibaldi, L. A., & Sait, S. M. (2014). Pollination and biological control research: Are we neglecting two billion smallholders. *Agriculture & Food Security*, *3*, 5.

Theisen-Jones, H., & Bienefeld, K. (2016). The Asian honey bee (*Apis cerana*) is significantly in decline. *Bee World*, *93*, 90–97.

Tibesigwa, B., Siikamäki, J., Lokina, R., & Alvsilver, J. (2019). Naturally available wild pollination services have economic value for nature dependent smallholder crop farms in Tanzania. *Scientific Reports*, *9*, p. 3434.

Timberlake, T. P. (2024). R code from: Agricultural specialisation increases the vulnerability of pollination services for smallholder farmers. *Zenodo Repository*. https://doi.org/10.5281/zenodo.12609151

Timberlake, T. P., Cirtwill, A. R., Baral, S. C., Bhusal, D. R., Devkota, K., Harris-Fry, H. A., Kortsch, S., Myers, S. S., Roslin, T., Saville, N. M., Smith, M. R., Strona, G., & Memmott, J. (2022). A network approach for managing ecosystem services and improving food and nutrition security on smallholder farms. *People and Nature*, *4*, 563–575.

Timberlake, T. P., Cirtwill, A. R., Sapkota, S., Bhusal, D. R., Devkota, K., Karki, R., Joshi, D., Saville, N., Kortsch, S., Baral, S., Roslin, T., & Memmott, J. (2024). Data from: Agricultural specialisation increases the vulnerability of pollination services for smallholder farmers. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.0rxwdbs91

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Map of Patarasi Rural Municipality.

Figure S2. Habitat composition of study sites.

Figure S3. Images of study sites.

Figure S4. Multi-Crop Pollinator Importance scores of each insect genus.

Figure S5. Plant Resource Importance scores of individual wild plant species.

Table S1. Nutritional and economic rankings of pollinator-dependent crops.

Table S2. Farmer questionnaire form.

Table S3. List of all pollinator-dependent crops cultivated in Jumla.

Table S4. Crops recorded in Jumla study sites.

Table S5. Pollinator-dependent crops and their key pollinators.

Table S6. Insect pollinators and their MCPI scores.

Table S7. Wild and ornamental plant species.

Appendix S1. Additional background on the study region.

Appendix S2. Detailed protocol for plant and pollinator sampling.

Appendix S3. Pollen quantification: methods and caveats.

Appendix S4. Details of nutritional and economic value estimation.

Appendix S5. Pollinator exclusion experiments.

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