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Managed honey bees as a radar for wild bee decline?

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Abstract – Wild and managed bees are essential for global food security and the maintenance of biodiversity. At present, the conservation of wild bees is hampered by a huge shortfall in knowledge about the trends and status of individual species mainly due to their large diversity and variation in life histories. In contrast, the managed Western honey bee *Apis mellifera* is one of the best studied and monitored insects in existence. Since similar drivers may be relevant for the decline of wild bees and losses of managed honey bees, this raises the possibility that monitoring of honey bees may help to detect threatened regions for wild bees, thereby fostering urgently required conservation measures. However, this possible relationship has not yet been explicitly tested for. Moreover, research currently focused on honey bees as a model species may yield important insights into wild insect susceptibility to stressors and vice versa. Here we use the bees of Europe as a model to show that managed honey bees are not suitable surrogates for detecting declines in wild bees. A direct comparison of the response of wild bees and honey bees to the same threats (nutritional deficiencies, parasites and pathogens, pesticides, and a changing climate) shows that, whilst some of their responses may be similar at the individual level, when considered at the reproductive level (individuals versus colonies), many of their responses diverge. These results reinforce the need for basic research into wild bee biology, the need for national monitoring schemes for wild bee populations, and the call for conservation actions tailored to the individual ecologies of wild bee species.

wild bees / indicator species / species specific / sociality / populations

1. INTRODUCTION

Declines in wild bee populations and losses in managed bee populations have been reported from around the world (Neumann and Carreck 2010; Cameron et al. 2011), but particularly from

Europe, where extensive records of historical bee distributions exist (Biesmeijer et al. 2006; Potts et al. 2010a; Senapathi et al. 2015). Evidence of declines in wild bee species has come primarily from studies that have assessed aggregate changes in species richness across regions over time; evidence from species-specific, quantitative, and year-to-year assessments of changes in population sizes is much rarer, though they are becoming the focus of more attention as the quality of both datasets and computational techniques improves (Ogilvie et al. 2017; Powney et al. 2019).

As the response of different species to a changing environment can vary hugely, even within the

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same genus (e.g. Kleijn and Raemakers 2008; Rasmont et al. 2015), a species-specific understanding of population trajectories is critical for selecting those bee species that are at greatest risk and for informing their conservation. However, creating species-specific assessments for a region requires considerable effort, with important taxonomic considerations—for example, some 2053 bee species are known from Europe (Rasmont et al. 2017). In common with other bee faunas, European species vary extensively in their spatial distribution (from just a few sites to spanning the entire continent, Nieto et al. 2014) and ecological traits (e.g. dietary breadth, social structure, emergence time, Hofmann et al. 2019). As for other insect groups, it is necessary to have a good understanding of the autecology of individual bee species in order to understand the drivers behind their decline and also to develop appropriate conservation strategies (Sutherland et al. 2004; Biesmeijer et al. 2006; Murray et al. 2009). For example, a high-resolution measurement of the quantitative pollen requirements of the specialist (Dipsacaceae) solitary bee *Andrena hattorfiana* was necessary in order to identify the minimum resource level needed to maintain stable populations (Larsson and Franzén 2007). Despite the importance of such data for informing bee conservation, detailed studies of the autecology of individual bee species are surprisingly uncommon (Murray et al. 2009).

Because of these knowledge gaps, and the huge quantity of work necessary to address them appropriately, it might be possible and preferable to be able to understand the response of bees in aggregate to the threats facing them by using model species as surrogates. The Western honey bee (*Apis mellifera*) is potentially one such model. It is found throughout Europe (Requier et al. 2019) and, as a domesticated and commercially important species, their populations are monitored by beekeepers (Brodschneider et al. 2018) and governments (FAO 2018; European Commission 2019). *Apis mellifera* was the first bee and just the fifth insect species to have its genome sequenced (Robinson et al. 2006). It has also been used as a model for the study of eusocial organisation, communication through pheromones and dance language, and for our understanding of neurological

and immunological development (e.g. Medrzycki et al. 2013; Kovac et al. 2014; Straub et al. 2015; Frias et al. 2016). Given the high diversity of wild bees, this level of detailed research will simply never be reached for the vast majority of species, and indeed there is no relationship between the species richness recorded in European bee genera and the number of papers published on them (Figure 1, see [Supplementary Materials](#)).

However, in broad terms, honey bees ultimately require the same things as wild bees: somewhere to nest with appropriate nesting materials and an adequate supply of flowers (pollen and nectar) to rear their young, and both groups of bees are directly sensitive to the pressures of parasites, pesticides, and a changing climate (Goulson et al. 2015). If the response of managed honey bee populations to these threats is similar to that of wild bee populations in aggregate, it suggests that some of the findings of honey bee research may be directly transferrable to foster the conservation of wild bees. However, this first requires a comparison between changes in both managed honey bee and wild bee populations across the same region.

