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Low-density migratory beekeeping induces intermediate disturbance effects on native bee communities in Tibetan Plateau alpine meadows

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Ecological disturbance can promote or reduce community biodiversity depending on its severity. Beekeeping activities represent a type of ecological disturbance when large numbers of honey bees are introduced to a landscape and interact with the local plant and pollinator community. In this study, we characterized the effect of immediate and long-term low-density migratory beekeeping on the diversity and abundance of native bees in the Qinghai-Tibet Plateau (China). We found that the presence of apiaries and the number of honey bees reduced native bee abundances in the local bee community, likely through displacement from floral resources. However, in locations where apiaries were previously kept for decades but are not currently present, native bee abundances recovered, and phylogenetic diversity increased; yet community relative abundances and dominant species were distinct from those that had never been stocked. Our results suggest that the presence of a transient, intermediate number of migratory honey bee colonies (60–100 colonies spaced ≥15 km from each other) may represent an intermediate ecological disturbance and not permanently reduce native bee abundances past a critical threshold that may lead to local extirpation. Yet, our study demonstrates the potential for even intermediate-scale low-density beekeeping to alter native bee communities in the long-term.

Key words: ecological disturbance, introduced species, community diversity, honey bees, native bees

低密度的放养蜜蜂对西藏地区高寒草甸本地蜂群落造成了中度水平的干扰

生态干扰引起群落多样性的增加或降低，其影响结果完全取决于干扰的程度. 放养蜜蜂作为生态干扰最重要的类型之一，通常会引起本地植物和传粉者群落发生变化.我们在青藏高原高寒草甸开展了系列试验， 监测了长期固定放蜂区域内低密度的放养蜜蜂对本地蜂群群数量和物种数目的影响情况，以期阐明放养蜜蜂对本地蜂群多度和丰富度的影响机制. 结果表明:在长期放蜂 (主要是意大利蜂) 区域内，意大利蜂的出现显著降低了本地蜂的多度和物种多样性，主要是通过竞争花资源来实现. 如果一旦移去意大利蜂群，本地蜂的多度和系统发育多样性会明显增加. 同时发现本地蜂群落的相对丰度和优势种与意大利蜂未移出前时的截然不同. 研究结果说明即时的少量迁徙蜜蜂群落 (60-100个蜂箱，间隔约15km) 可能代表一种中等程度上的生态干扰水平，这有利于将本地蜂的丰度维持在一定的安全水平，降低本地蜂的灭绝风险. 本研究表明，即使在小规模养蜂水平下如果长期固定在一个区域内放蜂也可能会改变当地蜜蜂的群落.

Introduction

Global insect declines can be attributed to several human-induced ecological disturbances, such as habitat alteration, agricultural intensification, and the introduction of exotic species (Wagner 2020). Yet understanding how these disturbances affect insect populations requires studies examining community effects beyond basic views of species gains and losses (Weisser et al. 2023). Ecological disturbances are a combination of biotic or abiotic factors that result

in perturbations in the structure and functioning of an ecosystem. At the community level, disturbance can result in changes in diversity, abundance, and composition that result in shifts in species interactions (Rykiel 1985). At the population level, disturbance may lead to species changes in phenotypes (e.g., morphology, phenology, behavior, and physiology) through either adaptation or plasticity (Mooney and Cleland 2001, Banks et al. 2013, Ruland and Jeschke 2020). While severe disturbances often have detrimental effects on communities and populations, intermediate disturbances often promote the diversity and the functioning of ecosystems (Petraitis et al. 1989, Hobbs and Huenneke 1992, Roxburgh et al. 2004, Catford et al. 2012).

Exotic species can be drivers of disturbance at different levels of severity and lead to ecologically positive or negative effects depending on context. For example, when plants become naturalized in a new area, they can provide ecological benefits to native pollinators and birds through additional floral and fruit resources, respectively (e.g., Gleditsch and Carlo 2011). However, when exotic species outcompete native species, changes in entire community composition may occur with negative effects on ecosystems (Hobbs and Huenneke 1992, Memmott and Waser 2002, Loehle 2003, Bartomeus et al. 2008, Morales and Traveset 2009, Vilà et al. 2009, Blackburn et al. 2011, Fortuna et al. 2022). Within a specific ecological niche, the introduction of exotic species may result in competition for resources with the native community. This results in the displacement of native species to new geographic areas, forcing them to non-preferred habitats, hosts, or food sources, or even increasing interspecific native species competition (Usio et al. 2001, Evans 2004, Kenis et al. 2009, Fortuna et al. 2022). These factors consequently may reduce population sizes of native species to undetectable levels that may make them vulnerable to local extinction.

The interdependence and stability of coevolved native plant-pollinator communities make their interactions particularly sensitive to the introduction of competitive nonnative species. One of the major drivers of disturbance to plant-pollinator communities around the world is the western honey bee (*Apis mellifera* L., Hymenoptera: Apidae; Mallinger et al. 2017, Iwasaki and Hogendoorn 2022), a managed bee species currently used globally for agricultural pollination and honey production (Aizen et al. 2009). With increasing market demands from pollinator-dependent crops, large-scale migratory beekeeping operations are needed to maximize pollination services in agricultural areas where native pollinators are not available or do not meet agricultural pollination demands due to the alteration of natural habitat (Kleijn et al. 2015). These operations generally house thousands of honey bee colonies that are contracted to farms during crop blooms, but in between pollination contracts are kept in locations with abundant floral resources to build colony strength and improve honey production. Therefore, the transient introduction of large numbers of honey bee colonies to nonagricultural areas results in a sudden increase in pollen demand to supply colonies comprising 10,000–80,000 individuals each, directly interfering with the already vast number of flowers needed to support the pollen requirements of local native bees (Hymenoptera: Anthophila; Müller et al. 2006, Cane and Tepedino 2017). Additionally, if this sudden introduction of honey bees reduces or displaces populations of native bee species, pollination services to the local floral community could remain compromised even after colonies have been removed from the site. Thus, there is global interest in characterizing the ecological consequences that introducing large numbers of honey bee colonies has on native bee populations. The goal is to develop guidelines enabling native pollinator biodiversity conservation while sustaining managed bees that provide critical pollination in large-scale agricultural landscapes.

