Global trends in the number and diversity of managed pollinator species

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ABSTRACT

Cultivation of pollinator-dependent crops has expanded globally, increasing our reliance on insect pollination. This essential ecosystem service is provided by a wide range of managed and wild pollinators whose abundance and diversity are thought to be in decline, threatening sustainable food production. The Western honey bee (*Apis mellifera*) is amongst the best-monitored insects but the state of other managed pollinators is less well known. Here, we review the status and trends of all managed pollinators based on publicly accessible databases and the published literature. We found that, on a global scale, the number of managed *A. mellifera* colonies has increased by 85% since 1961, driven mainly by Asia. This contrasts with high reported colony overwinter mortality, especially in North America (average 26% since 2007) and Europe (average 16% since 2007). Increasing agricultural dependency on pollinators as well as threats associated with managing non-native pollinators have likely spurred interest in the management of alternative species for pollination, including bumble bees, stingless bees, solitary bees, and flies that have higher efficiency in pollinating specific crops. We identify 66 insect species that have been, or are considered to have the potential to be, managed for crop pollination, including seven bumble bee species and subspecies currently commercially produced mainly for the pollination of greenhouse-grown tomatoes and two species that are trap-nested in New Zealand. Other managed pollinators currently in use include eight solitary bee species (mainly for pollination services in orchards or alfalfa fields) and three fly species (mainly used in enclosures and for seed production). Additional species in each taxonomic category are under consideration for pollinator management. Examples include 15 stingless bee species that are able to buzz-pollinate, will fly in enclosures, and some of which have a history of management for honey production; their use for pollination is not yet established. To ensure sustainable, integrated pollination management in agricultural landscapes, the risks, as well as the benefits of novel managed pollinator species must be considered. We, therefore, urge the prioritization of biodiversity-friendly measures maintaining native pollinator species diversity to provide ecosystem resilience to future environmental changes.

Keywords: *Apis*, *Bombus*, crop pollination, Meliponini, risk, overwinter mortality

1. Introduction

For most Angiosperm plant species, reproduction depends on pollination provided by a wide range of animal species, including insects, birds, and mammals (Ollerton et al., 2011). Through their contributions to global food security as well as farmer and beekeeper livelihoods and maintenance of wild plant biodiversity, pollinating insects are closely tied to human well-being (Potts et al., 2010, 2016; Hill et al., 2019), facilitating the yield of at least 87 out of the world's 107 leading crops (Klein et al., 2007).

Globally, the total agricultural area has expanded by around 41% from 1961 to 2016, with the area cultivated for pollinator-dependent crops having increased disproportionately (137%), making agriculture more pollinator-dependent than ever (33% of the agricultural area occupied by pollinator-dependent crops; Aizen et al., 2019). This has, however, been accompanied by a trend towards agricultural monocultures rather than diversification (Aizen et al., 2019), which could further lead to pollination deficits through habitat loss for wild pollinators. Regions projected to suffer from a mismatch of pollination demand and supply provided by wild insects include Europe and the United States (Schulp et al., 2014; Koh et al., 2016). Moreover, the dependency of agriculture on pollination is especially high in South America and parts of Southeast Asia (Aizen et al., 2019), where pollination supply has not been evaluated.

Another trend in agriculture, although not as well documented, is the increase in cultivated area under permanent covers, such as greenhouses, tunnels, and row covers. While official data reporting the area under covered environments are rare (e.g., FAO, 2020), Cuesta Roble (2020) estimated that in 1995 around 500,000 ha of crops were cultivated under permanent cover, which increased to 5,630,000 ha by 2019. Crops under cover are partly protected from extreme weather conditions, pathogens and pests, and can allow variety-specific seed production (Cuesta Roble, 2020). However, pollination services by insects are limited in enclosures without active pollinator management (Kendall et al., 2021). A particular challenge is that covers can negatively impact the health and foraging activity of managed honey bees placed in such conditions (Evans et al., 2019; Kendall et al., 2021).

In open fields, wild insects make an important contribution to crop pollination worldwide (Garibaldi et al., 2013, 2014; Rader et al., 2016, 2020). However, there have been ongoing reports of declines in the abundance of wild bees (Biesmeijer et al., 2006; Goulson et al., 2010; Dupont et al., 2011) and other wild insects (Powney et al., 2019; Seibold et al., 2019) as well as declines in insect diversity and biomass (Biesmeijer et al., 2006; Bommarco et al., 2012; Seibold et al., 2019; van Klink et al., 2020; Zattara and Aizen, 2021), representing a threat to the sustainable supply of pollination. By increasing landscape complexity (e.g., presence of wildflower strips, the cover of semi-natural habitat, distance to the nearest semi-natural habitat) and wildlife-friendly farming, the abundance, and diversity of pollinators can be enhanced, leading to higher crop yields (e.g., Holzschuh et al., 2012; Blaauw & Isaacs, 2014; Pywell et al., 2015). Another option to ensure pollination provision, though potentially less desirable, is managing formerly wild pollinator species through *in situ* promotion or active domestication (IPBES, 2016). However, pollinator domestication and associated trade pose novel threats, such as the promotion of insects that become invasive, with associated negative impacts on biodiversity and sustainable provision of pollination services (Aizen et al., 2020; Ghisbain et al., 2021; Russo et al. 2021).

One approach to ensuring sufficient pollination services is through hand pollination, which has been practiced at least since 800 BC, with an Assyrian-dynasty relief showing hand pollination of a date palm tree using a branch holding male flowers (Free, 1982). *Vanilla* is routinely pollinated by hand following the discovery of the method in the 1830s (Arditti et al., 2009). Griggs and Vansell (1949) first mentioned the use of honey bee-collected pollen for artificial pollination of deciduous fruit trees in the first half of the 20th Century. To date, hand pollination is known to have been employed for 20 different crops (Wurz et al., 2021). Artificial pollination with blowers and vibrating devices was an established method for the pollination of tomatoes grown under cover that, because it was labour-intensive and expensive, has nowadays largely been replaced by managed bumble bees (Velthuis and van Doorn, 2006). Nevertheless, artificial pollination remains a topical issue, for example through its accomplishment by mini-drones (Potts et al., 2018). However, by far the greatest attention has been paid to managing or otherwise enhancing the number of bees and other insects as pollen vectors.

For many years, the Western honey bee, *Apis mellifera,* has been the most widely used of managed pollinators (McGregor, 1976; Kevan et al., 1990). However, in recent decades, public and scientific attention has been drawn to abnormally high honey bee colony (particularly overwinter) mortality rates in Europe and the United States of America (vanEngelsdorp et al., 2008; Potts et al., 2016). Many stressors that negatively affect honey bee colonies have been hypothesised: lack of food (floral resources; Neumann and Carreck, 2010), climate change (Le Conte and Navajas, 2008), poor beekeeping practices (Neumann and Blacquière, 2017), chronic exposure to pesticides (Sánchez-Bayo et al., 2016; Battisti et al., 2021) and, most importantly, diseases and pests such as the exotic ectoparasitic mite, *Varroa destructor*, along with the viruses it transmits (Mondet et al., 2014; Brown et al., 2016). The dependence of pollination on a single, managed species, *A. mellifera*, is therefore of rising concern for food security (Winfree, 2008), especially in times of changes in the human diet, a growing world population, and higher per capita consumption (Godfray et al., 2010).