In order to address this central question, we focused our research on the comparatively well-known European bee fauna, for which both continental and country-level assessments of wild bee population changes are known (Nieto et al. 2014), in combination with assessments of managed honey bee colony abundance and rates of mortality (Brodschneider et al. 2018). Though similar assessments of honey bee mortality exist for other biogeographical regions such as the USA (Kulhanek et al. 2017), they are not accompanied by assessments of the population trends of the wild bee fauna. Using the patterns of spatial bee decline in Europe, we specifically compare trends in wild bees with those of managed honey bees to evaluate if they show the same pattern at a broad geographic (continental) scale. We review the threats facing wild bees and managed honey bees and assess their differential responses to common threats, in order to examine whether or not findings from honey bee studies can be generalised to wild bee species.

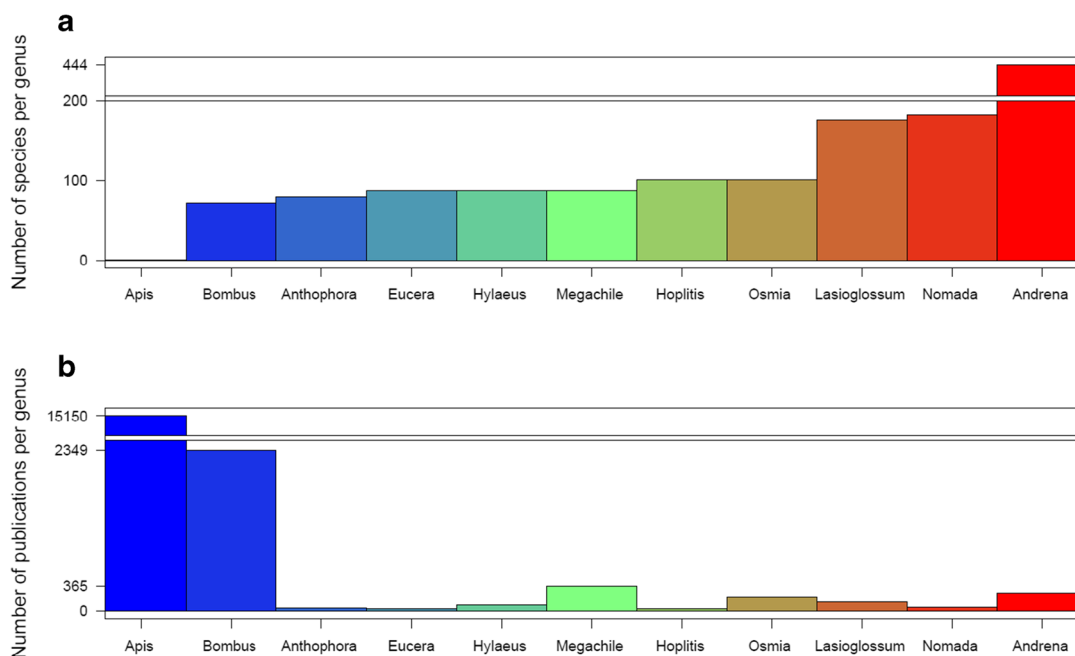


Figure 1. **a** The top 10 European bee genera with the highest species diversity. Only one species of *Apis* is found in Europe and it is included for comparison. **b** The number of publications recorded in Scopus for the top 10 most diverse European bee genera and for the genus *Apis*.

2. DO MANAGED HONEY BEES AND WILD BEES SHOW SIMILAR PATTERNS OF DECLINE AND LOSSES?

2.1. Population declines in wild bee species

We selected the work of Nieto et al. (2014) as a baseline as it is the only study considering the spatial distribution of wild bee declines at a continental scale for the European fauna (see Supplementary Materials, Figure S1). Of 1942 assessed bee species, a total of 77 (3.9%) were assessed as being ‘threatened’ across their European range based on IUCN criteria (vulnerable, endangered, or critically endangered). The highest absolute number of threatened species was found in south-central Europe eastwards to Crimea, whilst large parts of southern and northern Europe seem to have low numbers of threatened bees (Figure S2). This pattern is different from and contrasts with the overall picture of species richness (Figure S3). In part, this may be because an overall majority of species (1101, i.e. 56.7%) were classified as Data Deficient, most of which are

found in southern Europe (Figure 2). Given that Mediterranean Europe, the area with the highest species richness, has undergone large-scale changes in land use over the last few decades (Benoit and Comeau 2005), it is possible that many of the endemic and specialised bee species found there are genuinely threatened (Ortiz-Sánchez et al. 2018; Quaranta et al. 2018). However, where longer term studies have been conducted in undisturbed semi-natural habitats, the abundance of wild bees has actually increased over the past 20 years (Herrera 2019), though this study does not take species identity or turnover into account.