Previous research examining the interactions between native bees and honey bees has indicated negative or neutral interactions through competition for floral resources and changes in the availability and quality of floral rewards of native plants (Mu et al. 2014, Mallinger et al. 2017, Iwasaki and Hogendoorn 2022, Page and Williams 2023a, 2023b). The fewer studies analyzing honey bees' impact on entire native bee community composition often exhibit negative effects where honey bees suppress native bee richness and abundance (Angelella et al. 2021, Garibaldi et al. 2021, MacInnis et al. 2023, MacKell et al. 2023). However, these studies are often conducted in agricultural or urban land-use settings where honey bees have been naturalized or the native environment and ecology have already been disturbed by humans. These disturbances include pesticide use, pollution, and reduced floral and nest site diversity or availability (Goulson et al. 2015), which may exacerbate the negative effects of honey bees on native species populations and filter native bee populations to only those resilient to such disturbances. Thus, there is a gap in understanding how honey bees affect native bees in natural or semi-natural areas.

Here, we study the effects of transient introductions of low-density migratory beekeeping operations (60–100 colonies per apiary with apiaries spaced at ≥15 km) to nonagricultural rural landscapes on native bee population abundance and diversity. Specifically, we evaluated changes in community structure and phylogenetic diversity of native bee populations as a consequence of (i) honey bee abundance and (ii) long- and short-term beekeeping history. We predicted that sites where honey bee apiaries were either currently located or have been located previously would host lower native bee abundance and diversity, with shifted community composition. We found that the current presence of honey bee apiaries resulted in a suppression of native bee abundances and change in community composition. Contrary to our hypothesis, in sites where honey bees were kept previously, but currently removed, we found that native bee abundances rebounded with higher phylogenetic diversity, supporting an intermediate disturbance hypothesis.

Materials and Methods

Field Sites

We conducted our study in the rural open meadows of the Qinghai-Tibet Plateau (QTP), a biodiversity hotspot for bumble bees (Williams et al. 2018) and temperate plant species (Ding et al. 2020). We collected data in Hongyuan County in Sichuan Province, China (~32.7993, 102.5393; ~3,500 m altitude; Fig. 1A), a region lacking intensified agricultural practices except for rotational yak grazing (Mu et al. 2016). *Apis mellifera* is neither native nor naturalized to the QTP. However, migratory beekeepers have brought their colonies to Hongyuan yearly since 1981 for its cooler climate and higher floral abundance during the summer (Mu et al. 2014, Su et al. 2022). Beekeepers typically stock ~60–100 colonies per apiary (Mu, personal communication) and have been in the same locations along the main highway (S209) passing through the town Qiongxi. Thus, this site provides a unique study area, where native bee communities have been interacting with introduced honey bee colonies in a distance-based gradient from the road for ~35 years at the time of the study. In 2017, when the study was conducted, at the initiation of a local music festival, beekeepers moved their apiaries ≥10 km away from their previous locations (Fig. 1A).

The recent movement of apiary locations allowed us to study the effects of novel honey bee exposure on native bees vs. the long-term effect of honey bees following their removal. We collected data at six 500-m × 500-m sites (Fig. 1B). Two field sites were chosen in