Humans have a long history of managing bees for honey extraction, with perhaps the oldest association being with *A. mellifera.* Managed bees can be circumscribed as those that are provided with artificial nests (Kritsky, 2010). Under this definition, the oldest evidence of managed honey bees dates back to 2450 BCE in Egypt, where stone reliefs show beekeepers working with honey bee hives (Crane, 1999). Apiculture (the management of honey bees) developed independently in many parts of the world (Kritsky, 2017). In Asia, the cavity-nesting Eastern honey bee (*Apis cerana*) seems to have been first managed much later, with the first evidence of beekeeping with *A. cerana* dating to 158-166 CE in China (Kritsky, 2017) and 300 BCE in Afghanistan and Pakistan. In Mesoamerica, the Maya developed a beekeeping culture around the stingless bee *Melipona beecheii*, the first evidence for which dates between 300 BCE and 250 CE (Chase and Chase, 2005). Nowadays, a wide range of pollinator species is managed, including honey bees (*Apis* spp.), several bumble bees (*Bombus* spp.), stingless bees (Meliponini), solitary bees of the genera *Megachile* and *Osmia*, blow flies (Calliphoridae), and hover flies (Syrphidae). This increase in managed pollinator diversity reflects a shift in attention from managed honey bees to alternative pollinator species, driven not only by academic researchers but also by commercial and public interest (IPBES, 2016).

Here, we present the current status and trends of managed bee species, both regionally and worldwide, and examine changes in their numbers and diversity over time. We also highlight several risks that have arisen from managing pollinators. We hypothesise that (1) the use of managed pollinators has increased as the dependence of agriculture on pollination has risen and that (2) the diversity of manageable pollinators is increasing because of greater awareness of the potential negative effects of non-native species along with trends in agriculture (e.g., crops under permanent cover). We furthermore predict that (3) countries or regions with higher rates of *A. mellifera* colony overwinter mortality managed a wider range of alternative pollinators.

2. Materials and Methods

2.1 Number of managed pollinators

We performed a literature search using Web of Knowledge/Web of Science (ISI Thompson-Reuters, webofknowledge.com) and Google Scholar to identify the earliest-dated scientific record of a managed pollinator species (see Supplementary Table 01) in February 2020. We used search terms relevant for the species, for example for the Western honey bee: ("honey bee" OR "honeybee" OR "*Apis mellifera*") AND ("managed pollinator" OR "pollinator" OR ("managed" AND "pollination")). Search terms for each species can be found in Supplementary Table 01 under *species* and *common name/synonym*. Additionally, we used expert knowledge to seek out further publications not found in the above search strategy. We categorized every identified manageable pollinator as (i) current managed pollinator, (ii) potential managed pollinator, or (iii) abandoned managed pollinator. The categorization was based on expert knowledge. We categorized species as potential managed pollinators if we found experimental evidence in the published literature that management is possible but not yet established in practice. Species were categorized as abandoned in the case of bumble bees when we could not find a company any longer producing the species. We furthermore categorized pollinator species into their native geographical regions based on distribution data from Discover Life (https://www.discoverlife.org/) and expert knowledge.

Also using Web of Knowledge/Web of Science (ISI Thompson-Reuters, webofknowledge.com) we performed a literature search with the terms (manage* AND pollinat*) and extracted the number of publications per year to 2019 to address trends in all managed pollinators over time.

2.2 Trends in honey bee hives, honey production and price

The Food and Agricultural Organization of the United Nations (FAO) gathers annual information on crops, livestock, and their products at global, regional, and country levels, and from which we extracted data on the number of honey bee hives, globally and regionally, from 1961 to 2018 as well as the global production of natural (raw) honey in tonnes (FAO, 2020). We calculated the amount of honey harvested per hive (colony) by dividing the total production of honey by the total number of honey bee hives, assuming that honey was derived predominantly from honey bees as only *Apis* honey meets many of the international and regional standards for trading as honey (Vit et al., 2013). Also, we collected the producer price for natural honey in the United States of America from 1992 to 2017 in USD (FAO, 2020).

2.3 Mortality rates of *A. mellifera* colonies

We performed a systematic search of the literature using Web of Knowledge/Web of Science (ISI Thompson-Reuters, webofknowledge.com) and Google Scholar to identify studies providing data on annual and/or overwinter mortality of colonies of the Western honey bee. We used the search terms: ("*Apis mellifera*" OR "honeybee" OR "honey bee") AND ("annual mortality" OR "winter mortality" OR "wintering losses" OR "overwinter mortality" OR "CCD" OR "colony collapse disorder") AND ("survey" OR "question*"). Also, we used expert knowledge to unearth further publications not found in the above search strategy. The PRISMA flow diagram in Supplementary Figure 01 illustrates the detailed selection process, i.e., the number of studies identified and accepted. We only included papers presenting data on beekeeper-reported colony mortality surveyed across entire countries. Data were sorted by geographical region, country and year (see Supplementary Table 02), resulting in 55 studies. Most studies (n = 46; 83%) reported only overwinter mortalities while few (n = 9, 16%) reported annual mortalities; of these, one reported only annual mortality and eight both annual and overwinter mortality (Supplementary Table 02). We, therefore, focused on overwinter mortality in our data analysis described below.

To investigate whether overwinter mortality of honey bee hives differed between years and regions, we used a linear model (LM) in R (R Core Team, 2016) with region and year as fixed factors. The proportions of overwinter mortalities were square-root-transformed prior to analysis to fulfill assumptions of normality. A Tukey post-hoc comparison was used to investigate differences between regions using the R package *multcomp* (Hothorn et al., 2008). Model assumptions were verified by visual assessment using the plot(lm) function in R.

3. Results

Our survey identified a total of 66 insect species formerly or currently managed, or under consideration for management, to pollinate crops (see Supplementary Table 01). Two *Apis* species, nine *Bombus* taxa, eight solitary bee species, and three non-bees are currently managed for the pollination of crops (Fig. 1A). Many other species have been mentioned to have the potential to be managed, including six bumble bee, 15 stingless bee, 14 solitary bee, and four non-bee species (Fig. 1A). Five bumble bee species were managed in the past but are no longer commercially produced (Fig. 1A). We also find that most manageable pollinators are native to Europe (n = 20), Asia (n = 20), North America (n = 19), and South America (n = 19), while for Oceania, Africa and Central America we only recorded nine managed species per region (Fig. 1B). Native species in Africa, Asia, Europe, and North America have for many decades been considered to be suitable managed pollinators (Supplementary Fig. 02). In contrast, native species in Central America, Oceania, and South America have been considered or used only more recently for their pollination services (Supplementary Fig. 02). While *A. mellifera* and solitary bee management have a long history, managing stingless bees or non-bee pollinators is rather recent (see Fig. 2A; Supplementary Fig. 03). Also, the number of publications on managed pollinators and managing pollination services has risen rapidly in the last two decades, reflecting the growing interest in alternative pollinators (see Fig. 2B).

3.1 Honey bees

Of the eight widely recognized species of *Apis* (honey bees), only two are managed to any extent, with *Apis mellifera* of primary importance worldwide, and *A. cerana* much less frequently used in its native South and East Asia (Smith 1991; Engel 1999). Over the last 60 years, the number of honey bee colonies has steadily increased (Fig. 3A), with a global stock of more than 92 million colonies in 2018, mostly driven by East Asia (Fig. 3B). This represents an increase of more than 85% in the global number of managed honey bee hives. Europe experienced losses around 1990 but its numbers of managed colonies have increased from around 16 million in 2010 to almost 19 million colonies in 2018. They have not, though, returned to the pre-1990 high of ca. 22 million colonies (see Fig. 3B).