The large proportion of Data Deficient species in the bee fauna of southern European countries makes understanding patterns of decline across Europe challenging. An alternative approach to this continental-level assessment is to integrate the findings of national-level rarity assessments in order to identify priority species at a continental scale (Maes et al. 2019). Using national-level Red Lists, countries showing bee faunas with the highest percentage of threatened species are located in Western and Central Europe, with the bee

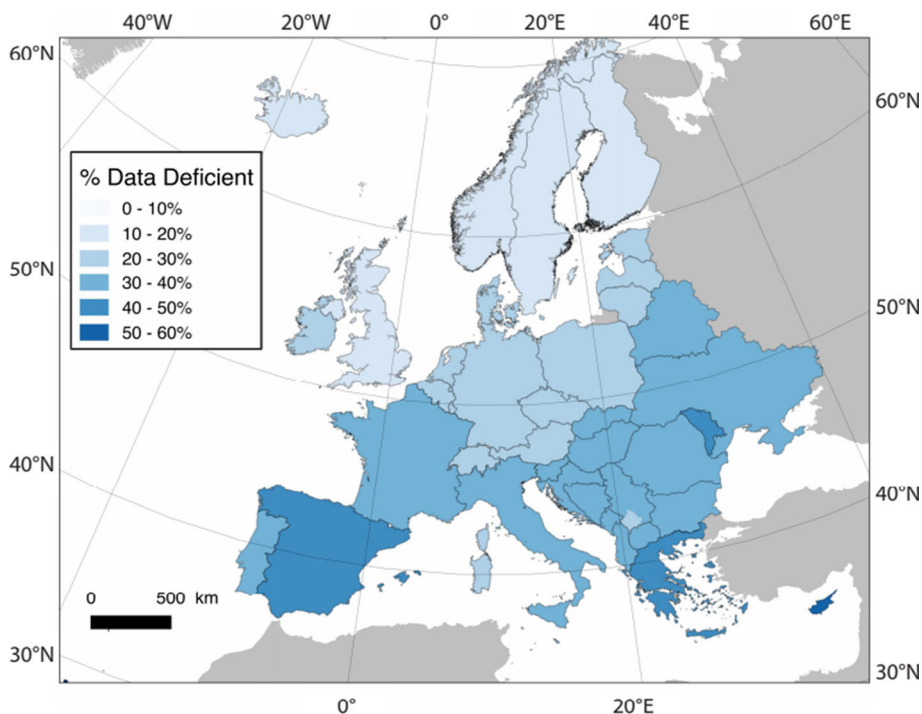


Figure 2. The distribution of European bee species assessed as Data Deficient by Nieto et al. (2014) as a percentage of national faunas.

faunas of Belgium, Czech Republic, Ireland, Germany, the Netherlands, and Switzerland, showing 30 to 40% of their faunas assessed as Vulnerable, Endangered, or Critically Endangered (Table I). In compiling national Red Lists of 34 European countries, Maes et al. (2019) produced a similar result for butterflies, with the faunas of Belgium, the Czech Republic, Denmark, and the Netherlands containing the greatest proportion of threatened butterfly species. However, directly comparing national Red List assessments for bee species is difficult because many of these national assessments are severely limited in scope. For example, Verdú and Galante (2006) considered just 32 of mainland Spain's more than 1000 bee species, finding eight to be Threatened (25.0%) and 15 Data Deficient (46.9%). Sároszpataki et al. (2005) and Wind and Pihl (2010) considered only bumble bees in the assessments for Hungary and Denmark respectively. Other assessments are relatively old and now partly outdated (e.g. Great Britain, Falk 1991) as the status of bee species may have changed considerably during this time, with for example species such as *Lasioglossum*

pauxillum increasing from scarce to abundant in Great Britain over the last 30 years (Else and Edwards 2018).

2.2. Colony mortality in managed honey bees

Though wild and feral populations of honey bees still persist in Europe, their populations are very small (Kohl and Rutschmann 2018; Requier et al. 2019). Because of a lack of information, the honey bee as a wild species was classified as Data Deficient by Nieto et al. (2014), and it is beyond the scope of this review to consider wild or feral *A. mellifera* populations in this comparison. For clarity, for the purposes of this review, use of the term 'honey bee' will refer only to managed populations of *A. mellifera*.

Rather than an assessment of threatened species as a percentage of a national or regional area, honey bee population trajectories can be measured with greater precision, at least theoretically. As the majority of honey bees in Europe live in managed colonies, their abundance can be measured from

Table I. National species diversity and Red List status in European countries. *N1*, number of nationally recorded species according to Nieto et al. (2014). *N2*, number of species on the National Red List (data from Drossart et al. 2019). *N3*, average winter mortality rates of managed honey bee colonies between 2008 and 2017 (data from COLOSS, see Section 4b). Faunas marked with an asterisk were not fully assessed

Country	N1	N2	N2/N1	N3	References for national level assessments
Estonia	179	0	0.0*	14.5	CNCEAS (2008)
Lithuania	295	2	0.7*	10.8	Rašomavičius (2007)
Spain (mainland)	1008	8	0.8*	17.6	Verdú and Galante (2006)
Slovenia	563	10	1.8*	17.1	Gogala (2018)
Hungary	704	12	1.8*		Sároszpataki et al. (2005)
Italy	879	16	1.8*	13.2	Quaranta et al. (2018)
Denmark	261	5	1.9*	12.9	Wind and Pihl (2010)
Malta	49	1	2.0*	2.6	Schembri and Sultana (1989)
Latvia	195	4	2.1*	13.4	Spuris (1998)
Belarus	124	3	2.4*	11.5	Prischchepchik (2008)
Moldova	127	10	7.9*		Timuş et al. (2017)
Norway	192	26	13.5	9.1	Kålås et al. (2010)
Great Britain	237	35	14.8	16.9	Falk (1991)
Poland	490	84	17.1*	13.2	Głowaciński and Nowacki (2009)
Finland	244	43	17.6	14.2	Rassi et al. (2010)
Slovakia	587	105	17.9*	7.9	Feráková et al. (2001)
Sweden	283	54	19.1	16.9	Gärdenfors (2010)
Belgium	403	112	29.1	17.5	Drossart et al. (2019)
Ireland	101	30	29.7	20.6	Fitzpatrick et al. (2006)
Switzerland	633	192	30.3	12.5	Cordillot and Klaus (2011)
Germany	585	194	33.2	16.5	Westrich et al. (2011)
Czech Republic	600	242	40.3	7.5	Farkac et al. (2005)
The Netherlands	331	135	40.7	18.0	Reemer (2018)

