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. New data suggest 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 seven European countries to model their autonomous population changes over ten-year periods, the time frame considered for population evaluation by the International Union for the Conservation of Nature (IUCN). Populations of wild honeybee colonies currently represent demographic sinks in six out of seven countries. With an estimated population decline of 56% per decade, the honeybee

should be considered "Endangered" in the wild in Europe. We believe that the formal recognition and study of honeybee populations beyond apiculture can have far-reaching consequences for the perception of this unique bee species and pollinator conservation in general.

Introduction

The western honeybee, *Apis mellifera,* is among the most abundant flower visitors across its cosmopolitan geographic range (Hung et al., 2018), so its persistence on the species level seems to be of little concern in conservation science. 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 a dozen species, most of which are confined to small distribution areas in (sub-)tropical Asia (Smith, 2021). 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 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 a phylogenetic perspective. Preserving its intra-specific genetic diversity and 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, likely because it is considered an entirely managed, or even domesticated, species, and thus, part of agriculture or the livestock sector (Geldmann & González-Varo, 2018). Unfortunately, such view neglects that there have always been both wild and managed honeybee colonies (Kohl & Rutschmann, 2018; Visick & Ratnieks, 2023; Niklasson et al., 2024). The mating of honeybee queens and drones takes place in free flight and is not usually controlled by beekeepers, and swarms from wild colonies have traditionally been a source of beekeeping operations, while, in turn, swarm emigration from apiaries is never completely prevented. Therefore, there has always been a genetic and demographic continuum between cohorts of wild and managed colonies and there is no scientific basis for a general biological distinction between managed and wild honeybees (Johnson, 2023).

What is typically confounded are the questions whether honeybees are native versus allochthonous on the one hand or living wild versus managed on the other hand. Certain subspecies of honeybee, mainly Italian (*A. m. ligustica*) and Carnolian bees (*A. m. carnica*) are preferred in modern apiculture. They have been introduced to countries outside their native ranges, and, due to a general lack of mating control, have hybridized with the native populations (De la Rúa et al., 2009). However, these commercially desired subspecies and their hybrids are, evolutionary speaking, not generally less wild than other honeybee populations. Furthermore, in most of the introduced regions, the respective native genetic backgrounds have not been completely replaced (Requier et al., 2019). Therefore, where *Apis mellifera* is native as a species, not considering the conservation of wild hybrid populations would mean applying a different standard compared to other taxa that are assessed on the species level. (Off course, considering wild honeybees on the species level, as we do here, does not preclude promoting the conservation of wild honeybees on the subspecies level, where this is applicable (e.g., Valentine et al., 2025).)

Apart from the question whether the attribute "wild" is appropriate for free-living colonies of honeybee within their native range, a simple reason for their neglect in conservation is the widespread belief that they have gone extinct. Due to habitat loss and/or the introduction of the invasive ectoparasitic mite *Varroa destructor* (starting around 50 years ago), the latter being a main driver of colony mortality in apiculture (Traynor et al., 2020), there would simply be no wild subpopulations left to protect. Unfortunately, there is no data documenting such alleged extinction in the wild (Kohl & Rutschmann, 2018), which is why *Apis mellifera* was listed as "Data deficient" in the "European Red List of Bees" by the International Union for the Conservation of Nature (IUCN) as of 2014 (Nieto et al., 2014). Throughout the last decade, however, motivated by the insight that temperate-adapted honeybees still form viable wild populations in their introduced range in the northeastern United States (reviewed by Seeley, 2019), researchers have started searching for, and (re-)discovered, wild honeybee colonies in Europe (Oleksa, Gawroński & Tofilski, 2013; Kohl & Rutschmann, 2018; Requier et al., 2020; Browne et al., 2021; Moro et al., 2021; Lang, Albouy & Zewen, 2022; Rutschmann et al., 2022; Albouy, 2024; Rutschmann, Remter & Roth, 2024; Visick & Ratnieks, 2024). The average colony density was estimated to be 0.26 colonies per km^2, equivalent to about 5.5 million colonies, 17.8% of the overall European honeybee population (which comprises ca. 25.4 million managed hives) (Visick & Ratnieks, 2023).