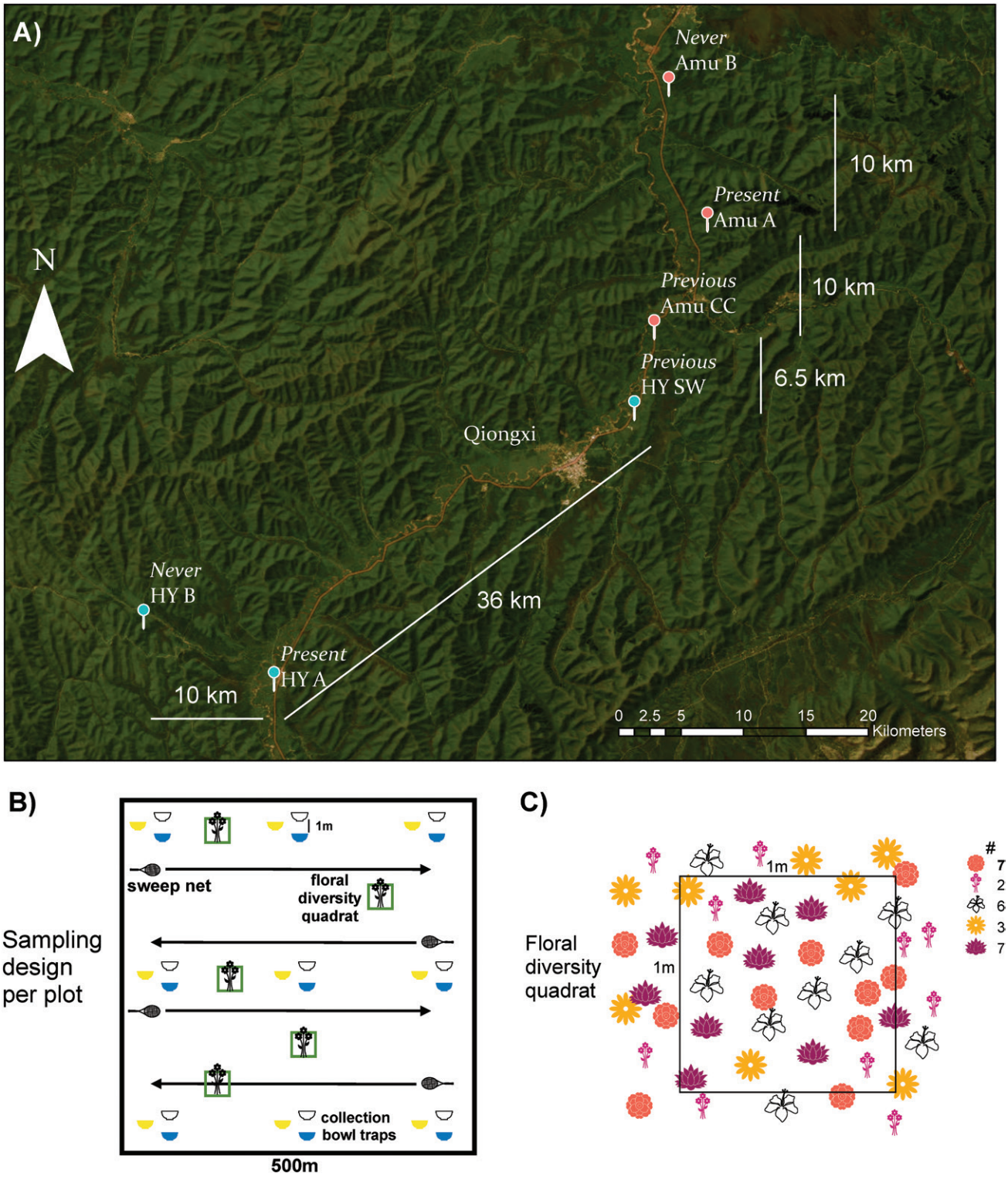

Fig. 1. Tibetan plateau field sites and sampling protocol. A) Map indicates locations and distances between sites and associated beekeeping history (*never*, *previous*, or *present*) surrounding Qiongxi in Hongyuan County, China. Site groups are represented by prefix "HY" or "Amu". B) Illustration of bee sampling protocol for each field plot, including passive bowl trapping and active sweep netting. Five randomly placed quadrats were placed at each site to survey floral diversity. C) Illustration of how the flower number of each genus was counted within and crossing the line of each quadrat.

each of three categories of honey beekeeping history (Fig. 1A): "previous" (sites where bees were kept for the previous decades, until 2017), "present" (~1 km away from the new current apiaries, ≥10 km from previous, 6.5 km from each other), and "never" (sites where honey bees have never been kept, ≥10 km away from present or any other known beekeeping sites; Fig. 1A). To verify that "never" sites had negligible honey bee presence or no other apiaries nearby, approximately three days prior to sample collection, three observers

patrolled wildflowers and the landscape for ~1 h for honey bee or apiary presence. The absence of honey bees would indicate that the sites had little pressure from honey bee abundances at the time of sampling. Our results further confirmed low honey bee occurrence, with a total of 2 honey bees caught within 6 days of sampling at *never* sites.

Sample Collection

We collected bees at each site on three separate days between July 12–22, 2017 (Fig. 1B). Each morning at 09:00, we placed nine groups of three bowl traps (filled with 100 ml soapy water and painted either fluorescent white, yellow, and blue) evenly throughout the plot, placed directly on the ground after clipping grass around the collection location. From 10:00–12:00 and 13:00–15:00, two collectors sampled bees by systematically sweep netting the plot for 10 min intervals, followed by 5 min of collecting bees from the sweep nets, resulting in 240 min of active collection per day. We euthanized each native bee in an individually labeled 2-ml tube and grouped honey bees in 20-ml tubes filled with 100% ethanol. At 15:00, we removed bees from the bowl traps, rinsed them with water, and placed them in individual 2-ml tubes filled with 100% ethanol. For each site, we counted the total number of flowers of each plant genus within five randomly placed 1-m × 1-m quadrats and calculated floral richness and Shannon diversity (Fig. 1C, Supplementary Table S1).

Bee Identification

We pinned and sorted all bee specimens to morphospecies and identified species for *Bombus* spp. (Apidae) and *Anthidium montanum* M. (Megachilidae), the only groups whose reference material was available (Supplementary Table S2; specimens are currently stored at the Chinese Academy of Sciences). Because the Asian honey bee *Apis cerana* F. has been reported in this area (Radloff et al. 2010), we randomly subsampled 100 collected honey bees (15%) and verified they were all *A. mellifera*. To verify native bee species identity, we removed one fore-, mid-, and hind leg per specimen and placed them in 100% ethanol. This material was sent to the Southern China DNA Barcoding Center (Kunming) for cytochrome c oxidase I (COI) DNA Sanger sequencing (Sanger et al. 1977) using standard LCO/HCO primers (Folmer et al. 1994). The raw COI Sanger sequences were processed (Geneious Prime® 2020.2.3, https://www.geneious.com) to remove poor-quality sequences, define ambiguous base calls, and trim primer and sequence tails. We aligned all sequences using MUSCLE v3 (Edgar 2004). From this alignment, we created a neighborhood-joining phylogenetic tree (nexus file in SI1) using the Tamura-Nei genetic distance model (Tamura and Nei 1993) starting at a random seed and using the consensus tree of 100 bootstrap iterations with a support threshold of 50%.

