European wild honeybee populations are endangered

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Abstract

The population trends of wild western honeybees (*Apis mellifera*) have been neglected by conservationists because the species has been considered to consist of managed colonies only, leading to its current European IUCN Red List category "Data Deficient". New data suggests that wild honeybee colonies (still) make up one sixth to one fifth of the overall European honeybee population. The population trends of wild cohorts can be evaluated like those of any other native wild species, albeit with some methodological adjustments to account for the bias introduced by swarms emigrating from managed cohorts. We used data on wild colony survival rates from six European countries to model their autonomous population changes over ten-year periods, the time frame considered for population evaluation by the IUCN. Populations of wild honeybee colonies currently represent demographic sinks in five out of six countries. With an average estimated population decline of 60% per decade, the honeybee should be considered "Endangered" in the wild in Europe. We believe that the formal recognition of wild honeybee colonies' existence and the explicit study of their population trends beyond apiculture can have far-reaching consequences for the evolution of this unique species and bee conservation in general.

Introduction

The western honeybee, *Apis mellifera,* is among the most abundant flower visitors across its cosmopolitan geographic range (Garibaldi et al. 2013; Hung et al. 2018), so its persistence on the species level seems to be of little concern in conservation science (Iwasaki and Hogendoorn 2021). It is rarely appreciated, however, that the existence of honeybees in regions with temperate climates is rather remarkable. The tribe of honeybees (Apini) only comprises about twelve species, most of which are confined to small distribution areas in (sub-)tropical Asia (Su et al. 2023; Kitnya et al. 2024). Only the western honeybee (in Europe) and, to a lesser degree, the eastern honeybee *Apis cerana* (in Asia) have evolved the peculiar ability to withstand long winters (Ruttner 1988). Forming perennial colonies, they are unique components of their respective temperate climate bee communities. Besides its colonisation of the temperate zone, *Apis mellifera* is further special because it is the only extant honeybee native to Africa, Western Asia and Europe. This shows that *Apis mellifera*, while common as a species, is uncommon from both a functional and phylogenetic perspective. Preserving its intra-specific genetic diversity and its potential to evolve naturally outside of apiculture can be seen as important goals in insect conservation (Fontana et al. 2018; Requier et al. 2019).

Interestingly, bee conservationists have not evaluated the conservation status of the western honeybee because they consider it a managed species, and thus, a part of agriculture or the livestock sector (Geldmann and González-Varo 2018). In fact, with the number of managed honeybee colonies increasing worldwide (Phiri et al. 2022), it seems unnecessary to promote the species beyond beekeeping and apicultural research. Furthermore, methods typically used to assess wildlife population trends seem unsuited for a managed, yet not truly domesticated species. This is reflected by the "European Red List of Bees" by the International Union for the Conservation of Nature (IUCN) as of 2014, in which *Apis mellifera* was listed as "Data deficient" because no data on wild honeybee populations were available (Nieto et al. 2014).

Throughout the last decade, however, several studies have provided evidence for the occurrence of wild honeybee colonies in Europe (Oleksa et al. 2013; Kohl and Rutschmann 2018; Browne et al. 2021; Moro et al. 2021; Oberreiter et al. 2021; Lang et al. 2022; Rutschmann et al. 2022; Albouy 2024; Niklasson et al. 2024; Rutschmann et al. 2024 Sep 17; Visick and Ratnieks 2024). Their average colony density was estimated to be 0.26 colonies per km^2, which would be equivalent to about 5.5 million colonies, 17.8% of the overall European honeybee population (managed hives: ca. 25.4 million) (Visick and Ratnieks 2023).

These figures suggest that wild honeybees are still ecologically and evolutionary relevant. Besides their foragers contributing to the species' overall flower pollination (especially in areas with low densities of manged hives) (Chang and Hoppenhauer 1991; Kohl and Rutschmann 2018) and the neglected biotic interactions associated with natural honeybee nests in tree holes or other cavities (Kohl et al. 2023), wild colonies are certainly relevant to the evolution of regional honeybee populations by acting as sources of local adaptations and as reservoirs for genetic variants of endangered subspecies (Requier et al. 2019; Panziera et al. 2022). Unfortunately, wild honeybee populations have received little attention so far from a conservation perspective.

In the context of ongoing updates to the European Red List of Bees (Ghisbain et al. 2023), the (re-)discovery of wild honeybees provides the opportunity to make the first informed assessment of their conservation status. Determining which IUCN Red List category currently applies to a species is an important formal step since it will help to objectively decide whether strategies to promote the respective populations are needed. The rationale is that wild species are assigned a category of threat ranging from "Least Concern" to "Extinct in the Wild" based on, for example, observed or estimated changes in population size within the last ten years (IUCN 2024).

