The wild honeybee population of Europe is in decline: evidence from monitoring studies

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Abstract

Populations of wild western honeybees (*Apis mellifera*) have been neglected because the species has been considered to consist of managed colonies only. New data suggest that wild colonies (still) make up at least one sixth of the overall European honeybee population. Their population trends can be evaluated like those of other species, albeit with some methodological adjustments to account for the bias introduced by swarms emigrating from apiaries. We used data on the annual survival rates of free-living colonies from seven European countries and assumed a realistic swarming rate of two swarms per colony per year to estimate the intrinsic growth rates of wild populations. Observed variation in nest site reoccupation rates among years was taken as a measure of environmental stochasticity in population performance. We then simulated the autonomous wild population changes over

ten-year periods, the time frame considered for assessments by the IUCN. Wild honeybee populations still exist in five of the seven countries with data, but they currently act as demographic sinks in most regions. With an estimated median population decline of 56% per decade, the honeybee can be considered "Endangered in the wild" at the European level. (For future updates on the population status see https://doi.org/10.5281/zenodo.18424042.)

Introduction

The western honeybee, *Apis mellifera,* is one of the most abundant flower visitors globally (Hung et al., 2018), so its persistence at 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. Furthermore, *Apis mellifera* is special because it is the only extant *Apis* species naturally occurring outside of Asia. Preserving its intra-specific genetic diversity and potential to evolve 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). On the one hand, this view is based on the inaccurate conflation of management and domestication. On the other hand, it neglects the fact that managed honeybee colonies have existed in sympatry with wild colonies since the beginning of apiculture about two thousand years ago (Kohl & Rutschmann, 2018; Niklasson et al., 2024; Visick & Ratnieks, 2023). The mating of honeybee queens and drones takes place in free flight and is not usually controlled by beekeepers (Koeniger et al., 2014), and swarms from wild colonies have traditionally been a source of beekeeping operations, while, in turn, swarm emigration from apiaries is never completely prevented (Crane, 1999). Due to a genetic and demographic continuum between both groups of colonies, there is no scientific evidence for a general biological distinction between managed and wild honeybees (Johnson, 2023).

The wild versus managed dichotomy is often confounded with the question of whether honeybees are native versus allochthonous. 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). Furthermore, some bee breeders intentionally create crosses between different subspecies to achieve short-term heterosis. These hybrids are commonly referred to as “Buckfast bees” after the first crosses intentionally created at Buckfast Abby in England starting in the 1920s (Costa et al., 2025). Nevertheless, from an evolutionary perspective, the subspecies overrepresented in apiculture and their hybrids are not intrinsically less wild than other honeybee populations.

Apart from doubts about whether the attribute “wild” is appropriate for free-living colonies of honeybee, a simple reason for the neglect of wild populations in conservation is the widespread assumption that they had long since become extinct anyway (Meixner et al., 2015; Stoeckhert, 1933). 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, researchers have started searching for, and (re-)discovered, wild honeybee colonies in Europe (Albouy, 2024; Browne et al., 2021; Kohl & Rutschmann, 2018; Lang et al., 2022; Moro et al., 2021; Oleksa et al., 2013; Requier et al., 2020; Rutschmann et al., 2022; Rutschmann, Remter & Roth, 2025; 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), their (re-)discovery provides the opportunity to make the first informed assessment of their conservation status in Europe. Determining a species’ Red List category is important since it helps to objectively decide whether strategies to promote 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).

As it is not generally possible to distinguish wild-living and managed honeybees based on morphology or genetics, the practical problem arises of how to specifically assess wild population trends. Even if the nesting sites of wild honeybees are known, directly assessing temporal changes in the number of colonies inhabiting an area still does not suffice: 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 (hypothetical) intrinsic population trend of the existing wild cohort. 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 et al., 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" 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, 2025). The (hypothetical) intrinsic change of the wild subpopulation per unit time can then be expressed by its finite growth rate (λ) (Krebs, 2013), which in turn can be derived from the average survival and reproductive rates of its members. Here, we use available data on free-living colony survival rates from seven European countries to model how their populations would change intrinsically over ten-year periods. Based on these projected population trends, we suggest an informed conservation category for the species in Europe.