The FAO database reports the number of beehives per country but does not distinguish between different honey bee (*Apis*) species. Data are likely dominated by *A. mellifera*, making it problematic to quantify changes in the number of Eastern honey bee hives (*Apis cerana*). In South Korea, *A. cerana* was widespread in beekeeping operations into the 1980s, but the current trend is toward managing *A. mellifera*, with an associated decline in the number of managed *A. cerana* colonies (Jung and Cho, 2015). It has been estimated that around 2 million *A. cerana* hives exist in China (Chen et al., 2017).

World annual honey production increased from 0.7 million tonnes in 1961 to ca. 1.86 million tonnes in 2018 (see Supplementary Fig. 04A). The average honey yield per colony, likely derived primarily from *A. mellifera*, can vary from year to year, but the overall trend is upwards (see Supplementary Fig. 04B); while less than 15 kg per colony per year was harvested around 1960, more than 20 kg per colony per year was harvested by 2018, an increase of 33% (see Supplementary Fig. 04B). We also report a slight increase in the real (inflation-adjusted) market value for honey (e.g., USA, see Supplementary Fig. 05).

We found 55 studies and reports presenting country-wide annual or overwinter mortalities of *A. mellifera* colonies for which data have been systematically collected since the winter of 2006/07. Before winter 2006/07, up to 30% annual colony losses were reported (see Fig. 4A and 4B, Supplementary Table 02), though this is based on few data points. Thereafter, colony mortality has fluctuated markedly (Fig. 4A and 4B), but there is no linear trend in mortality over time (LM, $t_{266} = -1.168$, $P = 0.244$, Fig. 4A).

There are, however, some general patterns that can be discerned from the data. North American beekeepers have experienced higher overwinter mortalities of 26% (±7% S.D.) than beekeepers in Europe (16% ± 8% S.D.), who themselves experienced higher losses than other regions (11% ±4% S.D.; post-hoc analysis, $P < 0.005$; Fig. 4A and Fig. 5). Fluctuations within regions can be large; within Europe, several countries reported annual overwinter losses above 30% in one or more years, for example during winter 2007/08 or winter 2009/10 (Fig. 4B). In the USA in recent years, annual losses have exceeded 50% (i.e. 2017/18; 2018/19; 2019/20, Supplementary Table 02). While Europe and North America are well represented in the literature, there are few documented studies on annual colony mortality in Central America, Africa, Asia, Oceania, and South America (Requier et al., 2018; Fig. 4B and Fig. 5; Supplementary Table 02). The first survey of colony losses of managed *A. cerana* in China revealed low overwinter mortality (average 12.8%; Chen et al., 2017) but slightly higher compared to *A. mellifera* (average 9.6 %) in China between 2011 and 2014.

3.2 Bumble bees (*Bombus* spp.)

Currently, seven different species or subspecies of *Bombus* are reared (Supplementary Table 03) and two additional species are trap-nested in New Zealand (Donovan, 2007) for pollination. We also found six additional bumble bee species under consideration for management as pollinators and five species that have already been abandoned as managed pollinators (Supplementary Table 01, Fig. 1A).

After the methods for commercial rearing of one bumble bee species, *Bombus terrestris*, were established in the 1980s in Europe, the number of managed colonies of this species traded annually had risen to one million by 2006 (Velthuis and van Doorn, 2006). The current number of *Bombus* colonies traded annually is not publicly known because information is withheld for commercial reasons, but likely exceeds 2 million colonies (IPBES, 2016).

3.3 Stingless bees

The potential of managing stingless bees for pollination services has been evaluated in several studies, particularly in Brazil (Supplementary Table 01), but their pollination management is not yet an established practice. Here, we report 15 species that have been or are under consideration as managed pollinators (Fig. 1A), mostly for crop pollination (of, e.g., strawberry, cucumber, tomatoes, habanero, and sweet pepper) in enclosures (Supplementary Table 01).

3.4 Solitary bees

Eight solitary bees, in particular leafcutter and mason bee species (family Megachilidae, genera *Megachile,* and *Osmia* respectively) but also the alkali bee (*Nomia melanderi*, family Halictidae), are currently managed for crop pollination (Fig. 1A). In addition, 14 other species are under consideration as managed pollinators (Supplementary Table 01, Fig. 1A). Leafcutter and mason bee species can be encouraged to nest in artificial media (e.g., drinking straws, bamboo canes, drilled wood blocks, and polystyrene boards; IPBES, 2016) while the ground-nesting alkali bee can be encouraged to nest in bee beds created by farmers adjacent to cropping fields (Johansen and Mayer, 1982). These latter measures allow the numbers of alkali bees to accumulate over successive years, enhancing the pollination of nearby crops in a very simple manner (Free, 1993; Delaplane and Mayer, 2000). However, management of solitary bees can also include the potentially more destructive commercial harvest, trade, and release beyond their native range (Richards, 1984; Bosch and Kemp, 2001).

Official figures on the size of the managed solitary bee industry (number of bees produced) are lacking, but there are estimates for several species (IPBES, 2016). Around 800 million alfalfa leafcutter bees (*Megachile rotundata*) are traded commercially per year in North America and an additional 1.6 million are promoted in and around alfalfa fields in the USA, making this species the most important managed solitary bee (Peterson et al., 1992; Reisen et al., 2009). *Osmia cornifrons* has been successfully managed since the 1940s in Japan, where it is native and employed in 70% of Japan's apple production area (Maeta, 1990). Populations of this species are also managed for orchard pollination in China and Korea (Xu et al. 1995, Lee et al. 2008) but the extent of its use is unknown. In 2002, trade of *Osmia bicornis* (=*rufa*) in Europe, *O. cornuta* in central and southern Europe, and *O. lignaria* in the US and Canada was estimated at over one million cocoons (individuals) per species per year for the pollination of orchard crops (Bosch and Kemp, 2002). Current numbers might be higher as a single company in France traded one million cocoons in 2020 (pers. comm. P. Ouvrard). In Korea, an estimate of 0.5 million *Osmia* spp. individuals (mostly *O. cornifrons* and *Osmia pedicornis*) were used to pollinate crops in 2007 (Yoon and Park, 2009).

3.5 Managing insects other than bees for pollination of crops

Currently, three fly species are available commercially for pollination (Fig. 1A): *Lucilia sericata* (common greenbottle fly; produced by, e.g., Koppert), *Eristalinus aeneus* (hover fly; produced by Polyfly), and *Eristalis tenax* (hover fly; produced by Polyfly). The extent of their use is not known as such commercially sensitive information is withheld and does not appear in public databases. In addition, we identify four other fly species under consideration as potential managed pollinators (see Supplementary Table 01; Fig. 1A). These flies have proven to be effective pollinators of crops grown in enclosures (cages or glasshouses) to promote cross-pollination for seed or fruit: the blow flies *Calliphora vomitoria* for onion grown for seed (Currah and Ockendon, 1984), *Calliphora vicina* for hybrid carrot seed production (Free, 1993; Howlett, 2012), *Calliphora albifrontalis* for the pollination of blueberries (Cook et al. 2020b), and the housefly *Musca domestica* for *Allium ampeloprasum* pollination (Clement et al., 2007).

4. Discussion

We clearly demonstrate an increase over the past seven decades in the number of insect species, particularly bees, which are managed as pollinators, as we expected. For the most numerous commercial insect pollinator, the Western honey bee (*A. mellifera*), the number of colonies worldwide has also increased over the past seven decades despite high overwinter colony losses in Northern temperate regions of the world.