When trying to determine the IUCN category for honeybees, practical problems arise due to its dual nature as wild and managed. Worker honeybees visiting flowers are easy to monitor, but bees from wild and managed colonies are indistinguishable. Finding the actual nesting sites of wild honeybee colonies is much more time consuming but can be achieved using the beelining technique (following forager bees to their homes) (Kohl and Rutschmann 2018), by specifically examining candidate nesting habitats (Oleksa et al. 2013; Kohl et al. 2022; Rutschmann et al. 2022; Visick and Ratnieks 2024), or by crowdsourcing data with the help of citizen scientists (Browne et al. 2021; Moro et al. 2021; Rutschmann et al. 2024 Sep 17). However, directly assessing temporal changes in the number of occupied nest sites in an area still does not suffice to estimate the wild honeybee population trend. Managed colonies can revert to the wild by leaving their apiaries as swarms and establishing natural nests in cavities of their choice during the reproductive season. This factor, which is comparable to the human-mediated supplementation of a wild population by captive stock in other species, can mask the autonomous population trend of the wild subpopulation. For example, approximately 10% of trees with black woodpecker (*Dryocopus martius*) cavities are occupied by honeybees in German forests each summer, suggesting the existence of a stable population of wild colonies.

However, studying the fate of many individual colonies revealed that only a few survive to the next spring; their relatively high abundance in summer could only be explained by the massive annual immigration of swarms from apiaries (Kohl et al. 2022).

The relevant question for determining the conservation status of wild honeybees is, therefore, "How would the population of wild colonies change over time if there was no immigration of swarms from managed colonies?". Understanding this requires the conceptual distinction between wild and managed cohorts and thinking of them as a metapopulation (Kohl 2023; Rutschmann et al. 2024 Sep 17). The autonomous change of the wild subpopulation is then expressed by a statistic called the net reproductive rate (R_0), which in turn can be derived from the average survival and reproductive rates of its members. Here, we use available data on wild colony survival rates from six European countries to model how their populations would change autonomously over ten-year periods. Based on these projected population trends, we suggest the first informed IUCN Red List category for the species in Europe.

Methods

Defining wild honeybee colonies

There is generally no physical or genetic barrier between managed (Fig. 1a) and wild honeybee colonies (Fig. 1b), and, contrary to common misconception, no stable "breeds" of domesticated honeybees exist (Seeley 2019). We therefore simply define wild *Apis mellifera* colonies based on their mode of living as colonies that live ownerless and unmanaged in cavities they have occupied themselves. In other publications, the same type of colonies has been described as "free-living" or "wild-living" to account for the possibility that a given population of colonies might not be self-sustaining (and thus not "truly wild"), just as the attribute "feral" has been used to highlight that wild colonies might be recent emigrants from apiaries (behavioural definition of "feral") or that the population under consideration was introduced by humans at some point in history.