These figures suggest that wild honeybees are still ecologically and evolutionary relevant. 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 in Europe. 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 periodically 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).

Given that a distinction between wild and managed honeybees can generally be based only on the current mode of living of their colonies rather than on morphology or genetics, the practical problem arises of how to specifically asses the population trends of wild subpopulations. Even if actual nesting sites of wild honeybees are known, directly assessing temporal changes in the number of colonies inhabiting 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, masking the potential autonomous population trend of the existing wild subpopulation. For example, approximately 10% of trees with black woodpecker (*Dryocopus martius*) cavities are occupied by honeybees in managed forests in Germany 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, Rutschmann & Steffan-Dewenter, 2022).

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 whether a population should be considered "wild" in the first place and thus be assessed: "*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, though a natural process, can be regarded as a regular supplementation of the wild population from captive stock. Therefore, the relevant question for determining whether a cohort of free-living colonies deserves the attribute "wild subpopulation" and whether its conservation should be assessed is, "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, Remter & Roth, 2024). 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 seven European countries to model how their populations would change autonomously over ten-year periods. Based on these projected population trends, we suggest an informed IUCN Red List category for the species in Europe.

Methods

Framework for studying the demography of wild honeybee populations

There is generally no physical or genetic barrier between managed (Figure 1a) and wild honeybee colonies (Figure 1b) and, contrary to common misconception, no stable "breeds" of domesticated honeybees exist (Seeley, 2019). We therefore define wild *Apis mellifera* colonies based on their mode of living as colonies that are ownerless and unmanaged and live in their natural comb nests, at sites they have occupied themselves (Rutschmann, Remter & Roth, 2024) (see supplementary information for further information).

To study the population demography of wild honeybee colonies, it is practical to consider regional honeybee populations as metapopulations consisting of cohorts ("subpopulations") of managed and wild colonies (Figure 1 c) (Kohl, 2023; Rutschmann, Remter & Roth, 2024). The size of the wild cohort is affected by immigration, emigration, survival, and natality. Immigration occurs when managed colonies swarm, disperse from their home apiary and occupy a cavity on their own, thus becoming 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 assume that this process is negligible in most regions since beekeepers usually obtain new colonies by splitting their own stock or trading with other beekeepers.) To understand how the size of the wild subpopulation would change intrinsically, the survival (s) and the natality (b) (i.e., reproduction) of the colonies that are already members of that cohort need to be considered. Given the annual survival and natality rates, the net reproductive rate (R_0) describes how the population would change from year to year if no immigration occurred, with values < 1 denoting population decline and values > 1 denoting population stability or increase. Since temperate honeybee colonies typically start reproducing after completing their first year (i.e., from the age of 1 year) and colonies are hermaphrodites (all colonies can, in principle, produce swarms with queens [female colony reproduction] besides drones [male colony reproduction]), the net reproductive rate of a wild honeybee subpopulation is (Kohl, Rutschmann & Steffan-Dewenter, 2022):

$$R_0 = s + s * b.$$

This index is the basis of our wild honeybee population trend projections.