year to year at a regional or national level, with the caveats that some organisations only report the number of hives producing honey, and not all hives managed by amateur beekeepers are registered and tracked. Though longer term declines in the number of managed honey bee colonies have been reported from Europe when compared with a historical baseline, particularly in central Europe (Potts et al. 2010b), the number of hives in Europe has increased over the past decade (FAO 2018, Figure 3), with a 5.5% increase between 2017 and 2018 alone (European Commission 2019). Much of this increase is driven by a rise in hive numbers in Eastern Europe in countries such as Poland and Romania. Because an increase in hive numbers is largely driven by socioeconomic factors such as

an increase in the demand for honey and demand for pollination (Aizen and Harder 2009; Aizen et al. 2019), the annual change in the number of beehives is not necessarily a good indication of threat levels that honey bees may face. Instead, the rate at which colonies die over the winter can be used as a proxy for threats faced, with pressure from parasites and reduced access to forage associated with higher mortality rates (van der Zee et al. 2014).

Using data from the COLOSS project (van der Zee et al. 2012, 2014; Brodschneider et al. 2016, 2018, Table I), we found that the average rate of honey bee colony winter mortality (Figure 4a) was not significantly correlated with the number of wild bee species assessed as threatened by

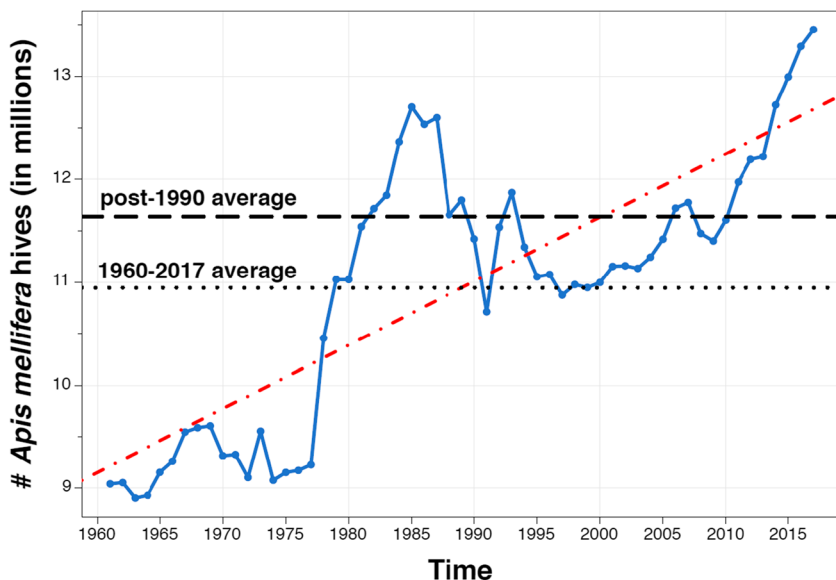


Figure 3. The number of managed honey bee colonies in Europe between 1961 and 2017 (data from FAO).

national Red Lists as a percentage of the national fauna (GLM, $t_{20} = 0.986$, $p = 0.337$, $R^2 = 0.049$, Figure 4b). Because of the severely limited scope of some of the regional assessments, restricting this analysis to those countries that assessed all of their species also shows no relationship (excluding those countries marked with asterisks in Table I, GLM, $t_9 = 0.089$, $p = 0.931$, $R^2 = 0.001$).

3. DO MANAGED HONEY BEES AND WILD BEES SHOW A SIMILAR RESPONSE TO COMMON THREATS?

Despite the lack of an apparent spatial pattern between managed honey bee losses and wild bee declines, there may still be important insights into wild bee ecology and population trends that can be gained from studies on honey bees, especially since they represent the bulk of research on bee ecology, with 78.4% of identified publications focusing on this species (Figure 1, Supplementary Materials). More broadly, including domesticated wild bee species, those species that can be easily reared represent 87.3% of publications, emphasising that most free-living bee species are chronically understudied. Here, we

review the threats facing honey bees and wild bees, and identify areas of similarity and difference in their respective responses, which may ultimately be reflected through parallels or differences in change in abundance with time. We then assess the extent to which findings are likely to be transferrable between honey bees and wild species.

