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Honeybees are far too insufficient to supply optimum pollination services in agricultural systems worldwide

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ABSTRACT

Evidence of a decline in wild pollinators is increasing across global and local habitats. However, with regional variation, the number of managed pollinators has increased globally. Whether these managed pollinators can sufficiently meet the agricultural pollination demand given wild pollinator declines remains unclear. Data on 49 honeybee-pollinated crops cultivated worldwide and stocked honeybee colonies were analysed to assess the pollination demand and pollination service capacity between 1989 and 2019. We found a rapidly increasing demand for honeybee pollination but a decreasing pollination service capacity of honeybee colonies. Globally, the demand for honeybee pollination rose approximately 2.3 times higher than the stocked number of honeybee colonies in 2019, growing 1.78% annually, almost 2 times faster than honeybee colonies (0.95%). On average, the pollination service capacity, growth rates of demands for honeybee colony stocks and honeybee pollination, and diversity of honeybee-pollinated crops varied regionally. Nevertheless, fluctuation of the honeybee-pollination demand increased with increased fluctuation of crop diversification. Oil crops accounted for over 70% of the world's honeybee-pollination demand in 2019, with soybean and rapeseed accounting for 39% and 16%, respectively. This was the case in less diversified countries, where a few crops dominated the demand for honeybee pollination, including American countries such as Argentina, Brazil, and the USA, compared to more diversified countries such as China, India, and Japan in Asia. Our study shows that managed pollinators are far too insufficient to adequately supply the agricultural pollination demand worldwide. This emphasises the importance of ongoing calls for protecting pollinators and the integrated management of honeybees and wild pollinator assemblages for a sustainable food-secure future world.

1. Introduction

Global concern about pollination demand and the decline of pollinators in many local and regional habitats (Potts et al., 2016, 2010), which is associated with widespread pollen limitation and pollination crises (Knight et al., 2005; Polce et al., 2013), has been increasing. The magnitude of pollen limitation has been worsening due to contemporary ecological factors, such as ecological perturbations and habitat fragmentation, which have changed the abundance and composition of pollinators (Knight et al., 2005). As a result, the quality and quantity of pollination services delivered have been declining over time due to degrading plant-pollinator interactions and functions, resulting in non-random pollinator species extinctions, loss of spatial co-occurrence between extant species in modified landscapes, and temporal mismatches (Burkle et al., 2013), which desynchronise the pollinator demand and supply. In this regard, studying the balance between the demand and supply of pollinators is vital, as its impacts are expected to affect the sustainability of ecosystem services such as crop pollination (Knight et al., 2005).

Pollinators are essential for maintaining the stability of the global food supply (Aizen and Harder, 2009; Garibaldi et al., 2011). Klein et al. (2007) reported that three-quarters of global food crops depend at least partly on animal pollination, particularly that by insects. Non-bee pollinators make a significant contribution to pollination, accounting for approximately 25–50% of total flower visits (Rader et al., 2016). However, the most ubiquitous and effective pollinators are bees (Venturini

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et al., 2016), as most plants (i.e., crops) exhibit pollen limitation in the absence of wild and managed bees, producing fewer fruits and seeds than would be produced with adequate pollen receipt (Hünicken et al., 2021; Knight et al., 2005). Honeybees provide much of this pollination workforce (Tylianakis, 2013) and are pollinators of choice for most crops due to their biology and characteristics (National Research Council (NRC), 2007). Their large perennial colonies provide a large number of generalist pollinators of many crops, foraging over long distances, and effectively communicate to enhance foraging efficiency and floral constancy (NRC, 2007). Therefore, they are preferred in large monocultures with high floral densities where other species (i.e., wild bees) are restricted to field margins due to limited foraging ranges (NRC, 2007; Rands and Whitney, 2011; Toivonen et al., 2021). Other bee species may be more efficient than honeybees, particularly on a flower-to-flower basis or in terms of pollen deposition per visit (NRC, 2007; Woodcock et al., 2013). However, this may not be important where honeybees are more abundant than other bees in a crop, as honeybees usually provide compensatory higher visitation rates (Rader et al., 2009; Woodcock et al., 2013). For this reason, managed honeybee colonies can be moved across landscapes and used as a mitigation measure against pollinator deficits (Woodcock et al., 2013) to enhance crop yield stability (Hünicken et al., 2021).

Global agriculture has increased reliance on pollination services (Osterman et al., 2021), as the proportion of land cultivated with pollinator-dependent crops has increased profoundly, affecting the supply of pollinators and pollination services (Aizen et al., 2019; Garibaldi et al., 2011). This increasing pollinator dependence does not appear to increase with crop diversification (e.g., crop richness and evenness of the area cultivated for these crops at different geographical scales) (Aizen et al., 2019). One possibility is that agricultural pollinator dependence could have been increasing not because of crop diversification but because of an increase in large-scale monocultures of pollinator-dependent crops. For instance, rapid expansions of pollinator-dependent oilseed crops such as soybean have occurred in several American and Asian countries (Aizen et al., 2019; Woodcock et al., 2013). Furthermore, while pollinator reliance is increasing, the agricultural practices that undermine pollination services are also expanding; as a result, an increasing shortage of pollinators in agricultural fields has been reported worldwide (Aizen et al., 2019). For instance, across Europe, the demand for honeybee pollinators increased approximately five-fold within half a decade (Breeze et al., 2014). Likewise, the number of honeybee colonies required to supply adequate crop pollination in China grew almost three times more than the number of stocked honeybee colonies in 2018 (Mashilingi et al., 2021).