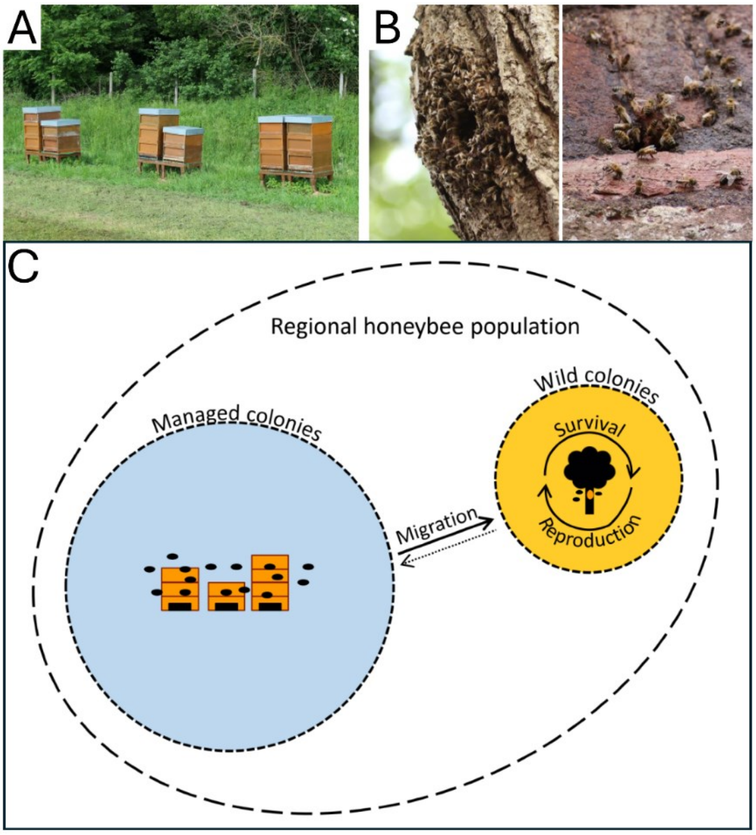

Figure 1. ***A)*** *Apiary with honeybee colonies managed in movable-frame hives.* ***B)*** *Examples of typical wild honeybee nesting sites: tree cavity (left) and hollow space in a wall (right).* ***C)*** *Metapopulation model of managed and wild honeybee colonies. Managed and wild colonies belong 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 current trends of populations of wild honeybee colonies

The annual survival rate in a population of wild honeybee colonies can be empirically studied by making repeated surveys of known nest sites (Seeley, 2017). Nine monitoring studies were available that provided information on the occupation histories of a total of 698 nesting sites of wild honeybee colonies in seven European countries gathered over several years (Figure 2, Table 1): Poland (Oleksa et al. 2013; A. Oleksa, pers. communication 2024), Germany (three studies) (Lang, Albouy & Zewen, 2022; Kohl, Rutschmann & Steffan-Dewenter, 2022; Rutschmann, Remter & Roth, 2024), France (Albouy, 2024), Spain (Rutschmann et al. 2022; Rutschmann & Kohl, unpublished data), England (Visick & Ratnieks, 2024; O. Visick, pers. communication 2025), Switzerland (Cordillot, 2024) and Luxembourg (J. Park & R. Dammé, pers. communication 2025). For each of the studied wild populations and for each country, we derived a point estimate of the average annual colony survival rate (s_{est}) from the available data (see supplementary information for details). The natality rate of wild honeybee colonies (the number of swarms produced per colony per year) is difficult to determine in the field. We therefore 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 (see Rutschmann, Kohl & Steffan-Dewenter, 2024 and references therein). However, it is well known that the swarming rate can vary strongly between years due to differences in weather, with zero to four swarms per colony being typical. Although no direct data on between-year variation in colony-level swarming rate was available, we had information on the annual variation in cavity re-occupations by wild colonies in Germany (Kohl, Rutschmann & Steffan-Dewenter, 2022) and Spain (Rutschmann et al. 2022; Rutschmann & Kohl, unpublished data). Assuming that such rates of nest re-occupation closely correlate with the average colony-level swarming rate in the respective year and region (since new nests are founded by swarms), we used the observed coefficient of variation in the annual nest re-occupation rate (12.5%), a dimensionless number, to derive a realistic level of annual variation in the natality rate. Specifically, we simulated environmental stochasticity in the annual natality rate (b_{sim}) by drawing from a normal distribution truncated between 0 and 4 (the minimum and maximum number of swarms per colony expected), with a mean of 2 and a coefficient of variation of 0.125 (standard deviation: 0.25).