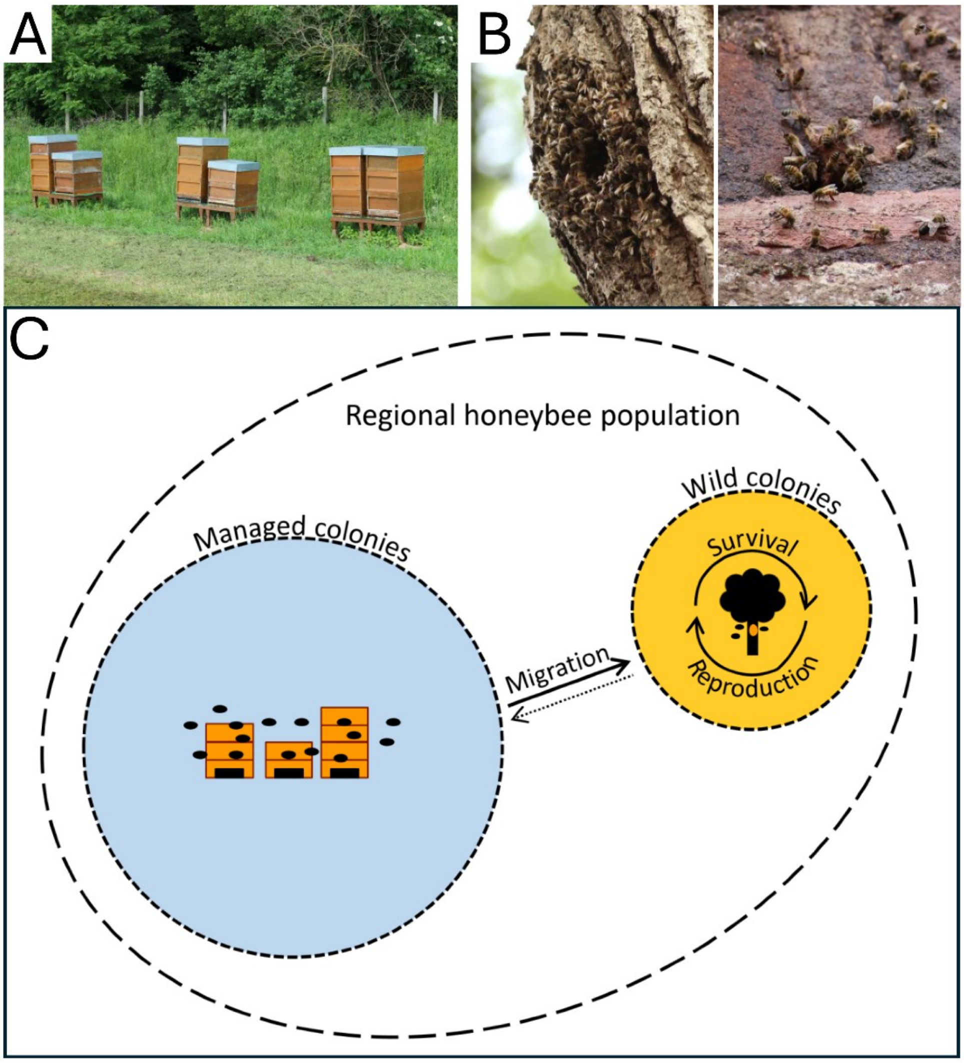

Figure 1. ***A)*** *Apiary with honeybee colonies managed in movable-frame hives.* ***B)*** *Examples of typical wild honeybee nesting sites: tree cavity (left) and hollow space in a wall (right).* ***C)*** *Metapopulation model of managed and wild honeybee colonies. Managed and wild colonies belong to one biological population; there is a genetic exchange through the random mating of queens and drones, and colonies can migrate between managed and wild cohorts ("subpopulations"). Selection pressure under apicultural management (natural and artificial selection) and under wild conditions (natural selection) are expected to differ. Figure modified after* (Kohl 2023).

Estimating population trends of wild honeybees

To study the demography of wild honeybees, it is practical to consider regional honeybee populations as metapopulations consisting of cohorts ("subpopulations") of managed and wild colonies (Fig. 1 c). Four variables affect the size of the wild cohort: immigration, emigration, survival, and natality. "Immigration" occurs when managed colonies swarm and become ownerless. By dispersing from the apiary and occupying a cavity on their own, they become members of the wild subpopulation. "Emigration" occurs when beekeepers capture swarms of wild colonies, be it directly or by luring swarms into bait hives. (We can assume that in most regions, emigration from the wild cohort is of minor importance, since beekeepers usually obtain new colonies by splitting their own stock or by trade with other beekeepers.)

To understand how the size of the wild subpopulation would change intrinsically, we needed to consider the survival (s) and the natality (n) (i.e., reproduction) of the colonies that are already members of that cohort. The annual survival rate of wild colonies can be empirically studied by making repeated surveys of known nest sites (Seeley 2017). We were able to make point estimates of annual survival rates because data on wild colony survival are now available for several regions in Europe (see below). The natality rate of wild honeybee colonies, the number of swarms produced per colony per year, is difficult to determine in the field. We assumed that wild colonies produce, on average, $n = 2$ swarms per year based on studies that examined the reproductive behaviour of unmanaged honeybee colonies living in hives with limited volumes (Gilley & Tarpy, 2005: 1.667 swarms/year; Lee & Winston, 1987: 2.2 swarms/year; Rutschmann, Kohl, et al., 2024: 1.7 swarms/year; Winston, 1980: 3 swarms/year), .

Given the annual survival and natality rates, we calculated the net reproductive rate (R_0) of the wild subpopulations. Since the generation time in temperate honeybee colonies is typically one year and colonies are hermaphrodites, this is:

$$R_0 = s + s * n.$$

This index describes how the population of wild colonies would change from year to year if no immigration occurred, with values < 1 denoting population decline and values > 1 denoting population stability or increase.

Sources of wild colony survival data

We consulted eight studies representing six European countries that provide information on wild colony survival rates (Fig. 2, Table 1). Oleksa et al. (2013) discovered wild colonies in trees along rural alleys in Poland, and these colonies were re-inspected over the next two years (Oleksa et al., unpublished). Continuous occupation by the same colonies, as opposed to re-occupation by new swarms, was tested using both mitochondrial and microsatellite markers. From an initial count of 67 colonies, 16 cavities remained occupied by the same colonies after the first year and 6 after the second year. We calculated an average annual survival rate for this population based on the average of the proportion of colonies remaining after the first and the second year.

