

# Mixed effects of honey bees on pollination function in the Tibetan alpine grasslands

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The global expansion of domesticated plant and animal species has profoundly impacted biodiversity and ecosystem functions. However, the spillover effect of non-native honey bees from mass-flowering crops into adjacent natural vegetation on pollination function within plant communities remains unclear. To address this, we conduct field experiments to investigate the ecological impacts of honey bees (*Apis mellifera*) and a mass-flowering crop (*Brassica rapa* var. *oleifera*) on pollinator communities, plant-pollinator interactions, and reproductive performance of wild plants in 48 pollinator-limited alpine grasslands. Our findings indicate that the transition of dominant pollinators from flies to honey bees enhances visitation fidelity of pollinator species and reconfigures pollination interactions due to an increase in competition between honey bees and native pollinator species. Additionally, honey bees increase, decrease or do not alter plant reproductive success, depending on the plant species. Here, we report the mixed effects of honey bees on pollination function in pollinator-limited alpine grasslands.

Nearly 90% of flowering plant species, including 75% of major crops, rely to some extent on animal pollination for their yield and quality<sup>1,2</sup>. The diversity and abundance of wild pollinators are declining<sup>3,4</sup>, while the global area of pollinator-dependent crops is expanding due to increasing agricultural activities<sup>5,6</sup>. This conflicting scenario of high demand and limited availability of pollinators could potentially result in insufficient pollination of flowering plant species<sup>7–9</sup>. To enhance the pollination success of flowering plants, non-native pollinators, such as honey bees and bumble bees, are predominantly utilized within mass-flowering crops (MFCs), including oilseed rape, sunflower, and orange<sup>10,11</sup>. The effects of honey bees on native pollinators and plant species have been extensively studied, showing that honey bees are detrimental to native pollinator communities and reproductive success of native plants<sup>12–14</sup>. However, the effects of co-occurrence and co-visitation of wild and non-native pollinators on the pollination function of plant communities remain an unresolved question in ecology<sup>15</sup> and plant science<sup>16,17</sup>.

Facilitation between plant species and competitive displacement among pollinator species have been postulated to affect the pollination function of plant communities amidst non-native crops and pollinator species<sup>12,18,19</sup>. In the first mechanism, facilitation, a positive interaction exists between plant species, but the benefits are mostly in one direction<sup>20</sup>. MFCs act as magnets for pollinators, attracting both native and non-native pollinators into nearby natural communities. These pollinators can visit flowers of rare native plant species, thereby enhancing the pollination success of these species<sup>20</sup>. The interaction is asymmetric because the native plant species have much less effect on the pollination of MFCs<sup>18</sup>. In the second mechanism, competitive displacement, non-native pollinators may influence other pollinator species through competition for shared plants, increasing the functional niche complementarity among pollinator species if native species switch to visiting alternative plants that are less preferred by the non-native pollinators<sup>12</sup>. For example, introduced Western honey bees (*Apis mellifera*) could visit a wide spectrum of wild plant species<sup>13</sup>,

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compete for flower resources with wild pollinators, and reshuffle wild pollinator diets<sup>12,13,21</sup>. This could either facilitate or impair the pollination success of co-flowering wild plant species<sup>12,13,22,23</sup>, depending on the differences of visitation fidelity and pollination effectiveness of native and non-native pollinator species<sup>24,25</sup>. The two mechanisms can affect the pollination success of flowering plants, either individually or combined.

Previous work has made suggestions of how non-native flowering plant species<sup>26,27</sup>, as well as pollinators<sup>12–14</sup>, might affect the richness and abundance of wild pollinators<sup>10–12,14,28</sup>, the structure of plant-pollinator interaction networks<sup>13,26,29</sup>, and the reproductive success of dominant plant species<sup>12,13</sup>. However, how non-native honey bees and MFCs change co-evolved wild pollinator communities and the associated plant species remains to be elucidated.

A recent study has demonstrated that non-native honey bees (*Apis mellifera*) exhibit significant spillover from rapeseed (*Brassica rapa* var. *oleifera*) into adjacent grasslands, and visit a multitude of flowering plant species during the blooming period of rapeseed in Tibetan alpine grassland communities<sup>30</sup>. This study system provides an optimal environment to test how the transition of dominant pollinators from flies to honey bees influences the pollination function of alpine plant communities. Initially, we predicted that (i) honey bees can influence native pollinator communities. We expected that honey bee spillover would decrease the pollinator species richness and pollination visits in pollinator communities<sup>14,23</sup> but enhance visitation fidelity and functional complementarity of pollinator communities by competitive displacement of native pollinators by honey bees<sup>12,13</sup>. Subsequently, we predicted that (ii) honey bee spillover can modify pollination interactions within plant-pollinator communities. Previous studies have shown that non-native honey bees diminished the diversity of pollination interactions in Tibetan alpine grasslands<sup>30,31</sup> and MFCs increased pollinator visitation to wild plants in neighboring alpine meadows<sup>32</sup>. Thus, we expected that the transition of dominant pollinators from flies to honey bees due to facilitation between plant species and competitive displacement among pollinator species would reduce the evenness and diversity of interactions in the pollination networks<sup>33,34</sup> and lead to the adaptive interaction rewiring in the plant-pollinator communities<sup>35,36</sup>. Finally, we predicted that (iii) honey bee spillover does increase the pollination function of plant communities because most flowering plant species are mainly visited by flies and undergo severe pollen limitation for sexual reproduction in the Tibetan alpine grasslands<sup>37,38</sup>. In particular, we expected that the spillover effect of honey bees would primarily enhance the reproductive success of numerous rare plant species. These species either lack pollinator species or have less effective pollinator functional groups in the alpine grasslands<sup>19,26,39</sup>.

In this study, we collect plant-pollinator interaction data in 48 Tibetan alpine grassland communities to evaluate the aforementioned predictions. Subsequently, we explore the ecological influences of the spillover of honey bees on pollination function by examining plots in seminatural areas in agroecosystems at different distances from apiaries. Our results reveal that honey bees enhance the pollination function of plant communities by altering the foraging behavior of native pollinators, highlighting the potential positive effect of honey bee spillover on the pollination services in alpine agroecosystems.

## Results

### The consistent spillover of honey bees from a MFC into nearby alpine grasslands

In the 48 alpine grassland communities (Fig. 1 and Supplementary Table 1), our study captured more than 83% of pollinator species richness (Supplementary Table 2 and Supplementary data 2) and about 73% of plant-pollinator interaction richness (Supplementary Fig. 1). We recorded 74,593 pollinator visits (Supplementary Table 1 and Supplementary data 1; 46.8% of which were honey bees) involving 104

flowering plant species (82.7% of these species were visited by honey bees) and 148 pollinator species or morphospecies (Fig. 1). Besides the *A. mellifera*, the most abundant native pollinator species were *B. supremus*, *B. kashmirensis*, and *Eristalis cerealis*, which were identified in 4440 (5.95%), 2,923 (3.92%), and 2,706 (3.63%) visits, respectively. The most visited flowering plants in the grasslands were *Carum carvi* (10,233 visits, 22.34% by honey bees), *Oxytropis ochrocephala* (6,003 visits, 52.21% by honey bees), and *Pedicularis kansuensis* (5,592 visits, 31.62% by honey bees).

