



# Are Bumblebees Relevant Models for Understanding Wild Bee Decline?

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The unsustainable use of ecosystems by human societies has put global biodiversity in peril. Bees are, in this context, a popular example of a highly diversified group of pollinators whose collapse is a major concern given the invaluable ecosystem services they provide. Amongst them, bumblebees (*Bombus*) have increasingly drawn the attention of scientists due to their dramatic population declines globally. This regression has converted them into popular conservation entities, making them the second most studied group of bees worldwide. However, in addition to have become relevant models in the fields of ecology, evolution and biogeography, bumblebees have also been used as models for studying wild bee decline and conservation worldwide. Integrating evidence from the comparative ecology and resilience of bumblebees and wild bees, I discuss the relevance of using *Bombus* as radars for wild bee decline worldwide. Responses of bumblebees to environmental changes are generally not comparable with those of wild bees because of their relatively long activity period, their inherent sensitivity to high temperatures, their relatively generalist diet breadth and many aspects arising from their eusocial behavior. Moreover, important differences in the available historical data between bumblebees and other bees make comparisons of conservation status even more arduous. Overall, these results reinforce the need for conservation actions that consider a higher level of understanding of ecological diversity in wild bees, highlight the need for an updated and more extensive sampling of these organisms, and emphasize that more caution is required when extrapolating trends from model species.

**Keywords:** bees, bumblebees, *Bombus*, conservation, decline, global change, resilience

## INTRODUCTION

The unsustainable use of ecosystems by human societies has made 75–95% of the terrestrial biosphere to be altered by anthropogenic stressors, with considerable impacts on its fauna and flora (Kennedy et al., 2019; Ellis et al., 2021; Wagner et al., 2021). Among the myriad of threatened organisms are bees (Hymenoptera: Anthophila), a highly diversified group of pollinators represented by more than 20,000 described species globally (Michener, 2007; Zattara and Aizen, 2021). Their collapse in both abundance and diversity is a critical issue for ecosystems and human societies given the invaluable ecosystem services they provide in the perpetuation of numerous wild plants and crops worldwide (Matias et al., 2017; Ollerton, 2017; Porto et al., 2020). As for most threatened insects (Wagner, 2020; Wagner et al., 2021), bee decline involves climate change,

landscape destruction, the misuse/overuse of pesticides, the arrival of invasive species and the transmission of pathogens as predominant drivers (Cariveau and Winfree, 2015; Carvalheiro et al., 2020; Mathiasson and Rehan, 2020; LeBuhn and Vargas Luna, 2021).

Bumblebees (*Bombus* spp.), known by ~270 species at the global scale, are a clade of bees mostly widespread across America, Europe and Asia, with distributions encompassing all biomes except extremely xeric deserts (Williams, 1998; Williams and Jepsen, 2021). These pollinators are increasingly used as models in a large array of scientific fields including ecology (Phelan et al., 2021), evolution (Tian et al., 2019; Wood et al., 2021b) and biogeography (Ghisbain et al., 2020; Potapov et al., 2021). Most concerningly however, bumblebees have increasingly drawn the attention of scientists worldwide due to the dramatic regressions of their populations across all continents they occupy (Bartomeus et al., 2013; Kerr et al., 2015; Aizen et al., 2019; Rasmont et al., 2021). These repeated patterns of decline have converted them into popular conservation entities, making them the second most studied bees worldwide after the honeybee *Apis mellifera* (Cameron and Sadd, 2020).

Against this context of global bee decline, Wood et al. (2020) discussed the relevance of using the *A. mellifera* as a sensor for wild bee decline. The authors showed that despite some of the responses of honeybees to anthropic stressors being similar to those of wild bees, this managed species is not a suitable surrogate for detecting declines in wild bees. In this review, I raise a similar concern for bumblebees, discussing their relevance as models to global changes for other wild bees.

## BUMBLEBEES AS FLAGSHIP SPECIES FOR BEE CONSERVATION

Bumblebees have always been immensely popular due to their great cultural value in north temperate regions (Rasmont et al., 2021). The overall colorful appearance, abundance and diversity of bumblebees in areas frequented by natural historians of the northern hemisphere have made them especially well-represented in museum collections (Kleijn and Raemakers, 2008; Cameron et al., 2011; Wood et al., 2019, 2021b). This has led scientists to rapidly acquire paramount quantities of data in comparison to other groups of wild bees (Nieto et al., 2014). As a direct benefit of having acquired so much biogeographic data on these culturally “cherished” animals is the speed at which their decline has been reported in Europe (Free and Butler, 1959; Williams, 1986; Rasmont and Mersch, 1988; Williams and Osborne, 2009). Among the array of insects that have shown dramatic declines since then, bumblebees showed an additional characteristic that would allow them to get even more attention: their ability to be domesticated (Velthuis and van Doorn, 2006). The immense economic importance of this management for global agriculture, and later the subsequent use of managed colonies for research purposes rapidly ranked bumblebees higher than ever in our conservation priorities (Cameron and Sadd, 2020; Rasmont et al., 2021). For all these reasons, bumblebees were intensively investigated compared to the rest of wild bees