Data Analysis

We created native bee species abundance (Supplementary Table S3) and presence/absence matrices. To define the native bee community at each site for both matrices, we conducted both unconstrained and constrained correspondence analysis (CA) in the R package "*vegan*" (Oksanen et al. 2022). First, for unconstrained CA, axes that best explain variation in community composition are first determined, then regressed against explanatory variables. We used the function *cca* to determine Eigenvalues and site scores (i.e., proximity in ordination space between sites). We then used the *envfit* function on the cca ordination object to test the relationship between site-level bee community composition and honey bee abundance, beekeeping history, and plant diversity. For constrained CA, where ordination axes are *first* fit to the explanatory variables, we used *cca* on the community matrix constrained by the number of honey bees, beekeeping history, and plant diversity of each site. We followed this by conducting ~720 permutation analysis of variance on the constrained CA object using the functions *permustats* and *anova*.

Using the native bee phylogenetic tree, we created a between-species phylogenetic distance matrix using the *cophenetic* function in the R package "*ape*" (Paradis and Schliep 2019). We determined native bee phylogenetic diversity at each site by calculating the standard effect size of the mean pairwise distance (SES MPD) both for presence/absence and weighted by abundance communities using the *ses.mpd* function and *phylogeny.pool* null model parameter randomized 1,000 times in the R package "*picante*" (Kembel et al. 2010). We ran independent analyses to estimate the effect of beekeeping history (ANOVA), honey bee abundance per site (regression), and plant diversity (regression) on the presence/absence and abundance-weighted SES MPD.

Results

The relative abundances of honey bees collected in the *never* sites (0%, 0.005% of total bees collected) were negligible compared to sites where apiaries are currently present (43% and 47%). At the *previous* sites, we collected an intermediate number of honey bees at one site (12%), while many at the other (47%) (Fig. 2, Supplementary Table S4), potentially arising from individual beekeepers with few colonies whom we did encounter sporadically in the region. The total number of native bees we captured was similar between *never* sites (N = 356, 405) and *previous* sites (N = 395, 364) yet were substantially lower than at sites where apiaries were currently present (N = 156, 201) (Fig. 2, Supplementary Table S4; $F_{2,5}$ = 31.4, P = 0.01). Plant genus diversity was lowest numerically at *previous* sites, but there was no evidence that it differed between sites with different beekeeping histories (Fig. 3, Supplementary Table S4; $F_{2,5}$ = 2.79, P = 0.21; genus richness—*never* = 15,12, *previous* = 10,11, *present* = 18,16).

For the unconstrained CA of the abundance matrix, components 1 and 2 explained approximately 51% and 25% of the variation of the data, respectively (Fig. 4, Supplementary Table S5). For the presence/absence matrix, unconstrained components 1 and 2 explained 40% and 22% of the variation (Supplementary Table S5). In the abundance and presence/absence matrices, there was moderate evidence that the number of honey bees between sites was related to changes in native bee relative abundances and species presence (R^2 = 0.95, P = 0.03 abundance; R^2 = 0.88, P = 0.07 presence/absence). Beekeeping history was also associated with the composition of native bee abundances by site (nonoverlapping centroids, Fig. 4, $F_{2,3}$ = 15.23, P = 0.027) but not in the presence/absence matrix (Supplementary Table S5, $F_{2,3}$ = 2.54, P = 0.23). In both abundance and presence/absence matrices, there was no evidence (R^2 = 0.72, P = 0.22, R^2 = 0.62, P = 0.3) that plant diversity was related to differences in bee communities (Figs. 3 and 4, Supplementary Table S5), likely because there was little difference between sites. Native bee communities in *never* sites clustered together as well as *present* sites, while *previous* sites showed differences in community composition (Fig. 4).

The constrained CA ordination accounted for 97% of the total variation in the abundance data and 89% of the presence/absence data (Supplementary Table S5). Components 1 and 2 explained 50% and 25% of the variation in the abundance data and 39% and 22% in the presence/absence data, respectively. Permuted ANOVA tests for the abundance data revealed strong and moderate evidence that differences in bee community composition between sites were explained by number of honey bees ($F_{1,8}$ = 15.23,