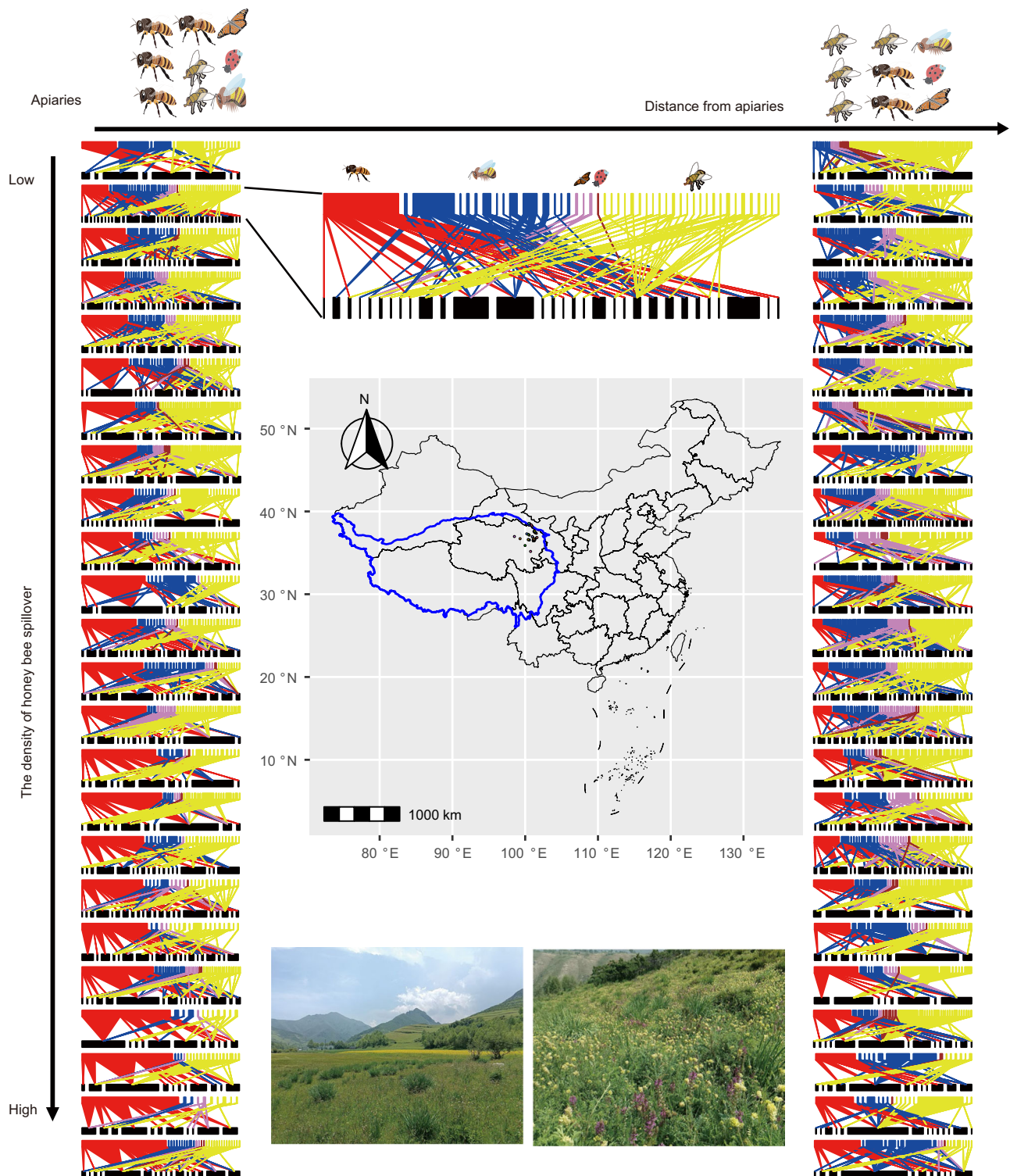
The proportion of flower visits by honey bees was  $43.15 \pm 27.99\%$  (Mean  $\pm$  1 SD,  $n = 48$ ) in the 48 plant communities, ranging from 0 to 93.35% (Supplementary Table 3 and Supplemental Data 3). Compared to the bee-far plots,  $28.05 \pm 14.02\%$  (Mean  $\pm$  1 SD,  $n = 8$ ) and  $15.63 \pm 13.65\%$  (Mean  $\pm$  1 SD,  $n = 16$ ) of visits involved in honey bees in high and low rapeseed cover plots, honey bee visits significantly increased in the bee-near plots,  $67.73 \pm 15.18\%$  (Mean  $\pm$  1 SD,  $n = 16$ ) of the interactions in the high rapeseed cover and  $64.09 \pm 16.82\%$  (Mean  $\pm$  1 SD,  $n = 8$ ) in the low rapeseed cover (Fig. 2a and Supplementary Table 4). This resulted in a clear dominance of honey bees in the bee-near plots regardless of the rapeseed cover (Supplementary Table 4).

### The effects of honey bees on pollinator communities and pollination interactions

The native pollinator communities were fly-dominated at both bee-near and bee-far plots (Fig. 1). The highest count of pollinator species was attributed to flies ( $15.75 \pm 5.82$  vs  $17.33 \pm 7.35$ , Mean  $\pm$  1 SD,  $n = 24$ ), followed by native bees ( $6.42 \pm 3.26$  vs  $8.13 \pm 3.10$ , Mean  $\pm$  1 SD,  $n = 24$ ), butterflies ( $2.71 \pm 2.24$  vs  $4.50 \pm 3.79$ , Mean  $\pm$  1 SD,  $n = 24$ ), and beetles ( $0.83 \pm 0.96$  vs  $1.08 \pm 1.10$ , Mean  $\pm$  1 SD,  $n = 24$ ) at both bee-near and bee-far plots (Fig. 1 and Supplemental Data 3).