Methods

Framework for studying the demography of wild honeybee populations

Based on what we know about honeybee biology, there is no general physical or genetic barrier between groups of managed (Figure 1a) and wild honeybee colonies (Figure 1b), and, contrary to common misconception, no stable "breeds" of honeybees exist (Johnson, 2023; Seeley, 2019). We therefore define wild *Apis mellifera* colonies based on their mode of living as colonies that are unmanaged and live in their natural comb nests at sites they have occupied themselves (Rutschmann, Remter & Roth, 2025) (see supplementary information for further information).

Since honeybees are eusocial insects, colonies can be viewed as superorganisms (Helanterä, 2016; Seeley, 1989), and colonies, not individual bees, are the relevant unit in population studies (Seeley, 2017). Colony reproduction is achieved via fission during the swarming season, whereby a fraction of the workers and a queen leave the old nest as a swarm to occupy a new nesting site. Newly founded colonies typically start reproducing in the next swarming season (at the age of approx. one year). Since young queen bees take over egg-laying in established colonies, colonies are rejuvenated annually and it is reasonable to assume that there is little effect of colony age on survival and reproduction after new colonies have passed the difficult establishment phase (Seeley, 1985).

To study the population demography of wild honeybee colonies, it is practical to consider regional honeybee populations as metapopulations comprising cohorts ("subpopulations") of managed and wild colonies (Figure 1c) (Kohl, 2023; Rutschmann, Remter & Roth, 2025). The size of a cohort of wild colonies is affected by immigration, emigration, survival, and reproduction (colony fission by swarming). 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 average annual survival (s) and birth rate (b) (i.e., the swarming rate) of the colonies that are already members of that cohort need to be considered. Colony survival and swarming determine the annual population growth rate λ:

$$\lambda = s + s * b.$$

This index describes how the population of 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 (see Kohl et al., 2022, where the same statistic was referred to as the net reproductive rate R_0). The annual rate of intrinsic population growth λ is the basis for our projections of wild honeybee population trends.