Using estimated survival and simulated natality rates, we then simulated annual net reproductive rate for each studied wild population and country as:

$$R_{0\_sim} = s_{est} + s_{est} \times b_{sim}$$

The relative wild honeybee population trend over a hypothetical decade without migration is given as ${R_{0\_sim}}^{x}$, with x denoting the year from 0 to 10, and with R_{0_sim} randomly varying among years. Accordingly, we estimated the rate of population change per 10 years as percentage by calculating $({R_{0\_sim}}^{10} - 1) * 100$. These steps were repeated 10000 times for each of the eight studied populations to account for random variation in population fate due to stochasticity in the swarming rate. We present the mean and the 90% confidence interval (CI) of the population trend projections for each studied population, for each of the seven countries, and for the whole of Europe (using the median of the seven country-level estimates of the survival rate). In accordance with IUCN guidelines (IUCN 2024), we then used the mean projected population change per decade to classify a population as "Least concern" (reduction: < 30%), "Vulnerable" (reduction: ≥ 30%), "Endangered" (reduction: ≥ 50%), "Critically Endangered" (reduction: ≥ 80%), or "Extinct in the Wild" (reduction: 100%) (see supplementary information for details).

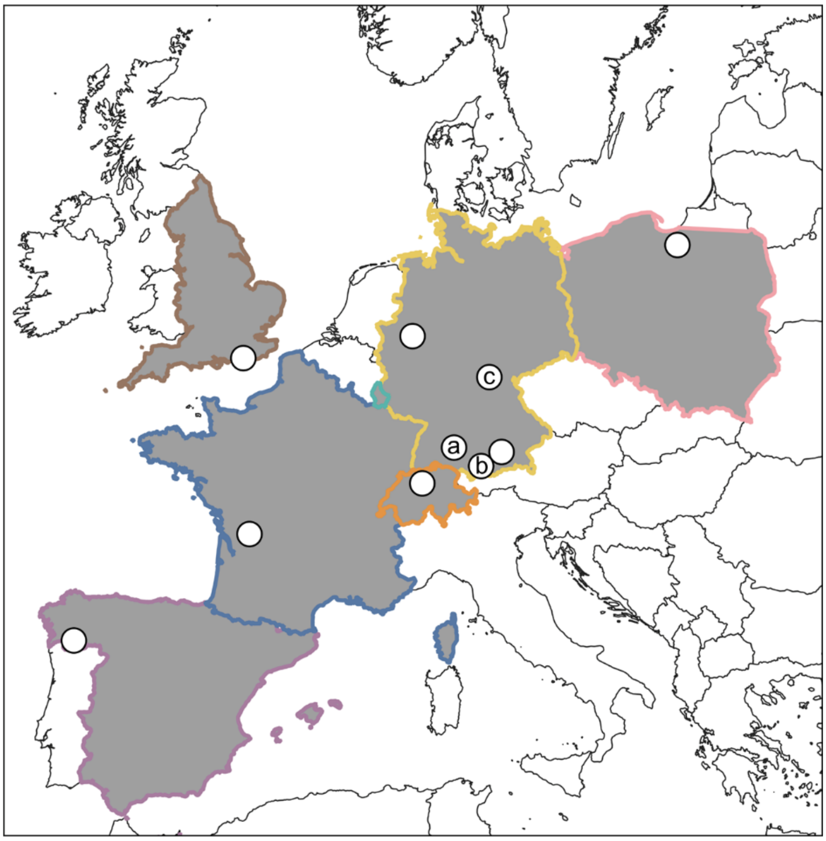

Figure 2. *Map of Europe highlighting seven countries with data on wild honeybee colony survival rates (grey) and the respective study regions (dots, except for Luxembourg). One*

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_{est}) are the values used in this study (corrected by us for potential silent colony turnovers, if necessary; see supplementary information).*