Experts worldwide agree that pollinator diversity and abundance are declining rapidly due to multiple stressors, including the large-scale prophylactic use of insecticides, pollution, habitat degradation from changing land use, and climate change (van der Sluijs and Vaage, 2016; Klein et al., 2017; Dicks et al., 2021; Osterman et al., 2021). For instance, over the past 120 years, environmental changes have disrupted plant-pollinator interactions and extirpated 50% of the bee species historically present in Illinois, USA (Burkle et al., 2013). Likewise, the occupancy of bumblebees declined by 46% in North America and 17% in Europe between 2000 and 2014 (Soroye et al., 2020). However, the population of honeybee colonies has increased globally despite the different trends exhibited at regional and country levels (e.g., a decline in Europe and the USA but an increase in Canada) (NRC, 2007; Osterman et al., 2021). Compared to wild bees, managed colonies are buffered to a certain extent from degrading environmental quality by the care and maintenance of beekeepers (NRC, 2007; Wakgari and Yigezu, 2021). Nevertheless, they remain more vulnerable to pests and pathogens such as the tracheal mite (*Acarapis woodi*) and the mite *Varroa destructor* (Klein et al., 2017; Wakgari and Yigezu, 2021), as well as replacement by other species. The inappropriate management practices applied to honeybee colonies are another important factor with negative effects, including the decline of honeybee colonies (Al-Ghamdi et al., 2016). In addition, the Western honeybee (*Apis mellifera*) has become dominant over other honeybee species, such as the Asian honeybee (*A. cerana*). For instance, it has replaced 55% of the *A. cerana* population, with more dramatic patterns in some countries, such as Afghanistan, where it has replaced over 95% of the population, and Pakistan, where less than 1% of the *A. cerana* population remains (Theisen-Jones and Bienefeld, 2016). Additionally, threatening severe diseases such as that caused by Thai sacbrood virus, among the most devastating threats, eliminated approximately 90% of *A. cerana* in southern India (Oldroyd and Nanork, 2009; Theisen-Jones and Bienefeld, 2016; Thomas et al., 2002). Furthermore, a few studies with contradictory findings have examined changes in feral honeybee populations over time. From infestation in 1952 and 1987 to the early 2000s, wild and feral honeybees were believed to have been cleared out by *V. destructor* in Europe and North America, respectively (Jaffé et al., 2010; Kraus and Page, 1995; Moritz et al., 2007). However, in the mid-2000 s, some wild and feral colonies were reported to survive interactions with *V. destructor* in France (Le Conte et al., 2007), Sweden (Fries et al., 2006), and the USA (Seeley, 2007). This increases concerns regarding the availability and stability of future honeybee pollination services (Potts et al., 2010).

As shown above, the current global trends of managed (honeybees) and wild pollinators are contradictory (Osterman et al., 2021). While the agricultural pollination demand is increasing, the pollinator supply is decreasing, which is likely exacerbating the current pollination crisis, ultimately putting global food security and stability at high risk (Garibaldi et al., 2011). Nevertheless, the growing beekeeping industry may serve the dual purposes of supplying hive products and agricultural pollination services. The present concern is whether the stocked honeybee colonies will be able to meet the increasing agricultural pollination demand and mitigate the pressure of a rising agricultural pollination deficit due to continuing declines in the wild pollinator community (i.e., diversity and abundance). Other studies, such as that of Aizen et al. (2019), have evaluated the association between changes in the cultivation area of animal-pollinator-dependent crops and agricultural diversity, aiming to connect agricultural expansion with agricultural diversification. However, with a focus on honeybee-pollinated crops, the present study evaluates the global demand for honeybee pollination using recommended colony densities and the relationship of honeybee-pollinated crop diversification with the stability of the demand for honeybee pollination. Therefore, in this study, we assessed 1) the global trends in agricultural honeybee-pollination demand and the honeybee-pollination service supply capacity, 2) the variation in and influences of honeybee-pollinated crop diversity on the increasing rate and stability of honeybee-pollination demand, and 3) the crops that drive agricultural honeybee-pollination demand. The findings of this study can help prioritise the integrated management of honeybee and wild pollinator assemblages for sustainable global agriculture and food security.

2. Materials and methods

2.1. Data collection

Data on the honeybee stock and area of cultivation for honeybee-pollinated crops were gathered from the FAO database from five FAO agricultural geographical regions over the past three decades (1989–2019) (FAOSTAT, 2021). However, not all countries have honeybee stock records in the FAO database; therefore, we focused on countries with honeybee stock records in the FAO database between 1989 and 2019. Additionally, because several countries became politically subdivided after 1989, we combined data on honeybee stocks and the area cultivated with each crop across the new countries. This was the case for countries of the former Union of Soviet Socialist Republics (USSR) (including Armenia), Czechoslovakia, People's Democratic Republic of Ethiopia (PDR Ethiopia), Socialist Federal Republic of

Yugoslavia (SFR Yugoslavia), and Belgium–Luxembourg (Supplementary 1). Mongolia was excluded due to abrupt extreme change in area which could influence the results. Thus, about 93 countries and former republics were included in this study. Moreover, most countries lack proper documentation of honeybee-keeping for pollination (e.g., migratory beekeeping). However, we considered situations in which honeybee colonies are supplied or have the potential to be supplied in agricultural systems for pollination services globally or at least in the world's major agricultural countries (i.e., agriculturally important countries) (Hitaj et al., 2018; Zheng et al., 2018) (Supplementary 1).

Following Klein et al. (2007) and Gallai et al. (2009), honeybee-pollinated crops were categorised into four pollinator-dependent classes: little (in the absence of insect pollination, production reduction >0 but <10%, pollinator-dependence (D) = 5%), modest (production reduction ≥10% but <40%, D = 25%), great (production reduction ≥40% but <90%, D = 65%), and essential (production reduction ≥90%, D = 95%). The recommended honeybee colony densities (RCDs) per hectare of each honeybee-pollinated crop were extensively searched for in sources of English and Chinese literature, including Web of Science, Google Scholar, PubMed, and CNKI (Breeze et al., 2014, 2011; Rollin and Garibaldi 2019) (Supplementary 1). Although we collected both minimum and maximum RCDs, we focused on the most extreme minimum RCDs per crop per hectare in our analysis. This is because we considered the most extreme lowest RCDs to be more representative of the supply of available honeybee colonies per unit area. The honeybee-pollinated crops for which RCDs were not found in the literature and that require buzz pollination (i.e., those pollinated by other pollinators, e.g., *Bombus* sp.), such as tomatoes, eggplants, chillies and peppers, were excluded. Therefore, the cultivated areas of 49 honeybee-pollinated crops worldwide were examined in this study (Supplementary 1). Furthermore, cultivars of some crops may not require any additional pollination from insects (i.e., honeybees) to achieve optimal yields. However, because it is unclear how widely these cultivars are used, the entire area of each crop was considered to require insect (i.e., honeybee) pollination (Breeze et al., 2014, 2011).

2.2. Honeybee-pollination demand and pollination service capacity

The total number of honeybee colonies required to provide adequate pollination services (honeybee-pollination demand) was estimated as the product of the area cultivated with honeybee-pollinated crops and the RCDs of these crops (Breeze et al., 2014, 2011): $TPDt = \frac{\sum_{it}(Ai \times RCDid)}{2}$. In the equation, *TPDt* represents the total honeybee-pollination demand, A*i* is the area of honeybee-pollinated crop *i*, and RCD*id* is the honeybee RCD for crop *i*. RCDs represent a more realistic assessment of pollination demand than covering insect-pollinated crops alone, as they consider differences in required pollinator densities between crops (Breeze et al., 2014). We focused on managed honeybee colonies because (1) the abundance and distribution of wild honeybees have been insufficiently studied; (2) the nesting behaviour of wild honeybees is complex, and their nests are difficult to find; and (3) the pollination impact of wild honeybees cannot be estimated at present (Breeze et al., 2011; Utaipanon et al., 2019). We assumed that within a year, a colony could be moved (*d*) at least once; thus, the pollination demand was divided by 2 to represent the capacity for hives to be moved once within year *t* for pollination purposes (Breeze et al., 2014). More than two moves of colonies for pollination are possible within a single year; however, this is considered unrealistic in many areas, and accounting for different crop phenologies in large and climatically variable areas can be complicated (Breeze et al., 2014, 2011).