Though our data do not address the cause or causes for the increase in the number of managed insect pollinator individuals or species, we hypothesise that the greater reliance of agriculture on insect pollinator-dependent crops (Aizen et al. 2009; 2019), the rise in crop cultivation under permanent cover (Cuesta Roble, 2020), and the rise in awareness of the negative effects of non-native pollinators on local species (Aizen et al., 2020) may all have been important in increasing the demand for managed pollinators, as outlined in our first two hypotheses. For those bee species that produce a surplus of stored honey or other products, increasing market prices might also have led to greater uptake of managed species. High overwinter mortality of *A. mellifera* might have a minor influence, as two-thirds of the species have been mentioned before 2007, when honey bee mortality became widely publicized (Oldroyd, 2007), and regions with higher honey bee overwinter mortality rates such as North America do not have particularly high numbers of native or alternative managed pollinator species.

4.1 Honey bees

Two honey bee species are used for the pollination of crops, the Western honey bee (*A. mellifera*), which is the most prominent pollinator worldwide (IPBES, 2016), and the Eastern honey bee, *A. cerana*, which is native to Asia, ranging from Afghanistan to Japan and south to most parts of Indonesia (Radloff et al., 2010). Both species have a long history of beekeeping management, mostly for honey production (IPBES, 2016). Data collected from the FAO on the number of honey bee hives per year and country are mostly dominated by *A. mellifera* and therefore disentangling the contribution of *A. cerana* is difficult. However, the introduction of *A. mellifera* to all Asian countries in recent decades (Requier et al., 2019) might have negatively affected the number of managed *A. cerana* (Theisen-Jones and Bienefeld, 2016). Colonies of *A. mellifera* are larger and produce more honey than *A. cerana* (Theisen-Jones and Bienefeld, 2016), leading beekeepers to convert from the management of the latter to the former. Nevertheless, *A. cerana* may show useful management traits such as disease resistance or tolerance, making it better adapted to management in tropical Asian countries (Lin et al., 2016; Theisen-Jones and Bienefeld, 2016). Furthermore, *A. cerana* has been shown to outperform *A. mellifera* in the provision of pollination services, e.g. pears in China (Gemeda et al., 2017), an argument for the maintenance of managed *A. cerana* where it is native.

We confirm the ongoing rise in the number of honey bee hives worldwide, with a total increase of more than 85% from 1960 to 2018; this dynamic supports our expectations as the dependency of agriculture on pollination has increased globally and, with it, potentially the demand for pollination services (Aizen and Harder, 2009b). This seems at odds with reports of high rates of colony mortality (e.g., Bruckner et al., 2019). An interesting question, therefore, concerns world honey bee health, for which data on trends in colony numbers are unreliable for many reasons (IPBES, 2016). First, colonies can be divided or reunited during the season (Root et al., 2006), leading to inaccuracy in the estimation of the number of colonies. Second, beekeepers can capture a passing honey bee swarm, increasing their number, or a colony may abscond, leading to colony loss (Root et al., 2006). Third, in Africa and South, Central and southern North America, large numbers of wild or feral honey bee colonies contribute to the population of *A. mellifera* and likely actively contribute to crop pollination (Vogel et al., 2021), though are not registered in databases. Fourth, many colonies are likely not registered, especially in small-scale apiaries, leading to inaccuracy in national estimates (IPBES, 2016).

In Europe, where *A. mellifera* is managed, feral honey bees are scarce (Jaffe et al., 2010). The number of registered honey bee colonies is therefore a product of the number of beekeepers. For example, the loss of *A. mellifera* colonies in Europe around 1990 has been attributed to societal changes (e.g., the collapse of socialist states, increasing wealth; see Moritz et al., 2010; Smith et al., 2013; van Engelsdorp and Meixner, 2010). As a consequence of great uncertainties in the total number of colonies at any one point in time, estimates of overwinter losses of honey bee hives might be a better indicator of honey bee health (IPBES, 2016).

Since monitoring by the science network COLOSS began in 2008, data have been collected on overwinter colony losses in a standardized way, although mostly for Europe. Both the United States of America and Canada have also introduced national programs that report their annual honey bee wintering losses. Data from Central America, Asia, Africa, Oceania, and South America are still scarce. For instance, cases of high colony losses have been reported in South America but, due to the lack of monitoring programs, a general overview is lacking (Requier et al., 2018).

This could have negative repercussions for this geographical region in which agriculture is highly pollinator-dependent (Aizen et al., 2019), limiting our ability to predict a pollination shortfall. In Africa, the density of feral honey bees is higher than in Europe (Jaffe et al., 2010). Therefore, colony mortality rates are hard to determine because many colonies go unrecorded and unobserved.

Interrogating the existing data on annual losses suggests some alarming trends; for example, in the USA, honey bee colony losses have exceeded 50% each year for the last three years (i.e., 2017/18; 2018/19; 2019/20; see Supplementary Table 02). There is obviously a need for ongoing documentation of colony losses to help understand their causes. Reported overwinter mortalities vary among geographical regions of the world, and might be a result of differences in beekeeping practices, weather conditions, the prevalence of pathogenic organisms, intensification of agriculture, inadequate nutrition, or the introduction of invasive species (Neov et al., 2019; 2021); these multifactorial drivers deserve to be further studied to understand better the threats to honey bee colony health. That novel pollinator species have been developed across the world and not predominantly in regions experiencing high honey bee overwinter colony mortality (e.g. North America; see Fig. 4 and Fig. 5) suggests that honey bee mortality *per se* does not spur interest in alternative pollinators, arguing against our third hypothesis. Alternatively, if honey bee mortality does promote research on alternative pollinators, then its impact is not limited to the country or region experiencing high colony mortality; global communication and awareness of the need for pollinators may be very effective.

Apis mellifera colony losses stand in contrast to the increasing global number of honey bee hives. However, colony losses might not have a direct effect on the standing number of colonies in a country because beekeepers may compensate for losses, as outlined above. Moreover, the price farmers have to pay for pollination services might well be affected by high annual rates of colony mortality, with an increase in price spurring an increase in the supply of colonies. In Central Europe (Germany), where average overwinter mortality is below 20%, farmers pay around US$35 per colony for pollination services (informal pers. comm. with farmers). In contrast, in the United States, where the average overwinter mortality is above 25%, farmers pay between US$ 74.3 and US$ 143.2 per honey bee colony for pollination services (USDA National Agricultural Statistics, 2017). In 2017, the summed US farm expenses for pollination services provided by honey bees has been estimated at more than US$ 300 million (USDA National Agricultural Statistics, 2017).

The overall pattern of increasing numbers of honey bee colonies worldwide may be either a consequence of an increasing market value of honey (see Supplementary Fig. 05 and Aizen and Harder, 2009a) or increasing demand for honey bee colonies as pollination 'units'. In a growers' survey in Europe, one-third of farmers owned managed honey bee colonies and almost half either owned or hired at least one managed pollinator species, including honey bees (Breeze et al., 2019). Similarly in Korea, honey bees have been used in 48% of cases by farmers to pollinate crops (Yoon and Park, 2009). In 2017, in the USA more than 2.6 million colonies were used to pollinate crops, particularly almonds grown in California (USDA National Agricultural Statistics, 2017). With the increased planting of pollinator-dependent crops at a rate greater than the rise in the global stock of domesticated honey bees (Aizen and Harder, 2009b), increasing demand for honey bees in the coming years is to be expected.

Interestingly, we found that honey production per colony has increased by 33% over the past seven decades. The growing production of honey might be a result of the increase in the human population and per capita demand for honey (Aizen and Harder, 2009b). An increase in mass-flowering crops and intensification in beekeeping (Aizen et al., 2019) could potentially also explain this consistent increase in yield per colony. Data collected from the FAO on the honey harvested per year and country do not distinguish its biological origin but will be dominated by *A. mellifera*. Honey harvested from other honey bee or stingless bee species likely represents a marginal proportion of the total world honey yield.