Country	**Region**	**Information provided**	**Number of nest sites monitored**	**Study period**	s_{est}	**Reference**
Germany	Three managed forest regions in southern Germany	Annual survival rate	77	2017–2021	0.106	(Kohl, Rutschmann & Steffan-Dewenter, 2022)
Germany	City of Dortmund	Annual survival rate	30	2018–2021	0.121	(Lang, Albouy & Zewen, 2022, Table 4 therein)
Germany	City of Munich	Summer, winter and spring survival rates	107	2016–2023	0.133	(Rutschmann, Remter & Roth, 2024, p. 14 therein)
Poland	Northeastern Poland	Proportion of colonies remaining after one and two years	67	2013–2015	0.307	(Oleksa, Gawroński & Tofilski, 2013), A. Oleksa, pers. communication 2024
Spain	Comarca de la Limia, Galicia	Annual survival rate	37	2019–2023	0.293	(Rutschmann et al., 2022) Rutschmann & Kohl, unpublished data
France	County of Saintonge	Summer, winter and spring survival rates	140	2018–2021	0.318	(Albouy, 2024, p. 623 therein)
Switzerland	Switzerland Regions north of the Alps	Annual survival rate	106	2020–2023	0.096	(Cordillot, 2024, p. 107 therein)
England	Southeast England	Annual survival rate	61	2021–2024	0.394	(Visick & Ratnieks, 2024; O. Visick, pers. communication 2025)
Luxembourg	Luxembourg	Summer, winter and spring survival rates	73	2019-2025	0.316	(J. Park & R. Dammé, pers. communication 2025)

Results

In six out of seven European countries, populations of wild honeybees were projected to be 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 disappear within 10 years without immigration (projected decline per decade [upper, lower 90% CI]: -100% [-100%, -100%]). In Spain and Poland, wild honeybee populations were projected to be declining by -78% [-68%, -87%] and -56% [-35%, -73%] per decade, meaning that they are "Endangered" according to IUCN red list criteria. The wild populations monitored in Luxembourg and France appear to be in moderate decline (-41% [-13%, -64%] and -38% [-7%, -61%] per decade); they can be classified as "Vulnerable". Only the wild honeybee population in South England appears to have the intrinsic capacity to increase in size (projected increase per decade: +432% [+692%, +230%]) and therefore is categorised as "Least Concern". The median population change per decade is -56% [-34%, -73%], meaning the overall wild honeybee population in Europe can be classified as "Endangered".

