Journal of Insect Conservation (2024) 28:389–400
https://doi.org/10.1007/s10841-023-00541-4

ORIGINAL PAPER

Free-living colonies of native honey bees (*Apis mellifera mellifera*) in 19th and early 20th century Sweden

Mats Niklasson[1,2,3] · Emil Svensson[4] · Sonja Leidenberger[5] · Niclas Norrström[5] · Elizabeth Crawford[1,3]

Received: 7 September 2023 / Accepted: 12 November 2023 / Published online: 7 December 2023

Abstract

Little information exists on the history and ecology of free-living colonies of European honey bees (*Apis mellifera* L.) in Europe, including its dark north-western subspecies (*Apis mellifera mellifera*). Our aim was to investigate the presence of colonies of free-living, native honey bees (*A. m. mellifera*) during the last two centuries in Sweden. For this we examined systematic interviews of beekeepers (176 answers from 158 questionnaires) performed in the years 1928–1981, with information dating back to the early 1800s. An overwhelming majority of answers (96%) confirmed the past presence of free-living colonies of honey bees in Sweden. While some stated that free-living colonies were simply absconded swarms from managed hives, the majority of interviewees (69%) believed that free-living colonies were of a truly wild origin. A decreasing trend in first-hand accounts of free-living colonies suggests that free-living populations underwent a dramatic decline at the end of the 19th century. This was also expressed in words by many interviewees, who in 14 cases stated that the loss of old forests and tree-cavity nest sites at the end of the 1800s was the primary cause of the decline. Direct accounts of perennial, free-living colonies, combined with detailed descriptions of the collection of large free-living colonies and/or wild honey, is strong evidence of free-living honey bees being well adapted to winter survival. These accounts contradict the officially supported view that the honey bee is a recently imported, domesticated, non-native species in Sweden. The results give a scientific underpinning and provide inspiration for the restoration of native forests which could facilitate populations of free-living colonies of *A. m. mellifera* exposed to natural selection. This could potentially lead to its return as a fully wild species. In an uncertain future, allowing for a natural lifestyle could increase resilience and reinstate characteristics that are otherwise lost in honey bees due to the increasing effects of artificial trait selection.

Implications for insect conservation Our results present strong evidence for populations of free-living colonies of *A. m. mellifera* in the recent past, which calls for a revised look at its conservation status and management. Allowing and supporting free-living colonies of this subspecies should be evaluated as a method for conservation.

Keywords Free-living honey bees · *Apis mellifera* · *Apis mellifera mellifera* · Wild honey bees · Old-growth forests · Hollow trees · Rewilding

✉ Mats Niklasson
mats.niklasson@nordensark.se

1 Foundation Nordens Ark, Research Department, Swedish University of Agricultural Sciences, Åby säteri, 456 93 Hunnebostrand, Sweden

2 Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, PO Box 190, Lomma, Sweden

3 Gothenburg Global Biodiversity Centre, Carl Skottsbergs gata 22B, 413 19 Gothenburg, Sweden

4 Gärsnäs, Sweden

5 School of Bioscience, Department of Biology and Bioinformatics, University of Skövde, Skövde, Sweden

Introduction

The European honey bee (*Apis mellifera*) (Linnaeus 1758) is one of several honey producing *Apis* species and is considered to be the most economically important globally, for pollination services as well as for honey production (Hung et al. 2018). Management of honey bees has a long tradition in Europe with a strong focus on high economic output using artificial hives, which has received significant scientific attention in recent years. However, the biology and ecology of wild colonies of honey bees have seldom been studied, even though these bees are an important member of Europe´s native insect fauna with a number of

well-described subspecies (Ruttner 1988). There are several possible explanations for the lack of such studies. For example, there is a presumed absence of wild colonies due to a massive loss of natural forests in earlier times and the expansion of agriculture over forests (Crane 1999; Banaszak 2009; De la Rua et al. 2009). Spillover of pathogens from managed to wild colonies, particularly via vectors like the *Varroa destructor* mite, is also a common explanation for the alleged disappearance of wild colonies of European honey bees (Anderson and Trueman 2000). Above all, its great economic importance and human attempts to control honey bee breeding have led to the view that *A. mellifera* is a highly domesticated species.

With the exception of some recent studies (Oleksa et al. 2013; Kohl and Rutschmann 2018; Requier et al. 2019; Dubaic et al. 2021; Kohl et al. 2022), there is a lack of fundamental ecological and biological information about free-living colonies of honey bees on the European subcontinent, such as their population densities, lifespans, sources of mortality, and nest properties. This situation has turned attention to free-living honey bees on other continents such as North America, where *A. mellifera* established populations of wild colonies in the early 1600s (Carpenter and Harpur 2021). These populations have been key to our understanding of the ecology and behaviour of honey bees living under natural, unmanaged conditions (Seeley 2019).

There is a long history of human management of *A. mellifera*, and the last two centuries have brought the introduction of more intensive beekeeping practices, including plastic hives, queen breeding, introgression of genes from non-native races, frequent medications for disease control, and winter feeding. Parallel with the onset of intensive beekeeping is the decline or local extinction of colonies of locally adapted subspecies (both managed and free-living) (Crane 1984; Weber 2013; Ellis et al. 2018). Together, these factors have contributed to the long-standing lack of scientific interest in Europe about free-living honey bees. Because of this, the past and present status of free-living colonies of native honey bees is largely unknown, even if there exists strong evidence of these bees, such as mediaeval collection of wild colonies (swarms), wild honey, and beeswax (Husberg 1994; Crane 1999).

The native Nordic subspecies of European honey bee, *Apis mellifera mellifera*, once had a large area of distribution in north and west Europe (Ruttner 1988). Native populations of *A. m. mellifera* (both managed and wild) are now extinct or close to extinction in many countries as a result of introgression by import of southern subspecies (De La Rúa et al. 2009). *A. m. mellifera* is locally adapted to the Nordic-Baltic's short summers and cold winters and has co-evolved with local flora and fauna (Ruottinen et al. 2014). Further adaptations, such as winter hardiness, good flight strength in cold and windy conditions, high levels of pollen collection, and low honey consumption in winter, may explain why *A. m. mellifera* is ecologically important in the Northern European climate (Ruttner 1988; Norrström et al. 2021).

We have analysed the situation in Sweden in the 19th and early 20th centuries regarding free-living populations of native honey bees, *A. m. mellifera*. We based our analysis on the records of systematic and extensive interviews with beekeepers, conducted in the years 1928–1980. In one section, the interviews specifically referred to wild colonies of honey bees and to the practice of harvesting honey from hollow tree nests in the 19th and early 20th centuries (a practice hereafter referred to as "bee hunting") (Husberg 1994). Based on the fact that Sweden in the 1800s still had vast areas of semi-natural forest (Eliasson 2002), we hypothesised that we would find records confirming the presence of populations of free-living colonies of *A. m. mellifera* at this time. In addition, we hypothesised that we could deduce temporal and spatial information about past population declines of free-living colonies, which has important implications for future conservation efforts for these bees.