3.1. Response to the loss of nutritional resources

Experimental studies on polylectic wild bees have shown that the nutritional quality of pollen (e.g. the concentration of protein, lipids, and sterols) can have an impact on the development and mortality of generalist bumble bee (Tasei and Aupinel 2008) and *Osmia* larvae (Sedivy et al. 2011). The floral diversity of pollen per se does not seem to be important, as bumble bees develop better on high-quality monofloral diets compared with low-quality polyfloral diets (Moerman et al. 2017). The pattern for honey bees appears to be similar at an individual level, with pollen quality having a positive impact on the physiology and survival of adult honey bees (Di Pasquale et al. 2013; Frias et al. 2016). However, when measuring foraging patterns in the field, honey bees often

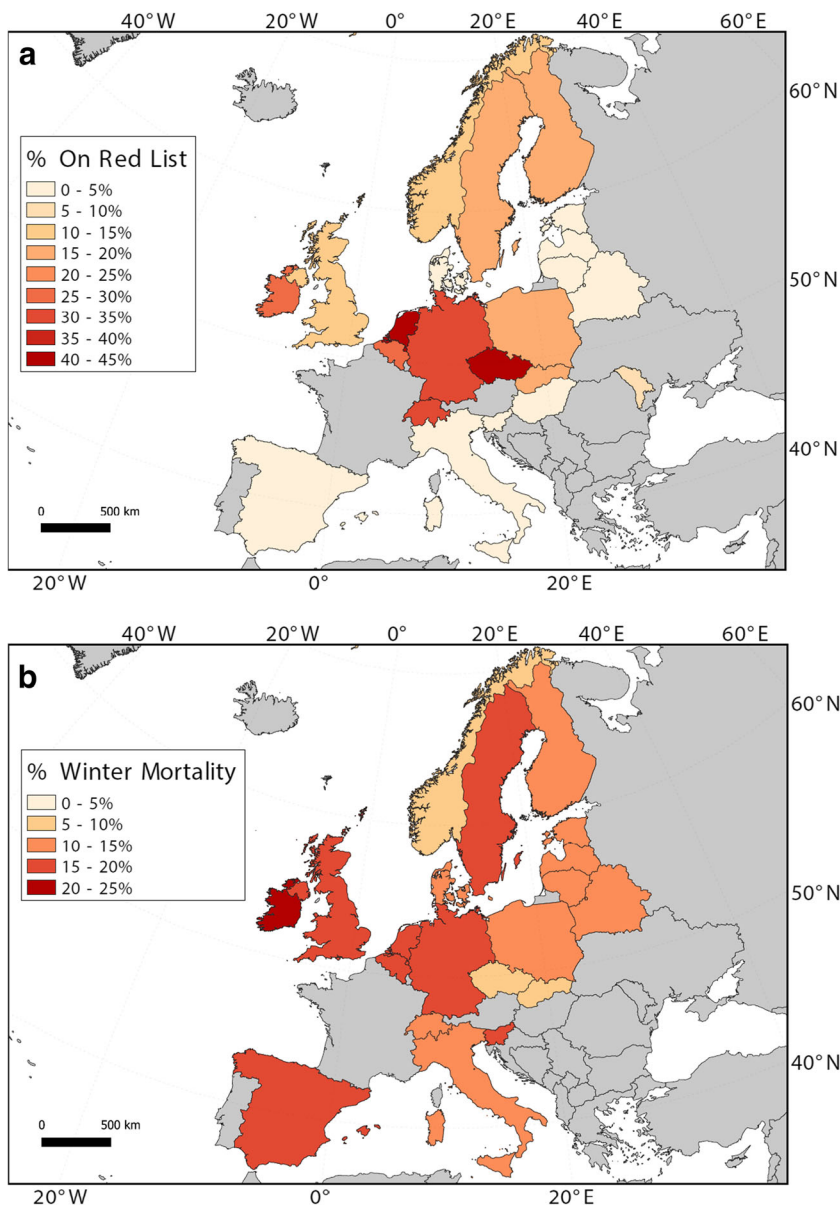


Figure 4. **a** The number of wild bee species assessed as threatened by national Red Lists as a percentage of the national fauna. **b** The average winter mortality of honey bee colonies between 2008 and 2017.

focus on highly available pollen sources regardless of their nutritional content (Leonhardt and Blüthgen 2012; Requier et al. 2015), yet honey bee colonies with access to a greater diversity and abundance of pollen sources throughout the season subsequently had higher rates of overwintering survival (Alaux et al. 2017).

The focus by bumble bees on pollen quality rather than quantity (Leonhardt and Blüthgen 2012) suggests that bumble bees may be more sensitive to a loss of high-quality resources compared with honey bees. Moreover, bumble bees vary in their dietary preferences, with those showing greater dietary specialisation having experienced greater declines in range and abundance in

Northwestern Europe and the Midwestern USA (Kleijn and Raemakers 2008; Wood et al. 2019), with more generalised species remaining stable. Likewise, solitary bees of the genus *Andrena* vary in their level of dietary generalisation, with more specialised species found less frequently on contemporary farmland than more generalised species (Wood and Roberts 2017).