Detailed demographic data were available for honeybee colonies nesting in cavities by the black woodpecker in southern Germany (Kohl et al. 2022). In that study, nest sites were controlled three times per year to determine summer (July–September), winter (September–April), and spring (April–September) survival rates. The annual colony survival rate was obtained by multiplication. The study also accounted for the possibility that the death of a colony in spring is followed by the quick re-occupation of the cavity by a new swarm, without being noticed during the monitoring, using microsatellite genetic data. The rate of such "silent spring turnovers" was reported to be 11.1% (one out of nine tested cases).

For the remaining studies, in case annual survival was not provided directly, we multiplied seasonal survival rates to obtain the "apparent annual colony survival rates". When the original study had not explicitly estimated the rate of unobserved colony turnovers during the swarming season, we further multiplied the "apparent annual colony survival rates" by the factor 0.889 (in line with the result from the German study, see above), to obtain corrected point estimates of annual colony survival rates.

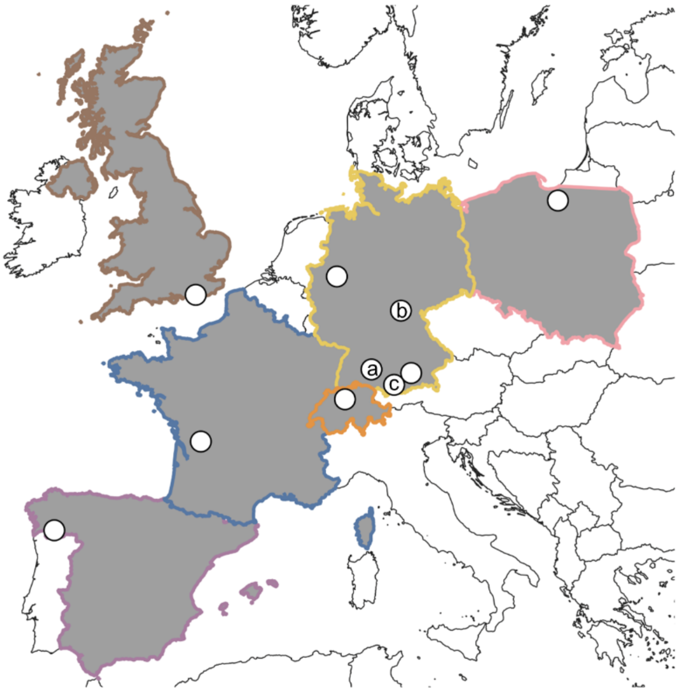

Figure 2. *Map of Europe highlighting six countries with data on wild honeybee colony survival rates (grey) and the respective study regions (dots). One study used data from three different forest regions ("German forest"; locations marked as "a", "b", "c").*

Table 1. *Overview of eight studies on wild honeybee population demography that provide wild colony survival data. The annual colony survival rates (s) are the values used in this study (corrected for potential silent colony turnovers, if necessary; see Methods text).*

Country	**Region**	**Information provided**	**Number of nest sites monitored**	**Study period**	***s***	**Reference**
Germany	Three managed forest regions in southern Germany	Annual survival rate	77	2017–2021	0.106	(Kohl et al. 2022)
Germany	City of Dortmund	Annual survival rate	30		0.121*	(Lang et al. 2022)
Germany	City of Munich	Summer, winter and spring survival rates	107	2016–2023	0.132*	(Rutschmann et al. 2024 Sep 17)
Poland	Northeastern Poland	Proportion of colonies remaining after one and two years	67	2013–2015	0.307	(Oleksa et al. 2013), A. Oleksa, pers. communication
Spain	Comarca de la Limia, Galicia	Annual survival rate	83	2019–2023	0.299	(Rutschmann et al. 2022) Rutschmann & Kohl, unpublished data
France	County of Saintonge	Summer, winter and spring survival rates	140	2018–2021	0.312	(Albouy 2024)
Switzerland	Regions north of the Alps	Annual survival rate	172	2020–2023	0.096	(Cordillot 2024)
England	Southeast England	Summer and winter survival rates	38	2021–2023	0.384*	(Visick & Ratnieks, 2024; O. Visick, pers. communication 2023)

* corrected for a potential silent colony turnover rate of 11.1%

Identifying the IUCN category of threat

The IUCN guideline (2024) lists five non-exclusive criteria that can be used to evaluate into which category of threat a given taxon belongs: (A) observed, estimated, inferred, or projected population size reduction over 10 years or three generations (whichever is longer); (B) small or declining geographic range; (C) a small remaining population *per se*; (D) a very small or spatially restricted remaining population, or (E) a statistical population viability analysis. We here evaluate wild *Apis mellifera* populations based on criterium (A), the change in population size over a 10-year period. (Honeybee colonies start reproducing within their first year of life, typically in their first spring after successful hibernation, and therefore, the duration of three generations is shorter than 10 years). Specifically, we used the criterium