Honeybee pollination service capacity (PSC) was estimated by dividing the honeybee stock by the total honeybee-pollination demand in year *t* (Breeze et al., 2014), that is, PSC*t* = HC*t*/TPD*t*, where PSC*t* is the pollination service capacity of the honeybee stock to provide adequate pollination services to honeybee-pollinated crops in year *t* and HC*t* is the honeybee colony stock in year *t*.

2.3. Trends in pollination demand and the service capacity of honeybees

Changes in honeybee-pollination demand and PSC were calculated annually from 1989 to 2019 (Aizen et al., 2019). The change in each dependent variable "*X*" (i.e., TPD and PSC) from 1989 until year *t* was represented as a percentage of the value of "*X*" in 1989 as $100(X_t - X_{1989})/X_{1989}$. The annual average growth rate of the honeybee-pollination demand was estimated from rates of TPD at the country level as $100 \times (e^{\left[\frac{\ln(X2019) - \ln(X1989)}{2019-1989}\right]} - 1)$ (Aizen et al., 2019). Fluctuations (i.e., variability) in honeybee-pollination demand, crop diversity, and evenness of the area devoted to these crops were estimated from year-to-year mean absolute changes (Δma) by $\Delta ma = \sum |Xt - Xt\text{-}1|/30$ from 1989 to 2019 (Foster, 1978; Ram, 1985).

2.4. Honeybee-pollinated crop diversification

The diversity of honeybee-pollinated crops was estimated as the effective number of honeybee-pollinated crops $e^{H'}$ (interpreted as the number of honeybee-pollinated crops with the same cultivation areas that result in the observed *H'*) (Aizen et al., 2019; Jost, 2006). The Shannon–Weiner diversity index *H'* was estimated as $H' = -\sum pi\ln(pi)$, where *pi* is the proportion of total cultivated area accounted for by crop *i* relative to the total for different cultivated honeybee-pollinated crops S. We also estimated crop evenness (i.e., how total cultivated area was portioned among different crops). Crop evenness was estimated by Pielou's index as $J = H'/\ln(S)$ (Jost, 2010). The value of *J* varies from 0 to 1, approaching 0 when most of the area is devoted to the cultivation of just one crop and equalling 1 when all cultivated crops occupy equivalent areas (Aizen et al., 2019).

2.5. Statistical analysis

Data were analysed using IBM SPSS 20 (Chicago, IL, USA). Shapiro–Wilk normality tests were used to test for normality, and Levene tests were used to test for homoscedasticity. Non-parametric Kruskal–Wallis one-way analysis of variance (ANOVA) was run to detect variations in honeybee PSC, diversity indices (i.e., effective number and evenness of honeybee-pollinated crops), and fluctuations (i.e., mean absolute changes) in the honeybee-pollination demand between geographical regions. To compare the annual growth rate of the honeybee colony stock and honeybee-pollination demand in different regions, general linear models were used with annual growth in the honeybee stock and honeybee-pollination demand as the response variables and region as a fixed factor. Duncan's post hoc method was used to test for significant differences among regions. Moreover, linear regressions were used to predict the relationships between a dependent variable (fluctuation in the honeybee-pollination demand) and explanatory variables (fluctuations in crop diversification and evenness).

3. Results

3.1. Global trends

A global decrease in honeybee PSC was observed from 1989 to 2019 (Fig. 1). The global honeybee stock in 1989 could supply approximately 56.9% of the global pollination demand; however, this value declined to 44.1% in 2019, decreasing the PSC by 22.5% at a global level. Different trends were observed in the global honeybee colony stock and honeybee-pollination demand from 1989 to 2019 (Fig. 1). From 1989–2019, the global pollination demand increased by 73.0%, with an average annual growth rate of 1.78%. In contrast, the honeybee colony stock increased by only 34.0%, with an average annual growth rate of 0.95%, which was only approximately half of the pollination demand

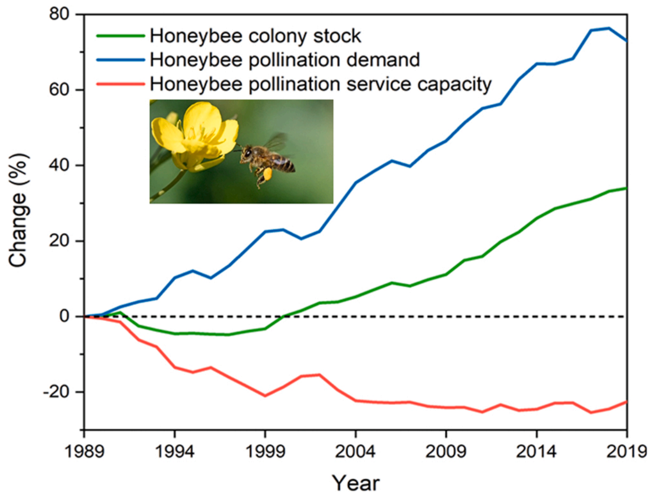

Fig. 1. Global changes in the honeybee colony stock, honeybee-pollination demand (estimated as the product of the area cultivated with the 49 honeybee-pollinated crops worldwide and the recommended honeybee colony densities of these crops), and honeybee pollination service capacity (estimated by dividing the honeybee colony stock by the total honeybee-pollination demand) between 1989 and 2019, based on crop area and honeybee colony stock data in the FAO dataset (FAOSTAT, 2021) and recommended honeybee colony density data from references. For each dependent variable, X, the change from 1989 to year t is represented as a percentage of the value of X in 1989, that is, $100(X_t\text{-}X_{1989})/X_{1989}$.

growth rate.