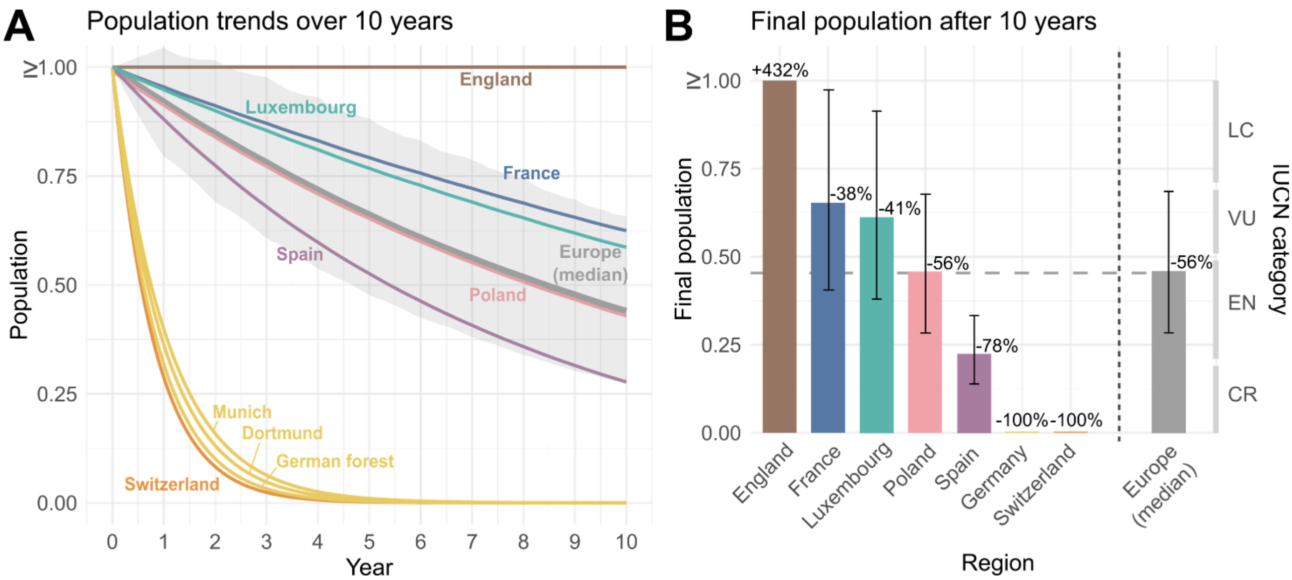

Figure 3. *A) Projected wild honeybee population trends over hypothetical ten-year periods for nine studied populations and for the whole of Europe. Relative changes in population size are based on net reproductive rates, which in turn rely on observed colony survival rates and an assumed average natality rate of two swarms per colony per year. Lines describe the mean trends based on 10000 simulations for each population. The grey shaded area describes the 90% confidence interval for Europe.* ***B)*** *Wild honeybee population remaining (means and 90% confidence intervals based on 10000 simulations) and their mean relative change (percentages) after hypothetical ten-year periods of intrinsic development (without migration) for seven European countries and the whole of Europe. The second y-axis shows the associated IUCN conservation categories: LC = Least Concern, VU = Vulnerable, EN = Endangered, CR =Critically Endangered. (The simulations for Germany were run using the*

average of the colony survival rates of the three studies. Confidence intervals for England, Germany and Switzerland are not visible because they are outside the y-axis range.)

Discussion

Using data on wild colony survival rates gathered in seven countries during the last decade, we modelled how the sizes of wild honeybee subpopulations would have intrinsically changed over a hypothetical period of ten years. While our estimate of a median population size reduction of -56% suggests that the overall wild honeybee subpopulation represents a demographic sink, a key insight is that it would clearly not have gone completely extinct within a decade. Therefore, on the European level, the cohort of wild *Apis mellifera* can be formally considered a "wild subpopulation" according to IUCN guidelines, and the assessment of its population trend for the Red List of bees is justified.

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 (Lang, Albouy & Zewen, 2022; Kohl, Rutschmann & Steffan-Dewenter, 2022; Cordillot, 2024; Rutschmann, Remter & Roth, 2024). Strikingly, these are clearly expected to go extinct within a hypothetical ten-year time window, given their low net reproductive rates. Therefore, 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 & Ratnieks, 2024), which seems to be stable on its own. Here, the projected excess population 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), Luxembourg (J. Park & R. Dammé, pers. communication 2025), Poland (Oleksa, Gawroński & Tofilski, 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 only. Depending on the spatiotemporal scopes, studies will be better or worse in representing the average demographics in the respective wider regions, the delineation of which is arbitrary. It also needs to be considered that wild subpopulations will be structured spatially, and since they can occupy more or less favourable habitats, there will be source-sink dynamics among such patches (Dias, 1996). For example, the study of the wild honeybee subpopulation in Galicia, Spain, was conducted in a landscape dominated by intensive agriculture, not representative of the province. Since colony winter survival is significantly lower in agricultural than in adjacent semi-natural habitats (Rutschmann et al., 2022), we might have overestimated the rate of decline for that population. Despite the uncertainty in the reliability of the country-level estimates, we believe that the combination of data from nine studies and seven countries lead 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.

One might argue that this intrinsic decline is not a problem insofar as the wild subpopulation 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 significant genetic differences to evolve between managed and wild populations due to the accumulation of minor allele frequency changes at many loci. Such variation can reflect adaptations to contrasting selection pressures or different demographic histories. For example, a lack of medical treatment can select for colonies resisting *Varroa* mites and/or their transmitted viruses in the wild population (Mikheyev et al., 2015), while frequent trade of managed colonies (or queen bees) across countries can lead to a higher proportion of non-native alleles in the managed compared to the wild subpopulation. In fact, beekeepers have largely altered managed 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, Kence & Kence, 2021). If native alleles have a selective advantage over non-native ones, promoting wild honeybee subpopulations can even lead to a progressive increase in the frequency of such alleles in the overall population (Wayne & Shaffer, 2016). In that case, conserving wild honeybee populations could be understood as a long-term means of conserving native honeybee subspecies.