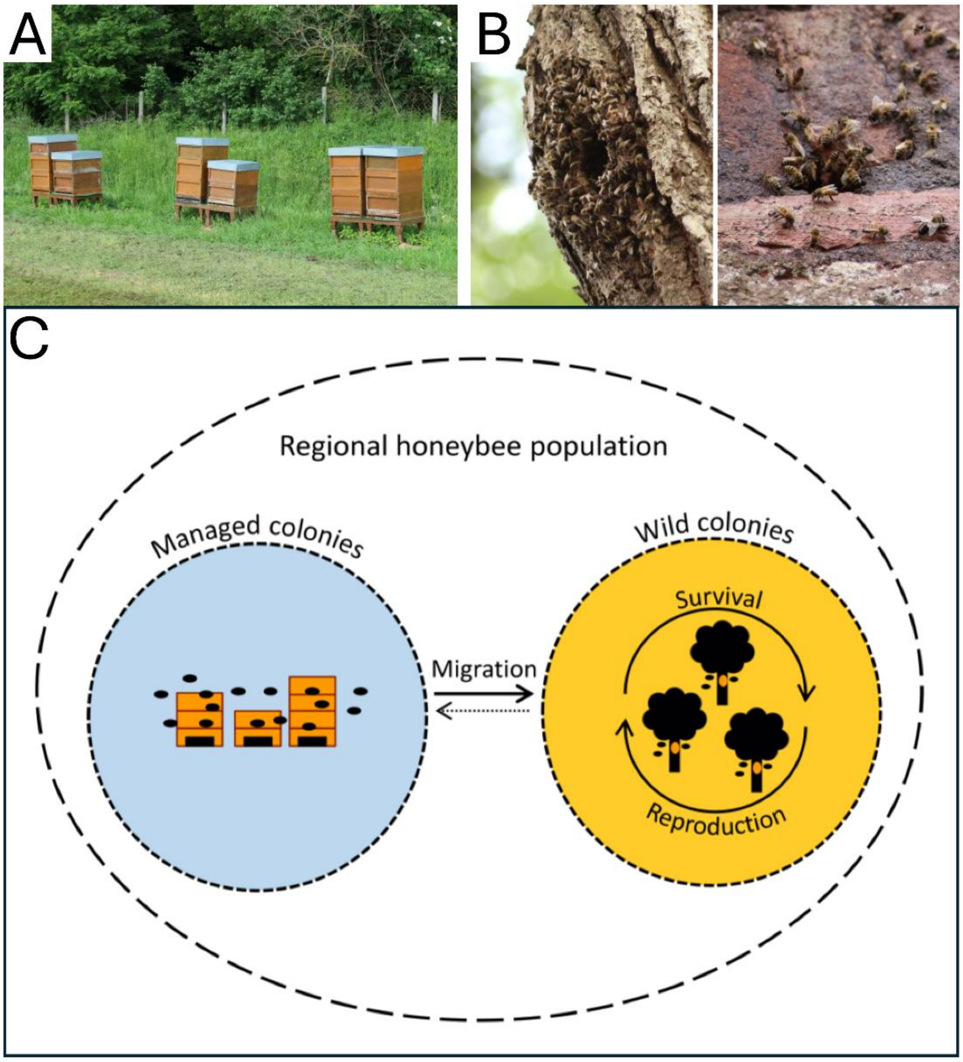

Figure 1. ***A)*** *Apiary with honeybee colonies managed in movable-frame hives.* ***B)*** *Examples of typical wild honeybee nesting sites: tree cavity (left) and hollow space in a wall (right).* ***C)*** *Metapopulation model of managed and wild honeybee colonies. Managed and wild colonies belong to one biological population; there is 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) is 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 700 nesting sites of wild honeybee colonies in seven European countries. The studies were conducted between 2013 and 2025, and within that period, they covered time windows of two to seven years (Figure 2, Table 1). 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), however, is difficult to determine in the field. We therefore assumed that wild colonies produce, on average, $b = 2$ swarms per year based on studies examining the reproductive behaviour of unmanaged honeybee colonies living in hives with limited volume (see Rutschmann, Kohl, et al., 2025, and references therein).

The average annual survival observed in a given population (s_{est}), and the assumed annual swarming rate (b) can be combined to calculate simple estimates of the annual population growth rate (λ_{est}), which, in turn, can be used to predict expected population growth over longer periods. Beyond such predictions of the mean, we wanted to obtain information on the uncertainty of population change given environmental stochasticity. For example, honeybee populations are affected by the weather conditions (e.g., Switanek et al., 2017), both directly and via its effect on floral resources. An appropriate indicator of the degree to which wild popualtions respond to such environmental fluctuations is the annual variation in the reoccupation rate of vacant nesting sites – information which typically comes with monitoring data. The number of new swarms occupying nest sites is affected by the previous survival of established colonies and their current swarming rate, and therefore, variation in nest reoccupation should mirror variation in annual net population growth, which is also a function of both survival and swarming. We simulated environmental stochasticity by drawing annual population growth rates from a normal distribution with mean λ_{est} (specific to each studied population) and a common coefficient of variation $CV = 0.132$ derived from the robust coefficient of variation (RCV) in nest site reoccupation (see Supplementary Material for details):

$$\lambda_{sim,y} \sim \mathcal{N}(\mu = \lambda_{est}, \sigma^2 = (\lambda_{est} \times 0.132)^2)$$

The relative population size over the course of a hypothetical decade without migration is given as

$$\prod_{y=1}^{10} \lambda_{sim,y},$$

with y denoting the year (1 to 10) and with $\lambda_{,y}$ randomly varying among years. The simulations were repeated 10000 times for each of the nine studied populations. 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).