Many solitary bee species have highly specialised diets and only collect pollen from just one or a few host plants (Westrich 1989; Müller and Kuhlmann 2008). Specialised bees have shown greater range declines in the UK and the Netherlands than generalised solitary bee species (Biesmeijer et al. 2006), and show greater sensitivity to changes in land use such as a loss of flowering plants (De Palma et al. 2015). However, it should be noted that dietary specialisation in and of itself is not a universal predictor of decline. Bees specialised on a plants that have remained common have persisted, and both generalist and specialist bee species that preferentially feed on declining plant species have declined (Scheper et al. 2014). These results suggest that a loss of particular host plants is more likely to affect bumble bees and solitary bees than honey bees, most acutely in those species that have a narrow dietary niche and are more dependent on specific resources. The more generalised the foraging behaviour of a particular bee species, the more likely it is to be able to switch to alternative host plants and persist in an area, even if those host plants are of a lower nutritional quality (Roger et al. 2017).

3.2. Response to parasites and pathogens

The pests and parasites (including micro-parasites) of honey bees have been extensively researched (Bailey and Ball 1991; Morse and Flottum 2013) and range from large insectivores such as bee-eaters (*Merops apiaster*) through to the submicroscopic; microparasites such as bacteria, fungi, and viruses. Increasing interest has been paid to viruses of honey bees, with over 24 viruses having now been recorded from *A. mellifera* (McMenamin and Genersch 2015). In temperate regions of the world, including Europe, the exotic *Varroa destructor* mite is considered to be the greatest scourge of beekeeping with *A. mellifera*

(Nazzi and Le Conte 2016). In feeding on hosts, the mite also transmits several viruses including *Deformed wing virus* (DWV) (Wilfert et al. 2016). DWV may be causal in the elevated over-winter mortality documented in temperate regions of the world over the past two decades (Berthoud et al. 2010; Natsopoulou et al. 2017).

Far less is known about the pests and pathogens of wild bees, which are generally not shared with honey bees, and vice versa. Those of bumble bees include conopid (Diptera) parasitoids of adults through to diverse protozoa of the *Bombus* intestinal tract (e.g. *Crithidia* and *Apicistis* spp.; Schmid-Hempel 1998). Brood cells of the solitary bee *Megachile rotundata*, adults of which are used extensively for commercial alfalfa (*Medicago sativa*) pollination (Pitts-Singer and Cane 2011), are destroyed by *Ascosphaera* spp. fungi, likely representing a major cause of off-spring mortality. Other wild bee species are often associated with a suite of cleptoparasitic bee and fly species (e.g. Paxton et al. 1996 for those associated with *Andrena scotica*) and many host enigmatic parasitoid Strepsiptera (e.g. Paxton and Pohl 1999). Microparasites of wild bees are largely unexplored, though the European *Andrena scotica* harbours the Microsporidian, *Antonosporea scoticae* which may cause the host populations to crash (Paxton et al. 1997). There is likely a wealth of undescribed parasitic species within European wild bees that await discovery.

Insectivorous predators like the bee-eater are generalists with a wide diet breadth that includes honey bees and wild bee species. Though they could in principle suppress both honey bee and wild bee populations, there is a paucity of data on their impact on populations of either honey bees or wild bees. In contrast, pests and parasites of bees are often considered to have a higher degree of host specificity. For example, wild bee species often host brood parasitic bees (e.g. members of the genera such as *Coelioxys*, *Nomada*, *Sphecodes*, and *Stelis*), many of which attack one or a few closely related host bee species (Westrich 1989), whilst only honey bees host *V. destructor* ectoparasitic mites (Nazzi and Le Conte 2016). The direct impact of these pests and parasites on honey bees is therefore

unlikely to be useful surrogates for impacts on wild bees and vice versa.

More recently, attention has focused on viral and microsporidian pathogens of honey bees, with evidence of their spill-over into wild bees (e.g. Tehel et al. 2016). Introduction of *V. destructor* mites into populations of *A. mellifera* has led to an astounding rise in the prevalence of DWV and in its titre per honey bee (Martin et al. 2012). DWV is also widespread in wild bee species (e.g. Radzevičiūtė et al. 2017), and its prevalence in bumble bees is correlated with DWV prevalence in honey bees (Fürst et al. 2014); viral sequencing demonstrates ongoing viral sharing between honey bees and bumble bees (Fürst et al. 2014), with transmission likely occurring through the shared use of and defecation on flowers (Alger et al. 2019). The introduction of *V. destructor* to host honey bee populations has led to greater DWV spill-over into bumble bees (Manley et al. 2019). Viral prevalence and intensity of infection (viral titre) in honey bees do vary geographically (Fürst et al. 2014) and therefore could in principle be used as a surrogate for pathogen challenge of wild bees. An outstanding question concerns the impact of honey bee viral pathogens on wild bee population fitness. For honey bees, viruses such as DWV are clearly pathogenic (McMahon et al. 2016). Though they similarly reduce the lifespan of *B. terrestris* workers in an experimental laboratory paradigm (Fürst et al. 2014), their impact on other wild bee species or population dynamics remains to be investigated.