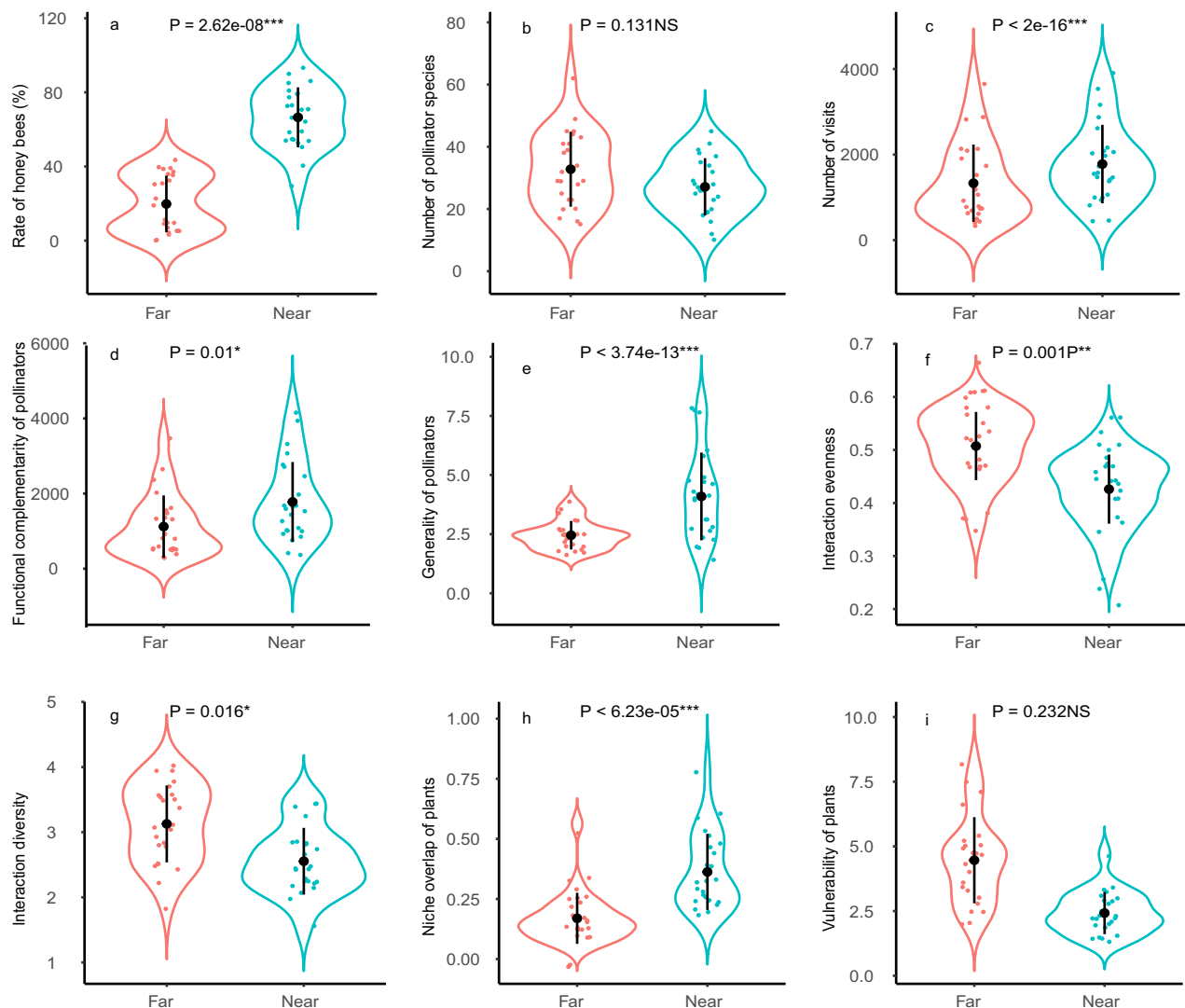
The dominance of honey bees significantly affected the visitation patterns of native pollinators (Supplementary Table 5). Competition between honey bees and the other pollinator species was higher in the bee-near plots (Supplementary Fig. 2). Despite the comparable diversity of pollinator species between bee-near and bee-far plots (number of pollinator species; Fig. 2b and Supplementary Table 6), all pollinator species (including visits by honey bees) exhibited a higher frequency of flower visits in the bee-near plots (number of pollinator visits; Fig. 2c and Supplementary Table 6). Furthermore, bumble bees visited 131.6% more flowers during individual foraging bouts in the bee-near plot ( $56.03 \pm 82.29$ , Mean  $\pm$  1 SD,  $n = 29$ ) compared to the bee-far plot ( $24.19 \pm 25.03$ , Mean  $\pm$  1 SD,  $n = 21$ ). Similarly, flies showed a similar trend, visiting 60.04% more flowers during individual foraging bouts in the bee-near plot ( $17.62 \pm 19.71$ , Mean  $\pm$  1 SD,  $n = 34$ ) than in the bee-far plot ( $11.01 \pm 11.32$ , Mean  $\pm$  1 SD,  $n = 28$ ). However, pollinator individuals showed higher plant species fidelity in bee-near plot (Supplementary Table 5). Pollinator fidelity was significantly higher in the bee-near plot compared to the bee-far plot (77.89% vs. 52.39%; GLMM;  $z_{314} = -2.46$ ,  $P = 0.014$ ,  $n = 318$ ), indicating greater pollinator fidelity under conditions of high honey bee spillover (Supplementary Table 5).

Honey bees significantly changed pollination interactions in the bee-near plots due to interaction turnover (Supplementary Fig. 3). This turnover caused a decrease in dissimilarity of pollination interactions within bee-near plots. Consequently, these dietary shifts resulted in enhanced functional niche complementarity among pollinators (functional complementarity of pollinators; Fig. 2d and Supplementary Table 6) in the bee-near plots. This suggests that pollinator species visited a greater variety of flowering plant species (generality of pollinators; Fig. 2e and Supplementary Table 6). The pollination networks in the bee-near plots exhibited lower levels of interaction evenness (Interaction evenness; Fig. 2f and Supplementary Table 6) and interaction diversity (Interaction diversity; Fig. 2g and Supplementary Table 6) compared to those in the bee-far plots. The spillover of honey bees resulted in an increase in the niche overlap of plants (Niche overlap of plants; Fig. 2h and Supplementary Table 6) in bee-near plots,



**Fig. 1 | The study sites and pollination networks.** Forty-eight typical alpine grassland communities were selected with 24 bee-near sites (high honey bee density: 1 km) and 24 bee-far sites (low honey bee density: 3 km) for the apiaries in the northeastern of the Tibetan alpine grasslands (blue line). At each of the 24 bee-near (From top to bottom, they are HCXSK, JFWJ, MCTC, QJK, TETC, MQCC, HKZ, XGJ, DYC, CHSC, ZLDS, XGLJ, XGL, XQC, ELJ, STL, TET, HCX, STMC, HMYDJ, GZH, QHHLB, QHHMSKZ, SJC) and bee-far sites (From top to bottom, they are BYC, DKEC, QSZFLZ, HSW, HMYDY, STMXG, DT, JFWY, MJWC, HEG, XLWTY, FXK, YLMDD, ET, LHC, BG, BHXXXXX, RYS, MDJ, XZC, XLWTC, BDK, NGZ, YGZ), we collected one pollination network between July and August 2021 or 2022. The networks consist of interactions between plants (bottom bar) and pollinators (top

bar). The full size of 48 networks includes in the Supplementary Fig. 8. The width of the links shows the number of pollination visits. There is a clear dominance of honey bees in the bee-near plots regardless of the rapeseed cover. Pollinator groups are depicted by colors: red, honey bees; blue, native bees; violet, butterflies and moths; brown, beetles; yellow, flies. All insect images belong to Pixabay (<https://pixabay.com>) under the Creative Commons Zero (CC0) license. The sample map was made using R 4.2.2. The base map was obtained from the Alibaba Cloud Data Visualization platform ([http://datav.aliyun.com/portal/school/atlas/area\\_selector](http://datav.aliyun.com/portal/school/atlas/area_selector)). Two landscape photos of the two plant communities © Lin-Lin Wang. Source data are provided as a Source Data file.



**Fig. 2 | The effects of honey bees on pollinator communities and pollination interactions.** The metrics (mean  $\pm$  SD) include the rate of honey bees (a), the number of pollinator species (b), and the number of visits (c), functional complementarity of pollinator species (d), generality of pollinator species (e), interaction evenness (f), interaction diversity (g), niche overlap of plant species (h), vulnerability of plant species (i) in the bee-near and bee-far plots. Differences in

metrics were estimated by two-sided linear mixed models (LMMs) or generalized linear mixed models (GLMMs). Error bars represent standard deviation.  $N = 24$  independent replicates. Single points show source data. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , NS not significant. Further statistical values are shown in Supplementary Table 6. Source data are provided as a Source Data file.

suggesting that few pollinator species visited plant species (vulnerability of plants; Fig. 2i and Supplementary Table 6).