Materials and methods

Questionnaire from institutet för Språk Och Folkminnen (Isof) and Nordiska Museet

In 1928, the Institutet för Språk och Folkminnen (Isof) (Institute for Language and Folklore) issued a questionnaire on beekeeping, "Bin och Biskötsel" (Bees and beekeeping) (Landsmålsarkivet 1928; for more details, see Online Resource 1). Answers to these questionnaires were found in the Isof archives in Lund and in Uppsala (Folkminnesarkivet), Sweden. The same questionnaire was also distributed by Nordiska Museet (Nordic Museum) in 1949 to a network of interviewees (questionnaire Nm 148, link: https://dokument.nordiskamuseet.se/, Online Resource 1). The questionnaire is a 7-page list of questions concerning beekeeping practices of the past (hive types, swarm handling, honey production, and honey use).

Questions evaluated in this study

For our study, we were mostly concerned with the first section of the questionnaire which asked about wild colonies of honey bees, specifically the harvesting of wild honey and/or wild colonies, and the collection of hollow tree sections with wild colonies and honey used for primitive log hives (Husberg 1994; Crane 1999). We also included any other reference to free-living colonies of honey bees from later sections of the questionnaire. The following questions were used in this study (here translated from their original Swedish to English). Note that the original wording is kept here

and at some places further in the text; "wild bees" meaning *free living colonies of honey bees* (not solitary bees), "wild honey" meaning *honey from free living colonies of honey bees* and "tame bees" meaning *managed honey bees*):

Section of the questionnaire titled 'Wild bees and wild honey?'

1. Are there examples of harvesting honey from wild bees in trees ("bee trees") in the forest?
2. Without killing the bees?
3. To harvest honey from trees, was an additional hole opened up?
4. If yes, in which position?
5. How was a tree marked when a bee colony was discovered, so that no one else would take the honey?
6. Were trees with bee colonies cut down and the log with the colony brought home?

Section of the questionnaire titled 'Bee houses?'

7. Were logs used for bee hives, more than temporarily?
8. Which tree species were used?
9. Were they used upright or lying down?
10. How were they produced?
11. What about their bee entrance hole and other arrangements for honey harvest?

A single question concerning wild [honey] bees was found in a different section of the questionnaire.

12. Bees, different types, wild bees, tame bees?

Extraction of data from questionnaires

In total, 176 (96 Isof + 80 Nm) answers were examined. Forty-nine of these answers did not contain any other information other than a title page with meta data, and 12 did not contain answers to the section on wild colonies of honey bees and were therefore excluded from the analysis. Thus, in total, 115 answers formed the basis for the analysis (76 Isof + 39 Nm).

The questionnaires were answered between the years 1928 and 1981 (mean = 1940, median = 1936). Fifty-one interviewees had provided birth dates, with a mean age of 75 years (Table 1; Fig. 1). All relevant text concerning wild colonies and their log homes was transcribed and translated from Swedish to English, and the key information was summarised into a Microsoft Excel spreadsheet. Categories for further analysis were created, and answers assigned to these accordingly. Place names mentioned in each answer were investigated (many names were no longer in use and could not be found through modern map services) and given the proper geographic coordinates, which were used as a basis for subsequent map creation in QGIS 3.28 (QGIS Development Team 2023).

Table 1 Descriptive statistics of the interviews and interviewees

Mean birth year	1865	Mean interview year	1941	Mean age	75
Median birth year	1865	Median interview year	1936	Median age	77
Earliest birth year	1841	Earliest interview year	1927	Youngest age	47
Latest birth year	1904	Latest interview year	1981	Oldest age	93

The original sequence of questions was rarely followed, and interviewees tended to answer several questions within one large paragraph. Additionally, many interviewees offered additional insightful information related to free-living honey bees that was not explicitly asked for. Therefore, instead of only analysing direct answers to the questions asked by the questionnaire, we searched the answers for information on several key topics: (i) presence of free-living honey bees; (ii) origin of free-living honey bees; (iii) cause of decline; (iv) nest types; (v) geographical location; (vi) approximate date when the transition from skeps (straw hives) to frame hives began, and (vii) approximate date that importation of non-native subspecies of honey bees began.

From the answers, it was clear that the term "wild honey bees" used in the questionnaire had variable meaning among interviewees, and it was not often clear whether the observations referred to bees of truly wild origin or bees that had absconded from a managed beehive. Undoubtedly, gene flow occurs between wild honey bee colonies, absconded colonies and managed colonies, and it is not feasible to make a clear morphological or genetic distinction between these categories. Therefore, we use the term "free-living" to refer to both wild honey bees and previously-managed honey bees which have become free-living (Browne et al. 2021). We use the terms "wild" and "feral" only when referring to the original statements from interviewees' in order to respect the range of opinions on the origin of free-living colonies (Table 2; Fig. 5). Where individuals referred to tracking or following recently absconded swarms from a certain and known hive, these bees were treated as managed rather than free-living and were excluded from the analysis.

The specific information we were searching for and considered important for the discussion of the past presence of free-living colonies of honey bees is as follows:

The presence of free-living colonies of honey bees

Accounts that referred to the presence of free-living colonies were categorised depending on the interviewee's degree of personal experience (Table 3).

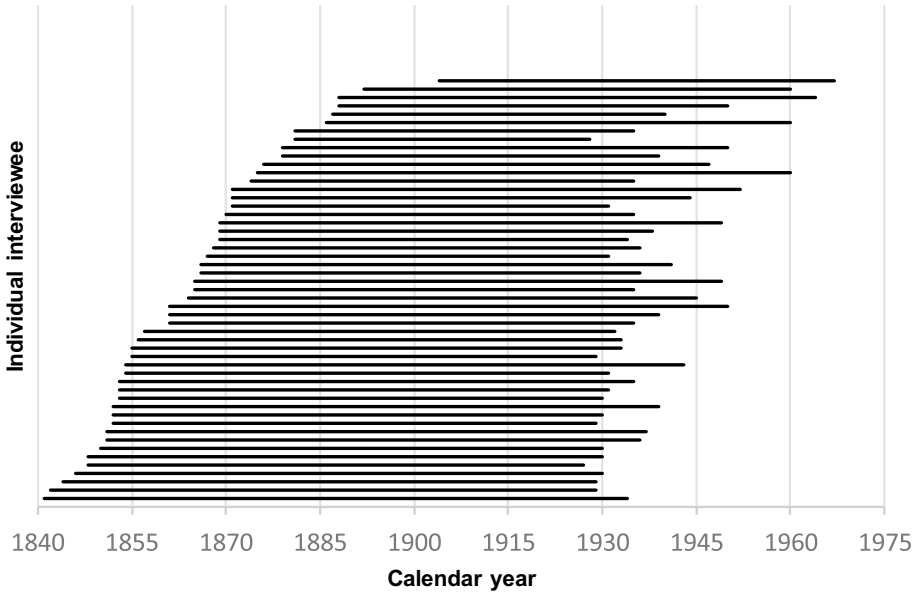

Fig. 1 Lifespan of each individual interviewee (that provided data for birth year) at the time of the interview (n = 51). The start of the line equals the birth year, and the end of the line equals the year of the interview. The majority of interviews were conducted from 1928–1950

Table 2 Number of accounts relating to different opinions on the origin of free-living honey bees

