Received: 18 September 2019 | Revised: 8 November 2019 | Accepted: 14 November 2019

DOI: 10.1111/conl.12693

Conservation Letters
A journal of the Society for Conservation Biology
Open Access
WILEY

LETTER

Contribution of European forests to safeguard wild honeybee populations

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Funding information
Deutsche Forschungsgemeinschaft; University of Wuerzburg

Abstract

Recent studies reveal the use of tree cavities by wild honeybee colonies in European forests. This highlights the conservation potential of forests for a highly threatened component of the native entomofauna in Europe, but currently no estimate of potential wild honeybee population sizes exists. Here, we analyzed the tree cavity densities of 106 forest areas across Europe and inferred an expected population size of wild honeybees. Both forest and management types affected the density of tree cavities. Accordingly, we estimated that more than 80,000 wild honeybee colonies could be sustained in European forests. As expected, potential conservation hotspots were identified in unmanaged forests, and, surprisingly, also in other large forest areas across Europe. Our results contribute to the EU policy strategy to halt pollinator declines and reveal the potential of forest areas for the conservation of so far neglected wild honeybee populations in Europe.

KEYWORDS

Apis mellifera, conservation, forest management, honeybees, native populations, protected forests, tree cavities, unmanaged broadleaved forests

1 | INTRODUCTION

In Europe, the western honeybee *Apis mellifera* exhibits a dual nature as managed and wild species (Requier et al., 2019a). Despite wild populations of *A. mellifera* being a threatened component of the native fauna, little attention has been paid to these populations (Kohl & Rutschmann, 2018; Requier et al., 2019a). Currently, *Apis mellifera* is classified as 'data deficient' in the *IUCN Red List of European bees* due to a lack of information on wild populations (De la Rúa et al., 2014). Although EU-wide pollinator monitoring schemes have been planned for assessing the status and trends of pollinator species (European Commission, 2018), little attention has been paid so far to the monitoring of wild honeybee populations (Requier & Crewe, 2019). Honeybee health issues (Potts et al., 2010) have primarily been discussed with respect to their impact on beekeeping and crop pollination (Potts et al., 2016), while wild populations are often not considered and even widely assumed as extinct (De la Rúa, Jaffé, Dall 'Olio, Mūnoz, & Serrano, 2009; Geldmann & González-Varo, 2018; Jaffé et al., 2010; Meixner, Kryger, & Costa, 2015). Nonetheless, recent studies have shown that wild colonies of *A. mellifera* can still be found in Europe (Kohl & Rutschmann, 2018; Oleksa, Gawronski, & Tofilski, 2013), underpinning the need to increase knowledge on these populations (Alaux, Le Conte, & Decourtye, 2019; Requier et al., 2019a; Requier & Crewe, 2019).

Wild honeybee populations are affected by the expansion of managed allochtone populations in Europe and associated spillover of nonlocal pathogens (De la Rúa et al., 2009; Muñoz et al., 2014; Moritz, Kraus, Kryger, & Crewe, 2007). Current beekeeping activities include the breeding of nonlocal subspecies and led to an introgressive hybridization, which can reduce both the colony health and survival of the local subspecies populations (De la Rúa et al., 2009; Meixner et al., 2015). Although the conservation of cavity-rich forests could foster the protection of native populations of *A. mellifera* in Europe (Moritz et al., 2007; Requier et al., 2019a), the coexistence with managed apiaries also exposes wild honeybee populations to exotic bee pests and pathogens (Fries, Imdorf, & Rosenkranz, 2006; Moritz et al., 2007). Conserving wild colonies could also favor naturally pathogen-resistant honeybee populations (e.g., *Varroa destructor)*, and wild honeybees colonies should be viewed as a genetic reservoir of resistance against biotic pressures (Seeley, 2019).