A2ab, a “population reduction estimated […] in the past where the causes of reduction may not have ceased or may not be understood or may not be reversible” based on “(a) direct observation” and “(b) an index of abundance appropriate to the taxon”. Our index is the net reproductive rate (R_0) of the wild subpopulation, which in turn is based on wild colony survival rates observed between 2013 and 2024. To obtain the relative wild honeybee population trend over a hypothetical decade without migration, we calculated ${R_0}^x$, with *x* denoting the year from 0 to 10. Accordingly, we estimated the rate of population change per 10 years as percentage by calculating $({R_0}^{10} - 1) * 100$. Depending on the modelled rate of change, we then classified a population as “Least concern” (reduction: < 30%), “Vulnerable” (reduction: ≥ 30%), “Endangered” (reduction: ≥ 50%), “Critically Endangered” (reduction: ≥ 80%), or “Extinct in the Wild” (reduction: 100%). These calculations were performed for the populations of each of the eight studies, for the six countries represented, and for the overall European wild subpopulation, as represented by the median net reproductive rate of the six countries.

Results

In five out of six European countries, populations of wild honeybees are in decline (Figure 3). In Germany (where data from three independent studies are in close agreement) and in Switzerland, wild honeybee populations must be assumed to (have) entirely disappear(ed) within any given period of 10 years without immigration (projected decline: ~ -100%/decade). In Spain and Poland, wild honeybee populations are predicted to be declining by 66% and 51% per decade, meaning that they are “Endangered” according to IUCN red list criteria. The wild population monitored in France appears to be in moderate decline (-30% per decade); it is at the brink between IUCN Red List criteria “Least Concern” and “Vulnerable”. Only the wild honeybee population in South England appears to have the intrinsic capacity to increase in size (projected increase per decade: +345%), and therefore is categorised as “Least Concern”. The median population change per decade is -60%, meaning the overall wild honeybee population in Europe can be classified as “Endangered”.

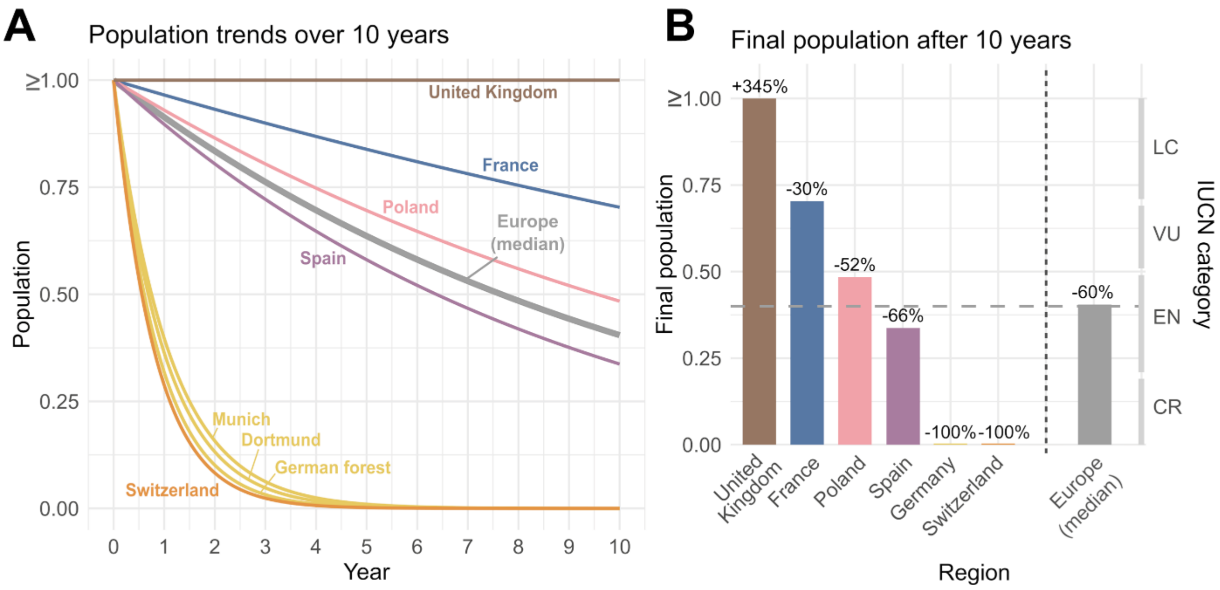

Figure 3. ***A)*** *Projected wild honeybee population trends over hypothetical 10-year-periods. Relative changes in population size are based on net reproductive rates, which in turn rely on observed colony survival rates and an assumed natality rate of 2 swarms per colony per year.* ***B)*** *Wild honeybee population remaining (bars) and their relative change (numbers above bars) after hypothetical 10-year-periods of intrinsic development (without migration) for six European countries and their average. The second y-axis shows the associated IUCN conservation categories: LC= Least Concern, VU= Vulnerable, EN= Endangered, CR=Critically Endangered.*