Category	Type of bee	Number of accounts
1	Free-living colonies of bees originate from managed colonies of bees	23
2	Both free-living (either "wild" or "feral" in the original phrasing) and managed colonies co-occur	8
3	Free-living colonies ("wild" but here excluding "feral" in the original phrasing) and managed colonies are the only existing types of honey bee colonies	50
4	Unsure if the bees in free-living colonies are truly wild or if they originated from previously managed colonies	3
	Total	84

Table 3 Categories of interviewees' experience with free-living bees and/or direct observation of free-living bees

Category	Quality of observation	Description
A	Direct/indirect experience	Direct, first hand observation of free-living colonies of honey bees Direct experience of bee hunting Indirect experience (observation or bee hunting by a family member, usually father) Free-living honey bees still found today
B	Detailed knowledge	Highly detailed description of free-living colonies of honey bees or of bee hunting, suggesting direct personal experience
C	Historical knowledge	Free-living colonies of honey bees and the practice of bee hunting were not observed by the interviewee personally, but it was known that they occurred, also in other areas Interviewee is aware that free-living colonies of honey bees were previously found in this area but are no longer or are rare
D	Wild colonies are unknown	Interviewee explicitly states that they do not know about free-living colonies or the tradition of bee hunting

Opinion on the origin of free-living colonies of bees

We categorised the interviewees' opinions on the origin of free-living colonies of bees, i.e., whether bees observed living in the wild were of a truly wild origin and differed from managed bees, or whether they were actually previously managed bees that had absconded from a hive and become free-living ("feral" in the original Swedish phrasing).

1. Free-living colonies of bees originate from managed colonies of bees.

2. Both free-living (either "wild" or "feral" in the original phrasing) and managed colonies co-occur.
3. Free-living colonies ("wild" but here excluding "feral" in the original phrasing) and managed colonies are the only existing types of honey bee colonies.
4. Unsure if the bees in free-living colonies are really wild or originated from previously managed colonies.

Cause of the decline of free-living colonies

We recorded the interviewees' opinions on the cause of the decline of free-living colonies of honey bees, if stated. This was not specifically asked for by the questionnaire but was stated regardless in several accounts.

Nest types of free-living colonies of honey bees

The nest type of free-living colonies was stated in many interviews, i.e., the structure in which free-living colonies were found. If the nest type was a hollow tree, then the species of tree was recorded if it was provided.

Geographical location

The location of free-living colony observations was recorded whenever stated. The Swedish Land Survey online search tool (https://minkarta.lantmateriet.se) was used to find the coordinates of place names. Where more precise geographical information on bee observations was missing, the home address or location of the nearest parish was used.

Timing of transition from skeps to frame hives for managed bees

Several interviewees noted when the change from skep to movable-frame hive beekeeping began in their region. This information is significant as skep hives promote swarming (which results in these bees becoming free-living if not caught), whereas movable-frame hive beekeeping tends to prevent swarming.

Importation of non-native subspecies

Any information on the importation of non-native honey bee subspecies was recorded (subspecies, date, location, etc.).

Results

The presence of free-living colonies of bees

The past presence of free-living honey bee colonies as interpreted from direct eyewitness accounts (category A) or detailed or historical knowledge (categories B and C) was confirmed in 110 out of 115 interviewees' accounts (96%, Table 4; Fig. 3). These accounts were almost equally distributed in categories A–C (38, 37 and 35, respectively; Fig. 4). The remaining 5 interviewees (4%) stated that they did not know about wild colonies and/or the tradition of using bee logs from the forest (category D) (Table 4). Example quotations from accounts for each category are found as Online Resource 2.

Table 4 Categorised observations of free-living colonies of honey bees

Category	Level of knowledge	Number of accounts
A	Direct/indirect experience	38
B	Detailed knowledge	37
C	Historical knowledge	35
D	Free-living colonies (originally named "wild bees" in the accounts) unknown	5
	Total	115

The majority of interviewees (72/115) who confirm the presence of free-living colonies refer to unspecified periods, usually before their own lifetime ("in the past"), which likely took place in the early to mid-1800s. Thirty-eight of these accounts were direct observations of free-living colonies with a date or with the possibility to tentatively assign an approximate date, which were unevenly distributed in time, with 30 observations in the late 1800s (Fig. 2) and only eight observations after 1900, after which a sharp decline was visible. A small number of accounts (4/115) suggested that free-living colonies were possible to find, albeit rare, at the time of the interview. No accounts stated that free-living colonies were common at the time of the interview. The earliest dated record (1817) was referring to a court verdict on burning an oak tree while collecting honey from a free-living colony (oaks were legally protected until 1830) (Eliasson and Nilsson 1999).

Opinion on the origin of free-living colonies

Out of the 115 accounts, 84 had an opinion on the origin and life history of free-living honey bee colonies (Table 2; Fig. 5). Fifty-eight of the 84 accounts (70%) acknowledged the existence of wild honey bees which are different from previously managed ("feral") or managed bees (categories 2 and 3). Two accounts were unsure if free-living bees should be classified as "wild" or "feral" (category 4). Only 23 of 84 accounts (28%) did not acknowledge the existence of wild bees, stating that free-living colonies (often called "wild" in quotation marks or "so called wild bees") were descendants of previously-managed ("feral") or absconded honey bees (category 1). Six out of 58 accounts that stated that

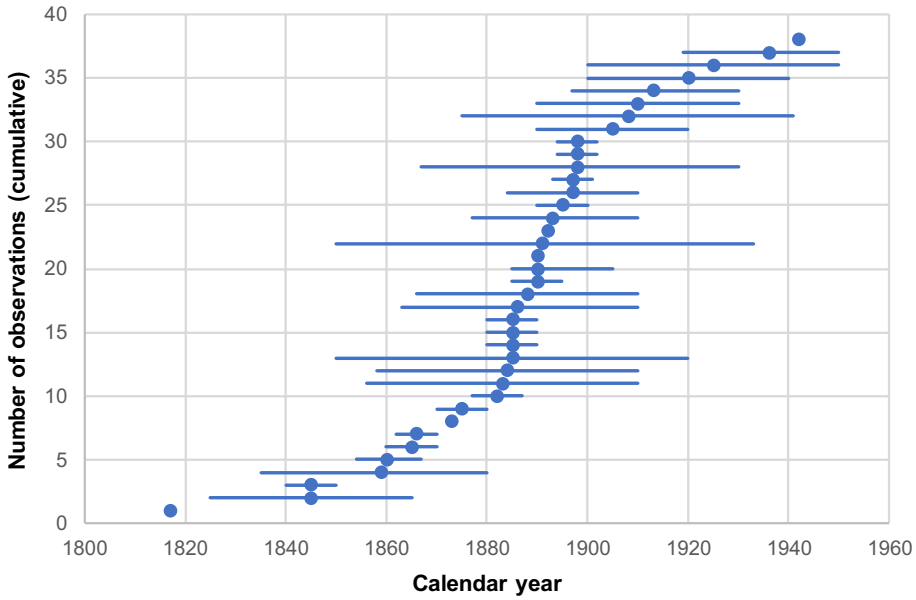

Fig. 2 Timing (cumulative presentation) of direct and indirect observations of free-living colonies (n = 38; horizontal lines represent timespan of observations reconstructed based on statements from interviewees ["in my childhood", "when I was young" (= more precise), "I once harvested", "in the 1800s" (= less precise)]. Dots are the centre date of the timespan. Free-living colony observations increased almost exponentially between 1875–1900 but showed a strong decline thereafter. The apparent lower frequency of observations pre-1880 is likely an effect of decreasing data for this period

wild bees were different from previously-managed ("feral") or managed bees stated that they had a different look or temper ("smaller and almost black", "small and reddish", "smaller", "more angry", "angrier", "more hardy and took the winter better"). Example quotations from accounts for each category are found as Online Resource 3.