Forest trees may bear many suitable cavities—either excavated by woodpeckers or as a result of wood decay (Kozák et al., 2018; Paillet et al., 2017; Remm & Lõhmus, 2011)—which constitute the primary nesting sites of the wild colonies of *A. mellifera* (Crane, 1999; Kohl & Rutschmann, 2018; Oleksa et al., 2013). However, the current availability of tree cavities is limited by production-oriented forest management in Europe (Bütler, Lachat, Larrieu, & Paillet, 2013; Paillet et al., 2017). Across the main European forest types, unmanaged areas generally host far more tree cavities than their managed counterparts (Kozák et al., 2018; Paillet et al., 2017, 2019). Records of wild honeybee colonies in tree cavities are mainly restricted to Northern Poland (Oleksa et al., 2013) and central Germany (Kohl & Rutschmann, 2018). Although wild colonies were also reported to colonize man-made tree cavities in Southern Urals forests (Ilyasov, Kosarev, Neal, & Yumaguzhin, 2015) and suspected in France (Bertrand et al., 2015), Ireland, and Italy (Jaffé et al., 2010), there is a critical lack of field data on the presence of honeybee occupied tree cavities. Consequently, it is still unclear to what extent such tree cavities could support wild honeybee populations across Europe.

We predicted the availability of tree cavities in forests at the European scale and derived the population size of wild honeybee colonies that could be sustained through reinforced conservation plans of cavity-bearing trees. We first synthesized the literature available on tree cavities in European forests. We analyzed how forest and management types affected tree cavity densities, and derived an European distribution of forest tree cavities. We then considered correction factors obtained from literature (cavity size and occupation rate) to estimate the potential size of the European population of wild honeybees. Finally, we gauged the representativeness of the presumed population size of wild honeybee colonies, discussing how conservation plans can foster these threatened populations. To support the design of robust field monitoring as an important step towards conservation policies of pollinators across Europe, we therefore identified potential hotspots of wild honeybee populations across Europe as priority areas for monitoring and conservation planning.

2 | MATERIALS AND METHODS

2.1 | Data synthesis of tree cavities in Europe

We extensively searched the published literature to gather data on tree cavities in Europe using the *Web of Knowledge* (Web of Knowledge, 2019). The complete search string was "[TS = (cavity OR hole) AND TS = Tree AND TS = (forest OR woodland) AND TS = density]" with TS meaning "Topic". We included all literature from 1991 until February 2019. The initial search identified 575 papers worldwide. Based on title and abstract, we then restricted our search to studies in Europe providing data on cavity densities. We defined tree cavity as all types of inventoried holes with a minimum entrance diameter of 2 cm, either in living or dead forest trees, including woodpecker-excavated and decayed cavities linked to wood rot and decomposition (Remm & Lõhmus, 2011). We finally selected studies that used plot-based sampling designs (excluding data based on active cavity search) and comparable cavity typologies. Data included in different papers were used only once. The data synthesis produced 12 references (see the complete list in Supporting Information, Table S1).

Overall, the dataset comprised 106 sites across Europe and 1,297 forest plots (Figure 1, more details in Table S1 and in Requier et al., 2019b). On each plot, all trees were systematically observed for decayed and excavated cavities. We recorded the time since the last human intervention (wood harvesting) or the forest state (e.g., unmanaged). Afterwards we attributed plots with no record of forest management for at least 50 years, as well as those qualified