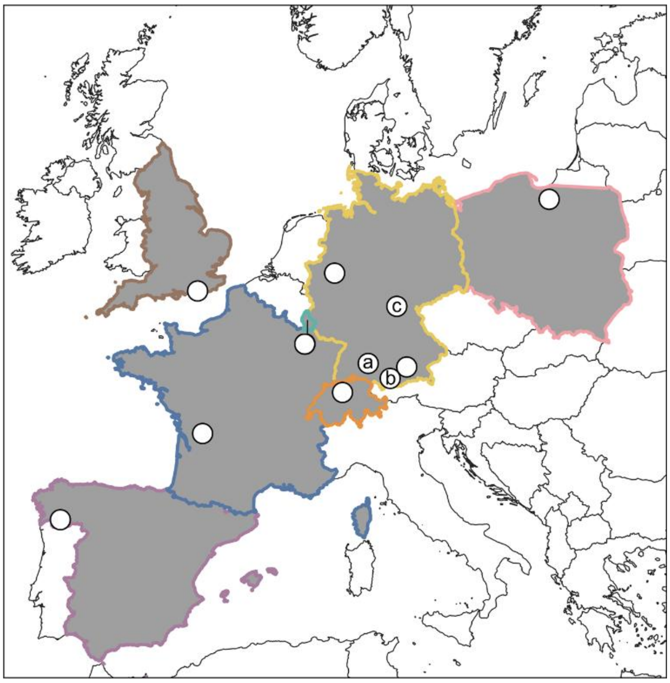

Figure 2. *Map of Europe highlighting seven countries with data on wild honeybee colony survival rates (grey) and the respective study regions (dots). For Germany, three studies were available, with one using data from three different forest regions (“German forest”; locations marked as “a”, “b”, “c”).*

Table 1. *Overview of nine monitoring studies on wild honeybee populations that provide wild colony survival data (ordered according to the year in which monitoring began). The estimated annual colony survival rates (s_{est}) are the values used in this study. If necessary, survival rates were corrected for potential "silent colony turnovers", the unobserved death of a colony followed by the quick reoccupation of its nest site by a new colony during the swarming season (see supplementary information for details).*

Country	Region	Information provided	Number of nest sites monitored	Study period	s_{est}	Reference
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 2024)
Germany	City of Munich	Summer, winter and spring survival rates	107	2016–2023	0.133	(Rutschmann, Remter & Roth, 2025)
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	2018–2021	0.121	(Lang, Albouy & Zewen, 2022, Table 4 therein)
France	County of Saintonge	Summer, winter and spring survival rates	140	2018–2021	0.318	(Albouy, 2024, p. 623 therein)
Spain	Comarca de la Limia, Galicia	Annual survival rate	37	2019–2023	0.286	(Rutschmann et al., 2022; Rutschmann & Kohl, unpublished data)
Luxembourg	Luxembourg	Summer, winter and spring survival rates	73	2019–2025	0.316	(J. Park & R. Dammé, pers. communication 2025)
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	63	2021–2024	0.370	(Visick & Ratnieks, 2026)

Results

In six out of seven European countries with data, 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 are highly likely to disappear within 10 years without immigration according to the simulations (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% [-61%, -90%] and -56% [-21%, -80%] per decade, meaning that they would fall into the "Endangered" category according to IUCN red list criteria. The wild populations monitored in Luxembourg and France appear to be in moderate decline (-41% [+7%, -73%] and -37% [+15%, -72%] per decade); they would 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: +346% [+717%, +98%]). It would be classified as "Least Concern". The median population change per decade is -56% [-20%, -80%], meaning the overall wild honeybee population in Europe would be classified as "Endangered" according to IUCN criteria.