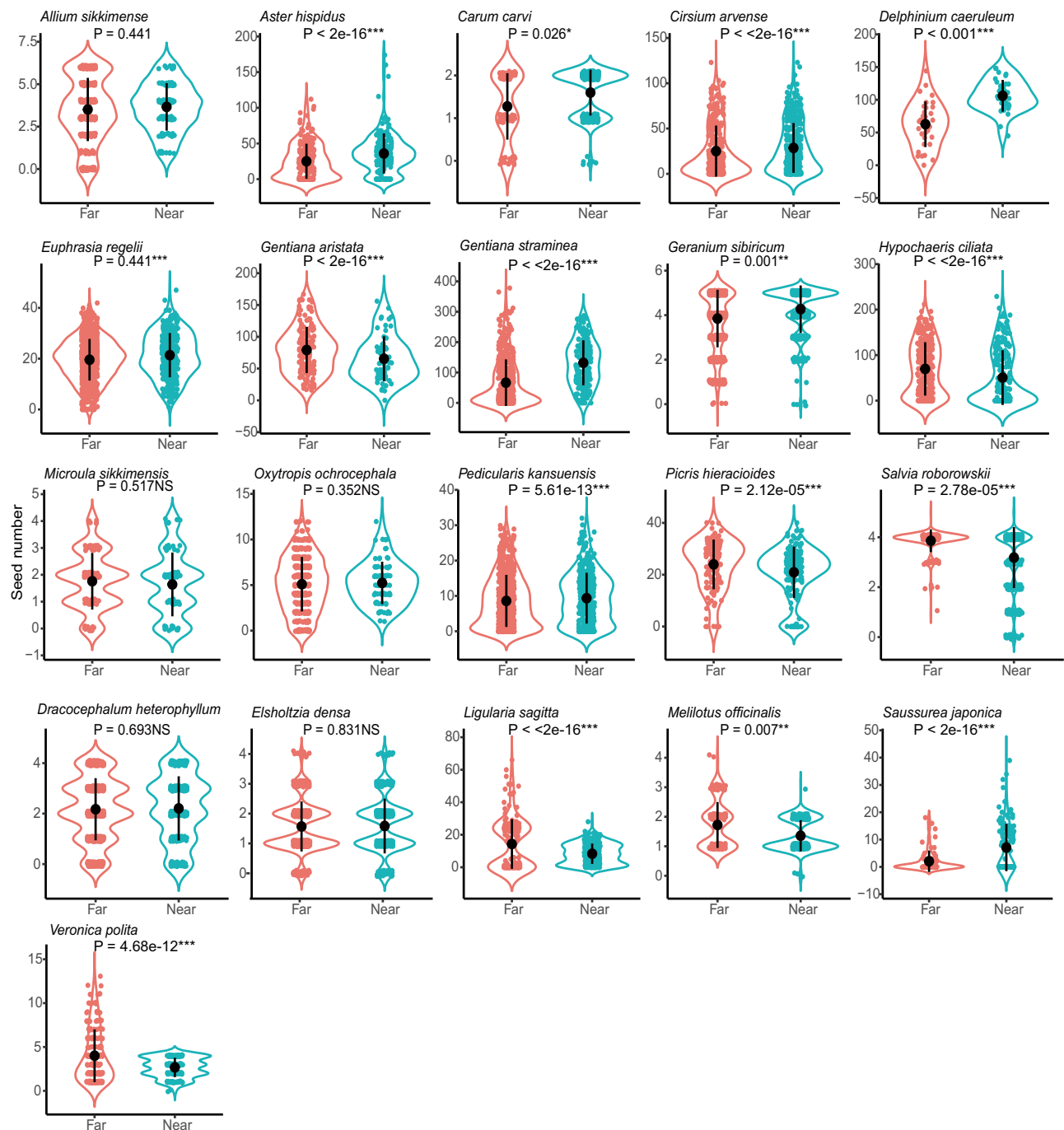
### The effects of honey bee spillover on the pollination function of plant communities

The introduction of honey bees and MFCs had a positive effect on the reproductive success of plant communities (Supplementary Table 7) due to facilitation between plant species and competitive displacement among pollinator species. These plant communities represented a significant limitation in pollination (PL = 0.29) on the alpine grasslands (LMM;  $t = -9.466$ ,  $P < 0.001$ ,  $n = 1257$ , Supplementary Table 8). Plants at bee-near plots produced a similar number of flowers (LMM;  $t = -0.565$ ,  $P = 0.575$ ,  $15382.08 \pm 6816.44$  versus  $13754.92 \pm 6603.8$ , Mean  $\pm$  1SD,  $n = 48$ ) but produced more fruit set (fruit set; Supplementary Table 7) and more seeds per fruit (seed numbers; Supplementary Table 7) across the 21 flowering plant species compared to the bee-far plots (Fig. 3 and Supplementary Table 7). Furthermore, the cultivation of rapeseed increased the seed number of plant

communities due to facilitation between plant species, with higher seed number in plots with high rapeseed cover (Supplementary Table 7).

The fruit set and seed number of plant species were affected by the native pollinator groups because of differences in pollination effectiveness between pollinator groups (Supplementary Table 9) but not flower abundance (rare vs. common) and mating system (self-compatible vs. partially self-compatible) (Supplementary Table 7). The pollination effectiveness of bumble bees was highest (100% of flowers set fruits;  $0.81 \pm 0.36$  of ovules became seeds, Mean  $\pm$  1SD,  $n = 55$ ), followed by honey bees ( $85.45\%$ ;  $0.67 \pm 0.43$ , Mean  $\pm$  1SD,  $n = 32$ ), and flies ( $63.48\%$ ;  $0.35 \pm 0.41$ , Mean  $\pm$  1SD,  $n = 115$ ) (Supplementary Table 9). Notably, compared with the bee-far plots, nine plant species that has a high visit rate of honey bees (Supplementary Tables 10), which were previously pollinated mainly by flies (*Carum carvi*, *Cirsium arvense*, and *Saussurea japonica*), bumble bees (*Delphinium caeruleum*, *Gentiana straminea*, and *Pedicularis kansuensis*), or by a mixture of flies and bumble bees (*Aster hispidus*, *Euphrasia regelii*, and *Geranium*





**Fig. 3 | Community-level plant reproduction success.** Differences in seed number (mean  $\pm$  SD) of 21 pollinator-dependent plant species in the bee-near and bee-far plots were estimated by two-sided generalized linear mixed models (GLMMs) with Poisson distributions. Plant species and individuals were assigned as random effects and were nested. Plants at bee-near plots produced more seed number across 21 flowering plant species (GLMM:  $t = -39.663$ ,  $P < 0.001$ , further statistical values are shown in Supplementary Tables 7). To test the effects of honey bee density (bee-near and bee-far) on seed number of each plant species, we fitted two-sided GLMMs with Poisson distributions. Plant individuals were assigned as random effects. Nine plant species (*Carum carvi*, *Cirsium arvense*, *Saussurea japonica*, *Delphinium caeruleum*, *Gentiana straminea*, *Pedicularis kansuensis*, *Aster hispidus*, *Euphrasia regelii*, and *Geranium sibiricum*) showed significant higher seed number

at the bee-near plots (GLMMs: all  $P < 0.05$ , further statistical values are shown in Supplementary Tables 11). The number of seeds of five species (*Allium sikkimense*, *Dracocephalum heterophyllum*, *Oxytropis ochrocephala*, *Elsholtzia densa*, and *Microula sikkimensis*) did not differ significantly between the bee-far and bee-near plots (GLMMs: all  $P > 0.05$ , further statistical values are shown in Supplementary Tables 11). The number of seeds of seven ecological and functional specialized plant species (*Melilotus officinalis*, *Salvia roborowskii*, *Gentiana aristata*, *Hypochaeris ciliata*, *Ligularia sagitta*, *Picris hieracioides*, and *Veronica polita*) was decreased in bee-near plots compared with those in bee-far plots (GLMMs: all  $P < 0.05$ , further statistical values are shown in Supplementary Tables 11). Error bars represent standard deviation. Single points show source data. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , NS not significant. Source data are provided as a Source Data file.