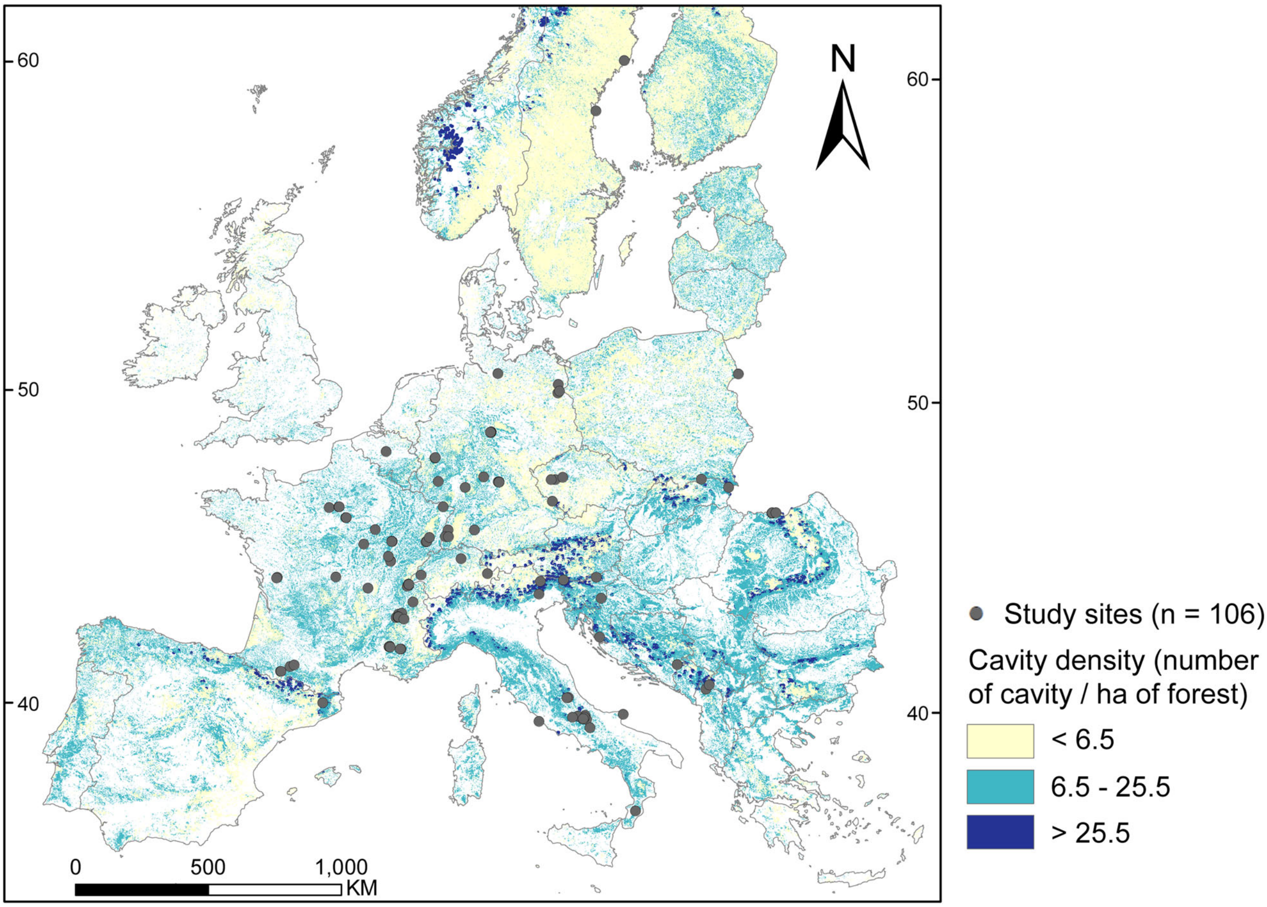

FIGURE 1 Predicted tree cavity densities across European forests. The predictions (color gradient) are based on a large data synthesis of cavity inventories over different forest and management types, including 106 sites across Europe (black dots). Pixels with high tree cavity densities (> 25.5 cav/ha, dark blue) have been highlighted (i.e., pixel borders have also been colored) to be visible. The northern limit corresponds to the native range of *Apis mellifera* in Europe (Ruttner, 1988)

as primeval and untouched, in an "unmanaged" category, while all the other plots were attributed to the "managed" category. We also recorded broad forest types according to the CORINE Land Cover's categories "Coniferous," "Broadleaved," or "Mixed forests" (CORINE Land Cover, 2018).

2.2 | Estimating the spatial availability of tree cavity densities

All statistical analyses were performed using the R software version 3.5.2 (R Development Core Team, 2018). To predict the spatial availability of tree cavities across Europe, we first estimated the density of cavities per forest type (broadleaved, conifers or mixed) crossed with management type (managed vs unmanaged). We fitted a generalized linear mixed-effects model (GLMM) with Gamma error distribution and log link function (*glmmTMB* function in the *glmmTMB* R-package, Brooks et al., 2017). Whenever the cavity density was null, we added a negligible random value (Gaussian distribution with mean = 0.01, SD = 0.001) to account for the assumptions of the gamma error distribution. We added a variance correction (calculated as number of plots × plot area) to account for the differences in sampling effort. Data source was added as a random parameter to account for the nestedness of data issued of the same source. We then tested the differences between levels of the fixed effects (i.e., forest type and forest management) with *a posteriori* multiple pairwise comparison (Tukey's test) using the *cld* function in the *emmeans* R-package (Russell, 2018).