The perspective suggested by the present analysis of explicitly conserving wild honeybee populations is currently not implemented. Usually, no difference is made between wild and managed honeybee colonies and the species is more often regarded as a problem, rather than a target, of European wild bee conservation (Geldmann & González-Varo, 2018). However, wild honeybee subpopulations likely suffer from the same environmental pressures as non-*Apis* wild bees (Goulson et al., 2015; Rutschmann et al., 2022; Kohl et al., 2023). In fact, local wild honeybees can be the bees most directly affected by long-distance apiary migrations, high densities of managed hives, and the trade of queen honeybees across countries (Requier et al., 2019; Panziera et al., 2022; Martínez-López, Ruiz & De La Rúa, 2022). Given that the number of managed colonies is currently growing (see supplementary information, figure S1), 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 positive (Requier et al., 2019; Panziera et al., 2022). Therefore, the decline of wild honeybees should not only be of concern for insect conservation but also for apiculture and crop pollination in agriculture. 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 & González-Varo, 2018; Henry & Rodet, 2018; Beaurepaire et al., 2025). For example, the existence of a wild honeybee subpopulation in a conservation area is an excellent argument for 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, Rutschmann & Steffan-Dewenter, 2022; Albouy, 2024; Moro et al., 2024; Rutschmann, Remter & Roth, 2024). 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.

Data Availability Statement

The data used for this work are referenced in the main text.

Author contributions

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

Conflict of interest declaration

We declare we have no competing interests.

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Supplementary information for

European wild honeybee populations are endangered

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Managed honeybee population trends

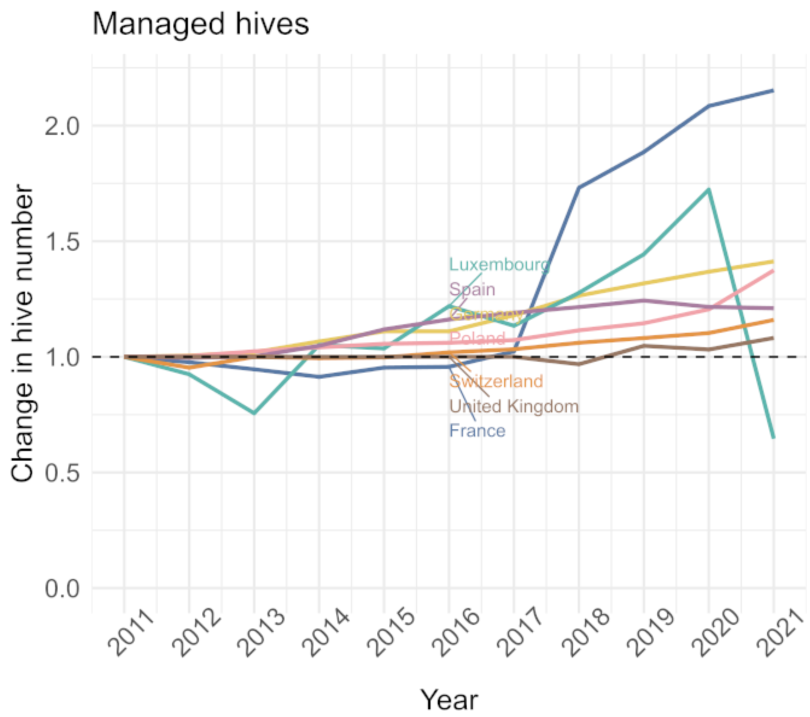

Figure S1: *Relative increase in the number of registered managed honeybee colonies between 2011 and 2021 in the seven European countries considered in this study (2017–2021 for UK). The number of hives registered is set to "1" in 2011 (or 2017 for UK). Data from the Food and Agriculture Organisation of the United Nations* (FAO, 2023) *and the National Bee Unit of the UK (*[*https://www.nationalbeeunit.com/bees-and-the-law/hive-count*](https://www.nationalbeeunit.com/bees-and-the-law/hive-count)*; date accessed: 27 September 2024).*