*sibiricum*), showed significantly higher seed numbers at the bee-near plots (Fig. 3 and Supplementary Tables 10 and 11).

The number of seeds of five species that were previously pollinated mainly by bumble bees (*Allium sikkimense*, *Dracocephalum heterophyllum*, and *Oxytropis ochrocephala*) and a mixture of bumble bees and flies (*Elsholtzia densa* and *Microula sikkimensis*) did not differ significantly between the bee-far and bee-near plots. This discrepancy can be attributed to the turnover in pollinator species (Fig. 3 and Supplementary Table 10 and 11). However, the number of seeds of seven plant species that are ecologically and functionally specialized, pollinated exclusively by bumble bees (*Melilotus officinalis* and *Salvia roborowskii*) or flies (*Gentiana aristate*, *Hypochaeris ciliat*, *Ligularia sagitta*, *Picris hieracioides*, and *Veronica polita*), decreased in the bee-near plots compared to those in the bee-far plots (Fig. 3 and Supplementary Table 10 and 11).

## Discussion

MFCs and domesticated pollinating insects are being introduced increasingly worldwide. Numerous studies have shown that the high density of honey bees diminishes the diversity and abundance of wild pollinators, particularly bumble bees<sup>14,23</sup> and reduces the reproductive success of the dominant of flowering plant species<sup>12,13</sup>. However, the current study demonstrates that the spillover of honey bees enhances the plant communities' pollination function by increasing the visitation fidelity of pollinator species and rewiring pollination interactions. These effects can only be observed when honey bees coexist with MFCs in the alpine grasslands, where most flowering plant species are mainly pollinated by flies and undergo severe pollen limitation for sexual reproduction<sup>37,38</sup>.

One notable finding is the weak effects of honey bee spillover on the richness of resident pollinator communities. This finding contrasts with previous studies, which have suggested that alien honey bees can displace native bees, thereby diminishing the diversity of wild pollinators in the plant-pollinator ecosystems<sup>13,23,28,40</sup>. A possible explanation for this might be the predominance of flies as native pollinators in Tibetan alpine grasslands (57.68% of pollinator richness)<sup>37,38,41</sup>. Additionally, the pollen and nectar standing crops in areas close to the apiaries, such as *B. rapa* var. *oleifera*, provides an additional food source for native pollinators. This allows these native pollinators to widen their foraging ranges when native nectar sources are scarce<sup>42</sup>. In our study, we observed that native pollinators visited more flowers and exhibited enhanced flower visitation fidelity during a flight bout at bee-near plot. This suggests that these bumble bees and flies may refine their foraging strategies to cope with increasing foraging competition from honey bees. Consequently, native pollinators can shift their food resources to less rewarding patches or MFCs when honey bees are highly abundant. However, our study did not consider the long-term impacts of honey bees on the diversity of native pollinators, such as the spread of pests and pathogens from honey bees to native pollinator communities, which can significantly reduce the diversity of local wild pollinators<sup>43,44</sup>. Future research should explore the response of pollinator communities to these perturbations.

Another important finding is that the spillover of honey bees alters the foraging behavior of native pollinators. Our results showed that wild generalized pollinators, such as bumble bees and flies, visited more flowers and exhibited greater pollinator fidelity during individual foraging bouts when the abundance of honey bees was high. This outcome may be attributed to the adaptive interaction rewiring of resident generalized pollinators<sup>45,46</sup>, which may prompt visits to other less rewarding flowering plants under high competition when super-generalized honey bees are highly abundant<sup>12,40</sup>. In line with our results, the effects of honey bee spillover after orange blooming led to a turnover of in interactions between wild plants and pollinators and changed the pollination network structure in Spain, such as decreased interaction evenness and link density<sup>12,13</sup>. Our study showed lower

interaction diversity and interaction evenness in the bee-near plots compared to the bee-far plots, indicating that honey bees did really compensate for the loss of some specialized pollinators and changed interaction links<sup>29,39,47</sup>. While some specialized species tend to disappear from networks through time, native highly generalized and mobile pollinator species can meet their energy needs by changing their foraging preferences or increasing the variety of plants they feed on<sup>47,48</sup>. Honey bee spillover has increased competition with other pollinator species for floral resources, leading to a greater complementarity of functional niches and a widening pollinator niche. Thus, a higher spillover of honey bees can increase the number of alternative interactions and interaction turnover, thereby making the network more robust to species loss or gain<sup>12,13</sup>. Although our study addresses the effects of honey bees on the pollinator communities and pollination interactions, the multidimensional stability of pollination networks<sup>49</sup>, such as persistence<sup>50</sup>, resilience<sup>51</sup> and robustness<sup>52</sup>, need to be examined under honey bees at the alpine grasslands in the future.

Perhaps the most unexpected finding is the enhancement of pollination function in plant communities. It is generally suggested that the introduction of alien pollinator species is likely to have negative consequences on pollination function of native plant species<sup>12,13</sup>. In alpine grasslands, flies are the most common pollinators<sup>38</sup>, yet they have lower flower fidelity and pollination effectiveness than other pollinators, such as native bumble bees and honey bees<sup>41</sup>. Our results revealed that the honey bees dominate in the bee-near plots and the seed numbers of numerous plant species (42.9% of plant species) have increased, but others have not changed (23.8%) or decreased (33.3%) in the 21 pollinator-dependent plant species.

Apart from the direct effect of honey bees on the pollination success of certain plant species<sup>8,53</sup>, the increased of pollination function in plant communities may be attributed to facilitation among plant species and competition among pollinator species due to honey bee spillover<sup>18–20</sup>. We discuss each of these mechanisms in turn below.

Firstly, maintaining natural habitats around agricultural land (particularly MFCs) can improve ecosystem services, such as crop pollination, biological pest and weed control<sup>11,54,55</sup>. In contrast to large field monocultures in Europe and North America, Chinese agroecosystems, particularly the Tibetan grassland agroecosystems, are characterized by relatively small fields and neighboring large (semi-)natural habitats (see Supplementary Fig. 4), which can benefit wild pollinator species by providing nesting sites and diverse floral resources<sup>54,56</sup>. Our results revealed an increase in the richness of pollinator assemblages and an increase of seed production in the plant communities under the high MFC cover (~30%) and bee-near plots. Thus, abundant flowering plants, such as MFCs, may act as a magnet species to attract wild pollinators into nearby natural communities and improve visitation rates of some rare plant species. This leads to improved reproductive success for these rare species<sup>18,32,57</sup>. The occurrence of pollination limitations in the rare plants, such as *D. caeruleum* and *G. straminea*, which are mainly pollinated by bumble bees<sup>58,59</sup>, suggests that bumble bee visits are insufficient for them to achieve maximum reproductive success. However, our results revealed that the flowers of *D. caeruleum* and *G. straminea* in the bee-near and high MFC cover plots had more bumble bee visits and improved the seed numbers in plot close to *B. rapa* var. *oleifera*. Therefore, such facilitation among flowering plant species might promote the coexistence of species in diverse plant communities, because rare plant species benefit from the presence of the abundant species.