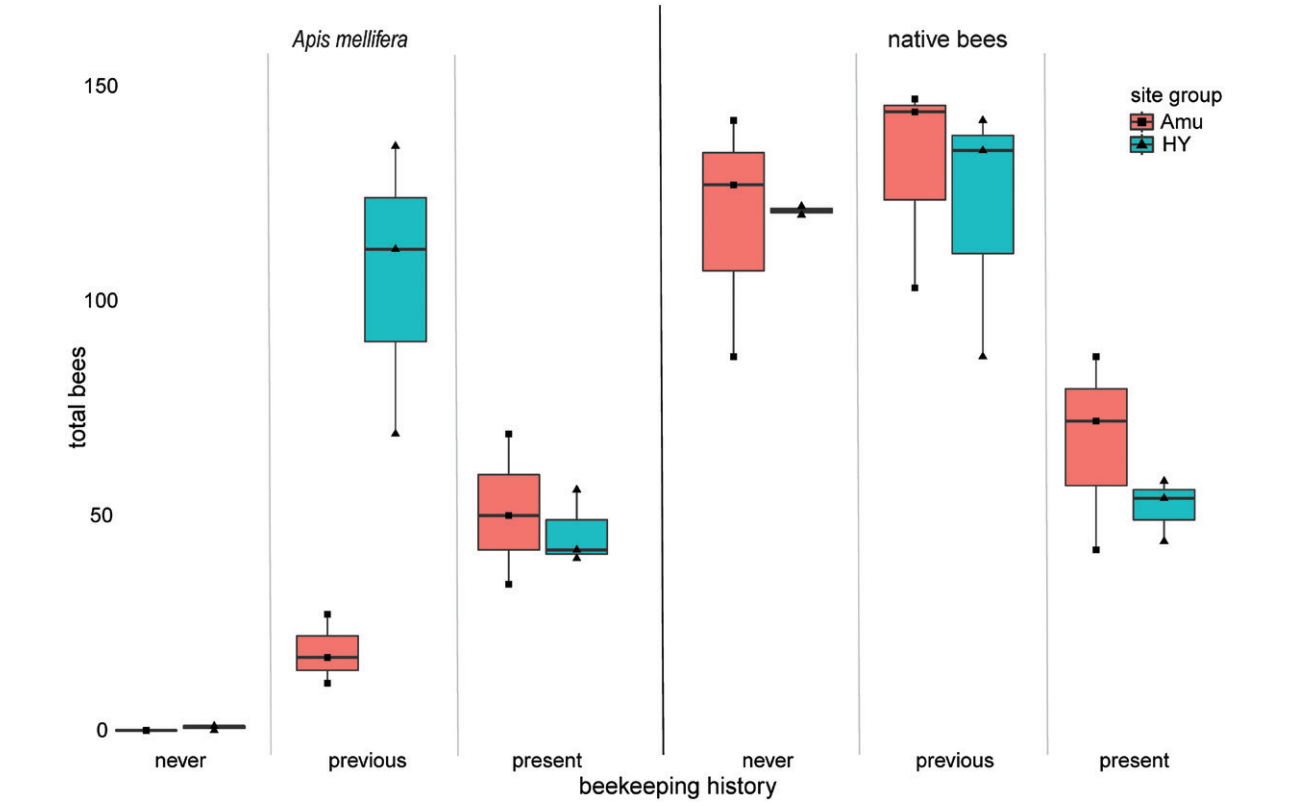

Fig. 2. Honey bee and native bee abundances by beekeeping history. Boxplot colors represent different site groups (see Fig. 1), and each marker represents each of three days of sampling.

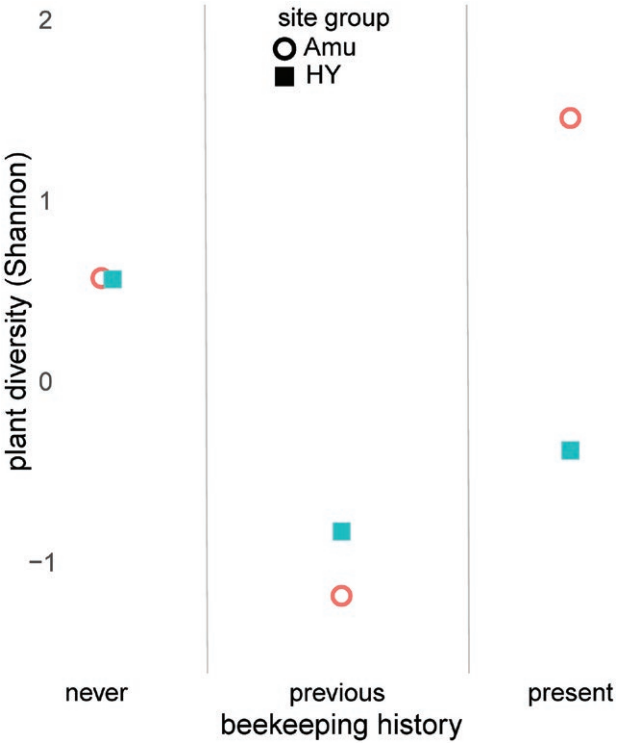

Fig. 3. Plant diversity (Shannon) at each sampling site (markers) organized by beekeeping history in each site group (color, see Fig. 1).

$P < 0.01$) and beekeeping history ($F_{2,8} = 8.31$, $P = 0.02$) respectively, yet little evidence that plant diversity was associated with native bee community composition ($F_{1,8} = 2.93$, $P = 0.11$; Supplementary Table S5). There was moderate evidence that honey bee abundance ($F_{1,8} = 3.18$, $P = 0.03$) explained differences in native bee species presence/absences between sites, yet no evidence that beekeeping history ($F_{1,8} = 1.92$, $P = 0.13$) or plant diversity ($F_{1,8} = 1.39$, $P = 0.39$) was associated with native bee presence (Supplementary Table S5). Interestingly, *never* and *previous* sites differed the most in native bee community composition.

At the composition level, we found evidence of shifts in the relative abundance of different species in the community. Many native bee species abundances were lower at *never* sites where honey bees were never kept than at *previous* sites where honey bees were kept previously (Fig. 5). However, many of the most abundant species were lowest at *present* sites near where apiaries were currently kept. Also, the dominant native bee species in *never* sites, *Andrena sp_3* (Andrenidae), was substantially lower at *present* sites where honey bees were currently kept and persisted at lower levels at *previous* beekeeping sites.