Cause of the decline of free-living colonies

Fourteen accounts stated a cause for the decline of free-living colonies. All fourteen attributed the decline to the loss of old forests with hollow trees by clear felling and thinning. Four accounts stated that the hollow tree decline was within the period 1880–1900. Two of these 14 accounts gave an additional cause for free-living colony decline: the introduction of modern frame-hive beekeeping resulted in less frequent swarming; also, beekeepers began to keep a careful watch to prevent swarms from escaping. Example quotations from accounts that state a cause for the decline of free-living colonies are found as Online Resource 4.

Nest types of free-living colonies

One hundred and eleven accounts described the nest type of free-living colonies. Eighty-seven of these were tree hollows, and the other 24 were: buildings (11), chimneys (5), churches/bells (2), dead trees or stumps (3), cliffs (2) and inside tree crowns (1) (Table 5). Hollows in trees were distributed over 11 species, with oak (*Quercus* sp.), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*) being the most common (Table 6). Nine accounts had the information that hollows were produced by woodpeckers,

Table 5 Frequency of different nest types of free-living colonies in interview accounts

Nest type	Frequency
Hollow tree	87
Building, wall	11
Chimney	5
Dead tree	3
Church-bell	2
Cliff	2
Inside dense tree crown	1
Total	111

Table 6 Frequency of different hollow tree species used as nests by free-living colonies in interview accounts

Hollow tree species	Frequency
Oak (*Quercus* sp.)	12
Scots pine (*Pinus sylvestris*)	11
Norway spruce (*Picea abies*)	9
Eurasian aspen (*Populus tremula*)	6
Lime (*Tilia* spp.)	4
European beech (*Fagus sylvatica*)	4
Birch (*Betula* spp.)	3
Common ash (*Fraxinus excelsior*)	2
Common alder (*Alnus glutinosa*)	2
Pear (*Pyrus communis*)	1
Willow (*Salix* sp.)	1
Total	55

with the black woodpecker (*Dryocopus martius*) mentioned in two cases.

Past geographic distribution of free-living colonies of honey bees

The answers that directly or indirectly confirmed that free-living colonies existed were evenly distributed over southern Sweden, barely exceeding the 60th parallel (Fig. 3). An exceptional case is the observation of a free-living colony on Alnön island, near the northern Swedish town Sundsvall (at 62° 25′N), some 300 km north of the main distribution of the honey bee. With the exception of this northern outlier, the main distribution coincides closely with the northern limit of the hemi-boreal vegetation zone, also being the northern distribution limit of oaks in Sweden (*Quercus robur*, *Quercus petraea*) (Figs 4 and 5).

Timing of transition from skeps to frame hives for managed colonies

Fifty-nine accounts had provided information on the date that beekeepers transitioned from using skeps to frame hives, ranging from 1865 to 1935, with a high frequency from 1880 to 1915 (Fig. 6).

Importation of non-native subspecies

Five accounts provided dates of importation of non-native *A. mellifera* subspecies and genetic material, during 1885–1895 (Fig. 6). Their origins were Carniolan (*A. m. carnica*) Italian (*A. m. ligustica*), and German dark bee ("Heath bee") (A. m. *mellifera*).

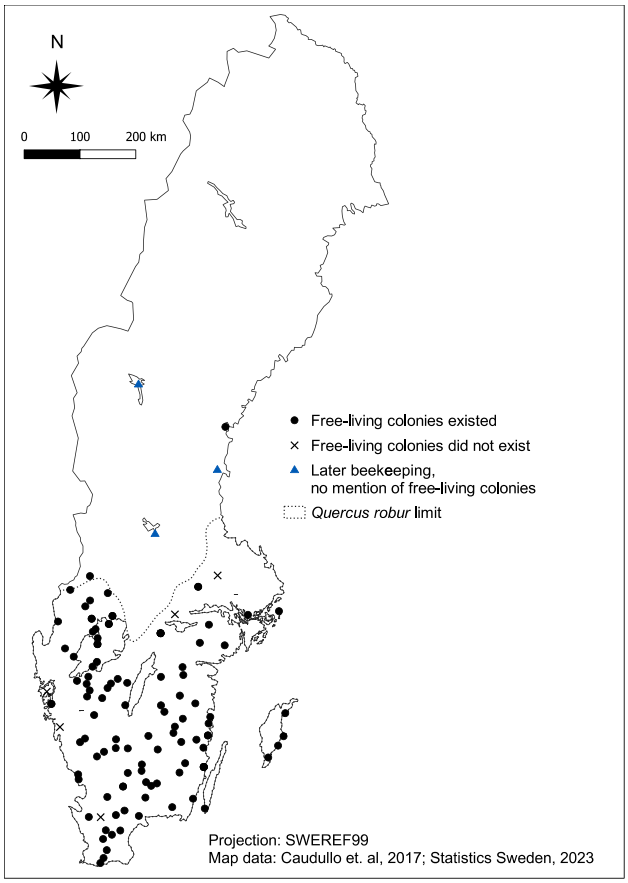

Fig. 3 Map showing the distribution of observations of free-living (wild) colonies from 1817–1942. Filled circles (filled circle) represent observations (both direct and indirect), crosses (×) confirmed non-presence of wild colonies ("I have not seen any wild colonies" etc.), and triangles (filled triangle) are areas where beekeeping only recently started at the time of the interview, with no previous tradition and no information (or explicit no observation) given on free-living colonies. The dashed line represents the approximate northern limit of Quercus robur , which also constitutes the northern border of the boreo-nemoral vegetation zone (Sjörs 1999). Map created using QGIS (version 3.28).

Discussion

With an overwhelming majority (110 out of 115) of direct or indirect accounts describing the presence of free-living colonies of honey bees, we confirmed our hypothesis that free-living colonies (defined as either wild or previously managed) were present in 19th and 20th century Sweden. To our knowledge, this is the most comprehensive evidence of a wild original lifestyle of honey bees in Europe presented to date.

Present day records of free-living honey bee colonies and perennial free-living colonies are rare but do exist (Banaszak and Jaroszewicz 2009; Kohl and Rutschmann 2018; Kohl et al. 2022). To our knowledge, no serious attempts to systematically gather data on free-living colonies of honey bees have been conducted in Sweden, thus it is uncertain whether there has been or still are any truly wild populations (not originating from managed honey bees) present. The commonly held, and officially supported, view of authorities in Sweden is that the honey bee is a domesticated, non-native, alien or invasive species[1] (cf. http://www.artportalen.se). This most likely reduces the interest to report findings of free-living honey bee colonies today and in the past, and it may have strengthened disinterest in reporting these colonies among entomologists. Therefore, the abundance of free-living honey bee colonies today may have been underestimated.

[1] Swedish zoologist and taxonomist Carl von Linné was the first descriptor of the honey bee *Apis mellifera* in 1758 in his Systema naturae.