Secondly, competitive displacement of some native pollinator species by honey bees improve the complementarity of functional niches within pollinator communities<sup>60,61</sup>, thereby increasing the reproductive success of plant species<sup>62</sup>. For example, bumble-bee-pollinated and fly-pollinated plant species, such as *G. sibiricum* and *E. regelii*, that have also been visited frequently by honey bees showed significant increases of seed numbers. This suggests enhanced

reproductive performance of these plant species when honey bees are integrated into the pollinators of these plant species. Functional enhancement within a pollinator species due to honey bee spillover can improve the quantity or quality of pollen transferred between flowers and plant individuals and increase the reproductive success of plant species<sup>19</sup>. In our study of Tibetan alpine grasslands, we found that most native pollinator individuals within one pollinator species showed a higher degree of specialization in the bee-near plot due to floral fidelity over the short term<sup>30</sup>, which could improve the deposition of conspecific pollen<sup>30,63</sup>. In addition, our results showed that most of flowering plant species were self-compatible in the alpine grasslands. While honey bees can appear as competitors when they are foraging, they can increase visitation fidelity for certain native pollinators, such as bumble bees and flies. This increased fidelity leads to a decrease in heterospecific pollen transfer and an increase in conspecific pollen transfer, ultimately resulting in increased plant reproductive success of some self-compatible flowering plant species<sup>8</sup>. For example, the seed number of fly-pollinated plant species (e. g. *S. japonica*) increased in the bee-near plots due to the higher visitation fidelity of pollinator individuals.

However, generalist flowering plant species often share pollinators and receive pollen grains from various species in natural communities<sup>12,64</sup>. The reproductive success of these flowering plant species can be altered when there is interaction rewiring<sup>35,65</sup>. For instance, when less efficient honey bees replace more efficient bumble bees as the pollinators of native plant species, the reproductive success of these native plant species can be decreased<sup>40,66</sup>. Indeed, bumble bee-pollinated plant species that were visited frequently by honey bees (such as *S. roborowskii* and *M. officinalis*) showed significant decreases of seed number in plots close to *B. rapa* var. *oleifera*. This is consistent with previous research showing reduced reproductive performance of native plants after introduction of honey bees<sup>12,13</sup>. Therefore, to understand the effects of non-native plants and pollinators on reproductive success at the plant community level, it is necessary to consider the types of native pollinator species and the pollination effectiveness of the main pollinator species within the community.

In summary, in contrast to the conclusions of other studies<sup>11–13,47</sup>, our research reveals that honey bees can alleviate pollination limitation of wild plants and complement the activities of wild pollinators. Moreover, honey bees enhance the pollination function of plant communities in the alpine grasslands (Supplementary Table 12). Importantly, honey bees alter pollination function of wild plants with species-specific consequences, detailed as increasing seed production of some plants whose main pollinators are flies, but decreasing seed production of some plants pollinated mainly by bumble bees. However, our study did not consider the long-term impact of honey bees on the diversity and abundance of native pollinators. Numerous studies have shown that the pests and pathogens associated with the spillover of honey bees can significantly reduce the diversity and richness of local wild pollinators and override the benefits obtained from their pollination services. Therefore, we urge future studies to examine the response of the diversity and abundance of pollinator communities to agricultural activities (such as MFCs and beekeeping activities) at different temporal and spatial scales in alpine grasslands.

## Methods

All sampling sites were located in non-protected areas. Following the national laws, permits for sampling were obtained from Haibei Alpine Grassland Ecosystem Research Station, Northwest Institute of Plateau Biology, Chinese Academy of Sciences.

## Study sites

This study was conducted in the alpine grasslands (latitude: 35.1689°–38.5433°N, longitude: 98.5169°–101.6225°E) of Tibet, China (Supplementary Fig. 5). The research area has a typical plateau continental

climate with short and cool summers and long and cold winters. The peak flowering period of native flowering plants extends from late June to late August. The flowering plant species are mainly Ranunculaceae, Fabaceae, Asteraceae, and Gentianaceae. Species such as *Ranunculus tanguticus*, *Oxytropis ochrocephala*, *Pedicularis kansuensis*, *Cirsium lanatum*, and *Gentiana straminea* are abundant from mid-June to early September. The dominant pollinator species are Western honey bees (*Apis mellifera*) and native bumble bees (e.g., *Bombus supremus* and *B. kashmirensis*), flies, and butterflies<sup>38</sup>. No feral *A. mellifera* or *A. cerana* were found in our study sites<sup>30</sup>. *Brassica rapa* var. *oleifera* is widely cultivated in the Tibetan Plateau, covering more than 160,000 hectares with an annual production of about 360,000 metric tons over the past thirty years. In parallel with the flowering period of rapeseed and wild plants from July to August, non-native pollinators (mainly western honey bees) have also been introduced into the field for more than thirty years to assist in the pollination of rapeseeds<sup>23,30</sup>.

## Setup of experimental plots

The effects of beekeeping activities on the plant-pollinator communities in natural ecosystems remain a subject of controversy due to the difficulty of finding an ideal control site free from honey bees and conducting rigorous manipulative experiments in replicated field trials<sup>13,66</sup>. Two main experimental designs are currently used to explore the impact of beekeeping on the plant and pollinator communities<sup>12,13,23,67–69</sup>. One is the before-and-after approach, which allows for investigating the effects of beekeeping on pollination systems by comparing differences between pre- and post-beekeeping at the same site<sup>12,13,47</sup>. However, this method makes it difficult to rule out the effects of phenological turnover of plant and pollinator species between periods because the absent period always precedes the present period<sup>13</sup>. The other commonly used method is to select study sites with different distances to the apiary at a spatial scale, since the dominance of honey bees is negatively related to the distance to the apiary, with high density at near sites and low density at far sites<sup>13,23,67–69</sup>. However, this method makes it difficult to avoid the effects of differences in plant and pollinator species between bee-near and bee-far plots. We chose space-for-time method<sup>13,23,40,67</sup> but not before-and-after method<sup>12,13</sup> because the blooming period of wild plants and rapeseeds (July–August) overlapped strongly in our alpine grasslands, and honey bees were only stocked during the flowering period of wild plants and rapeseeds.

To examine the effects of honey bees on the plant and pollinator communities, we established two contrasting honey bee abundance regimes with sufficient replications in the northeastern Tibetan alpine grasslands (Fig. 1). First, following Torné-Noguera et al.<sup>68</sup> and Mu et al.<sup>69</sup>, we selected 48 alpine grassland communities from 21 apiaries (1–7 plant communities per apiary) with 24 “bee-near” sites (high honey bee density: 1 km from the apiaries) and 24 “bee-far” sites (low honey bee density: 3 km away from the apiaries) in 2021 (Fig. 1). The selection criteria for the study sites were an altitude between 2700 and 3400 m above sea level, size greater than 1 ha, similar native plant communities, and accessibility. All study sites had typical alpine grassland vegetation and comparable climate across the northeastern of the Tibetan Plateau. Thus, by selecting the same number of bee-near and bee-far sites at equal distances from apiaries, we could avoid confounding factors such as distance to the apiaries and the number of hives that may affect the general conclusions.