3.2. Regional trends

The PSC varied greatly among regions (Fig. 2, Supplementary 2: Fig. S1; Kruskal–Wallis test: H = 110.095, df = 4, $p < 0.000$). On average, during the past 30 years, the honeybee colony stock in Africa and Europe could supply 138.8% and 124.3% of the regional pollination demand, respectively. However, in Oceania and Asia, honeybee colonies could supply only 54.7% and 50.0%, respectively, and comparably, the Americas faced the most severe deficiency, as only 15.8% of the regional honeybee-pollination demand could be supplied. Nevertheless, the PSC declined across regions between 1989 and 2019. It declined greatly in Oceania by 64.8%, followed by Africa (47.7%), the Americas (35.4%), Asia (9.4%), and Europe (4.4%). In the first 10 years (1989–1999), the honeybee PSC declined rapidly in all regions, but it has shown a general upwards trend in Asia and Europe since 2000. In Africa and the Americas, the PSC showed a short period of increase from 1999 to 2002 and rapidly declined beginning in 2003. The most rapid decline in pollination capacity was observed in Oceania from 1989 to 1999, after which the capacity remained steady until 2019 (Fig. 2, Supplementary 2: Fig. S1).

The honeybee colony stock and honeybee-pollination demand were also unevenly distributed among regions and countries (Fig. 3). In the past three decades, Asia had the largest honeybee colony stock, accounting for 47.3% of the global honeybee colony population, followed by Africa (20.8%), Europe (16.9%), the Americas (13.9%), and Oceania (1.1%). At the same time, more than 85% of the global honeybee-pollination demand was accounted for by Asia (43.4%) and the Americas (41.7%); Africa and Europe accounted for 7.3% and 6.3%, respectively, while Oceania accounted for only 1.2% of the global pollination

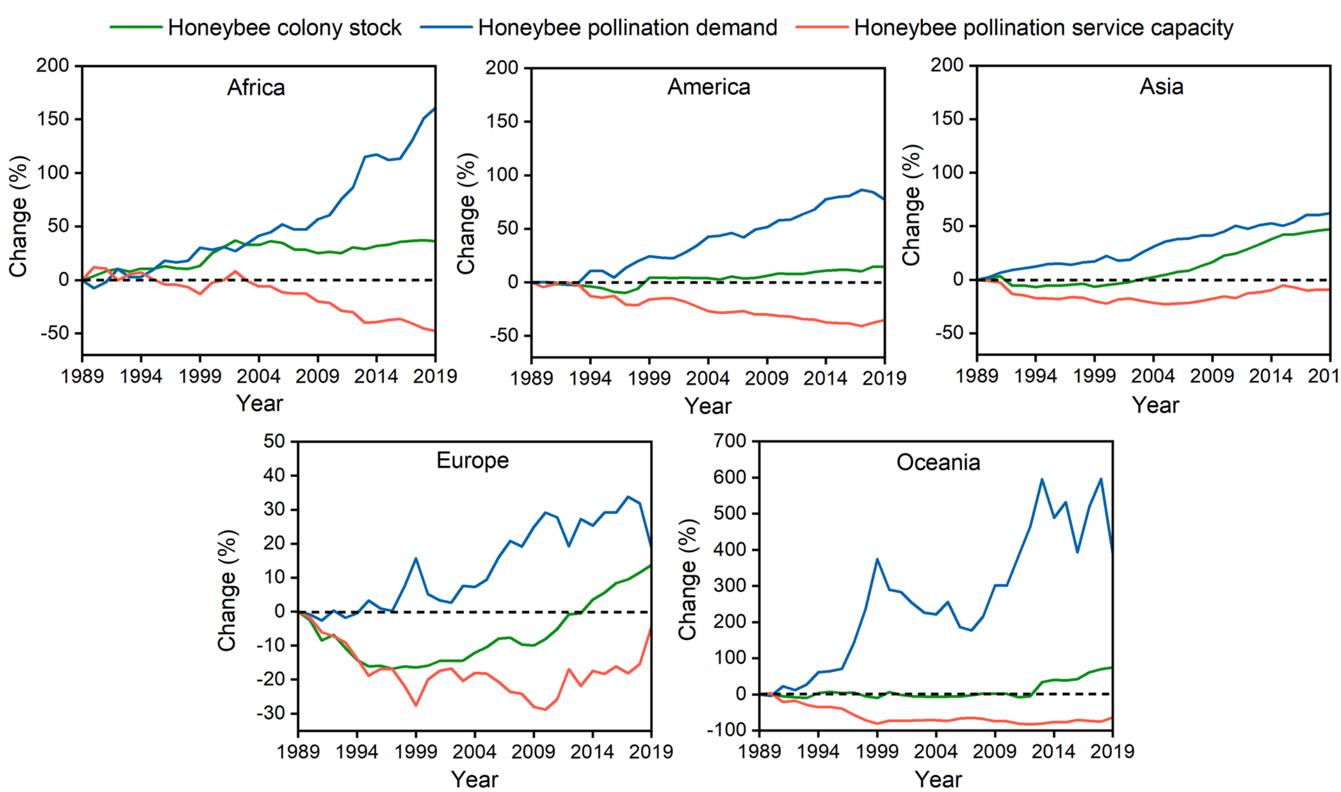

Fig. 2. Regional changes in the honeybee colony stock, honeybee-pollination demand (estimated as the product of the area cultivated with the 49 honeybee-pollinated crops worldwide and the recommended honeybee colony densities of these crops), and honeybee pollination service capacity (estimated by dividing the honeybee colony stock by the total honeybee-pollination demand) between 1989 and 2019, based on crop area and honeybee colony stock data in the FAO dataset (FAOSTAT, 2021) and recommended honeybee colony density data from references. For each dependent variable, X, the change from 1989 to year t is represented as a percentage of the value of X in 1989, that is, $100(X_t - X_{1989})/X_{1989}$.