We subsequently extrapolated the results of the GLMM at the European scale, with a resolution of one squared kilometer pixels. We used the CORINE Land Cover (2018) map of forest types at the European scale as our independent variable of forest type. We used the map of European potential primary forests proposed by Sabatini et al. (2018) with a threshold of 0.9 occurrence probability—the threshold value that optimizes the predictive power of primary forest distribution (Sabatini et al., 2018)—as our managed versus unmanaged independent variable. We addressed the predicted density of cavities for each pixel resulting from the intersection of both maps.

2.3 | Estimating the population size of wild honeybees

Based on the predicted density of tree cavities across Europe, we estimated the population size of wild honeybees considering two correction factors: (*i*) the cavity size and (*ii*) the occupation rate of wild honeybees. Honeybees need a volume of at least 20 L to hoard enough honey to overwinter (Seeley, 1985). In European forests, such suitable (large) tree cavities result either from wood decay or excavation by the Black woodpecker (*Dryocopus martius*) (Kohl & Rutschmann, 2018). Based on the rare studies assessing different tree cavities sizes in forest areas, we estimated that approximately 0.4%–0.8% of all cavities available are large enough to host viable wild honeybees colonies (see e.g., Andersson, Domingo Gómez, Michon, & Roberge, 2018; Kohl & Rutschmann, 2018; Kosinski & Kempa, 2007; Kosiński, Bilińska, Dereziński, & Jeleń, 2010). We conservatively considered the lower bound estimate of 0.4%. Based on the rare studies assessing the occupation rate of wild honeybees in suitable tree cavities across Europe (Kohl & Rutschmann, 2018; Oleksa et al., 2013), we conservatively assumed that only 1% of the suitable cavities were actually occupied (Section S1, Supporting Information). Finally, we estimated population size of wild honeybees per country (as the area unit of the study) as follows:

$$\text{Number of wild colonies per country} = f \times d \times p \times o$$

with *f* the forest land cover of the country recorded following CORINE Land Cover (2018); *d* the predicted density of tree cavities in the forest area of the country; *p* the proportion of suitable cavities across all cavities available (estimate of .004, see above); and *o* the conservative occupation rate of tree cavities by wild honeybees (average estimate of .01, see above).

2.4 | Gauging the representativeness of the estimated populations

Given the lack of field data on the proportion of tree cavities occupied by honeybees, we performed an expert-based survey to record empirical observations across Europe. We submitted a questionnaire to 131 experts working with tree cavities across 19 European countries (6.9 ± 7.1 experts per country, mean ± SD, Table S2). We invited experts to record their observations of honeybee-occupied cavities in European forests across a 100 × 100 km square designed questionnaire (Section S2, Supporting Information). The aim was to get a first estimate of the occurrence of wild honeybees living in tree cavities across European countries. On the other hand, we measured the representativeness of the presumed population size of wild honeybee colonies compared with that of colonies managed by beekeepers. We used data out of the extensive FAO dataset of the United Nations (FAOSTAT, 2018), in particular the number of managed colonies per European country for the last five years available in the database (2012–2016 in order to get an average and incertitude value) and the country area. The dataset was restricted to 26 European countries with information for the number of managed colonies.

2.5 | Identifying conservation hotspots of wild honeybees

We identified the potential conservation hotspots of wild honeybee colonies on the basis of the predicted densities of suitable tree cavities across Europe. Based on the same raster (see Section 2.2), we selected forest areas (i.e., clusters of adjacent pixels) larger than 10,000 ha, for which we assume a sufficient minimum population size and isolation from risks of human-mediated hybridization and pest transmission from managed colonies (Requier et al., 2019a). Thereafter, we merged the 6-km neighboring patches as a single area, representing a population unit. We then estimated the total surface of each conservation hotspot and the amount of wild colonies that could be hosted. Finally, we selected the 30 most important conservation hotspots relatively to their capacity to host wild honeybee colonies (i.e., the total amount of colonies in the defined area).