To ensure the similarity of the plant and pollinator communities, we then selected three transects (100 × 2 m each) in a large plot (100 × 100 m) with the closest possible similarity in orientation and vegetation at each bee-near and bee-far site. The number of flowering plant species was similar between bee-near and bee-far sites (ANOVA;  $F_{1,47} = 0.21$ ,  $P = 0.65$ ; mean ± SD; 16.25 ± 4.88 versus 15.63 ± 4.63). The mean number of native pollinator species also did not differ between bee-near and bee-far plots (ANOVA;  $F_{1,47} = 3.35$ ,  $P = 0.07$ ; 27.16 ± 9.23 versus 32.79 ± 12.05).

Species similarity of plant and pollinator communities (proportion of co-occurring species to the total number of species at two paired sites) was similar across the 24 bee-near and 24 bee-far sites, and between bee-near and bee-far sites (LMM; all  $P > 0.05$ ;  $0.37 \pm 0.08$ ,  $0.38 \pm 0.10$ , and  $0.36 \pm 0.09$ , respectively). There was no correlation between the spatial distance among sites ( $96.14 \pm 78.04$  km) and the composition of plant or pollinator communities (Mantel tests; plants  $r = -0.04$ ,  $P = 0.62$ ; pollinators  $r = 0.117$ ,  $P = 0.10$ ) (Supplementary Table 13). Thus, diversity and composition of plant and pollinator species were spatially similar and independent across the 48 sites.

### The effects of honey bees on pollinator communities

To investigate the effects of honey bees on the richness and abundance of flower visitors, flower visitors were observed along three transects at 28 sites in 2021 and 20 sites in 2022 from early July to late August during the peak flowering period of native flowering plants and *B. rapa* var. *oleifera* in the Tibetan alpine grassland. Each transect in each plot was surveyed for 60 min per day on four clear days (9:00–19:00) without strong wind for a total of 720 min per plot (60 min  $\times$  four different days  $\times$  three transects). The mass-flowering area of *B. rapa* var. *oleifera* within 1 km of each plot was also recorded<sup>67</sup>. Of the 48 sample plots, we defined the 24 plots with the larger rapeseed areas as high MFC plots and the other half as low MFC plots. If an insect visited anthers or stigmas of flowers, we recorded pollination visits regardless of pollination effectiveness<sup>30</sup>. We did not observe pollinator visits at night because few pollinators visit flowers under low temperatures<sup>70</sup>. Total number of visits to flowering plants by all pollinator taxa per sample plot was used to determine pollinator abundance. All unidentified pollinators in the field were collected for identification by the expert taxonomists.

To investigate the effects of honey bees on the fidelity of pollinators to visit flowers, following Wang et al.,<sup>30</sup> we constructed four small plots (10  $\times$  10 m) to observe the foraging behavior of pollinators within two large plots (100  $\times$  100 m), with one near and one bee-far site from the apiary in Huangyuan County (Supplementary Fig. 6). Because the effective pollen dispersal distance of pollinators in our alpine grassland was less than 10 m<sup>70</sup>, a fixed quadrat of 1  $\times$  1 m was set up at the center of the small plots (10  $\times$  10 m). We waited for possible pollinators to visit open flowers in the fixed quadrat and tracked pollinator movement between flowering plants, because pollinators tended to forage on nearby plant species<sup>30</sup>. When a pollinator entered the selected fixed quadrat (1  $\times$  1 m) and visited the flowers, the pollinator was followed as long as it stayed in the chosen small area (10  $\times$  10 m). Each quadrat (1  $\times$  1 m) was monitored for 120 min per session, totaling four sessions over four different days. Flower-visiting insects were followed from 9:00 to 19:00 on clear, windless days mid-July to late August, during the peak season of pollinator activity. Because low temperatures at high altitudes limit pollinator activity, we did not observe outside this period. We only recorded flower-visiting insects that came into contact with the anthers and stigmas of at least two flowers, since effective pollinator-mediated pollination mainly occurred between different flowers<sup>71</sup>. All pollinators were insects of the orders: Diptera, Hymenoptera, and Lepidoptera. With the help of expert taxonomists, we collected and identified all continuous flower visitors after they left the selected plot. We recorded the identity of the insect species, the number of flowers visited, and the number of visitation turnover. We defined visitation turnover as pollinating from one flower of one plant species to a flower of another plant species. We defined floral visit fidelity as 1 when there was no turnover (only one plant species visited) and 0 when turnover happened. We determined fidelity of 318 pollinators (of 44 pollinator species) visiting 12,769 flowers.

### The effects of honey bees on pollination interactions

To capture the effects of honey bees on the pollination interactions in the bee-near and bee-far plots, we first assembled 48 plant-pollinator

interaction networks (Fig. 1) using a standardized transect sampling protocol for observing plant-pollinator interactions in heterogeneous vegetation. We summed the number of pollinators observed visiting flowers over 12 h per network, as described above. Each pollination network was composed of a quantitative adjacency matrix that indicated the total number of visits of each pollinator to each plant species. We recorded 104 flowering plant species (Supplementary Table 14) and 148 pollinator species (Supplementary Table 15). Then, we extracted two pollination interaction metrics at the network level for each network: interaction evenness and interaction diversity (Supplementary Table 16). The metrics interaction diversity and interaction evenness of the networks characterize aspects of complexity in diversity and distribution of interactions between plants and pollinators<sup>60,72</sup>.

To identify the effects of honey bee spillover on the level of niche breadth of these flowering plant and pollinator species in the networks, these metrics, functional complementarity of pollinators, generality of pollinators, niche overlap of plants, and vulnerability of plants were assessed in each network (Supplementary Table 16). Functional complementarity of a pollinator species measures the niche complementarity of a pollinator species and is computed as the total branch length of a “functional dendrogram” based on qualitative differences in interactions between one level with another<sup>73</sup>. Niche overlap of plant species is the mean similarity in interaction patterns between plant species<sup>74</sup>. Generality of pollinators means the effective number of flowering plant species per pollinator species and vulnerability of plants means the effective number of pollinator species per flowering plant species<sup>75,76</sup>. There was no correlation between the spatial distance among sites and all these network metrics (Mantel tests; all  $P > 0.05$ ), indicating no inherent site-related bias or spatial autocorrelation (Supplementary Table 12).

To examine the effects of honey bees on the dissimilarity of plant-pollinator interactions between the bee-near and bee-far sites<sup>77</sup>. We focused on the dissimilarity explained by interaction turnover ( $\beta_{OS}$  measure in Poisot et al.<sup>77</sup>, which corresponds to rewiring of species interactions) among shared species between the two networks. This metric ( $\beta_{OS}$ ) ranges from 0 to 1, with a value of 1 indicating that the composition of interactions is completely different.