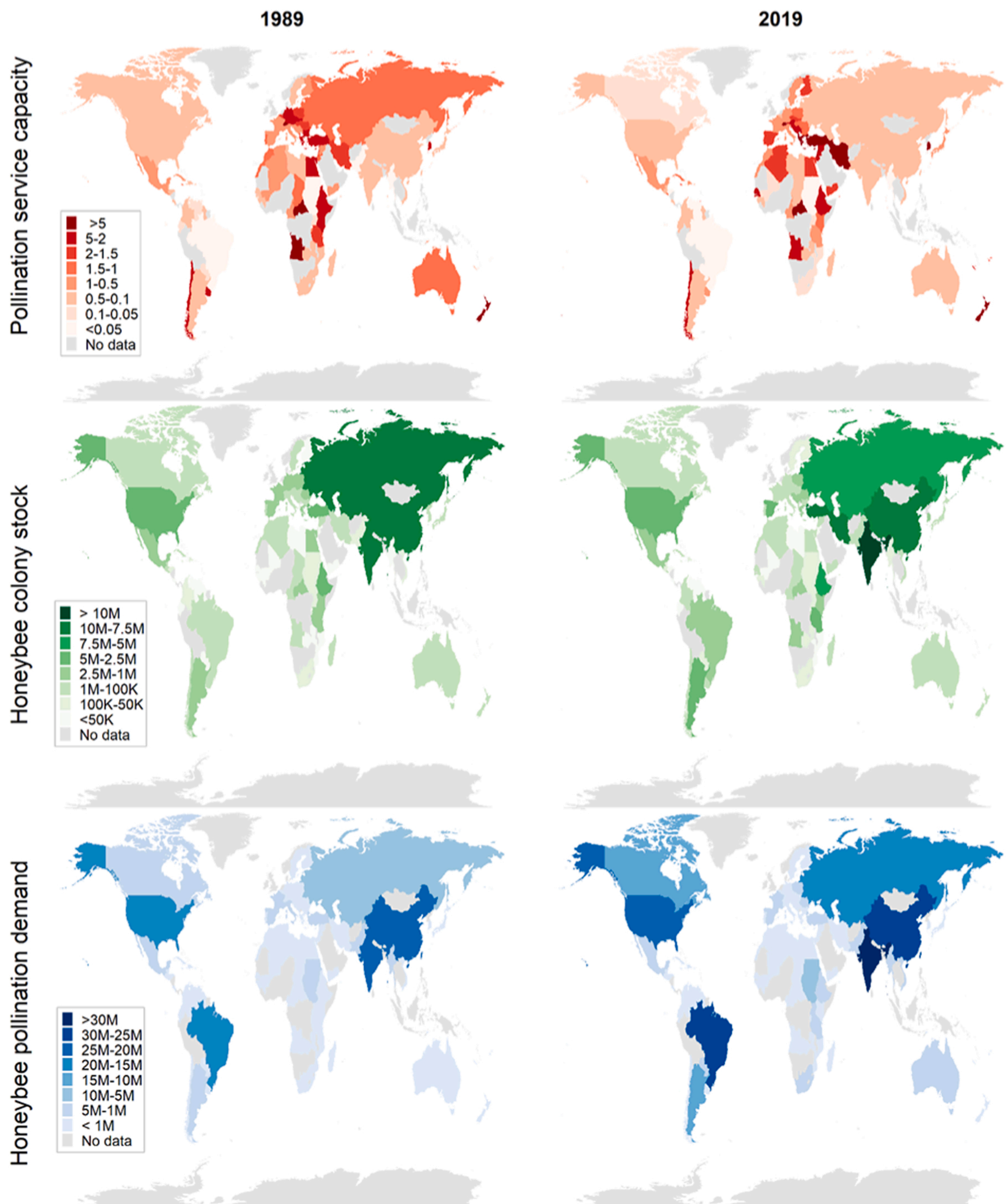

Fig. 3. World maps of countries' pollination service capacity (estimated as the ratio of honeybee stock to honeybee-pollination demand), honeybee colony stock, and honeybee-pollination demand (the sum of the products of honeybee-pollinated crop area and recommended colony densities) from 1989 to 2019.

demand.

Significant differences in the annual growth of the honeybee colony stock and pollination demand were found between regions for the past 30 years (Supplementary 2: Fig. S2; Annual growth of the honeybee colony stock: GLM, $F_{4,88} = 4.901$, $p = 0.001$; Annual growth of the pollination demand: GLM, $F_{4,88} = 4.587$, $p = 0.002$). Oceania was the only region with a decline in pollination demand and had a limited influence on global increasing trends in the past 30 years. Asia was the only region where the honeybee colony stock grew faster than the pollination demand. Stocked honeybee colonies increased by 47.0% in Asia, with the most rapid growth from 1989 to 2019. Countries in Europe and the Americas had quite slow and even negative honeybee colony growth, where colonies increased by only 13.7% and 14.4%, respectively (Fig. 2). A gentle increase in the pollination demand was observed in most regions, with African countries showing the fastest average annual growth rate. However, Oceania exhibited relatively sharp increasing and declining trends from 1989 to 1999, 2000–2007, and 2008–2013 and a fluctuating decline from 2013 to 2019 (Fig. 2).

3.3. *Honeybee-pollinated crop diversification and pollination demand*

Significant differences in honeybee-pollinated crop cultivation were observed between agricultural geographical regions (Supplementary 2: Fig. S3). We found statistically significant variations in the diversification of honeybee-pollinated crops (Kruskal–Wallis test, H = 28.420, df = 4, $p < 0.0001$), evenness of areas devoted to these crops (Kruskal–Wallis test, H = 27.505, df = 4, $p < 0.0001$), and fluctuations in the demand for honeybee pollination (Kruskal–Wallis test, H = 15.884, df = 4, $p < 0.01$). On average, in the past 30 years, regions with high crop diversification and evenness, such as Asia, have exhibited a steadier pollination demand (i.e., low fluctuations). Africa and Europe exhibited high fluctuations in pollination demand with relatively low crop diversification and evenness. Low crop diversification and evenness and fewer demand fluctuations were also observed in Oceania. In addition, we further found that such relatively low regional demand fluctuation, for instance in Asia, was associated with high crop diversification in most agriculturally important countries in the region, such as China ($e^{H'}$=13.06), Japan ($e^{H'}$= 13.01), and Turkey ($e^{H'}$=12.12), as well as others, such as Iran ($e^{H'}$ = 18.91), Israel ($e^{H'}$ = 15.47), Lebanon ($e^{H'}$ = 13.70), and Jordan ($e^{H'}$ = 12.91), compared to most agriculturally important American and European countries with low crop diversification, such as Argentina ($e^{H'}$ = 2.34), Brazil ($e^{H'}$ = 3.51), Canada ($e^{H'}$ = 2.25), and Germany ($e^{H'}$ = 2.17).

The linear regression results showed that fluctuations in the honeybee-pollination demand increased with fluctuations in the diversification of honeybee-pollinated crops ($F_{1,78}$ = 3.941, p = 0.050) and evenness of the area cultivated with these crops ($F_{1,78}$ = 3.272, p = 0.074) (Fig. 4). Heterogeneity within regions was observed; however, extremely high fluctuations in honeybee-pollination demand (Δma > 100000) were observed in major agricultural countries. For instance, India showed fluctuations in demand (Δma = 946267) that were stronger than those in other countries across the world but fluctuations in crop diversification (Δma = 0.169) and evenness (Δma = 0.005) that were weaker than those in other major agricultural countries. Similar extremes were also observed in the USA (demand Δma = 914550, diversity Δma = 0.101, evenness Δma = 0.011), Brazil (demand Δma = 859907, diversity Δma = 0.154, evenness Δma = 0.013), Canada (demand Δma = 676938, diversity Δma = 0.117, evenness Δma = 0.015), and the USSR (demand Δma = 637815, diversity Δma = 0.267, evenness Δma = 0.013). Moreover, other agriculturally important countries, such as Mexico, Germany and France, showed strong fluctuations in diversification (0.869, 0.198, and 0.250, respectively) and evenness (0.027, 0.023, and 0.017) but variable fluctuations in demands (159201, 96247, and 113309). The small agricultural countries with relatively strong fluctuations in demand were Australia, Sudan (former), and Tanzania; those with strong fluctuations in diversity were Egypt, Italy, and South Africa; and that with strong fluctuations in evenness was Burundi.