3 | RESULTS

3.1 | Spatial availability of tree cavity densities

Broadleaved forests were the most represented forest type across the 106 sites in 12 European countries (Figure 1), while pure coniferous and mixed stands were the rarest (Table S1). The density of cavities varied widely among forest and management types (Table 1). Coniferous forests had smaller cavity densities than the other forest types. Unmanaged forests had much higher cavity densities than managed forests, independently of the forest type (Table 1). Extrapolated at the European scale (Figure 1), the predicted mean density of cavities also varied among countries (from 8.5 cav/ha in Sweden to 25.2 cav/ha of forest in Kosovo, Figure S1, Supporting Information). In particular, high densities of cavities were found in mountainous areas with continuous forest areas: the Carpathians, the Alps, and the Pyrenees (Figure 1).

3.2 | Estimated population size of wild honeybees

Based on the spatial predictions of cavities, the density of wild colonies ranged from 0.4 colony per thousand ha of forest in Liechtenstein to 1.0 colony per thousand ha of forest in Croatia, Hungary, and Serbia (Figure 2a). Thus, we estimated that 81,248 wild honeybee colonies could be sustained in European forests, which would represent on average 2% of the current managed honeybee population of European countries (Figure 2b). No correlation was detected between predicted

TABLE 1 Estimated mean cavity densities per hectare of forest issued from a generalized linear mixed model with gamma error distribution (log link, results have been back-transformed), variance correction for sampling effort (plot number × plot area) and random data source effect. CLC = Corine Land Cover; SE = standard error of the mean; N = number of sites × CLC type combinations; CI = 95% confidence interval. Different letters indicate significantly ($p < .05$) different cavity densities values based on post hoc Tukey's test

Management type	CLC type	Estimated mean	SE	N	Lower CI	Upper CI	
Managed	Coniferous	6.47	1.46	7	3.06	13.7	*a*
Unmanaged	Coniferous	7.67	1.56	6	3.19	18.43	*ab*
Managed	Mixed	20.34	1.36	20	10.98	37.70	*bc*
Unmanaged	Mixed	61.18	1.42	9	30.62	122.26	*d*
Managed	Broadleaved	25.51	1.32	45	14.74	44.17	*c*
Unmanaged	Broadleaved	63.92	1.35	19	35.14	116.24	*d*