### The effects of honey bees on the pollination function of plant communities

To investigate pollination limitation at the plant community level, we selected 12 species of flowering plants (Supplementary Table 8) at the Haibei Alpine Grassland Ecosystem Research Station (37° 36'N, 101° 12'E, 3,250 m above sea level), Qinghai, China. These species were highly dependent on pollinators for fruit set, and their flowering periods overlapped with that of rapeseed<sup>31,38</sup>. For each species, about 30 flowers were randomly selected to be hand-pollinated to test whether additional pollination increased seed production, and another ~30 flowers were selected as controls. Pollen grains used for hand-pollination were taken from newly opened flowers and were sufficient to fertilize all the ovules in a flower. There was more than 10 m between pollen donors and hand-pollinated flowers to ensure cross-pollination. To estimate the number of mature seeds per fruit, all fruits were collected before dehiscence and the number of mature seeds was counted. Our calculation of pollination limitation (PL) is as follows:  $PL = 1 - Sc/Sh$ , where  $Sc$  and  $Sh$  denote the seed number of natural and hand-pollinated flowers, respectively. We determined the seed number of 1397 flowers across 12 flowering plant species.

To measure the seed production of honey bees, bumble bees, and flies in a single visit, 30 individuals of four plant species were randomly selected from those that were fully bloom during the vegetation period at the Haibei Alpine Grassland Ecosystem Research Station. *Gentiana aristata* and *Parnassia trinervis* are mainly visited by flies, while *Delphinium caeruleum* and *Gentiana straminea* are mainly visited by



bumble bees and honey bees<sup>30,31,58,59</sup>. All opened flowers were removed from the targeted plants, and pollinators were excluded by covering the plants with nylon netting. When the flowers opened and stigmas ripened, they were individually removed from the bag and observed until each was visited by an insect. The types of visitors (honey bees, bumble bees or flies) were noted, and the flowers were marked and re-bagged. After about 30 days, all the fruits of the marked flowers were collected, and the number of mature seeds was counted.

To determine whether the dominance of honey bees and rape-seed change the pollination function of native plant communities, we selected 21 insect-pollinated plant species (Supplementary Table 10) according to two criteria. First, those plant species were shared between the bee-near and bee-far large plots, and had more than 30 individual flowering plants in each plot from mid-July to mid-August, which covered the peak of the flowering period of wild plants and rapeseed. Second, all 21 flowering species were hermaphrodites that depend on pollinators (mainly bees and/or flies) to deliver pollen to ensure their pollination success<sup>31,38</sup>. Therefore, some common species were excluded such as *Aconitum gymnanthum*, *Halenia elliptica*, *Comastoma pulmonarium* and *Taraxacum* which were subject to wind-pollination, self-pollination, or apomixis<sup>31,78–80</sup>. The details of the plant abundance (common vs rare), reproductive system (self-compatible and partially self-compatible), native pollinator groups (flies, bumble bees, or both) and pollinator visitation (honey bees vs native pollinators) of the 21 plant species are shown in Supplementary Table 10. In each plot, we tagged 30 flowering plants for each species. We collected three branches per individual plant or whole plant (number of branches <3) to determine fruit set (the proportion of flowers that set fruit) in mid-September 2021. First, we recorded the number of flowers and fruits per individual per species when all flowers had wilted. Then, more than 30 pre-marked ripe fruits (one fruit per branch) were collected for seed number per fruit. Finally, we defined the reproductive performance of native plants as fruit set and seed number per fruit. Changes in fruit set and seed number revealed functional changes driven by beekeeping activity because of similar natural vegetable and environmental conditions between bee-near and bee-far plots. We determined the reproductive output of 11,749 fruits nested in 877 plants of 21 species.

## Data analysis

Analyzes were conducted in R (version 4.2.2) (R Core Team, 2022; <http://www.R-project.org>), using the following packages: bipartite 2.13<sup>72</sup>, lme4 1.1-21<sup>81</sup>, betalink 2.2.1<sup>77</sup> and vegan 2.4-6<sup>82</sup>. In all models, we first checked the normality of the variables. If they did not follow a normal distribution, we used log-transformation to improve normality.

We tested the effects of honey bee density (bee-near and bear-far plots) and MFC (high MFC cover and low MFC cover) and their interactions on pollinator communities (rate of honey bees, the number of pollinator species and the number of pollinator visits) and pollination interactions (interaction evenness, interaction diversity, functional complementarity of pollinators, generality of pollinators, niche overlap of plants, and vulnerability of plants) using linear mixed models (LMMs) or generalized linear mixed models (GLMMs). Year was assigned as a random effect. The LMMs were used to evaluate rate of honey bees, interaction evenness, interaction diversity, niche overlap of plants, functional complementarity of pollinators, generality of pollinators, and vulnerability of plants (Supplementary Table 6). The GLMM tests used a Poisson distribution and log-link function for the number of pollinator species and the number of pollinator visits (Supplementary Table 6).

We tested the effects of honey bee density (bee-near and bear-far plots) on pollinator fidelity using a GLMM with binomial distributions. Honey bee density (bee-near and bear-far) was treated as a fixed effect. Pollinator groups (honey bees, bumble bees, and flies) and pollinator species were treated as random effects and were nested.

We fitted a LMM to analyze pollination limitation of plant communities. To allow for a meaningful comparison between species, the number of seeds per fruit was divided by the mean number of seeds per plant ('relative seed production'), which was fixed at one for each species<sup>83</sup>. Pollination treatments (supplementary pollination and control treatments) were assigned as a fixed factor and plant species as random effect.

We fitted GLMM to test the single-visit seed production of honey bees, bumble bees, and flies and assumed a Poisson distribution in the model. The pollinator group (honey bees, bumble bees, and flies) was assigned as a fixed factor. We included pollinator species as a random factor.

To test the effects of honey bee density (bee-near and bee-far), MFC (high MFC cover and low MFC cover), native pollinator groups (flies, bumble bees, and both flies and bumble bees), mating system (self-compatible and partial self-compatible), and flower abundance (rare and common) on fruit set and seed number of plant communities, we fitted GLMMs with binomial and poisson distributions, respectively. Plant species and individuals were assigned as random effects and were nested. The year was also assigned as a random effect. To test the effects of honey bee density (bee-near and bee-far) on fruit set and seed number of each plant species, we fitted GLMMs with binomial and Poisson distributions, respectively. Plant individuals were assigned as random effects.

We check the suitability of the models by using residual plots and QQ plots in the (G)LMMs (Supplementary Fig. 7). The best model was selected based on AICc. Also presented are the AICc weights (AICcWt) that indicate the probabilities of the models. We computed the adjusted  $R^2$ , marginal, and conditional  $R^2$  (G)LMM as goodness-of-fit measures for linear and linear mixed models. Marginal and conditional  $R^2$  (G)LMM are coefficients of determination for mixed models that describe the proportion of variance explained by the fixed factors only (marginal  $R^2$  (G)LMM) and by both the fixed and random effects (conditional  $R^2$  (G)LMM). We fitted in all (G)LMMs because the models of the quadratic terms showed a poorer fit (>AICc) compared to the linear fit.

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

The data related to analyzes are available on Figshare (<https://doi.org/10.6084/m9.figshare.24564775>). Source data are provided with this paper.

## Code availability

The R codes for the analyzes are available on Figshare (<https://doi.org/10.6084/m9.figshare.24564775>).

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## Author contributions

L.L.W., Y.Y.P., and Y.W.D. designed research; L.L.W. and W.F.D. performed research; L.L.W. and Y.W.D. analyzed data; L.L.W. wrote the paper; Z. Y. H., Y.Y.P., and Y.W.D. edited the paper.

## Competing interests

The authors declare no competing interests.

## Additional information

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