Discussion

The first Red List category assessment of wild Apis mellifera

It is an established belief that wild populations of *Apis mellifera* have gone extinct in Europe due to habitat loss (Stoeckhert 1933) and/or the introduction of the invasive ectoparasitic mite *Varroa destructor* (starting around 50 years ago) (Thompson et al. 2014; Meixner et al. 2015), the latter being a main driver of colony mortality in apiculture (Traynor et al. 2020). However, motivated by the well-established insight that temperate-adapted honeybees still form viable wild populations in the northeastern United States (reviewed by Seeley, 2019), researchers recently started searching for, and (re-)discovered, wild honeybee colonies in Europe, too. Using data on wild colony survival rates gathered in six countries during the last decade, we modelled how the sizes of these wild honeybee subpopulations would have intrinsically changed over the last 10 years. Our estimate of an average population size reduction of -60%

suggests that the overall wild honeybee subpopulation represents a demographic sink, and therefore, according to IUCN guidelines, wild *Apis mellifera* should be considered "Endangered" in Europe.

Wild honeybee populations still exist but are endangered

Given that many more honeybee colonies live in managed hives than in the wild in Europe (Visick and Ratnieks 2023) and that "wild" colonies can be recent emigrants from apiculture ("feral" colonies) (Kohl et al. 2022), the first obvious question raised by our perspective is whether it is justified to consider European honeybees as "wild" in the first place. There is a qualitative reply ("yes") and a quantitative answer ("it depends") to that question. The honeybee is a native bee in most of Europe; it was a member of the European fauna long before humans. Since the beginning of beekeeping culture about two thousand years ago, there have always been both wild and managed honeybee colonies (Crane 1999). This is testified, for example, by the distinction between "house bees" (managed in hives) and "forest bees" (living in tree cavities) that was common in Germany until the beginning of the 19th century (Schirach 1774). The mating of honeybee queens and drones takes place in free flight and is not usually controlled by beekeepers (Koeniger et al. 2014). Swarms from wild colonies have traditionally been a source of beekeeping operations and swarm emigration from apiaries is not completely prevented. Therefore, we can assume that there has always been a genetic and demographic exchange between wild and managed subpopulations, so one might as well claim that honeybees managed in hives are essentially wild animals (Moritz and Crewe 2018; Seeley 2019). These considerations show that quantitative rules must be applied to formally decide when to use the attribute "wild" for honeybees.

In awareness of the problems that arise when dealing with species that contain managed populations, the IUCN (2024) has determined the following threshold to decide for or against considering a population as "wild": "*Subpopulations dependent on direct intervention are not considered wild, if they would go extinct within 10 years without "intensive" management such as [...] regularly supplementing the population from captive stock to prevent imminent extinction".* The emigration of honeybee swarms from apiaries, even though a natural process, can be regarded as a regular supplementation of the wild population from captive stock. Therefore, it must be modelled how the cohort of free-living colonies would change in size over a hypothetical period of 10 years without such supplementation by feral swarms. That is what we did here. In fact, the first important result of this study is that the overall European free-living honeybee subpopulation, despite likely population size reduction, would clearly not go extinct within a decade, and therefore, formerly qualifies to be considered "wild".

What holds for the whole of Europe, however, is not true for each of the individual populations studied. In fact, our second key insight is that there are remarkable differences in wild population demographics among regions. On the low end of the spectrum, there are the populations studied in Germany and in Switzerland north of the Alps (Kohl et al. 2022; Lang et al. 2022; Cordillot 2024; Rutschmann et al. 2024 Sep 17). Strikingly, these are clearly expected to go extinct within a hypothetical 10-year time window, given their current low net reproductive rates. Conditional upon the discovery of populations with higher average colony survival rates, the honeybee can be considered "Extinct in the Wild" in these countries. On the other end of the spectrum, there is the population studied in southeast England (Visick and Ratnieks 2024), which seems to be stable on its own. Here, the projected excess population reproduction of +345% per decade means that it can act as a demographic source for other populations (including the managed subpopulation), and that it has strong evolutionary potential. Between these extremes are the populations studied in France (Albouy 2024), Poland (Oleksa et al. 2013), and Spain (Rutschmann et al. 2022), which apparently fare much better than the ones in Germany and Switzerland, but also represent demographic sinks.