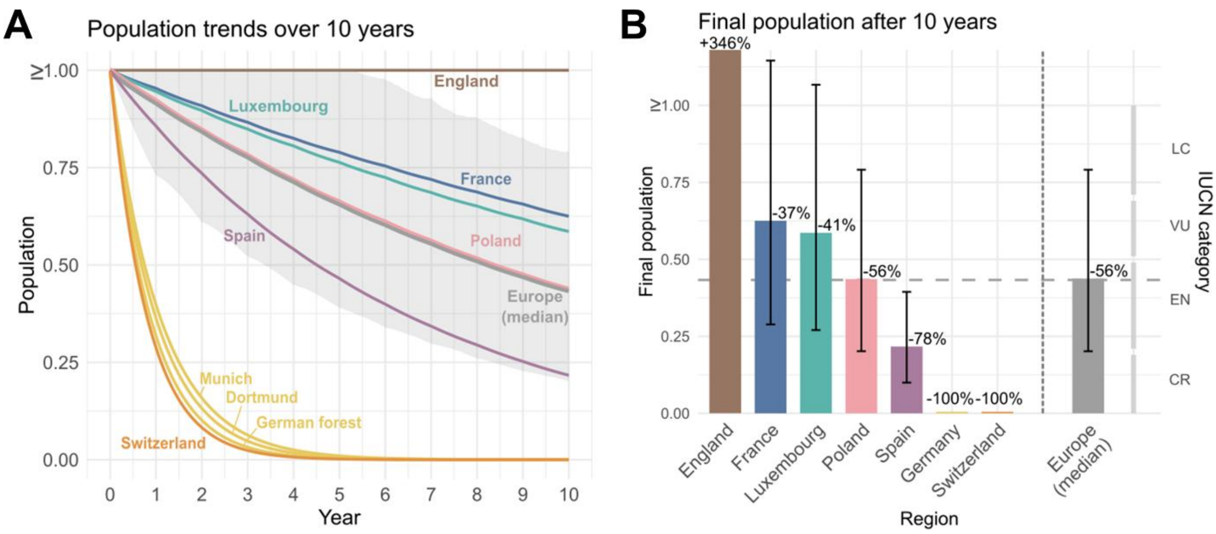

Figure 3. *A) Projected wild honeybee population trends over hypothetical ten-year periods for nine studied populations and for the whole of Europe. Relative changes in population size are based on intrinsic population growth rates, which in turn rely on observed colony survival rates and an assumed average natality 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 some*

countries are not visible because they are outside the y-axis range (England) or too small to be seen at this scale (Germany and Switzerland)).

Discussion

In species with both managed and free-living individuals, and in which managed individuals frequently revert to the wild, any demographic definition of what constitutes a "truly wild" subpopulation is arbitrary. The IUCN has dealt with this problem and defined wild subpopulations as those that do not become extinct within 10 years (or three generations, whichever is longer) (IUCN 2024). 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 intrinsically change over a hypothetical period of ten years. While our estimate of a median population decline of 56% indicates that the overall wild honeybee subpopulation functions as a demographic sink, an important conclusion is that complete extinction within a single decade is highly unlikely. Therefore, according to IUCN guidelines, the cohort of wild *Apis mellifera* can be formally considered a "wild subpopulation" at the European level, and the assessment of its population trend for the Red List of bees is justified.

Accepting the existence of wild honeybee populations solely because some *colonies* live wild, combined with an arbitrary criterium of population survival, might be difficult for some readers. The common linguistic distinction between honeybees and "wild bees" and the fact that most people have only ever seen colonies in hives makes it hard to change the image of the species. However, wild honeybees have most likely always made up a significant fraction of the overall population of the species (Visick & Ratnieks, 2023). Furthermore, when analysing apiculture and its history in detail, it becomes evident that successful beekeeping is based on the continuous manipulation of colonies using all sorts of tools and techniques rather than the biological change of the bees through breeding (Crane, 1999; Seeley, 2019). Of course, with increasing management intensity, selection pressure will differ more profoundly between beekeeping and wild conditions. Nevertheless, widespread domestication is rather unlikely given that managed honeybees are usually not completely isolated from wild ones (Johnson, 2023). Accordingly, no genetic markers are available that can reliably distinguish wild from managed honeybees. These considerations suggest that wild honeybees are currently best defined in demographic terms as we do here. In this light, the data indicate that a wild honeybee population still exists in Europe, although it is in decline.