We found moderate evidence that bee phylogenetic diversity (SES MPD) weighted by abundance increased from *never* to *present* to *previous* beekeeping history ($F_{2,3} = 15.04$, $P = 0.03$), and was positively correlated with honey bee abundance ($F_{1,4} = 6.09$, $P = 0.07$). In contrast, we found no evidence that phylogenetic diversity was influenced by plant diversity ($F_{1,4} = 2.69$, $P = 0.18$, Fig. 6, Supplementary Table S6). There was no evidence that SES MPD for presence/absence was related to beekeeping history ($F_{2,3} = 0.79$, $P = 0.53$) or plant diversity ($F_{1,4} = 2.32$, $P = 0.2$), yet moderate evidence that phylogenetic diversity increased with honey bee abundance ($F_{1,4} = 8.24$, $P = 0.05$, Supplementary Table S6).

Discussion

In this one-year study, we investigated how the introduction of honey bee colonies via intermediate-scale migratory beekeeping

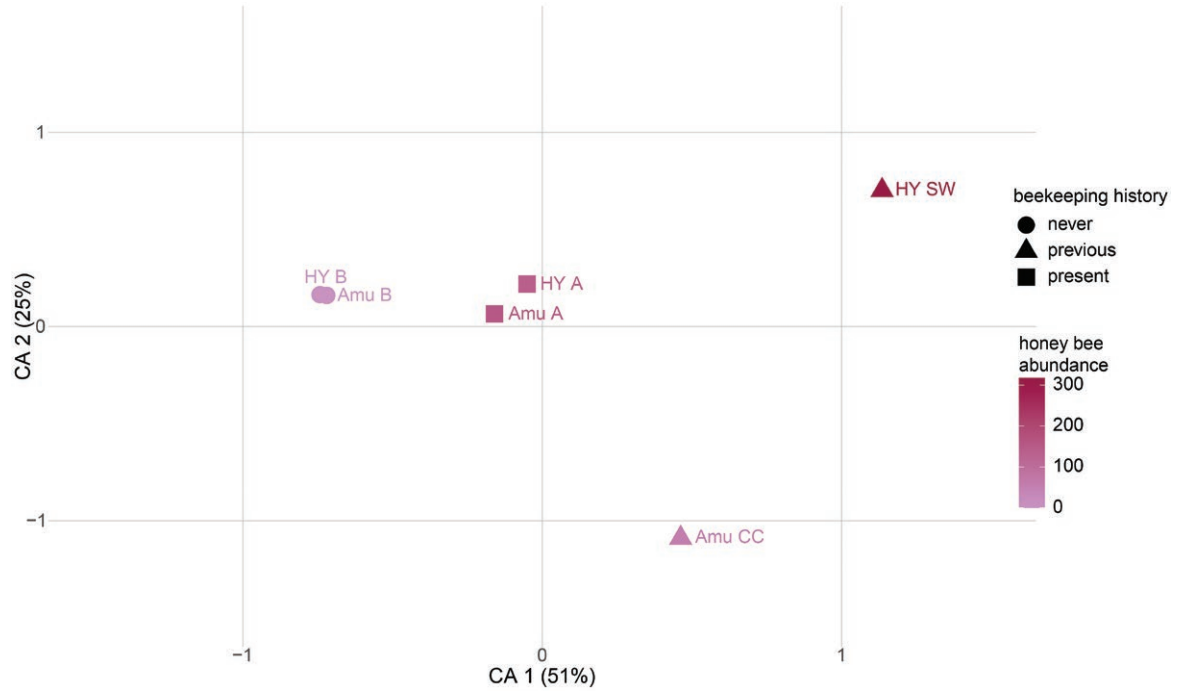

Fig. 4. Unconstrained correspondence analysis (CA) of native bee community abundances for each field site. Each marker represents an individual field site (see Fig. 1) and its associated bee community, shaped by beekeeping history, and opacity along a gradient of honey bee abundance. The percentage of variation in the bee community data explained by each component (axis) is provided.

impacts native bee community diversity and abundance in areas with low-density of beekeeping. We found that native bee abundance was lowest at *present* sites, and similarly higher among *never* and *previous* sites. However, compared to the undisturbed sites where honey bees were never kept, native bee species diversity increased at sites where apiaries were placed currently (*present*) and increased further after they were removed (*previous*), indicating that beekeeping activities in the region shifted relative abundances between native bee species over time. These changes in the native bee community suggests that beekeeping activities in this context have functioned as an intermediate ecological disturbance.

Although this study represents a snapshot in community compositions in the region, our data suggest that within a short distance (~1 km), the immediate presence of beekeeping (i.e., the first introduction of honey bees in the current season) reduces the overall population abundance of native bee species in the community. While we did not investigate specific mechanisms for this change, reductions in native bee abundance in the presence of large numbers of honey bees are likely due to direct or indirect competition for floral resources (Cane 2024). In our study, the presence of managed honey bee colonies was associated with a severe reduction in the most dominant native bee species (*Andrena sp_3*; Fig. 5). This association with a reduction of the dominant species restructured local native bee community composition and increased phylogenetic diversity, possibly because the suppression of *Andrena sp_3* allowed other species to occupy limited foraging or nesting habitat (Fig. 5). After colonies were removed from sites the previous year, we observed that community abundances rebounded, phylogenetic diversity increased, but the abundance of the dominant species *Andrena sp_3* remained low compared to the *never* sites. The interactions between introduced honey bees and the dominant native bee species in this study exemplify similar findings that low community evenness is associated with lower community species richness and diversity (Garibaldi et al. 2021). In these scenarios, a disturbance that reduces the abundance of the dominant species may cause some downstream community effects discussed below.