4.2 Bumble bees

The rising number of managed bumble bee species and number of colonies might be driven by a trend towards more cultivated area under permanent cover (Cuesta Roble, 2020), as honey bees do not perform well in these environments. Moreover, honey bees are unable to buzz pollinate (Buchmann, 1983) and, therefore, are unlikely to provide an adequate pollination service to buzz-pollinated crops like tomato that are regularly grown under cover. Estimates of two million *Bombus* spp. colonies traded annually across the world, presented in the IPBES report (2016), might be an underestimation as data on the current number of traded colonies are not available. Most likely, bumble bees are the second most common managed pollinators (after the Western honey bee) used for pollinating approximately 240 crops worldwide (IPBES, 2016), particularly those grown under enclosure (e.g., in glasshouses), but increasingly also for semi-enclosed or open field pollination (Murray et al., 2013). For example, tomatoes are cultivated mostly in enclosed greenhouses, a crop that is now primarily pollinated by bumble bees (*Bombus* spp.) (Morandin et al., 2001). In Europe, tomatoes were planted on around 0.5 million ha in 2017 (FAOSTAT, 2017). If farmers use recommended rates of 10 to 15 bumble bee colonies per hectare (van Ravestijn and van der Sande, 1991), this would suggest that at least 5 million *Bombus* colonies are needed for the pollination of tomatoes grown in greenhouses in Europe alone. This number of colonies is likely an underestimate, given that *Bombus* spp. colony survival time is only around 4 to 6 weeks whereas glasshouse-grown tomato plants survive for several months. Also, bumble bees have been reared not only for agricultural purposes but also as part of conservation strategies. For example, *Bombus subterraneus*, which became extinct in Great Britain in the 20th Century, has been reared in New Zealand for reintroduction to Great Britain, which ironically was the source of New Zealand's *B. subterraneus* founder population in the 19th Century (Howlett et al., 2009).

4.3. Stingless bees

There are many reasons why stingless bees are considered suitable as managed pollinators in the tropics, where they are native. First of all, some species have been traditionally managed for centuries in clay or wooden pots and harvested for honey (Free, 1982; Crane, 1983, 1999; Cortopassi-Laurino et al., 2006; Vit et al., 2013). One species in particular, *Melipona beecheii*, has been managed by the Maya of the Yucatan Peninsula for the past two millennia, if not longer

(Quezada-Euán et al., 2001). Rearing techniques for their management might therefore be adapted from indigenous knowledge.

Stingless bees are social; a colony comprises 100s to 10000s of workers (Roubik, 1989), providing many potential pollinators compared to bumble bees (whose colonies comprise 50-500 workers) or solitary bees. Moreover, stingless bees may be more suited for management in the tropics. For instance, although the Africanized honey bee dominates in the Neotropics, it is not suitable for management of crops grown under permanent cover (e.g. greenhouses) as it exhibits extreme defensive behaviour (Danka and Rinderer, 1986). In addition, when relocated (e.g., to a greenhouse), an Africanized honey bee colony frequently absconds (Danka et al., 1987), making beekeeping problematic. In contrast, stingless bees are considered efficient pollinators that are able to buzz pollinate and likely contribute greatly to the pollination of many crops, especially in the Neotropics (Heard, 1999; Slaa et al., 2006) and especially for crops such as tomatoes and eggplants that rely on buzz pollination (Abak et al., 2000; Velthuis and Van Doorn, 2006). Though bumble bees are efficient buzz pollinators, they are not native to all parts of the world and are costly to purchase. There are therefore many reasons why stingless bees should be considered for management as pollinators where they are native and widespread. Their use would also reduce the risks and known negative impacts on native fauna, including on native bumble bee species, through the introduction of exotic bumble bee species (Aizen et al., 2018, 2020).

4.4 Solitary bees

Solitary bees have long been managed as they are efficient pollinators, partly for crops that honey bees pollinate poorly (IPBES, 2016). The best-known case of a managed solitary bee is the alfalfa leafcutter bee, *Megachile rotundata*, managed for the pollination of alfalfa (*Medicago sativa*), a Eurasian crop introduced to North America as an important fodder plant for cattle but for which honey bees provide inadequate pollination (Free, 1993). *Megachile rotundata* was likely unintentionally introduced from its native range in Europe and Asia to East Coast North America in the 1930s, from where it spread naturally to alfalfa seed-producing regions of Central-Western USA and proved to be an excellent alfalfa pollinator. Through detailed research on its biology, facilitated by its gregarious nesting in artificial domiciles, a viable alfalfa leafcutter bee industry became established in the USA and Canada (Bohart, 1952; Stephen, 1962, 1961; Stubbs and Drummond, 2001; Pitts-Singer and Cane, 2011). Apart from *M. rotundata*, farmers can manage their land surrounding alfalfa fields by creating bee beds for the ground-nesting alkali bee *N. melanderi* (Halictidae) in the USA and for *Rhophitoides canus* (Halictidae) in Eastern Europe (Ptacek, 1989; Bosch, 2005), both of which are efficient alfalfa pollinators. Both species have not been commercialized to any extent (IPBES, 2016).

Other solitary species such as carpenter bees (genus *Xylocopa*) have been experimentally managed as pollinators of crops such as passion fruit (*Passiflora edulis*) (Junqueira et al., 2012, 2013) and tomatoes (Hogendoorn et al., 2000). For example, in Australia, honey bees and bumble bees are not native whereas *Amegilla chlorocyanea,* the blue banded bee, is a very efficient native pollinator of tomatoes grown in glasshouses (Hogendoorn et al., 2006). These are good cases for how a diverse range of native pollinators can be used to enhance crop pollination services whilst reducing the risks to native fauna inherent to the introduction of a new species through, for example, competitive displacement or pathogen spillover (Aizen et al., 2020, LeCroy et al., 2020; Russo et al., 2021).

Other examples of solitary bees used for pollination services include mason bees (*Osmia* spp.) that are mostly used to pollinate early-flowering fruit trees (Supplementary Table 01), where they increase fruit yields in apples, sweet cherries, and pears (Torchio 1985, Monzón et al. 2004, Bosch et al. 2006). For strawberry pollination, *O. cornuta* was shown to have a positive impact on fruit quality under experimental conditions (Herrmann et al., 2019) and the active management of *O. lignaria* in strawberry fields enhances fruit quality (Horth and Campbell, 2018).

Wild populations of solitary bees can be enhanced by active landscape and field management, particularly by creating nesting habitats and providing floral resources (habitat improvement for pollinators or 'ecological intensification'). This is a sound alternative that should always be preferred, in terms of both conservation and economic perspectives, to the trading of pollinators. Trading in pollinators can lead to the introduction of new species that especially bear risks through the competitive displacement of native fauna and pathogen spillover (Aizen et al., 2020, LeCroy et al., 2020; Russo et al., 2021). Also, the yield of pollinator-dependent crops tends to increase with the abundance and diversity of wild pollinators (Garibaldi et al., 2013).