For DWV, its higher prevalence in honey bees than bumble bees suggests that its direction of transmission is largely from honey bees to bumble bees (Fürst et al. 2014, see also Alger et al. 2019). By the same argument, transmission for some other so-called honey bee viruses might be in the reverse direction because they are more prevalent in *Bombus* than *Apis* (McMahon et al. 2015). Some bumble bee species are managed, and their use in commercial pollination also leads to pathogen spill-over into native conspecifics and congeners (Colla et al. 2006; Murray et al. 2013). For the widespread *Crithidia bombi*, not only does its interspecific transmission occur regularly among native species (Ruiz-González et al. 2012), its transmission from imported, exotic *B. terrestris*

colonies to South America has been suggested as a factor behind the decline of native South American *Bombus* (Schmid-Hempel et al. 2014). Thus, though pathogens seem to play an important role in regulating bee populations, we lack data on *Bombus* pathogen distribution, or that of any other wild bee species, with which to inform on wild bee population fitness in Europe.

3.3. Response to pesticide exposure

The majority of studies that have assessed the acute impact of pesticides on bees have measured their toxicity to honey bees (Medrzycki et al. 2013), such as the assessment of acute oral LD₅₀s for neonicotinoids (Godfray et al. 2014). Given the large variation in wild bee species, from their body size and level of social organisation to their dietary breadth, the relative sensitivity of different wild bee species to pesticides has become a focus of attention (Franklin and Raine 2019).

Detailed studies measuring LD₅₀s for wild bees are available for a very limited suite of species, with a focus on social species that can be easily reared in captivity. Meta-analyses have shown that on average wild bees have lower acute sensitivity to pesticides compared with honey bees (Arena and Sgolastra 2014), though there is large variation in response, with small-bodied species showing greater sensitivity than large-bodied species. Direct comparisons between these species and honey bees show that acute sensitivity to a range of insecticides is broadly similar, with wild bees generally less sensitive on an individual basis (Heard et al. 2017; Thompson and Pamminer 2019).

This approach has been criticised as incomplete because the mortality of individuals is not an equivalent metric of fitness between solitary and eusocial species because, for honey bees, it requires field-based studies to detect colony level effects (Franklin and Raine 2019). European field studies assessing the impact of real-world pesticide exposure have also converged on *B. terrestris* and *O. bicornis* as species for comparison with honey bees. Studies measuring the impact of proximity to pesticide-treated crops on these three model bee species have found a reduction in colony growth (*B. terrestris*) and reproductive output (*O. bicornis*), with honey bee

colony size and health unaffected or showing inconsistent patterns of expansion or contraction (Rundlöf et al. 2015; Woodcock et al. 2017). Though contrasting with studies that find no difference for any of the three species (Rolke et al. 2016), these results suggest that the use of honey bees as models for measuring the effects of pesticides on wild bee species in the field is limited, probably at least in part because of the fundamental buffering effect inherent to a social lifecycle with many thousands of workers per colony (Straub et al. 2015), and possibly in part because worker honey bees may effectively filter out toxins before feeding brood food to their larvae (Lucchetti et al. 2018).

The majority of pesticides tested for negative effects on bees have been insecticides. A smaller number of studies have measured the effects of fungicides on bee health, either alone or in combination with insecticides (Carnesecchi et al. 2019; Iverson et al. 2019). Certain fungicide and insecticide combinations are known to have synergistic effects, leading to increased toxicity to honey bees (Pilling et al. 1995; Thompson and Wilkins 2003). Only a few studies are available that investigate pesticide/fungicide synergy in *B. terrestris* and *O. bicornis* (Robinson et al. 2017; Sgolastra et al. 2017), in which synergies were found for both species in addition to *A. mellifera*, but with the strongest effects seen in *O. bicornis* (though see also Azpiazu et al. 2019). With the limited number of studies, it is difficult to determine if synergies pose a greater risk to wild bees than honey bees.

3.4. Response to a changing climate

The effects of climate change can be broken down into two main elements: (i) an increase in average parameter values (e.g. annual mean temperature) and (ii) an increase of the frequency of extreme events (e.g. heat waves). The impact of increasing average parameter values has been assessed by modelling the future distribution of species based on their current ecological niches and distributions (Kerr et al. 2015; Rasmont et al. 2015), but this effort has largely been limited to bumble bees. For these predominantly cold-adapted species, studies predict sharp

distributional regressions even under optimistic predictions. For species that are more adapted to xeric conditions, we might expect an equivalent expansion (Rasmont et al. 2015; Dew et al. 2019), but for the vast majority of species, no assessments of their likely future distributions have been made. For most species, our understanding of distributional trends has been limited to biological recording efforts that have observed range expansions across the northern range edges over the last 20–30 years, such as for *Andrena flavipes* and *Lasioglossum malachurum* in Britain (Else and Edwards 2018). However, as this recording effort is not standardised and varies greatly from country to country, it is difficult to draw firm conclusions at a wider European level.

As heterothermic organisms, exposure to elevated temperatures during heat waves can cause physiological perturbations in bees at several development stages (Tautz et al. 2003). Whilst adult bees can tolerate a wide range of temperatures, the ability of social species to thermoregulate their nest, a behaviour that is crucial for larval development (Heinrich 2004), can be disrupted when exposed to high temperatures (Vogt 1986) and result in health-compromised workers that eclose from heat-stressed pupae (Medina et al. 2019). As the number of workers required for such task increases (e.g. via wing fanning), fewer bees are available for nest maintenance, larval feeding, and foraging (Brian 1952), potentially reducing the fitness of the colony. High temperatures, even during a short time, could therefore disrupt thermoregulation and could have a negative effect on colony development (Vogt 1986).