When referring to the individual populations by their countries of origin, it needs to be highlighted that each is represented by one or a few studies that cover a part of the respective population. Depending on the spatiotemporal scope and the number of nest sites monitored they will be better or worse in representing the average demographics in the respective wider regions, the delineation of which is arbitrary. Wild populations themselves will be structured spatially and represent metapopulations on smaller spatial scales. Wild colonies can occupy more or less favourable habitats, so that there will be source-sink dynamics among such patches (Dias 1996). For example, the rate of decline of the wild honeybee subpopulation in Galicia, Spain, might be overestimated because the respective study was conducted in a landscape dominated by intensive agriculture, not representative of the province, and colony winter survival is significantly lower in agricultural than in adjacent semi-natural habitat (Rutschmann et al. 2022). In fact, most of the available studies were conducted in highly anthropogenically altered agricultural or urban landscapes. Despite the uncertainty in the reliability of the country-level estimates, we believe that the combination of data from eight studies and six countries leads to an informative estimate of the overall wild honeybee population trend. Based on the best data available, we must assume that the overall population of wild honeybees is in decline in Europe. More research and conservation actions are needed to understand, and halt that decline.

Evolutionary significance of wild honeybee subpopulations

The intrinsic decline of wild subpopulations might not be considered a problem insofar as they could be (partly) replenished annually by feral swarms from the managed subpopulation. This view makes sense when considering that wild and managed honeybees are intrinsically the same. However, it lacks appreciation for the potential of populations to evolve. Any pair of wild and managed *colonies* might be difficult to distinguish genetically because subpopulations of wild and managed honeybees will always share alleles. However, this does not contradict the potential that significant genetic differences exist on the level of the *population* due to the accumulation of minor allele frequency changes at many loci. These can reflect adaptive differences to contrasting selection pressures. For example, a lack of medical treatment against *Varroa* mites can select for colonies resisting *Varroa* mites and/or their transmitted viruses in the wild population (Mikheyev et al. 2015; Bozek et al. 2018 Dec 19). Another source of genetic variation is the rate of exchange with other populations. Frequent trade of managed colonies (or queen bees) across countries can lead to a higher proportion of non-native alleles in the managed subpopulation, whereas native genotypes are more likely to be retained in the wild subpopulation (e.g., Malagnini et al., 2023).

Wild honeybee conservation on the species level

Our analysis takes place on the species level and thus does not take into consideration that different subspecies of honeybee exist in Europe. Consequently, a potential argument against our perspective is that many extant honeybee populations are not native and thus do not represent conservation cases in the first place (Carreck 2008). While it is true that beekeepers have altered honeybee populations through the importation of non-native subspecies and subsequent introgressive hybridisation in many regions (De la Rúa et al. 2009; Requier et al. 2019; Espregueira Themudo et al. 2020; Kükrer et al. 2021), wild honeybee conservation should include populations with admixed genetic backgrounds for several reasons.

First, it needs to be highlighted that native honeybee genotypes are unlikely to have been replaced completely in any region, so the issue is generally about the conservation of hybrids rather than merely about non-native subspecies (Moritz 1991). Whether hybrid populations should be protected is a common dilemma in conservation (Allendorf et al. 2001), however, most cases are about between-species rather than within-species hybrids (Piett et al. 2015).

Deciding to neglect subspecies-hybrids in the honeybee would mean applying a different standard compared to other taxa that are assessed on the species level. For example, there is no debate about whether wild populations of the buff-tailed bumblebee (*Bombus terrestris*) should be protected despite evidence of widespread introgression of non-native subspecies via colonies used for greenhouse pollination (Kraus et al. 2011; Seabra et al. 2019).

Besides "only" being subspecies-hybrids, admixed populations of wild honeybees also meet other criteria in favour of their conservation (Wayne and Shaffer 2016). For example, we can expect that many European honeybee subspecies and their hybrids represent ecological equivalents because a main driver of the original differentiation of subspecies was geographic barriers rather than environmental gradients (Ruttner 1988; but see Coroian et al. 2014). In general, we can expect that extant honeybees hybrid populations interact with ecosystems the same way as the original native subspecies did. In case native alleles have a selective advantage over non-native ones, promoting wild hybrid subpopulations can even lead to a progressive increase in the frequency of such alleles in the population (Wayne and Shaffer 2016; Malagnini et al. 2023). In that case, conserving wild honeybees could be understood as a long-term means of conserving native honeybee subspecies.

Finally, in a (hypothetical) context in which local wild populations have gone extinct and are to be re-established (see the German and Swiss cases above), a local, admixed feral founder population may have advantages over a non-local source population comprising pure stock. Regardless of the subspecies or the hybridization level, extant populations may already have evoloved local adaptations (Büchler et al. 2014), and through higher genetic diversity, admixed populations have a higher likelihood of containing alleles that are adaptive in the context of climate change, land use change, and novel parasites (Chan et al. 2019). Apart from these considerations, it needs to be stressed that conserving wild honeybees on the species level does not preclude assessing the conservation status of wild honeybee subspecies, where this is applicable (Oleksa et al. 2013; Browne et al. 2021; Malagnini et al. 2023; IUCN 2024; McCann and McCormack 2024).