4.5 Managing insects other than bees for pollination of crops

Managing non-bees as pollinators has great potential (Kevan et al., 1990; Howlett, 2012; Howlett and Gee, 2019; Cook et al., 2020a) as these insects play a significant role in global crop production (Rader et al., 2016, 2020). The potential of hover flies to pollinate crops was shown by Garratt *et al*. (2016), although they were less effective than honey bees, bumble bees, or solitary bees. Eight percent of global food crops reliant on pollinators are favoured by non-bees and another 77% are visited both by bees and non-bees (Rader et al., 2020). Oil palm (*Elaeis guineensis* Jacq) is an example of a crop completely reliant on non-bee pollinators. To improve the yield of oil palm where it is non-native, manual pollination was undertaken until the weevil *Elaeidobius kamerunicus* was discovered in oil palm's native West Africa as the main pollinator and introduced into the non-native growing areas of oil palm (Syed et al., 1982). Since then, the oil palm pollination strategy has relied on the feral populations of *E. kamerunicus*. But its fluctuating populations have led to concerns, raising the issue of more active management of the weevil to sustain yield by, for example, by manipulating male palm inflorescence density (Li et al., 2019).

Despite their contribution to pollination services, the management of non-bee pollinators currently occurs on a far smaller scale than that of their bee counterparts. But it might have great potential, for example for pollination of crops grown under cover.

4.6 Risks associated with pollinator management

An important risk associated with pollinator management is the introduction for crop pollination of an alien pollinator species that subsequently becomes invasive (Ghisbain et al., 2021; Russo et al., 2021). The mechanisms by which introduced (but also native) managed pollinators and their trade can affect native species and ecosystems include (a) exploitative or interference competition for flower resources and nesting sites (Hansen et al., 2002; Inoue et al., 2008; Howlett and Donovan, 2010; Morales et al., 2013; Hudewenz and Klein, 2015; Lindström et al., 2016; Torné-Noguera et al., 2016; Ropars et al., 2019), (b) inadequate pollination of native flora, leading to changes in the reproduction of native plants (Gross and MacKay, 1998; Dohzono et al., 2008; Valido et al., 2019), (c) undesirable pollination of exotic flora (Barthell et al., 2001; Stout et al., 2002; Morales et al., 2014), (d) transmission of parasites or pathogens to wild or native populations, including the co-introduction of natural enemies (Colla et al., 2006; Morales et al., 2013; Murray et al., 2013; Fürst et al., 2014; Schmid-Hempel et al., 2014), and (e) genetic introgression or reproductive disturbance of native pollinator species (Tsuchida et al., 2010; Kraus et al., 2011). Managed pollinators can even have a negative impact on wild plant reproduction and crop yields when they become superabundant (Aizen et al., 2020; Russo et al., 2021). For instance, high visitation rates of the invasive *B. terrestris* to commercial raspberry in Patagonia resulted in a negative impact on fruit set (reviewed in Aizen et al., 2020). Risk assessments should therefore be implemented before introducing a non-native pollinator species, especially since managed species may have a marked negative effect on native pollinators (Russo et al., 2021).

On the other hand, there has been an increase in the number of manageable pollinator species over time, which highlights the potential or perceived need for additional suitable pollinator species. These could be chosen according to their traits, e.g. their ability to buzz-pollinate in the case of tomato pollination, or ability to nest in the vicinity of a field-grown crop. For successful trait-matching, crop-pollinator networks could be used to identify common flower visitors of that crop, paired with quantification of pollinator efficiency of the species itself or related species with similar traits (e.g., short-tongued vs. long-tongued bumble bees). Such trait matching could pinpoint native species that can be prioritized for investigation and assessed for risks they might pose to other native pollinators and their ecosystems if the managed species becomes invasive.

Given the potential risks associated with pollinator management, and that a combination of species provides better pollination assurance than a single species (e.g., Garibaldi et al., 2013), it is logically more sustainable to enhance and/or manage multiple native pollinator species, e.g., through the creation of habitat for native pollinators in or around crop fields. Habitat enhancement to benefit pollinator abundance and diversity in agricultural landscapes aims to protect and restore favorable habitats, increase the quality and quantity of floral resources, reduce intensive mechanical practices, reduce chemical inputs, and provide nest sites for pollinators (reviewed in Garibaldi et al., 2017; Kleijn et al., 2019). Furthermore, by coupling knowledge of the most efficient pollinators of specific crops with knowledge of their lifecycle requirements, habitat can be specifically designed to support targeted bee and non-bee pollinators for improved pollination (Howlett et al., 2021). Using these approaches, native wild pollinator populations can be enhanced and promoted, resulting in increased pollination of adjacent crops (Blaauw and Isaacs, 2014; Forbes and Northfield, 2017).

4.7 Knowledge gaps and future research

We found the majority of reports on *A. mellifera* mortality from North America and Europe and limited information for Africa, Asia, South America and Oceania. Further surveys in understudied regions and a continuation of the monitoring in well-studied regions as well as investigation of the causes of mortality can help to achieve better understanding of honey bee health across the world. While the number of *A. mellifera* hives is reported worldwide, we lack data for other managed pollinators on the extent of their use so as to identify trends over time. The health of other pollinators and their responses to threats (diseases, pesticides, nutritional deficiencies and climate change) can differ from honey bees, which emphasizes the need to monitor several pollinator species (Wood et al., 2020). Furthermore, while there is increasing research on manageable pollinators and their effects on crops, there is limited information on the pollination management practices of farmers (Breeze et al., 2019) and their willingness to include new species into their pollination management, information which could be important to understand practicable species for farmers. Also, most manageable pollinator species are native to North America, Europe, and Asia. Only recently have a greater number of native species been considered in South America, despite the high dependence on pollinators by agriculture in that geographical region (Aizen et al., 2019). Few species from Central America, Africa, and Oceania are known as manageable pollinators. Previous practices that introduced non-native species to those regions could be avoided in the future if more native pollinators were investigated as manageable species.

5. Conclusions

The number of insect species managed for pollination, especially bees, has increased markedly over recent decades, paralleled by a growing number of honey bee colonies and commercially-reared bumble bee colonies. Currently, 66 species are known as manageable pollinator species globally. While some taxonomic groups (e.g., solitary bees) and species native to geographical regions (e.g., North America) have long been used as managed pollinators, others have only been considered rather recently (e.g., stingless bees and species from South America). The rise in consumer demand for pollination-dependent fruits, nuts, and seeds is likely driving the increasing dependence of agriculture on pollinator-dependent crops and the trend towards crops cultivated under permanent cover. At the same time, there is growing awareness and recognition of the negative effects of non-native species on local pollinators. Only a few bee species are commonly used in pollination, which represents a challenge for food security and farmer livelihoods. For instance, we demonstrate high mortalities of *A. mellifera* colonies, the most widely used managed pollinator, especially in North America. This highlights the need to preserve wild pollinators, e.g., through pollinator-sympathetic land management, as well as to consider a more diverse set of managed pollinator species. Though the management and deployment of novel pollinator species are not without risks, particularly if employed in locations where a pollinator is non-native, crop-specific and sustainable management of a diversity of new pollinator species may contribute to safeguarding future crop yields and food security.