The global honeybee-pollination demand was influenced mainly by oil crops, which accounted for 73.0% of the global honeybee-pollination demand in 2019, with two crops (i.e., soybean and rapeseed) accounting for 38.9% and 15.7% of the global pollination demand (Fig. 5). In 2019, 65% (in Asia) to 92% (in the Americas and Oceania) of the regional honeybee-pollination demand was accounted for by approximately five honeybee-pollinated crops, which also contributed 82% and 71% of the regional honeybee-pollination demand in Europe and Africa, respectively (Fig. 5). The crops with the highest pollination demand were soybean in the Americas, rapeseed in Europe and Oceania, sesame in Africa, and soybeans and rapeseed in Asia. These crops also determined the magnitude of the honeybee-pollination demand at the country level. For example, soybean was the major contributor crop that accounted for > 80% of the honeybee-pollination demand in Argentina, Brazil, and the USA and a leading high-pollination demand crop in Japan and India in 2019 (Fig. 6). Rapeseed was responsible for > 80% of the pollination demand in Canada and Germany and > 60% of that in France, and it was responsible for the high pollination demand in China. Other crops, including sunflower, accounted for > 42% of the demand in the USSR and > 25% in Turkey, and beans accounted for > 20% in Mexico in 2019.

4. Discussion

4.1. Increasing honeybee-pollination demand but decreasing honeybee colony supply capacity

Pollinators are increasingly becoming insufficient because of declines in their populations and diversity as well as an increase in the magnitude of pollination demand (Aizen et al., 2019; Klein et al., 2017; NRC, 2007), with the potential to worsen the prevailing pollination deficiency crisis (Knight et al., 2005; Shivanna et al., 2020). At present, the demand for pollination services exceeds the available pollination service supply capacity due to persisting pollinator shortages (NRC, 2007) (Fig. 1 and Supplementary 2: Fig. S2), which are intensifying. For instance, many native bee species that were once common in particular geographical regions have declined or gone extinct (Ollerton et al., 2014; Pereira et al., 2012).

Nevertheless, pollinator shortages can often be overcome by providing a sufficient number of managed pollinators, particularly honeybees (Osterman et al., 2021). Even though some wild pollinator species are more efficient than honeybees, especially on a flower-by-flower basis (Garibaldi et al., 2013; Hung et al., 2018), honeybees remain the preferred pollinators for most plants (i.e., crops) (Burkle et al., 2013; Hung et al., 2018; NRC, 2007). As a result, the colony stock of honeybees has increased globally, associated with both the increasing market value of honey and the demand for honeybee colonies as pollination units (Osterman et al., 2021). In 2019, almost half of the world's honeybee colonies were stocked in Asia (Fig. 3), driving the world population (Osterman et al., 2021). Our analysis result adds to evidence that in the past three decades, the annual average growth rate of the colony stock was rapid in Asian countries but slower in European and American countries, which experienced high overwinter mortality rates of honeybee colonies (Osterman et al., 2021) (Fig. 2 and Supplementary 2: Fig. S2).

Despite these variations in growth rates, the increase in honeybee stocks is still not keeping pace with the increase in the agricultural pollination demand (Aizen and Harder, 2009; Wakgari and Yigezu, 2021). For instance, the global agricultural honeybee-pollination demand rose approximately 2.3 times higher than the worldwide stocked number of honeybee colonies in 2019. Similar to those of Aizen and Harder (2009), our results show that in the past three decades, the pace of honeybee stock growth (0.95%) was almost two times slower than that of agricultural pollination demand growth (1.78%). High demands beyond available honeybee colony stocks have also been observed in the UK (Breeze et al., 2011), in China (Mashilingi et al., 2021), and across Europe (Breeze et al., 2014). However, as mentioned above, the honeybee stock grew rapidly in Asian countries, although the demand for honeybee pollination grew significantly faster in African countries and slowly in Oceania (Supplementary 2: Fig. S2). Furthermore, the observed growth rate of the honeybee-pollination demand may be attributed to a rapid rate of agricultural expansion in African countries and retraction in other regions, such as Europe (Aizen et al., 2019), which influences the magnitudes of honeybee-pollination demands.

In addition, the observed mismatch in growth rates between the colony stock and pollination demand could indicate a worsening pollination shortage and an increase in the pollination crisis (Aizen and Harder, 2009; Martin, 2015; Shivanna et al., 2020). This results in a low capacity of honeybee stocks to supply sufficient pollination services in agricultural systems. As a result, the pollination service supply capacity has declined globally and regionally (Figs. 1, 2, 3, and S1).

4.2. More fluctuation in the diversification of honeybee-pollinated crops, more fluctuation in the honeybee-pollination demand

Honeybee-pollinated crop diversification and evenness and their influence on the honeybee-pollination demand varied statistically between geographical regions (Fig. 4, S2, and S3). Over the last three

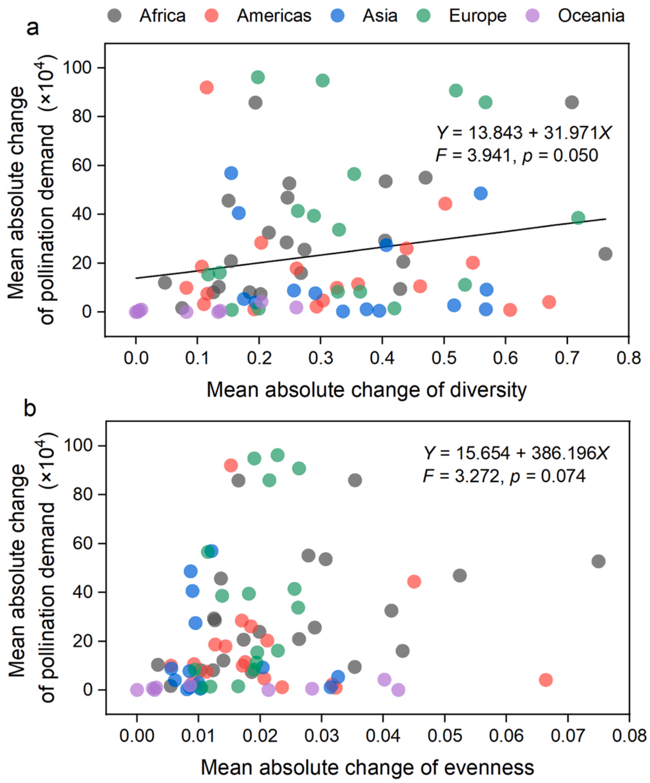

Fig. 4. Predictions of the effect of fluctuations in (a) honeybee-pollinated crop diversity (estimated as effective number) and (b) evenness (estimated as Pielou's index) on the fluctuation of honeybee-pollination demand. Fluctuation (variability) was estimated as the mean absolute change ($\Delta ma = \sum |Xt - Xt\text{-}1|/30$ in the crop effective number, evenness, and honeybee-pollination demand between 1989 and 2019. Extreme changes were removed during regression; thus, 80 out of 93 countries and unions with honeybee colony stock records in the FAO database in 2019 were regressed. The F test statistics are provided in Supplementary 2 (Table S1).