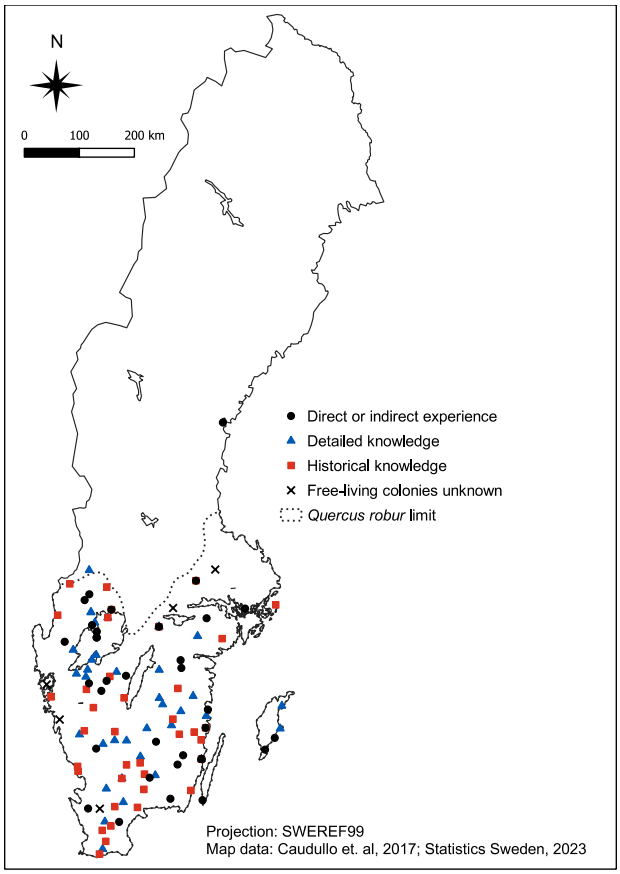

Fig. 4 Presence and absence of free-living colonies of honey bees. Observations of presence sorted according to degree of personal experience. Filled circles (filled circle) represent answers containing direct or indirect experience with wild colonies, triangles (filled triangle) detailed knowledge, squares (filled square) historical knowledge, and crosses (×) lacking knowledge of wild colonies. The dashed line represents the approximate northern limit of *Quercus robur*, which also constitutes the northern border of the boreo-nemoral vegetation zone (Sjörs 1999). Map created using QGIS (version 3.28)

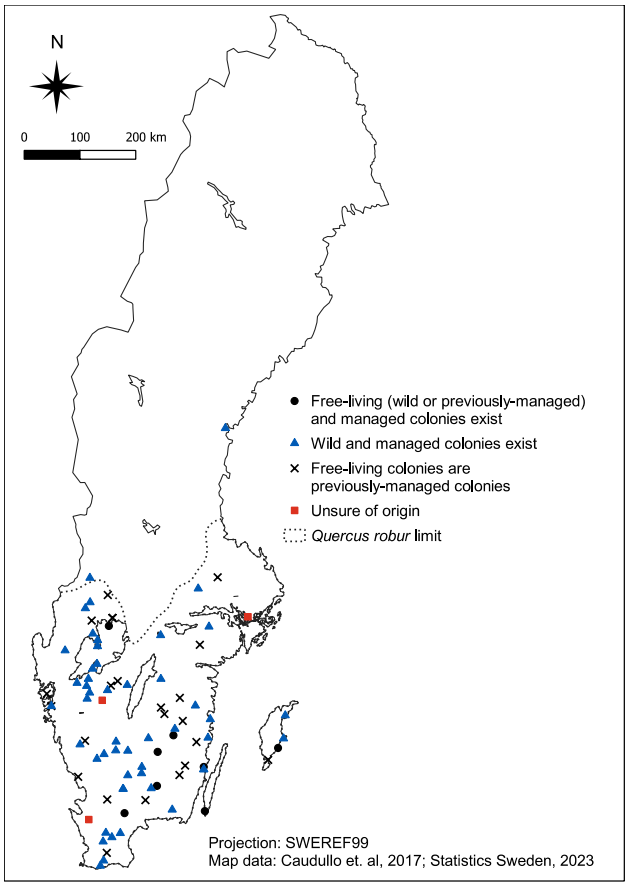

Fig. 5 Map of interviewees' opinions on the origin of free-living colonies. Filled circles (filled circle) represent the opinion that free-living (either wild or previously managed) and managed colonies all exist, triangles (filled triangle) that wild and managed colonies exist, crosses (×) that free-living colonies are previously managed colonies, and squares (filled square) that there is uncertainty regarding their origin. The dashed line represents the approximate northern limit of *Quercus robur*, which also constitutes the northern border of the boreo-nemoral vegetation zone (Sjörs 1999). Map created using QGIS (version 3.28)

The apparently sudden and strong decline of free-living colonies that occurred in the 1880s and 1890s as interpreted from accounts was, according to many interviewees, caused by loss of hollow trees and old-growth forests (Online Resource 4). In fact, this is a plausible explanation; in strong contrast to neighbouring countries, south Sweden in the early-mid 1800s still had vast areas of forest (Eliasson 2002) and extensive wood pastures with high densities of hollow oaks (Eliasson 2002; Ranius et al. 2008). However, in the late 1800s the fast developing forest industry and onset of organised forest management introduced methods focused on timber and pulpwood-production, which put a strong pressure on remaining old-growth forests (Eliasson and Nilsson 1999; Enander 2007). This directly and negatively influenced the availability of hollow trees on which free-living colonies of honey bees and many other organisms depend, such as bats and other small mammals, beetles and a number of cavity-dwelling bird species (Nilsson et al. 2001; Ranius 2002; Michaelsen 2016). Several studies have shown that availability of suitable hollow trees for nesting is a critical factor for free-living honey bee presence in Europe (Oleksa et al. 2013; Kohl and Rutschmann 2018) and only a small fraction of existing tree hollows are suitable for nesting in terms of volume, height above ground and thermal properties (Seeley 2017; Seeley 2019). Forests managed for wood and pulp production since the end of the 19th century have extremely low availability of suitable hollow trees compared to old-growth forests (Linder and Östlund 1998; Walankiewicz et al. 2014; Andersson et al. 2018; Kohl et al. 2022). Therefore, the availability of suitable tree cavities may be a major limiting factor for the occurrence of natural and