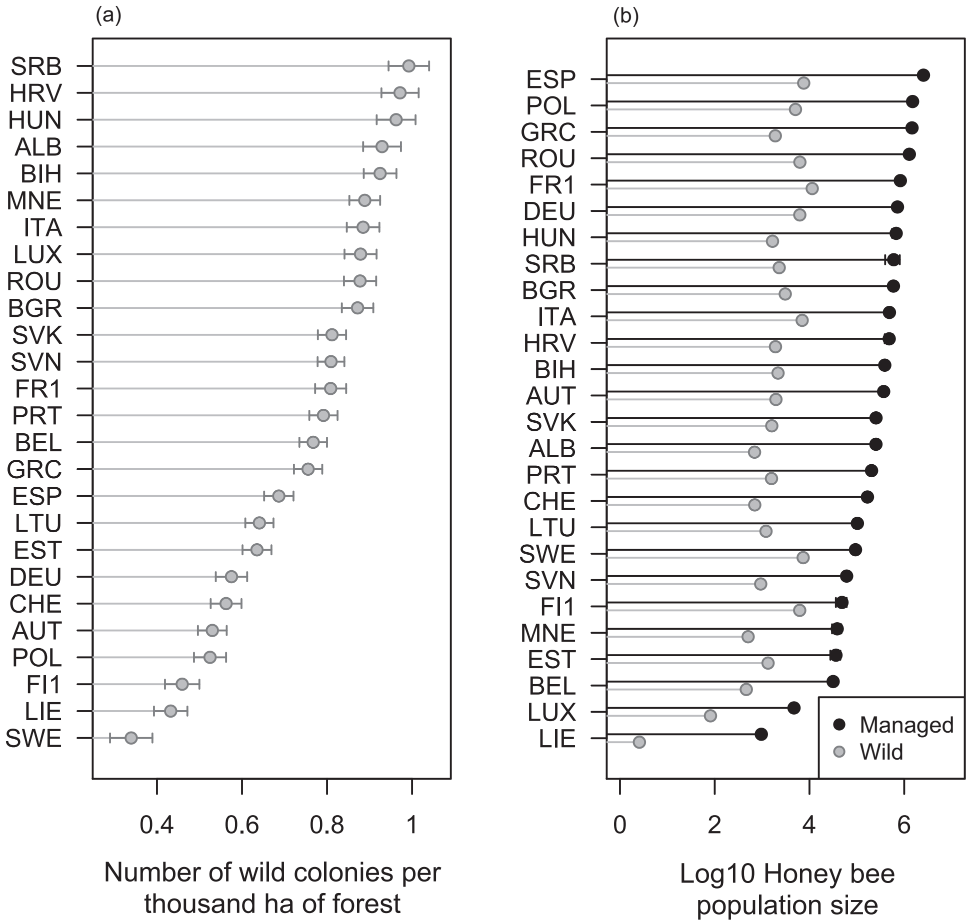

FIGURE 2 Estimated population size of wild honeybees across Europe. (a) The density of wild colonies per thousand ha of forest, and (b) the nation-wide population size of wild versus managed colonies. Countries are named according to the ISO 3166-1 alpha-3 convention. Values are means ± SD. The absence of visible SD on the b graph is related to the low data variability (the mean dots overlap the SD)

wild and managed colony densities ($t = .24$, $p = .81$, $R^2 = .05$), suggesting that the capacity of countries to conserve wild honeybees is independent of current beekeeping activities. Thirty-five experts participated in the field-validation survey of honeybee-occupied tree cavities, representing a participation rate of 27% from 12 different European countries (Table S2). Most experts (72%) observed honeybees in tree cavities in 11 out of 12 countries, and for more than half of the European squares (i.e., 48 out of 92) wild colonies in tree cavities were reported (Figure 3).

3.3 | Conservation hotspots of wild honeybees

Conservation hotspots were identified all over Europe (Figure 4). As expected, most of these hotspots were located in the same mountain areas as mentioned above (Figure 1).

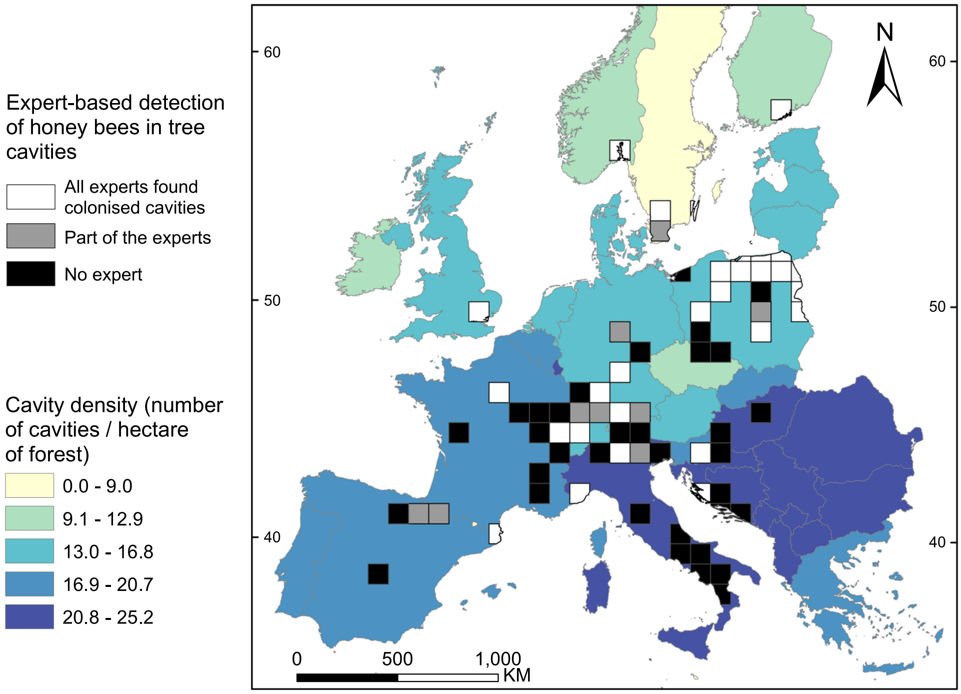

FIGURE 3 Expert-based survey of wild honeybee colonies across European forests. Given the extreme rarity of data available on the occupation rate of tree cavities by wild honeybee colonies in forests, we carried out an expert-based survey to record observation from experts in forest ecology and/or on woodpecker ecology across Europe (Table S2, Supporting Information). The aim of this survey was to roughly assess the presence of tree cavities potentially occupied by honeybee colonies within each 100 × 100 km square of a European grid. This spatial resolution was determined as the best compromise between effective participation and data quality (Section S2). The color gradient in the background represents the national average of cavity density (in number of cavities per hectare of forest).