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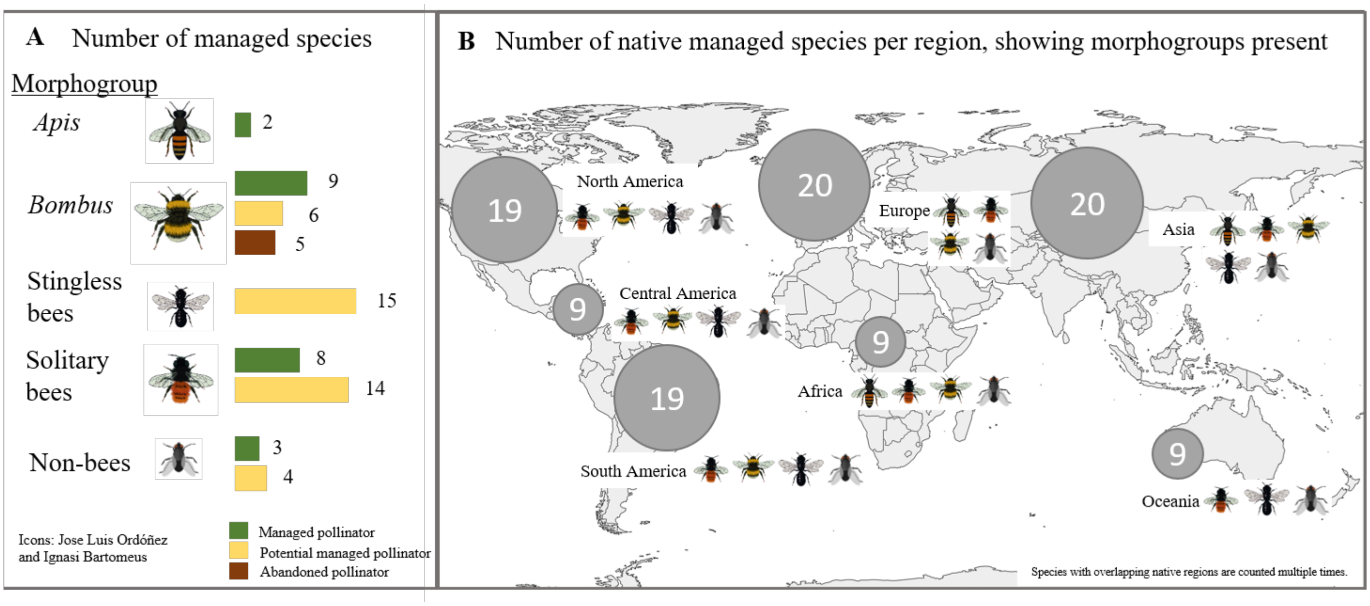

Figure 1 | Number of managed pollinator species (A) per morphogroup divided into the current management status and (B) native per geographical region. Icons under the geographical region represent morphogroups in that region. Species with overlapping native regions are counted multiple times.

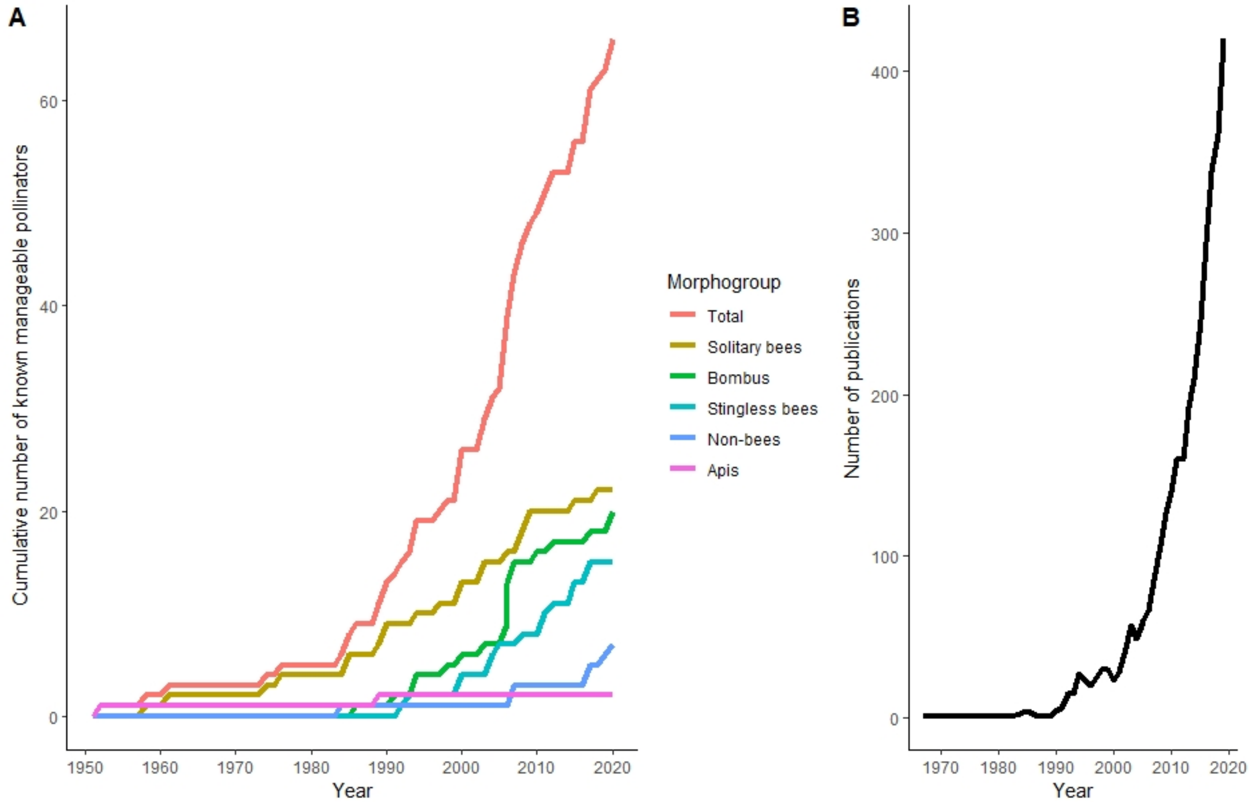

Figure 2 | (A) the cumulative number of known pollinator species in total and divided into morphogroups and **(B)** the **increase in the number of publications on managed pollinators per year** (using the search term manage* AND pollinat*)**.**