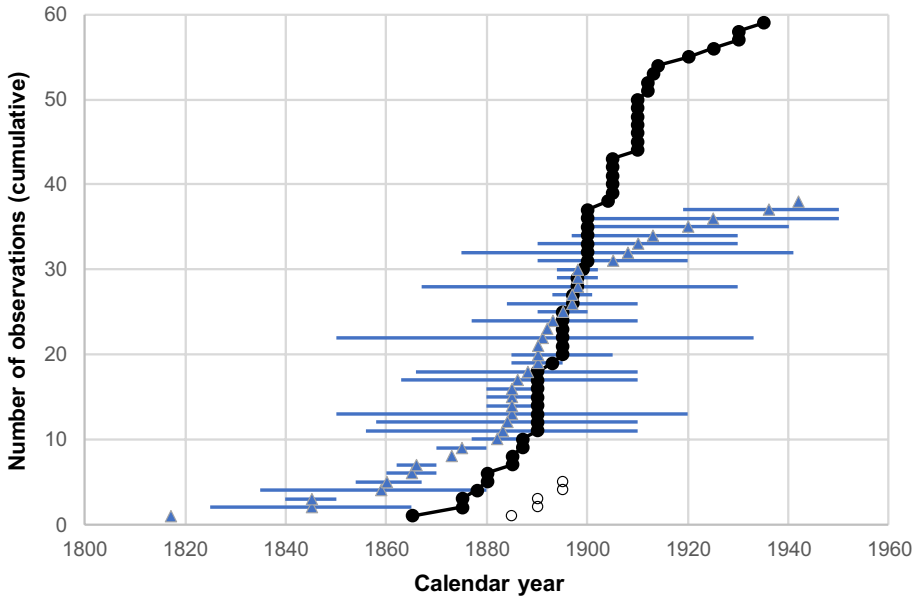

Fig. 6 Onset of beekeeping with frame hives (cumulatively presented) (n = 59, filled circles); and importations of foreign subspecies (n = 5, open circles). For reference and comparison, cumulative presentation of direct and indirect encounters with free-living colonies (n = 38, triangles, see Fig. 2) is shown underneath. The figure shows that the onset of frame-hive beekeeping began later than the early observations of free-living colonies. Onset of frame-hive beekeeping increased exponentially from approximately the year 1880. Observations of free-living colonies were also increasing until the early 1900s when observations of free-living colonies began to level off and transition to frame-hive beekeeping continued to increase

free-living honey bee populations in modern managed forest landscapes (Seeley 2017; Seeley 2019; Requier et al. 2019; Kohl et al. 2022). The abundance of free-living colonies of honey bees was probably already in decline before the time of the interviewees, as the majority of the accounts referred to colonies living in tree cavities during previous generations or "in the past". In summary, our data suggest a strong decline in free-living colonies of honey bees in the 1800s, but they do not present proof of complete extinction of these colonies either. Several interviewees indeed stated that free-living colonies of honey bees were still to be found at the time of interview.

Although we believe loss of nesting sites was a primary reason for the decline of free-living colonies of honey bees, there are also other variables that may have contributed. In the late 1800s, frame hives gradually replaced skeps (Fig. 6) which probably considerably reduced the number of absconded swarms and thus the number of managed colonies which could have become free-living, as was suggested by two of the interviewees. The introduction of frame hives was also a prerequisite for more controlled beekeeping practices, such as queen breeding and importation of foreign subspecies, which is likely to have started in Sweden in the 1860s at the very earliest (Dahm 1878; Nielsdatter et al. 2021). Importation was recorded in a few cases in our material at the very end of the 19th century, but major effects of genetic introgression are likely to have occurred only much later. Commonly imported *Apis mellifera* subspecies in Sweden include *A. m. ligustica*, *A. m. carnica,* and the Buckfast hybrid. The gradual hybridisation with other subspecies with lower winter hardiness may, for example, have negatively affected winter survival in the wild. But this must remain as speculation.

Disease transmission from intensely managed colonies to free-living colonies may be yet another cause for the decline in the abundance of free-living honey bee colonies (Potts et al. 2010; Pirk et al. 2017). Also, the hunting of free-living colonies for both honey and colonies/bee logs, as documented in this study, probably had a direct negative impact on both nest availability and the abundance of free-living colonies. With disappearing old-growth forests and hollow trees, bee hunting likely exacerbated the impacts on free-living populations. Historical records suggest that this population decline may have started already in the late mediaeval period in Sweden when previously large yields of wild honey sold to the royal court were drastically reduced (Husberg 1994, p. 246, graph on p. 244).

There is not a uniform picture of the perceived origin of free-living colonies. For someone chasing a swarm as it absconded from a hive and then settled in a tree, it was obvious that it originated from a managed colony. At the same time, colonies that are randomly encountered in hollow trees in forests and meadows do not have a known origin, and are thus named by the interviewee as either "wild", "feral" or of

uncertain origin, probably depending on the experience of the witness. Interestingly, some (n = 8) state that "both feral and wild" honey bees were found, indicating that there could be a perceived difference between them. However, our data suggests that in the early part of our study period, before importation and change over to frame hives became firmly established, there was a continuous gene exchange between free-living colonies and colonies living in log hives or skeps. On the one hand, bees in hives were swarming away to settle in hollow trees, and on the other hand, hollow trees with bee colonies were cut down and brought home. Thus, it is questionable if it is even possible to establish that there existed a difference between these populations, genetic or behavioural.

Hollow trees were by far the most common nest site. The preference of honey bees for selecting trees for nesting is well documented in literature (Seeley and Morse 1976; Ruttner 1988; Crane 1999). We could not see any clear preference for a certain tree species out of a total of eight tree species that were reported as nest trees, which is in line with previous findings (Oleksa et al. 2013). The three most common species (oak, pine, spruce) were likely dominating in south Sweden during this time period as well as today (SLU 2023), but since we do not have any data on the frequency of different tree species from these times, it is difficult to conclude if some tree species were preferred over others. Interestingly, the high number of tree species used for nests indicate that honey bees in Sweden were less selective of host tree species but more selective of hollow properties (Seeley 2017; Seeley 2019). Most of the observations of free-living colonies in trees were within forests, however, some observations clearly show that nest trees were also found in other habitats such as fields and tree alleys (See Online Resource 3, account NM8541, and Online Resource 2, account NM11226). The observations of honey bee nests found in cliffs and buildings is good evidence of large flexibility in choice of nests. Even today, escaped managed honey bees in Europe have a strong ability to adapt to life in the wild when habitat requirements are met, for example, in Poland (Oleksa et al. 2013), Germany (Kohl and Rutschmann 2018), and Ireland (Browne et al. 2021). Indeed, there have been recent finds of perennial free-living colonies in Europe, which supports this finding (Kohl and Rutschmann 2022). In peri-urban areas, human structures are the most common nest sites for free-living honey bees (Browne et al. 2020; Dubaić et al. 2021).

First- and secondhand testimonies of free-living honey bee colonies were recorded across southern Sweden, up to a latitude approximately 60 degrees north, closely following the northern border of the oak *Q. robur and Q. petraea*. The natural range of *A. m. mellifera* in Sweden has earlier been suggested to follow the distribution of the common hazel *Corylus avellana* L. (Hansson 1955; Crane 1999). Our data suggest that the natural northern limit of *A. m. mellifera* was further south, and closer to the northern limit of the pedunculate oak (*Quercus robur* L.) (Fig. 3). Spatial modelling such as Maximum Entropy modelling (e.g., Dudik et al. 2007) would likely provide higher accuracy for such predictions, but we considered this beyond the scope of this present study. Several accounts suggested that beekeeping had not reached areas north of this line until the early 1900s, implying that the potential of observing absconded managed swarms was very unlikely. Nor were there observations of truly wild bees (not previously managed bees) recorded in the north. This indirectly supports our suggestion that the general distribution of free-living colonies did not surpass the northern distribution of oak.