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. At the low end of the spectrum, there are the populations studied in Germany and in Switzerland north of the Alps (Cordillot, 2024; Kohl et al., 2022; Lang et al., 2022; Rutschmann, Remter & Roth, 2025). Conditional upon the discovery of populations with higher average colony survival rates, model projections are consistent with high local extinction risk in these countries. At the other end of the spectrum, there is the population studied in southeast England (Visick & Ratnieks, 2026), 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 et al., 2013), and Spain (Rutschmann et al., 2022), which apparently fare much better than the ones in Germany and Switzerland, even if they still represent demographic sinks.

When referring to individual populations by country of origin, it is important to note that each is represented by only one or a few studies. Depending on their spatial and temporal scope, these studies may provide stronger or weaker approximations of average demographic patterns in the broader regions, whose delineation is to some extent arbitrary. Moreover, wild subpopulations are spatially structured, and because they occupy habitats of varying quality, source–sink dynamics are likely to occur among different 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.

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; Espregueira Themudo et al., 2020; Kükrer et al., 2021; Requier et al., 2019).

The presented analysis takes place at the species level, and therefore, a potential argument against our case is that many extant honeybee populations might not be native and thus do not represent conservation cases in the first place (Carreck, 2008). Apart from the rule that population assessments are first made at the level of the species before lower taxonomic ranks are considered (IUCN 2024), there are ecological arguments in support of the species-level assessment. Native honeybee genotypes are unlikely to have been replaced completely in any region (Moritz, 1991; Requier et al., 2019), so the issue generally includes hybrids rather than merely non-native subspecies. 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). Furthermore, deciding to neglect non-native subspecies and subspecies-hybrids in wild honeybee population assessments would mean applying a different standard compared to other taxa that are assessed at 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. 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 honeybee hybrid populations interact with ecosystems the same way as the original native subspecies did. Where 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 (Malagnini et al., 2023; Wayne & Shaffer, 2016).

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 evolved 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 at the species level does not preclude assessing the conservation status of wild honeybee on the subspecies level, where this is applicable (Browne et al., 2021; Malagnini et al., 2023; McCann & McCormack, 2024; Oleksa et al., 2013; Valentine et al., 2025)

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 honeybees 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; Kohl et al., 2023; Rutschmann et al., 2022). 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 (Martínez-López et al., 2022; Panziera et al., 2022; Requier et al., 2019). 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. The evolutionary role of wild subpopulations in shaping the long-term resilience and adaptability of the overall honeybee population remains uncertain, yet their contribution is likely to be beneficial (Panziera et al., 2022; Requier et al., 2019). 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 (Beaurepaire et al., 2025; Geldmann & González-Varo, 2018;

Henry & Rodet, 2018). For example, the existence of a wild honeybee subpopulation in a conservation area could provide arguments to consider restrictions of beekeeping in that area.