Classifying the levels of disturbance (i.e., from minor to intermediate to severe) that honey bees and beekeeping practices exert on native bee communities is often difficult because of the many agricultural and urban land use practices that may exacerbate such disturbances, including agricultural chemicals, pollutants, and reduced floral and nesting resources (Goulson et al. 2015). By studying a relatively undisturbed landscape in the QTP, we inferred the direct effects of migratory beekeeping disturbance through honey bee abundance and beekeeping history. These reductions in native diversity associated with the presence of abundant honey bees suggest that the placement of migratory apiaries represents a disturbance to native bee communities that has long-lasting effects. In this region, honey bee pressure from apiaries to the native bee communities was localized to specific areas as no other apiaries were present for long distances. Because we found that *previous* sites rebounded in native bee abundance only one year after the beekeeping disturbance, our results suggest that the underlying mechanism of disturbance is the displacement of native bees and not local extinction (Fortuna et al. 2022). This rebound in native bee abundance is likely possible because of the open florally diverse landscape with minimal agricultural input, pesticide use, habitat loss, and lack of persistent widespread apiaries outside of the localized areas of beekeeping. However, our results cannot be extrapolated to other situations where floral diversity and the carrying capacity of the environment are lower and higher density of managed honey bee colonies are kept (e.g., Mandelik and Roll 2009, Klein et al. 2012). In areas where migratory beekeeping introduces thousands of colonies to wild and natural habitats after pollination contracts, we expect disturbance of local bee species to be more pronounced with long-lasting and possibly irreversible effects, pushing already less abundant species

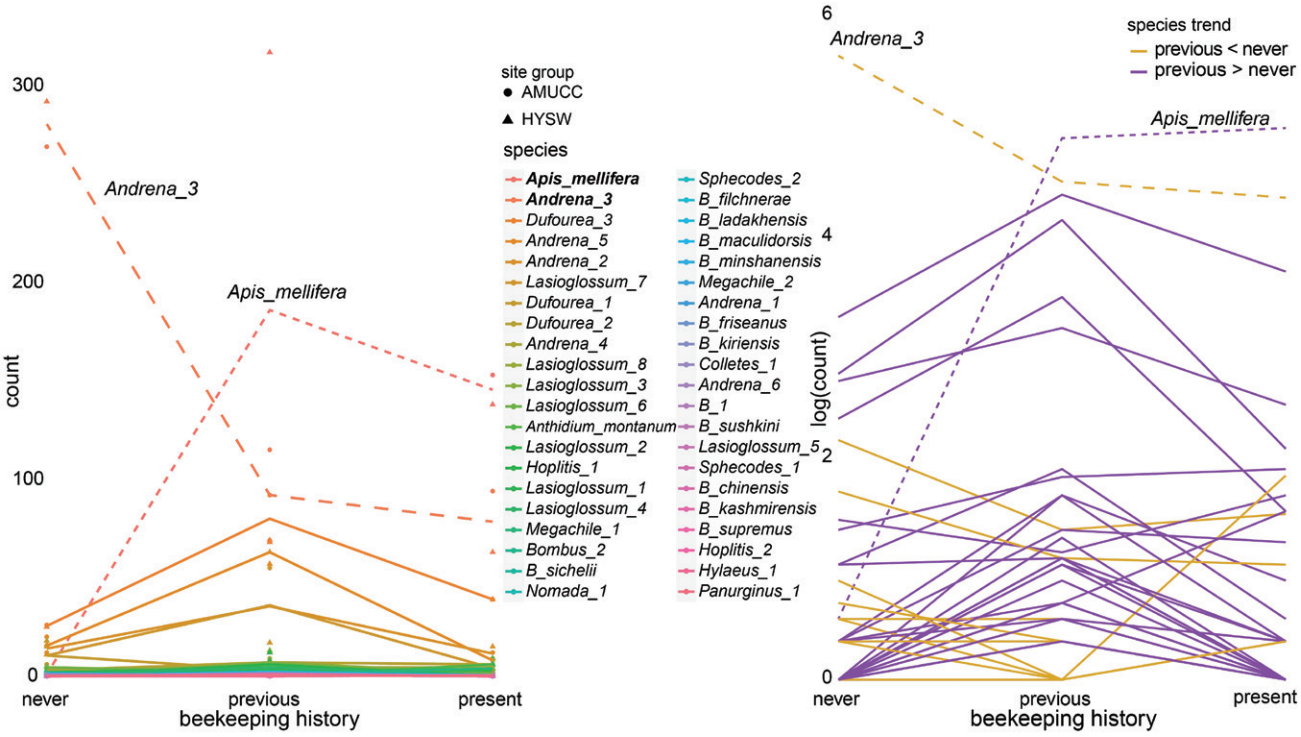

Fig. 5. Individual bee species' abundances at sites differing in beekeeping history. Left panel indicates actual abundances at each site (shape, see Fig. 1) with lines representing average trends. Right panel highlights the trend that most species' abundances (log scale) were higher at sites where honey bees were previously kept vs sites where honey bees were never or presently kept (see "species trend" legend). Note how nearly all bee species abundances were lowest at sites where honey bees were kept at the season of the study. Honey bees and the dominant native bee *Andrena sp_3* are emphasized by dashed lines.