Introgression has had far-reaching consequences for the European honey bee as a whole with several subspecies becoming locally extinct and/or hybridised, resulting in loss of genetic diversity and local adaptations (De la Rúa et al. 2009; Soland-Reckeweg et al. 2009). In Scandinavia, *A. m. mellifera* is severely impacted by competition from imported subspecies (Ruottinen et al. 2014, Nielsdatter et al. 2021). However, the few surviving pure-bred *A. m. mellifera* populations in Sweden show a high degree of uniqueness and very little introgression from other subspecies (Jensen et al. 2005), indicating potential for further developed conservation efforts. *A. m. mellifera* populations in Sweden, Norway, Denmark, Ireland and Scotland have been targeted for conservation due to their isolation, which has allowed colonies to retain genetic purity. Sweden has a hive density of 0.2 hives per km^2, compared to 10–20 hives per km^2 in Central Europe (Ruottinen et al. 2014).

Isolated areas may have an additional benefit for preventing disease transmission and increasing resistance to the *Varroa destructor* mite. Current beekeeping methods within apiaries, such as management to prevent swarming, may increase the occurrence and severity of honey bee diseases (Brosi et al. 2017). As suggested by several authors, conservation of locally adapted bees with higher resistance to *Varroa* transmitted pathogens can be achieved by assigning areas where human trait selection is removed in favour of natural selection (Requier et al. 2019; Panziera et al. 2022). Several studies have shown the remarkable plasticity and ability of the honey bee to rapidly select for *Varroa* resistance under natural and unmanaged conditions (Fries et al. 2006; Seeley and Smith 2015). However, when used to promote *Varroa*-resistance, natural selection-based programmes may still require human intervention to optimise genetic diversity and ensure survival of desirable selected populations (Guichard et al. 2023).

An increasing number of 'rewilding' projects are being established, whereby free-living honey bee colonies are reintroduced to nature and left completely unmanaged (examples: https://www.freelivingbees.com/projects). The rich evidence presented here of free-living colonies in

the recent past may encourage and guide future rewilding efforts. Restored native forest and other tree-bearing habitats in southern Sweden (such as wooded meadows, parks, and alleys) could support populations of free-living colonies of native honey bees. This in turn would improve conservation of the threatened *A.m. mellifera* subspecies and promote the reinstatement of its natural characteristics and selective processes (Blacquière and Panziera 2018; Requier et al. 2019).

Conclusions

To conclude, we found strong evidence that free-living colonies of native honey bees existed in southern Sweden in the 19th and 20th century. The results also suggest that *A. m. mellifera* underwent a strong population decline during the 1900s. We believe that the decline was mainly driven by loss of nest habitats. Together with earlier research, we reinforce the view that free-living populations of native honey bees can thrive in southern Sweden if habitat requirements are met, and we suggest that it is yet another hollow-tree dependent species which has become locally extinct in the wild due to massive habitat loss. Our results support ongoing and future honey bee rewilding projects in Sweden, as a broad outlook of past long-term population dynamics, geographic distribution, and as evidence of the original wild lifestyle of this native honey bee subspecies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-023-00541-4.

Acknowledgements We would like to acknowledge Milkywire and Trädgårdsresan for their support in the conservation of the native Nordic honey bee. We are also grateful to Professors Tom Seeley and Andrzej Oleksa who provided valuable feedback during review.

Author contributions MN was responsible for the study conception and design. Material preparation, data collection and analysis were performed by MN and ES. The first draft of the manuscript was written by MN and EC All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by Swedish University of Agricultural Sciences. This work was financially supported by INTERREG project 2020–1923 "Bistånd till Nordiska bin" to MN, NN, SL and Trädgårdsresan (MN, EC). Milkywire provided financial support to MN for conservation of the Nordic Bee.

Declarations

Competing interests The authors declare no competing interests.

References

Anderson D, Trueman J (2000) *Varroa jacobsoni* (Acari: Varroidae) is more than one species. Exp Appl Acarol 24:165–189. https://doi.org/10.1023/A:1006456720416

Andersson J, Domingo Gómez E, Michon S, Roberge J-M (2018) Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. Scand J for Res 33:233–244. https://doi.org/10.1080/02827581.2017.1360389

Banaszak J (2009) Pollinating insects (Hymenoptera: Apoidea, Apiformes) as an example of changes in fauna. Fragm Faunist 52:105–123

Banaszak J, Jaroszewicz B (2009) Bees of the Białowieża national park and adjacent areas, NE Poland (Hymenoptera: apoidea, apiformes). Pol J Entomol 78:281–313

Blacquière T, Panziera D (2018) A plea for use of honey bees' natural resilience in beekeeping. Bee World 95:34–38. https://doi.org/10.1080/0005772X.2018.1430999

Brosi BJ, Delaplane KS, Boots M, De Roode JC (2017) Ecological and evolutionary approaches to managing honeybee disease. Nat Ecol Evol 1:1250–1262. https://doi.org/10.1038/s41559-017-0246-z

Browne KA, Geary Hassett J, Moore M, Henriques E, Soland-Reckeweg D, Loughlin E, O'Brien E, O'Driscoll S, Young P, Pinto MA, Mccormack GP (2021) Investigation of free-living honey bee colonies in Ireland. J Apic Res 60:229–240. https://doi.org/10.1080/00218839.2020.1837530

Carpenter MH, Harpur BA (2021) Genetic past, present, and future of the honey bee (*Apis mellifera*) in the United States of America. Apidologie 52:63–79. https://doi.org/10.1007/s13592-020-00836-4

Caudullo G, Welk E, San-Miguel-Ayanz J (2017) Chorological maps for the main European woody species. Data Brief 12:662–666. https://doi.org/10.1016/j.dib.2017.05.007

Crane E (1984) Ch. 65: honeybees. In: Mason IL (ed) Evolution of domesticated animals. Longman Group, London

Crane E (1999) The world history of beekeeping and honey hunting. Routledge, London

Dahm OEL (1878) Biet, dess natur och vård samt några drag ur bikännedomens historia. P.A.Norstedt & Sons, Stockholm

de la Rúa P, Jaffé R, Dall'olio R, Muñoz I, Serrano J (2009) Biodiversity, conservation and current threats to European honeybees. Apidologie 40:263. https://doi.org/10.1051/apido/2009027

Dubaić JB, Simonović S, Plećaš M, Stanisavljević L, Davidović S, Tanasković M, Ćetković A (2021) Unprecedented density and persistence of feral honey bees in urban environments of a large SE-European city (Belgrade, Serbia). Insects 12:1127. https://doi.org/10.3390/insects12121127

Dudík M, Phillips SJ, Schapire RE (2007) Maximum entropy density estimation with generalized regularization and an application to species distribution modeling. J Med Entomol 8:1217

Eliasson P (2002) Skog, makt och människor. En miljöhistoria Om Svensk Skog. Lund University, Lund, pp 1800–1875

Eliasson P, Nilsson S (1999) The Swedish oak during the 18th and 19th centuries–quantities, qualities and biodiversity. Bebyggelsehistorisk Tidskrift 37:33–64