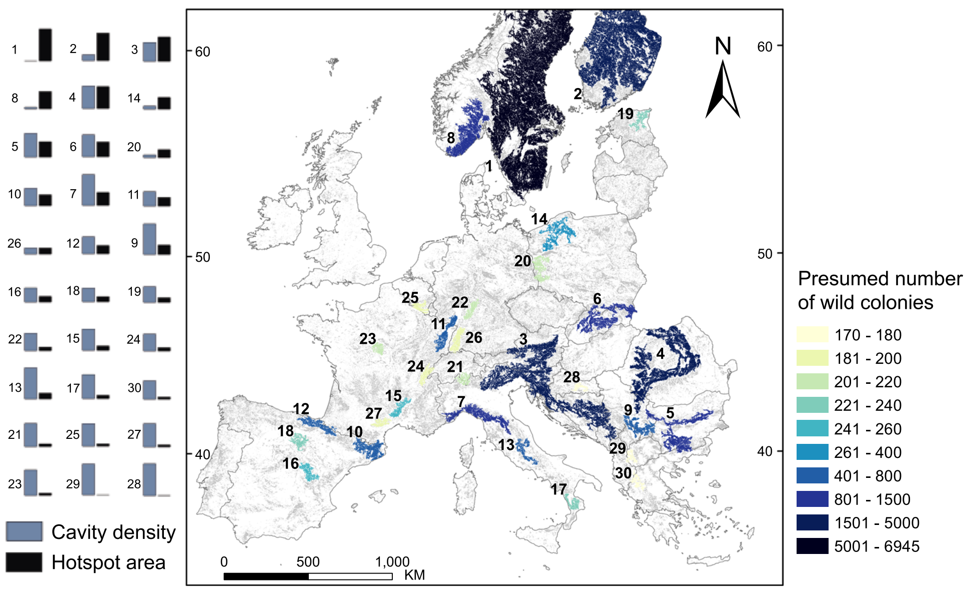

FIGURE 4 Identification of forest areas with the highest conservation value for wild honeybees across Europe. The 30 most important hotspots were ranged regarding their potential to host wild honeybee colonies (color gradient, in number of colonies). Characteristics of each hotspot are given on the left, in particular to inform whether the population size of wild honeybees in a hotspot is rather related to the density of cavities in the hotspot (in blue) or to the size of the hotspot (in black). More details are available in Table S3, Supporting Information.

Surprisingly, however, some hotspots were also identified in areas with lower cavity densities such as in Sweden, Finland, Norway, Poland, and Germany (Figure 4, Table S3), but with large continuous forest areas. Overall, the capacity of these hotspots to host wild honeybees varied widely from 170 colonies in Greece to 6,945 colonies in the connected forest areas of Sweden (Figure 4, Table S3). Interestingly, most of the identified conservation hotspots were congruent with observations of honeybee colonies by experts (Figure 3).

4 | DISCUSSION

Using data synthesis, model predictions and expert-based surveys, we showed that a substantial population of wild honeybee colonies could be sustained through the conservation of cavity-bearing trees in European forests. The density of tree cavities differed greatly among forests and management types in Europe. Our results showed that conifer-dominated forests are generally poorer in microhabitats, especially in tree cavities (see also Paillet et al., 2017). This is likely related to the foraging and nesting habits of cavity excavators, which tend to prefer broadleaved trees (e.g., Kosinski et al., 2018; Rolstad, Rolstad, & Saeteren, 2000), as well as to the higher persistence of decayed cavities on broadleaved trees (Paillet et al., 2019; Wesołowski, 2011). Unsurprisingly, unmanaged forests displayed significantly higher cavity densities than their managed counterparts, due to the higher occurrence of large trees and snags in these forests (Kozák et al., 2018; Paillet et al., 2017). As a result, we predict that most European forests are cavity-poor except for some rare areas of unmanaged forest (Sabatini et al., 2018).