A novel perspective on honeybee conservation

The western honeybee has so far been regarded as a problem, rather than a target, of European wild bee conservation (Geldmann and González-Varo 2018; Herrera 2020). In fact, several modern beekeeping practices have been identified to be potentially harmful to wild bee populations (Goulson and Hughes 2015; Lindström et al. 2016; Iwasaki and Hogendoorn 2022; Martínez-López et al. 2022). However, the bees that are potentially most strongly affected by long-distance apiary migrations, high local densities of managed hives and trade in queen honeybees across countries, are the local wild honeybees (Requier et al. 2019; Panziera et al. 2022). The diversity of bees and population sizes of many non-*Apis* bees are known to be in decline (Aizen et al. 2016; Zattara and Aizen 2021), and we demonstrate that wild honeybee subpopulations can be considered to be in decline in Europe, too. Wild honeybee populations likely suffer from the same environmental pressures as other wild bees(Goulson et al. 2015; Rutschmann et al. 2022; Kohl et al. 2023). This contrasts with changes in populations of managed honeybee colonies, which rather reflect socio-cultural and socio-economic developments (Potts et al. 2010; vanEngelsdorp and Meixner 2010; Moritz and Erler 2016).

Given that the number of managed colonies is currently growing (Fig. 4), there is probably an ongoing shift in the relative importance of selection pressure in the overall honeybee population, with conditions under management gaining importance over wild conditions. We do not know which evolutionary role the existence of a wild subpopulation plays in the long-term health and adaptability of the overall honeybee population, but it is likely to be negative (Requier et al. 2019; Panziera et al. 2022). Therefore, the decline of wild honeybees should not only be of concern in conservation but also in apiculture. Furthermore, the perspective that honeybees could be a subject of conservation themselves also has an impact on the conflict between apiculture and non-*Apis* bee conservation (Geldmann and González-Varo 2018; Henry and Rodet 2018): highlighting the existence of a wild honeybee subpopulation in a conservation area is an excellent argument to restricting apiculture in that area.

We suggest that wild honeybee monitoring programs should be continued and adopted in many more regions to allow for better inference of population trends (Seeley 2017; Kohl et al. 2022; Albouy 2024; Moro et al. 2024; Rutschmann et al. 2024 Sep 17). Furthermore, we need to know which factors limit wild honeybee colony survival (e.g. Kohl et al., 2023), and why wild subpopulations fare so much better in some regions compared to others. According to the principle that we can only conserve what we understand, we believe that recognising wild honeybee subpopulations as real and tangible subjects of population demographic studies is a key step in the conservation of this unique component of the European bee fauna.

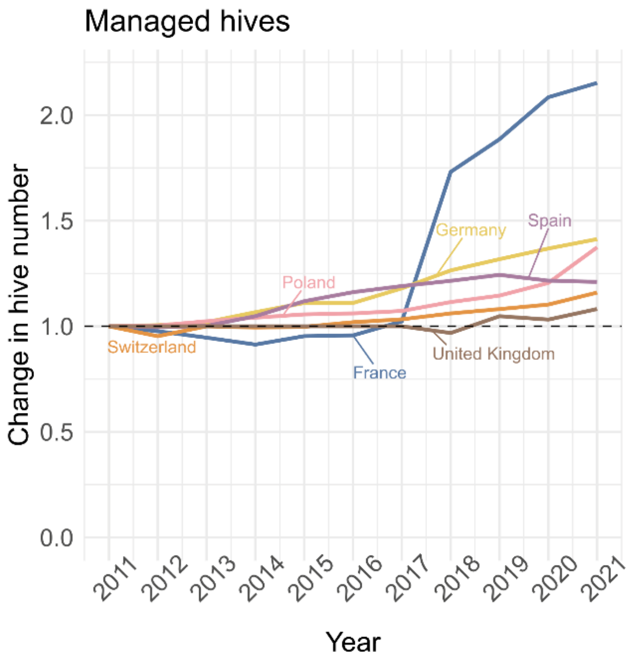

Figure 4: *Relative increase in the number of registered managed honeybee colonies between 2011 and 2021 (or 2017–2021 for UK) in the six countries considered in this study. The number of hives registered in 2011 (or 2017 for UK) is set to "1". Data from the Food and Agriculture Organisation of the United Nations* (FAO 2023) *and the National Bee Unit of the UK (https://www.nationalbeeunit.com/bees-and-the-law/hive-count; date accessed: 27 September 2024).*

Data Availability Statement

The data used for this work are either directly listed or reverenced in the text.

Author contributions

Patrick L. Kohl was involved in conceptualization, methodology, investigation, formal analysis, writing– original draft. Benjamin Rutschmann was involved in conceptualization, methodology, investigation, formal analysis, visualization, writing– review & editing.

Conflict of interest declaration

We declare we have no competing interests.

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