Furthermore, not all bee species are equally affected by heat stress (Martinet et al. 2015; Oyen et al. 2016). Species with a lower level of social complexity and species that have evolved in thermally stable environments may be particularly susceptible (Heinrich 2004; Kovac et al. 2014). As *A. mellifera* is a species adapted to hot environments, global warming may affect it comparatively less than for the genus *Bombus*, a group largely adapted to cold environments (Heinrich 1975). Bumblebees become distressed when the temperature reaches 35 °C and die when it exceeds 44 °C (Heinrich 1979), whilst *A. mellifera* can survive up to 50 °C (Kovac et al. 2014).

In addition to the direct effects of climate change on species distributions, climate change might also increase the chance of losing appropriate floral resources by differentially altering the phenology of bees and plants and increasing temporal mismatches between them (Schleuning et al. 2016; Ogilvie and Forrest 2017). Though our understanding of this phenomenon is largely theoretical and based on model predictions, empirical work suggests that access to high-quality resources can mitigate the impact of heat stress (Vanderplanck et al. 2019).

3.5. Response to management

Finally, a principle factor determining the health of a managed organism is the management itself. Beekeepers play the key role determining the spread, diagnosis, and control of diseases (Mutinelli 2011; Neumann et al. 2016). For example, chemical treatment of colonies against the ubiquitous ectoparasitic mites *V. destructor* is usually to prevent mortality (Rosenkranz et al. 2010), but this also prevents host-parasite co-evolution (Neumann and Blacqui re 2017), and such treatments also add to colony pesticide exposure thereby also possibly compromising colony health (Boncristiani et al. 2012). This also holds true for antibiotic treatments which will almost certainly interfere with the population dynamics of endosymbionts and other beneficial microbiota (Aebi and Neumann 2011; Engel et al. 2016).

The artificially high density of colonies kept in apiaries is in sharp contrast to the more widely spread nests in wild honey bee populations, which almost certainly promotes disease transmission and impact (Seeley and Smith 2015). Moreover, regular prevention of swarming can result in truly gigantic honey bee colonies compared with natural ones, which may also have a negative impact on health (Loftus et al. 2016). Beekeepers inevitably break the natural propolis envelope of *A. mellifera* colonies during colony inspections, thereby possibly compromising an integral part of social immunity (Simone-Finstrom et al. 2009). Like with any other managed species, beekeepers also govern colony nutrition either by placing stationary apiaries in suitable or unsuitable areas or by translocating colonies in migratory beekeeping. Replacing the often diverse honey stores with plain sugar water may also impact honey bee health (Erlor

et al. 2014), and inadequate feeding is a well-documented reason for honey bee colony mortality over winter (van Engelsdorp et al. 2011). Last but not least, beekeepers routinely import and export colonies and queens over large distances thereby negating any local adaptations which the bees may have had and probably compromising colony health (B chler et al. 2014).

Besides the fundamental differences in life history between solitary and social bee species, it seems clear that management itself sets managed honey bees even further apart from non-managed wild bees. Given that the management of honey bees has the potential to be a principle stressor in a way not experienced by wild bees, it is perhaps not surprising that there is no obvious relationship between the population trajectories of these two groups in Europe.

4. CONCLUSIONS

Though some broad spatial patterns of decline can be found at a continental scale, with more central-northern European countries having a greater proportion of threatened wild bee species, there is no overall similarity with observed mortality rates in managed honey bee colonies. Though at the individual level, there can be insights gained about generalised bee biology from research into managed honey bees, at the colony level, the ecology and therefore the response of *A. mellifera* to stressors can diverge strongly from that of other bee species. The fundamental nature of honey bees as superorganisms (Seeley 1995; Straub et al. 2015) and their status as managed bees means that a targeted and taxon-, or at least genus-specific approach to research and monitoring is needed to understand and conserve wild bees.

Globally, the organisation of bee reference collections at a national scale is extremely incomplete, even for the intensively studied Europe fauna (Nieto et al. 2014). For countries or regions where the national fauna and its distribution are better known, there is a need for the establishment of a standardised field monitoring protocol applied across a representative number of locations (Drossart et al. 2019), though such efforts are still in their infancy (O'Connor et al. 2019). Meeting these more targeted research objectives will

require additional support for basic ecological research and taxonomy, as well as the establishment of a wider range of model bee species as the conclusions drawn from the study of honey bees are taxonomically limited.

CONTRIBUTIONS

DM, RJP, PN, DM conceived the review. TJW led the writing, with all other authors contributing sections. All authors read and approved the final manuscript.

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Les abeilles domestiques peuvent-elles être un radar pour le déclin des abeilles sauvages ?

abeilles sauvages / espèces indicatrices / espèces spécifiques / socialité / populations.

Können imkerlich gehaltene Bienenvölker ein Radarschirm für den Rückgang der Wildbienen sein?

Wildbienen / Indikatorart / artspezifisch / Sozialität / Populationen.

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