We estimated that more than 80,000 wild honeybee colonies could be sustained by cavity-bearing trees in European forests. While such an estimate is rather encouraging since wild populations of honeybees were widely assumed as extinct (De la Rúa et al., 2009; Geldmann & González-Varo, 2018; Jaffé et al., 2010; Meixner et al., 2015), this figure represents only 2% of the managed colonies and underpins the need for dedicated conservation plans to increase this proportion. However, our approach may underestimate the actual population size and support a conservative prediction. First, we intentionally restricted our estimations to forest nesting sites; but other cavity types can be used, for example, in trees outside forests, rocks, or man-made structures, that would consequently increase substantially wild population estimates. Unfortunately, no field data are yet available on these potential habitats. In addition, the occupation rate of wild honeybees was based on two studies that only estimated lower limits of wild colony densities (Kohl & Rutschmann, 2018; Oleksa et al., 2013), although real occupation rates should be higher. Moreover, the ecological parameters used to predict the population size of wild colonies have been spatiotemporally restricted to sparse available data. For instance, we used a fixed estimate of cavity size used by wild honeybees, although it could vary with latitude and elevation, given that climate (and in particular winter duration) could affect the colony size and the amount of food reserve needed to overwinter (Nürnberger, Härtel, & Steffan-Dewenter, 2018). We also used a fixed-occupation-rate estimate due to a lack of data on variability among different forest and management types, or on the potential competition between woodpeckers, honeybees, and other secondary cavity nesters for access to large cavities (see Broughton et al., 2015 for an analysis of competition between taxa).

Encouragingly, our large-scale expert-based survey showed that most experts detected occupied cavities in conservation hotspots, in accordance with the predicted patterns of cavity-nesting wild colonies across European forests. Surprisingly, the larger hotspots have been predicted in low cavity density, but well-connected forest areas, such as in Sweden and Finland where conifers are dominant (except for some birch—*Betula* spp.—and aspen—*Populus tremula*—dominated forests). As expected, other important hotspots were detected in areas of unmanaged forests allowing high cavity densities (Kozák et al., 2018; Paillet et al., 2017, 2019), for which wild honeybees should be added to the list of unmanaged forest-dependent species. It is important to note that our estimates do not include other determinants of wild honeybee population densities, particularly the flower resource quality of forests, which is mainly unknown for European forests.

Reinforcing conservation plans of cavity-bearing trees in such large forest areas can promote the conservation of wild honeybees as a threatened component of the native fauna in Europe. The spatial distribution of hotspot areas and the predicted number of wild colonies reveals a lack of potential forest areas in the Iberian peninsula, Southern Italy, and Greece, indicating that subspecies of *Apis mellifera* with Mediterranean distribution ranges are particularly threatened (De la Rúa et al., 2009, Requier et al., 2019a). Our results help to fill a knowledge gap regarding the threat status of wild honeybees in Europe (De la Rúa et al., 2014) and contribute to the aims of the EU pollinators initiative (European Commission, 2018). In particular, they provide the basis for a systematic monitoring of potential wild honeybee habitats, the targeted set-up of protected forest areas, improved forest management to maintain critical nesting and food resources, and the inclusion of wild honeybees and their regional subspecies in national and European conservation policies.

ACKNOWLEDGMENTS AND DATA

This publication was funded by the German Research Foundation (DFG) and the University of Wuerzburg in the funding programme Open Access Publishing. We are greatful to

D. Kozak and B. Regnery for sharing their data on cavities, and F. M. Sabatini for helpful comments on the map of primary forests in Europe. We also thank all the volunteer experts who participated in the survey and the two anonymous reviewers for constructive comments on the manuscript. The data presented in this manuscript are available through the Dryad Digital Repository (Requier et al., 2019b).

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SUPPORTING INFORMATION

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How to cite this article: Requier F, Paillet Y, Laroche F, et al. Contribution of European forests to safeguard wild honeybee populations. *Conservation Letters*. 2019;e12693. https://doi.org/10.1111/conl.12693