decades, highly diversified cultivation of honeybee-pollinated crops has occurred in Asia. Aizen and colleagues reported that crop diversification occurred in regions or countries that have undergone slower expansion in agricultural areas, particularly those planted with honeybee-pollinated crops (Aizen et al., 2019). For example, the rapid growth of the honeybee-pollination demand in Africa (Supplementary 2: Fig. S2), which has been linked to high rates of agricultural expansion in African countries (Aizen et al., 2019), may be associated with low diversity and strong fluctuation in the total demand for honeybee pollination (Supplementary 2: Fig. S3). This evidence indicates that a more diversified crop system slows the demand for honeybee pollination, agreeing with the findings from other authors that an increase in the diversity of crop types promotes the diversity and abundance of pollinators (Aguilera et al., 2020) and fosters indirect crop-to-crop facilitative interactions and pollinator species coexistence (Gavini et al., 2021).

Fluctuations in crop diversification positively influence the fluctuations in pollination demand (Fig. 4). This finding further suggests that diversifying honeybee-pollinated crops reduces year-to-year fluctuations in the total demand for honeybee pollination. This was observed in more diversified agriculturally important countries in Asia, such as China, Japan, and Turkey, which fluctuated less in crop diversification and pollination demand than agriculturally important countries in the Americas, such as Argentina and Brazil. Aizen et al. (2019) similarly noticed a decrease in agricultural areas' expansion rate with an increase in crop diversification. Furthermore, heterogeneous fluctuations were observed within regions; for instance, high diversification and fewer demand fluctuations were observed in countries such as Algeria and Egypt in Africa; Chile in the Americas; Jordan, Lebanon, and Israel in Asia; Albania and Portugal in Europe; and New Zealand in Oceania.

Nevertheless, the extreme demand fluctuations under relatively low diversity and diversity fluctuation in the major agricultural countries, such as Argentina, Brazil, Canada, and the USA, indicate large-scale monocultures of honeybee-pollinated crops. The highest year-to-year demand fluctuation with less crop diversity fluctuation (but high diversification) in India could indicate the cultivation of the same crop types in an approximately equal proportional area that greatly varied between years. Thus, larger agricultural expansions not accompanied by agricultural diversification would pose a high risk of future pollination deficits (Garibaldi et al., 2014), as they could cause instability in pollinator demand.

Fluctuation of the evenness of cultivated areas with honeybee-pollinated crops also influenced the fluctuation of pollination demand (Fig. 4). Higher evenness (and diversity) but lower fluctuations were observed in India, Japan, China, and Turkey compared to less diversified but more fluctuating major agricultural countries in the Americas and Europe. Asia had more evenly cultivated honeybee-pollinated crops; however, such uniformity (i.e., evenness) of the area cultivated with honeybee-pollinated crops declined in other regions. This can further be attributed to increased agricultural expansion, suggesting a trend towards increasing monoculture associated with highly variable demand (Aizen et al., 2019). For example, in the important Asian and American countries mentioned above, the demand for honeybee pollination fluctuated less in countries showing increases in the evenness of areas cultivated with honeybee-pollinated crops.

Moreover, the high interannual variabilities could have influenced the fluctuations in honeybee-pollination demands across regions. This could provide the most direct evidence of interannual variation in pollen limitation in animal-pollinated crops (e.g., honeybee-pollinated crops) (Garibaldi et al., 2011), which is also consistent with the observed contemporary variations in pollen limitation for wild plant species (Knight et al., 2005). High variability in the pollination demand may further indicate an unstable pollination service supply, contributing to limited yield improvement of crops that rely on animal pollination (Garibaldi et al., 2011; Mashilingi et al., 2021), since these crops tend to produce fewer fruits or seeds than they would produce with adequate pollen receipt (Hünicken et al., 2021).

Furthermore, such pollen limitations in plants (e.g., crops) vary in time and space, since the magnitude of pollen limitation can vary between years and among populations, significantly explained by pollinator activity (Cosacov et al., 2008; Jiang and Xie, 2020; Knight et al., 2005). For example, Koch et al. (2020) show that pollinator-dependent crops currently receive adequate pollination services (i.e., they are not pollen limited) north of the Arctic Circle. However, increasing spatial-temporal evidence shows intensifying pollen limitation (Chen and Zhao, 2019; Chen and Zuo, 2019, 2018; Jiang and Xie, 2020; Li et al., 2020; Reilly et al., 2020), which is influenced by various factors, including changes in land use and agricultural pollinator dependence (Bennett et al., 2020), in turn affecting pollinator activity and populations (Cosacov et al., 2008; Potts et al., 2010).

4.3. *Pollinator-dependent monocultures might threaten pollination service stability*

Expansions of agricultural areas and an increased honeybee-pollination demand may be associated with monocultures of honeybee-pollinated crops. Our results showed that the honeybee-pollination demand was highly accounted for by oil crops (oilseed crops) from the global to country levels (Figs. 5 and 6). This result is consistent with findings by other authors about the increasing effect of oilseed crops on agricultural systems (Aizen et al., 2019; Breeze et al., 2014). For example, almost 39% and 16% of the global population of honeybee colonies required to supply sufficient agricultural pollination services in 2019 could be used to pollinate only two crops worldwide: soybean and rapeseed, respectively. However, only a few