Our inference of the wild honeybee population trend for Europe is based on colony survival data from nine studies from seven countries only, and we had to rely on fixed assumptions about colony swarming rates and environmental stochasticity. Hence it is obvious that significant uncertainty remains about the actual population demography of the species on the whole continent. Nevertheless, the monitoring data of free-living colonies analysed here likely represented an unbiased picture. They were conducted during the pioneering phase of this field of research and started without prior knowledge of how favourable their respective study areas would be for wild honeybees. In fact, some studies were performed by citizen or hobby scientists near their homes. In the next phase of research, scientists will probably search for, and subsequently focus on, those (rare) wild populations that are thriving. Therefore, any future population assessment will need to carefully evaluate whether the relevant monitoring studies can provide an accurate picture of the overall population. We strongly recommend that monitoring programs not only be continued but also expanded to a much broader range of regions regardless of habitat quality, thereby enabling more robust inferences on population trajectories in the future (Albouy, 2024; Kohl et al., 2022; Moro et al., 2024; Rutschmann, Remter & Roth, 2025; Seeley, 2017). To support a continuous evaluation of wild honeybee populations and to facilitate the regular update of their conservation status according to the methods presented here, we created a living data base of nest site monitoring studies: https://doi.org/10.5281/zenodo.18424042. Apart from the mere monitoring of wild populations, it will be equally crucial to identify the ecological and evolutionary factors that constrain wild colony survival (e.g. Kohl et al., 2023) and explain why wild subpopulations persist successfully in certain regions but decline in others. Guided by the principle that effective conservation is only possible when underpinned by sound ecological knowledge, we argue that explicitly recognising wild honeybee subpopulations as legitimate subjects of demographic and ecological study is essential. Such recognition is a prerequisite for evidence-based conservation strategies aimed at safeguarding this irreplaceable and evolutionarily significant component of Europe's bee fauna.

Data Availability Statement

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

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

The wild honeybee population of Europe is in decline: evidence from monitoring studies

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Managed honeybee population trends