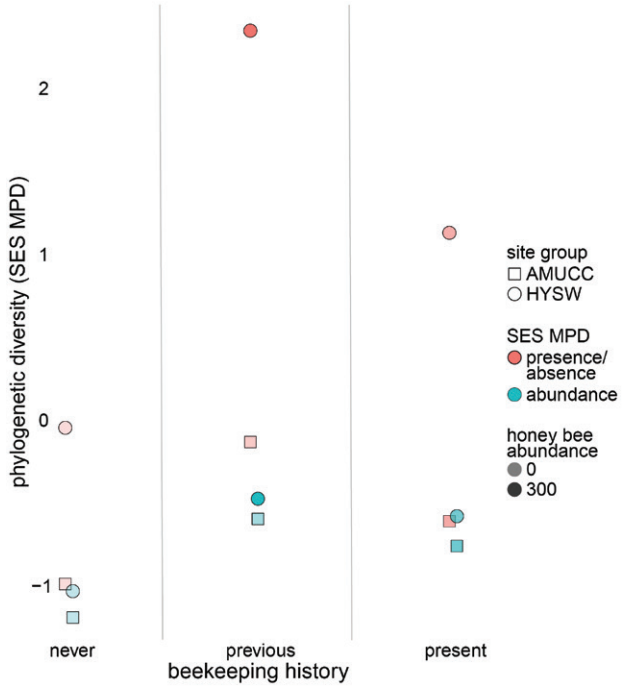

Fig. 6. Phylogenetic diversity (MPD SES) of the native bee community at each site by beekeeping history. Each marker represents a different field site, shaped by site group (see Fig. 1), colored by abundance weighted or presence/absence data, and opacity by honey bee abundance at each site.

below critical population thresholds (i.e., local extirpation; Mooney and Cleland 2001, Portman et al. 2018). This is conceivable, given the sheer quantity of nectar and pollen resources honey bees require. It is estimated that "a 40-hive apiary residing on wildlands for three months collects the pollen equivalent of four million wild bees" (Cane and Tepedino 2017). Therefore, we recommend that the location of large-scale commercial beekeeping operations be limited to areas where crops or pasture are grown for agricultural purposes.

The long-term effect of beekeeping in the study region was exemplified at the sites where apiaries were previously kept for decades but forced to move in the year of the study. At these sites, native bees repopulated displaced habitats and recovered to abundances observed at sites with no beekeeping history, but with new species compositions and different relative abundances (including the persistent reduction in the dominant *Andrena sp_3*). Native bees were not only likely displaced from the habitat, but community compositions were altered by repeated seasonal pressure. In this scenario of intermediate-scale migratory beekeeping with low densities, although some species may have experienced significant and persistent displacement from the presence of managed honey bees, the overall community experienced an increase in abundance, and phylogenetic diversity. These seemingly positive effects of the transient presence of honey bees on native bee communities support predictions of an intermediate ecological disturbance (Connell 1978, Galand et al. 2016, Mu et al. 2016).

An important point to highlight is that the long-term ecological effects of introducing large numbers of honey bees can manifest in more nuanced ways that may be more apparent in studies over longer timeframes. For example, long-term displacement of native pollinators may perturb pollination services provided by native bee species that honey bees may not replace (Magrach et al. 2017, Page and Williams 2023b). Concurrently, long-term selection by honey bees on floral traits may lead to evolutionary shifts in floral reward quantity, quality, and potential accessibility of native plants (Mu et al. 2014), disrupting interactions with native pollinators. Species

displacement from sites near apiaries may further create or exacerbate competition for resources between native species in habitats with low honey bee pressure. Pollen nutritional value differs between host plants, and bees likely have nutritional niches fulfilled by preferred pollen hosts (Vaudo et al. 2024). If displaced from preferred nutritional hosts, shifts in diet quality may have long-term physiological and fitness effects that may negatively affect the fitness of native bees, especially when displaced species compete with each other. This has been exemplified in bee communities through shifts in body size and nutritional storage of bees in agricultural systems where diverse floral resources are limited (Grab et al. 2019, Smart et al. 2019).

Conclusions

This study contributes to the growing body of literature demonstrating that the introduction of intermediate numbers of honey bee colonies to nonagricultural habitats decreases the abundance of native bees, most likely via ecological competitive displacement. However, the long-term effects of these negative associations between the presence of transient beekeeping operations and native bees likely depend on the density of honey bee colonies introduced, the duration of their presence in these habitats, and habitat-specific carrying capacity. Therefore, results of studies investigating the impact of beekeeping on the native bee community need to be interpreted in a context-specific fashion and not as generalizable. In our context, our results indicate that intermediate-scale low-density migratory beekeeping was associated with higher native bee diversity but lower abundance in a landscape with abundant floral resources and no other major agricultural stressors. Future studies should explicitly investigate the effects of stocking densities and the duration of honey bee pressure on native bee abundance, community composition, and pollination services, especially over multiple seasons. Although not studied directly, our study supports this potential impact for beekeeping in open natural ecosystems as well, where low to intermediate stocking density of apiaries at low densities may only displace native bee communities for short periods of time and long-term population effects on native bees may be potentially avoided with changing apiary locations intermittently or leaving apiaries in primarily agricultural areas.

Supplementary data

Supplementary data are available at *Journal of Insect Science* online.

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