Notes on the definition of wild honeybee colonies

We here considered all colonies of *Apis mellifera* as "wild" that are ownerless and unmanaged and live in their natural comb nests at sites they have occupied themselves. Therefore, our definition is solely based on the colonies' current mode of living, regardless of whether they, or their ancestors, have a history of management. We think that this is the most useful definition given that there has always been a genetic and demographic exchange between wild and managed subpopulations. The western honeybee is a native bee in most of Europe and 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), so there is no genetic barrier between wild and managed subpopulations. Furthermore, swarms from wild colonies have traditionally been a source of beekeeping operations and swarm emigration from apiaries is not completely prevented so there is frequent migration between wild and managed cohorts. In other publications, what we refer to as "wild 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" (Daniels & Bekoff, 1989)) or that the population under consideration was introduced by humans at some point in history (in case of the Americas, Australia and New Zealand). Note that we here refer to all wild-living *colonies* of honeybee as "wild" but use the IUCN's demographic criteria (no extinction within 10 years, see main text) to test whether a *population* of wild-living colonies should be considered a "wild subpopulation".

Sources of wild colony survival data

We consulted eight studies representing six European countries that yielded information on wild colony survival rates. 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, Rutschmann & Steffan-Dewenter, 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 information on the *annual* survival was not provided directly, we obtained it by multiplying information on seasonal survival rates (i.e., summer, winter, spring survival). In the cases of the studies from Dortmund (Lang, Albouy & Zewen, 2022) and Munich (Rutschmann, Remter & Roth, 2024), the original study had not accounted for unobserved colony turnovers during the swarming season, and therefore, we further multiplied the “apparent” annual colony survival rates by the factor 0.889 (in line with the result from the other German study, see above), to obtain corrected point estimates of annual colony survival rates.

Notes on the IUCN category of threat and population projections

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. 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 2025. All calculations for the population projections as detailed in the main text were conducted in R version 4.4.2 (R Core Team, 2024).

As shown by the following considerations, evaluating population change over 10 years makes sense because this approximately matches the time of three consecutive generations in honeybees (it is *colonies,* not individual worker or queen bees that is the unit of interest here). According to the IUCN definition (2024),

> “*Generation length is the average age of parents of the current* [age] *cohort (i.e., newborn individuals in the population). Generation length therefore reflects the turnover rate of breeding individuals in a population. Generation length is greater*

than the age at first breeding and less than the age of the oldest breeding individual, except in taxa that breed only once. Where generation length varies under threat, such as the exploitation of fishes, the more natural, i.e. pre-disturbance, generation length should be used."

Temperate-adapted honeybee colonies usually start reproducing just after having completed their first year of life, i.e. in the swarming season following their first winter survival, and they are expected to produce swarms every year until death. Therefore, the generation length of honeybee colonies is equal to the average age of established colonies (those having completed at least one year) at the time of swarming. Like average colony lifespan, average age of reproduction of established colonies can be calculated based on data of annual colony survival rates: by summing over a range of plausible age classes the products of age in years times the probability of dying at that age. (See Kohl, Rutschmann & Steffan-Dewenter (2022) for corrected versions of the formulas initially proposed by (Seeley, (1978)).

In the following formula for generation length (*G*), *A* is colony age in number of completed years, and *e* is the annual probability of survival for established colonies:

$$G = \sum_{A=1}^{10} A(e)^{A-1}(1-e)$$

We arbitrarily restrict the summation to the maximum age class of ten because we think it uncommon that colonies live longer (Kohl, Rutschmann & Steffan-Dewenter, 2022). Currently, there is detailed data on age-related colony survival probability from only two self-sustaining populations of European honeybees, one living in temperate forests of New York State, USA (Seeley, 2017), and one in Wyperfield National Park in Southeastern Australia (Oldroyd et al., 1997) (for an overview see table 1 in Kohl, Rutschmann & Steffan-Dewenter, 2022). Since the survival statistics for these populations are very similar, we assume that they reflect temperate honeybees' "natural" demographics. In New York State, the annual survival rate of established colonies was found to be 0.79, so generation length is 3.36 years. In Wyperfield, annual survival rate of established colonies was found to be 0.76, leading to the estimated generation length of 3.26 years. Accordingly, the duration of three consecutive generations is wild honeybee populations is approximately 10 years (10.09 years and 9.78 years, respectively).

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