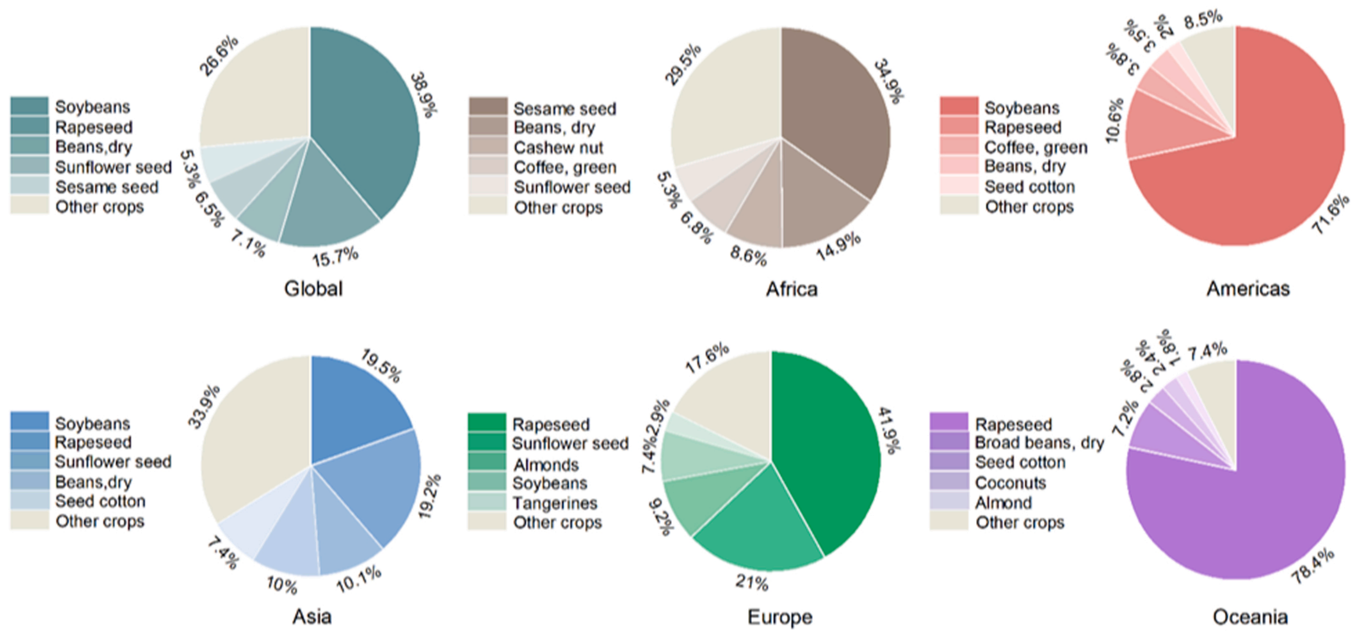

Fig. 5. The five crops with the highest pollination demand at the global and regional levels in 2019. The pollination demand ratio was estimated as the ratio of crop *i* pollination demand to the total demand of all crops in a region in year *t* as 100 (X_{it}/X_{Tt}).

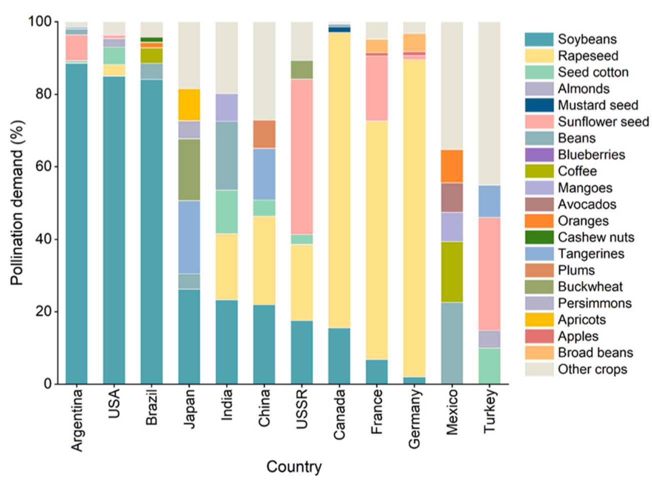

Fig. 6. Crops of large agricultural countries with high pollination demands in 2019. The pollination demand ratio was estimated as the ratio of the pollination demand of crop *i* to the total demand of all crops in a country in year *t* as 100 (X_{it}/X_{Tt}).

(approximately five) crops with a honeybee-pollination demand, mostly oil crops, could require a range of 65–92% of the total regional demand for honeybee colonies to supply sufficient pollination services in agricultural systems (Fig. 5). Such a small number of crops dominating the honeybee-pollination demand could further be observed at the country level. For instance, in 2019, soybean required > 80% of all honeybee colonies demanded to supply sufficient agricultural pollination services in the major agricultural countries with less diversified honeybee-pollinated crops, such as Argentina, Brazil, and the USA (Fig. 6).

Large cultivation areas of one or a few honeybee-pollinator-dependent crops decrease agricultural diversity at both the landscape and country scales (Aizen et al., 2019; Curtis et al., 2018; Fitzherbert et al., 2008). Moreover, such large pollinator-dependent monocultures, associated with the clearing of natural areas (Molotoks et al., 2020), occupy vast agricultural areas and dominate agriculture in several countries or entire regions, such as the Americas (Aizen et al., 2019; Lautenbach et al., 2012). For example, soybean expansion has been implicated in high deforestation and biodiversity loss rates, for instance, in countries such as Brazil, Argentina, Paraguay, and Bolivia, showing the positive association between the cultivation of oil crops and the high environmental cost it implies (Aizen et al., 2019; Curtis et al., 2018; Fitzherbert et al., 2008).

As a result, biodiversity is declining. Wild pollinators are increasingly at risk of decreasing abundance and diversity, but the simultaneous overreliance on managed honeybee pollinators is increasing (Osterman et al., 2021). For instance, in regions such as Oceania (e.g., in countries such as New Zealand and Australia), honeybees were introduced for commercial pollination purposes (Iwasaki et al., 2015). Compared to that in other regions, such as Africa, agriculture in Oceania countries (e.g., horticulture in Australia) relies heavily on managed honeybees (*A. mellifera*) for crop pollination (Cook et al., 2020; Cunningham et al., 2002). This shows evidence that the shortage of stocked honeybee colonies may profoundly affect socioeconomics in these countries (Iwasaki et al., 2015, Hristov et al., 2020) and globally, especially in countries with increasing agricultural expansion, pollinator dependence, and pollination benefits (Aizen et al., 2019; Lautenbach et al., 2012).

5. Conclusion

Our results showed that the honeybee-pollination demand increased while the pollination service supply capacity decreased worldwide. The annual growth rate and fluctuation of the honeybee-pollination demand varied between geographical regions. However, the fluctuation of the pollination demand increased with an increase in the fluctuation of crop diversification. Oil crops were the drivers of the honeybee-pollination demand from the global to country levels. These findings emphasise the importance of global and local efforts in conserving declining wild pollinators. Additionally, the findings further support the importance of integrated management of single species and wild pollinator assemblages for a sustainable and food-secure future world.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108003.

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