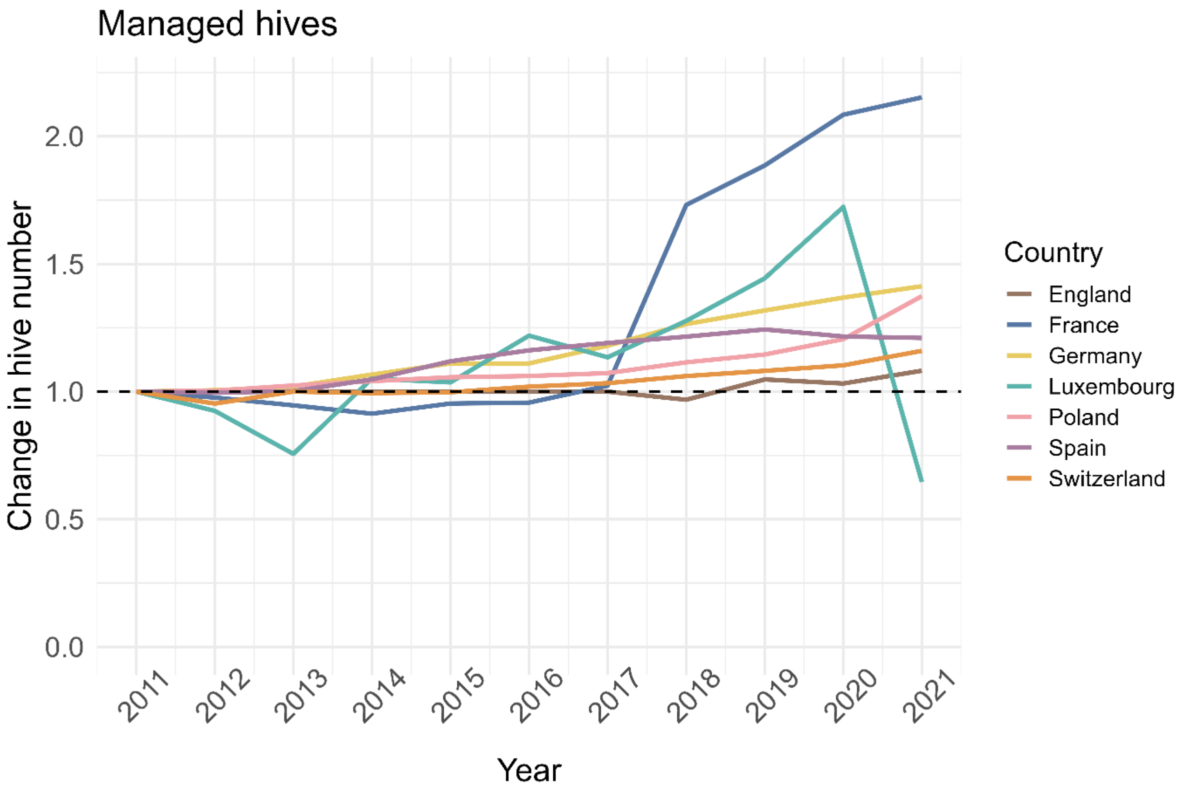

Figure S1: *Relative change in the number of registered managed honeybee colonies between 2011 and 2021 in seven European countries relative to 2011 (or between 2017 and 2021 and relative to 2017 for UK). The countries are those for which data on wild honeybee populations were available. Data from the 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).*

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 be "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 nine studies representing seven 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 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 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 et al., 2022), Munich (Rutschmann, Remter & Roth, 2025) and Luxembourg (J. Park & R. Dammé, pers. communication 2025), 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.

Data on variation in nest site reoccupation rates

Variation in the rate at which vacated honeybee nesting sites are reoccupied by new swarms can be seen as a measure of how strongly wild honeybee populations are affected by interannual environmental stochasticity, since it reflects variation in both the survival and swarming rates in the population. We were able to obtain data on variation in nest site reoccupation from five (out of nine) monitoring studies. Given the limited information, we decided to derive a robust general estimate of interannual population fluctuations that we would use for all population simulations. To that end, we calculated the median annual reoccupation rate for each study as well as the median absolute deviation (MAD) in reoccupation, which is a robust measure of the standard deviation (using the "mad" function in R). Dividing the MAD by the median yields the robust coefficient of variation (RCV) (Arachchige et al., 2020). The mean RCV in nest site reoccupation across five studies was 13.2% (see Table S1 for an overview of reoccupation rate data from five studies). We hence simulated environmental stochasticity by drawing annual population growth rates from a normal distribution with mean λ_{est} (specific to each studied population) and a common coefficient of variation $CV = 0.132$ derived from the robust coefficient of variation (RCV) in nest site reoccupation:

$$\lambda_{sim,y} \sim \mathcal{N}(\mu = \lambda_{est}, \sigma^2 = (\lambda_{est} \times 0.132)^2)$$

Table S1: *Overview of nest site reoccupation data from seven monitoring studies. The number of years refers to the number of swarming seasons in which reoccupation rates could be determined. MAD= median absolute difference, RCV = robust coefficient of variation.*

Country	**Ref.**	**Number of years**	**Median number of vacant sites/year**	**Median reoccupation rate**	**MAD reoccupation rate**	**RCV reoccupation rate**
Germany	(Rutschmann, Remter & Roth, 2025)	7	16	0.692	0.086	0.124
Germany	(Kohl et al., 2022)	3	32	0.656	0.007	0.010
France	(Albouy, 2024, p. 623 therein)	6	69	0.509	0.086	0.169
Spain	(Rutschmann et al., 2022; Rutschmann & Kohl, unpublished data)	4	22.5	0.508	0.176	0.347
England	(Visick & Ratnieks, 2026)	3	17	0.652	0.008	0.012

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 annual rate of intrinsic growth of the wild subpopulation, which in turn is based on wild colony survival rates determined by nine independent monitoring studies in seven countries. The period covered by the studies was from 2013 to 2025, with each study looking at a time span of between two and seven years. 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 the generation length of *colonies,* not individual worker or queen bees that is the unit of interest here). According to the IUCN definition (IUCN Standards and Petitions Committee, 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 at 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 et al., 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 et al., 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 et al., 2022). Since the survival statistics for these populations are very similar, we here assume that they reflect temperate honeybees' natural, pre-disturbance 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). These considerations show that using 10-year periods for conservation status assessment in the western honeybee is reasonable.

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