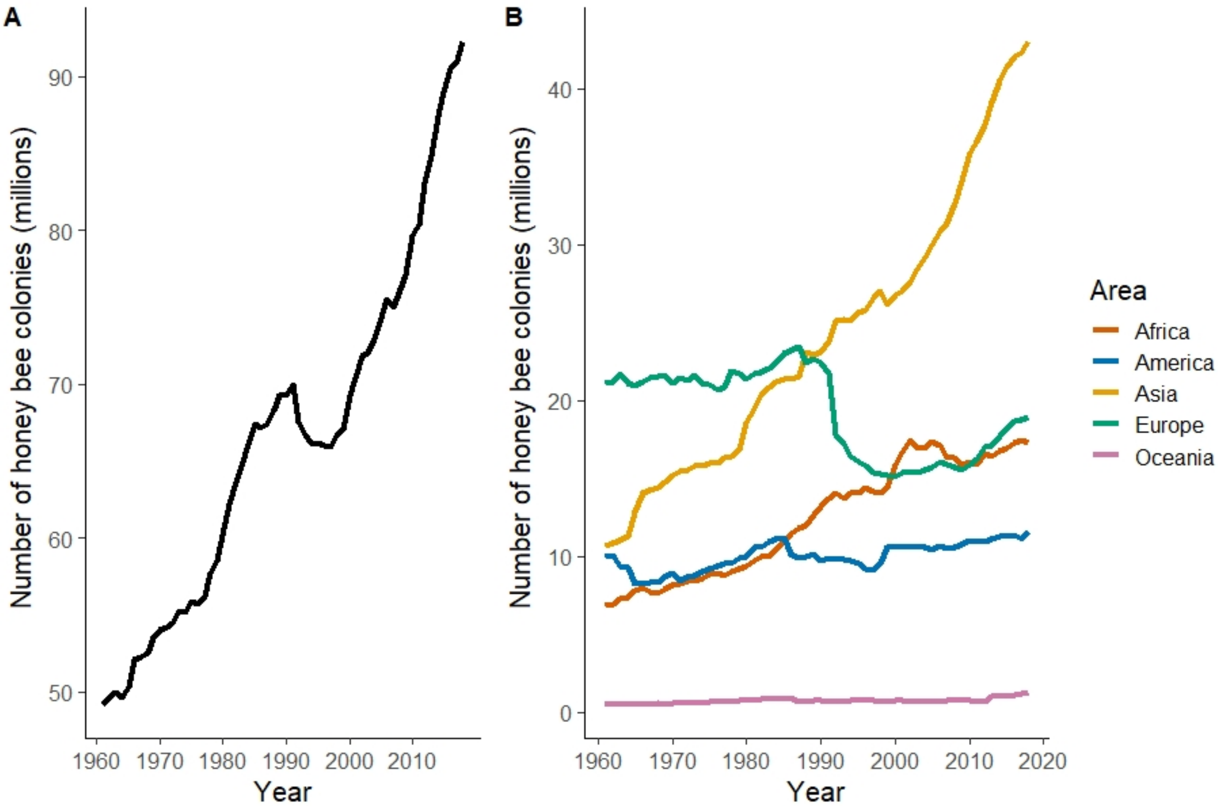

Figure 3 | Numbers of managed honey bee colonies (in millions) **(A) worldwide and (B) divided by geographical region** from 1961 to 2018 (FAO, 2020)

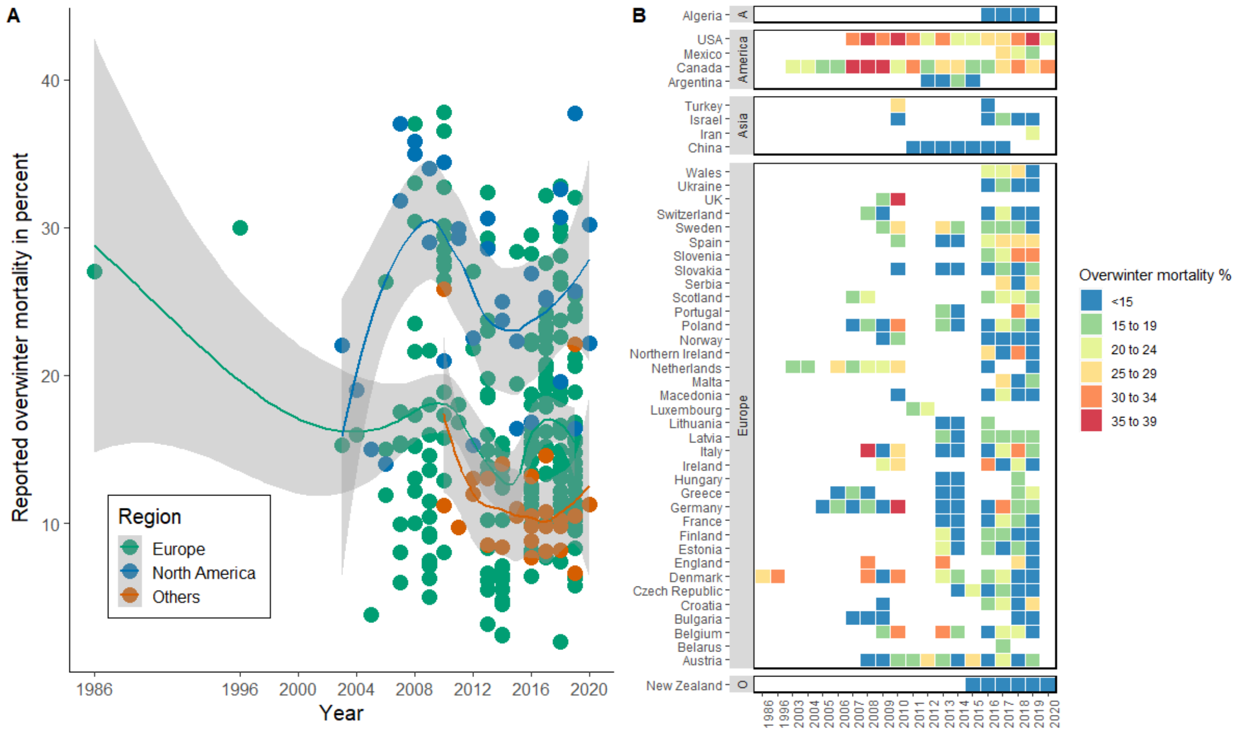

Figure 4 | Overwinter mortality of managed honey bee colonies (A) separated by geographic region over time and (B) by country and year. The category ‘Others’ includes Africa, East Asia, West Asia, Oceania and South America. Shaded areas represent 95% confidence intervals around locally weighted loess smoothing regression lines. The heat map illustrates overwinter mortality (%) per year and country in six colour categories. Countries are grouped by continents: Africa (A), America, Asia, Europe and Oceania (O). Data and corresponding sources are presented in Supplementary Table 02.

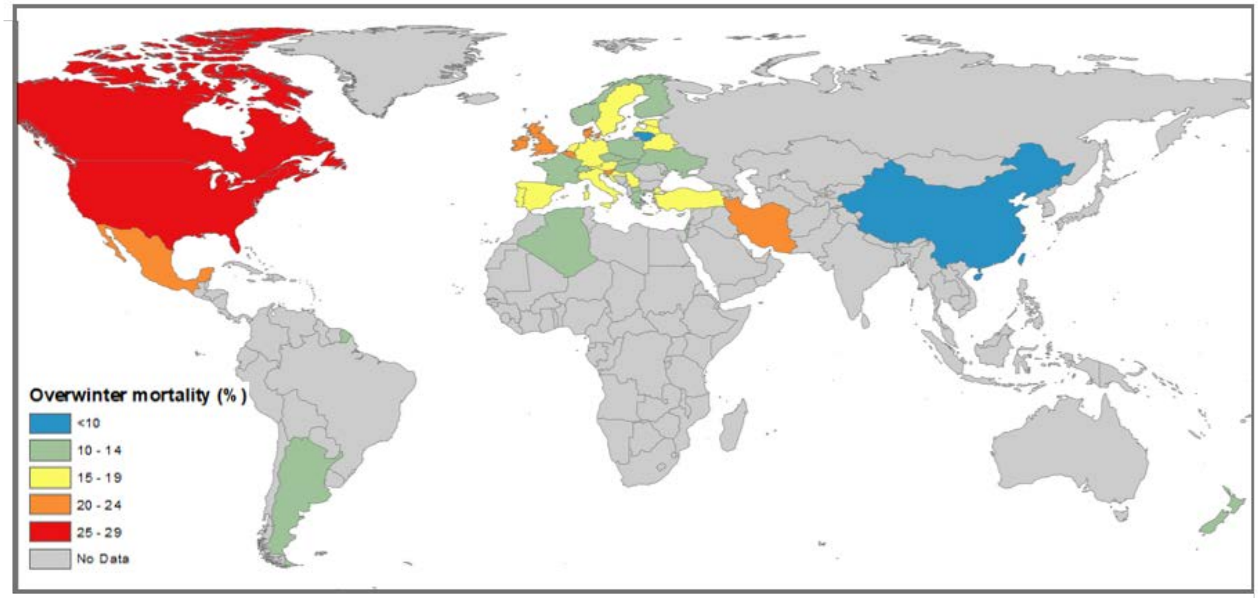

Figure 5 | Average overwinter mortality per country. Grey represents no data available. Number of years per country differ between 1 (Iran, Belgium) and 18 (Canada). Data and corresponding sources are presented in Supplementary Table 02.