Ellis JS, Soland-Reckeweg G, Buswell VG, Huml JV, Brown A, Knight ME (2018) Introgression in native populations of *Apis mellifera*

mellifera L.: implications for conservation. J Insect Conserv 22:377–390. https://doi.org/10.1007/s10841-018-0067-7
Enander KG (2007) Skogsbruk på samhällets villkor. Institutionen för skogens ekologi och skötsel, Sveriges lantbruksuniversitet. Available at: http://urn.kb.se/resolve?urn=urn:nbn:se:slu:epsilon-e-288 . Accessed 01 Jul 2023
Fries I, Imdorf A, Rosenkranz P (2006) Survival of mite infested (*Varroa destructor*) honey bee (*Apis mellifera*) colonies in a nordic climate. Apidologie 37:564–570. https://doi.org/10.1051/apido:2006031
Guichard M, Dainat B, Dietemann V (2023) Prospects, challenges and perspectives in harnessing natural selection to solve the 'varroa problem' of honey bees. Evol Appl 16:593–608. https://doi.org/10.1111/eva.13533
Hansson Ã (1955) Finns honungsbiet kvar i vilt tillstånd i Norden. Nordisk Bitidskrift 8:123–126
Hung K-LJ, Kingston JM, Albrecht M, Holway DA, Kohn JR (2018) The worldwide importance of honey bees as pollinators in natural habitats. Proc Royal Soc B: Biol Sci 285:20172140. https://doi.org/10.1098/rspb.2017.2140
Husberg E (1994) The history of beekeeping: honey, beeswax and mead in Sweden during the middle ages and the sixteenth century. Avhandlingar fraan Historiska Institutionen i Goeteborg, Sweden
Jensen AB, Pedersen BV (2005) Varying degrees of *Apis mellifera ligustica* introgression in protected populations of the black honeybee, *Apis mellifera mellifera*, in northwest Europe. Mol Ecol 14:93–106. https://doi.org/10.1111/j.1365-294X.2004.02399.x
Kohl PL, Rutschmann B (2018) The neglected bee trees: European beech forests as a home for feral honey bee colonies. PeerJ 6:e4602. https://doi.org/10.7717/peerj.4602
Kohl PL, Rutschmann B, Steffan-Dewenter I (2022) Population demography of feral honeybee colonies in central European forests. Royal Soc Open Sci 9:220565. https://doi.org/10.1098/rsos.220565
Landsmålsarkivet (1928) Bin och Biskötsel, Uppsala, Almqvist & Wiksells Boktryckeri AB. 283504
Linder P, Östlund L (1998) Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. Biol Conserv 85:9–19. https://doi.org/10.1016/S0006-3207(97)00168-7
Michaelsen TC (2016) Aspen *Populus tremula* is a key habitat for tree-dwelling bats in boreonemoral and south boreal woodlands in Norway. Scand J for Res 31:477–483. https://doi.org/10.1080/02827581.2015.1133844
Nielsdatter MG, Larsen M, Nielsen Nielsenlg MM, Rasmussen C (2021) History of the displacement of the European dark bee (*Apis mellifera mellifera*) in Denmark. J Apic Res 60:13–18. https://doi.org/10.1080/00218839.2020.1826111
Nilsson SG, Hedin J, Niklasson M (2001) Biodiversity and its Assessment in Boreal and Nemoral forests. Scand J for Res 16:10–26. https://doi.org/10.1080/028275801300090546
Norrström N, Niklasson M, Leidenberger S (2021) Winter weight loss of different subspecies of honey bee *Apis mellifera* colonies (Linnaeus, 1758) in southwestern Sweden. PLoS ONE 16:e0258398. https://doi.org/10.1371/journal.pone.0258398
Oleksa A, Gawroński R, Tofilski A (2013) Rural avenues as a refuge for feral honey bee population. J Insect Conserv 17:465–472. https://doi.org/10.1007/s10841-012-9528-6
Panziera D, Requier F, Chantawannakul P, Blacquière T (2022) The diversity decline in wild and managed honey bee populations urges for an integrated conservation approach. Front Ecol Evol 10:767950
Pirk CWW, Moritz RFA (2017) Risks and benefits of the biological interface between managed and wild bee pollinators. Funct Ecol 31:47–55. https://doi.org/10.1111/1365-2435.12768
Potts SG, Roberts SPM, Dean R, Marris G, Brown MA, Jones R, Neumann P, Settele J (2010) Declines of managed honey bees and beekeepers in Europe. J Apic Res 49:15–22. https://doi.org/10.3896/IBRA.1.49.1.02
QGIS Development Team 2023. QGIS geographic information system. Open Source Geospatial Foundation Project. URL: http://qgis.osgeo.org
Ranius T (2002) Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol Conserv 103:85–91
Ranius T, Eliasson P, Johansson P (2008) Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. Biodivers Conserv 17:2371–2381. https://doi.org/10.1007/s10531-008-9387-3
Requier F, Garnery L, Kohl PL, Njovu HK, Pirk CW, Crewe RM, Steffan-Dewenter I (2019) The conservation of native honey bees is crucial. Trends Ecol Evol 34:789–798. https://doi.org/10.1016/j.tree.2019.04.008
Ruottinen L, Berg P, Kantanen J, Kristensen TN, Praebel A, Groeneveld F (2014) Status and conservation of the nordic brown bee: final report. NordGen publication series 2014:02, Nordic Genetic Resource Center
Ruttner F (1988) Morphometric analysis and classification. In: Ruttner F (ed) Biogeography and taxonomy of honeybees. Springer, Berling
Seeley TD (2017) Life-history traits of wild honey bee colonies living in forests around Ithaca, NY, USA. Apidologie 48:743–754. https://doi.org/10.1007/s13592-017-0519-1
Seeley TD (2019) The lives of bees: the untold story of the honey bee in the wild. Princeton University Press, Princeton. https://doi.org/10.2307/j.ctvc7749q
Seeley T, Morse R (1976) The nest of the honey bee (*Apis mellifera* L.). Insectes Sociaux 23:495–512
Seeley TD, Smith ML (2015) Crowding honeybee colonies in apiaries can increase their vulnerability to the deadly ectoparasite *Varroa destructor*. Apidologie 46:716–727. https://doi.org/10.1007/s13592-015-0361-2
Sjörs H (1999) The background: geology, climate and zonation. Acta Phytogeograph Suec 84:5–14 In: Sjögren, E, Rydin H, Snoeijs P, Diekmann M (1999) Swedish plant geography. Acta Phytogeograph Suec 84:5–14
Skogsdata SLU (2023) Sveriges Lantbruksuniversitet, Umeå: SLU Institutionen för skoglig resurshushållning. Available at: https://www.slu.se/globalassets/ew/org/centrb/rt/dokument/skogsdata/skogsdata_2023_webb.pdf . Accessed 14 Aug 2023
Soland-Reckeweg G, Heckel G, Neumann P, Fluri P, Excoffier L (2009) Gene flow in admixed populations and implications for the conservation of the western honeybee, *Apis mellifera*. J Insect Conserv 13:317–328. https://doi.org/10.1007/s10841-008-9175-0
Statistics Sweden (2023) Digitala gränser. Available at: https://www.scb.se/hitta-statistik/regional-statistik-och-kartor/regionala-indelningar/digitala-granser . Accessed 3 Aug 2023
Walankiewicz W, Czeszczewik D, Stański T, Sahel M, Ruczyński I (2014) Tree cavity resources in spruce-pine managed and protected stands of the Białowieża Forest, Poland. Nat Areas J 34:423–428. https://doi.org/10.3375/043.034.0404
Weber E (2013) *Apis mellifera*: the domestication and spread of european honey bees for agriculture in North America. Univ Mich Undergrad Res J 9:20–23