and are therefore usually used as main examples to illustrate the decline of other bee species. Research about their decline is now extensively cited in the scientific literature to illustrate the regression of other native/wild bees (e.g., literature cited in Carvalheiro et al., 2020; Reilly et al., 2020; Kammerer et al., 2021; Zattara and Aizen, 2021) but also of pollinators in general (e.g., in Potts et al., 2010; Sevenello et al., 2020; Dicks et al., 2021), and of even higher taxonomical levels such as insects and arthropods (e.g., in Harvey et al., 2020; Høye, 2020; Wagner, 2020; Halsch et al., 2021). It is not uncommon that works exclusively focusing on bumblebees are cited as references to support statements about threats to wild, native bees (e.g., in Winfree, 2010; Phelps et al., 2018; Vega-Hidalgo et al., 2020) or to pollinators in general (e.g., in Potts et al., 2016; Dicks et al., 2021). However, are bumblebees objectively that convincing as models for wild bee decline?

## BUMBLEBEES ARE ABERRANT BEES

### Stronger Together?

Displaying a social behavior is more the exception than the rule in bees (around 1,000 social species over the 20,000 known bee species, cf. Michener, 2007; Wcislo and Fewell, 2017). Outside the fundamental aspect of this divergence in a life history trait, the fact that bumblebees fall into this relatively rare category of sociality makes their responses to global changes completely different to those of solitary bees (Schweiger et al., 2010).

Eusocial pollinators such as bumblebees mostly present both more flexible and longer activity periods, extending across several months from the time of nest foundation until sexuals are produced (Goulson, 2003). In contrast, wild solitary bees tend to have much narrower activity windows, with an increased likelihood to suffer from temporal mismatches (Gérard et al., 2020). In *Bombus*, this long activity period imposed by their sociality implies dietary generalism, a characteristic that allows the colony to benefit from resources all along its lifetime (Goulson, 2003). With few exceptions, bumblebees are not strictly restricted to the consumption of plants from a single species or even genus (Kleijn and Raemakers, 2008; Rasmont et al., 2021). Despite obvious dietary requirements for their survival (Wood et al., 2021b), bumblebees do not fall into the “oligolectic/monolectic” category encountered in many other bee genera (Rasmussen et al., 2020; Cane, 2021). This is a considerable advantage as specialized bees have shown greater range declines and higher sensibility to land use in comparison to more generalist bees (Biesmeijer et al., 2006; Palma et al., 2015). In addition to a certain degree of generalism, larger bees such as bumblebees are expected to cope well with patchy resources requiring longer flight ranges (cf. Greenleaf et al., 2007). This foraging success enables colony growth and enhances food storage, another invaluable buffer against the inclement weather or periods of sparse availability of adequate flowering plants (Wcislo and Fewell, 2017).

Another fundamental privilege given by sociality in a context of climate change is colony homeostasis. In contrast with solitary bees, worker bumblebees keep the ability to take shelter in a thermoregulated nest during unfavorable weather conditions. In

a case of heat waves, groups of worker bumblebees use their wings to fan when temperature rises above optimal (Heinrich, 1985; Westhus et al., 2013; Wynants et al., 2021). Alternatively, the endothermic nature of bumblebees can also be helpful to warm up the nests in especially cold periods (Heinrich, 2004). Overall, temperatures in bumblebee nests are carefully regulated to setpoints conducive to optimize larval development, regardless of environmental challenges (Heinrich, 1985, 2004). In solitary bees however, homeostasis remains an individual matter.

Although many other “universal” advantages of sociality exist (e.g., increased defense against predators, brood care, etc), the so-called “superorganism resilience” of eusocial organisms is still not optimal in *Bombus*. For instance, while the effects of pesticides could be buffered by the high number of workers in social colonies compared to solitary bees, the solitary phase of the bumblebees’ life cycle still makes them susceptible to face these chemicals (Straub et al., 2015).

## Bear Wasps<sup>1</sup> in a Warming World

Understanding the metabolism of bumblebees requires to understand their evolutionary history. It is most likely that bumblebees appeared about 25–40 million years ago in high-altitude regions of Northeast Asia (Hines, 2008). This period coincides with the sharp decline in temperature of the Eocene-Oligocene transition (about 34 million years ago), a period well-known to have caused a major extinction and turnover of organisms, replacing many tropical taxa organisms adapted to cooler climates. Except for a few species, bumblebees still constitute a mostly cold-adapted lineage to day. This trait leads to key difference in their distribution ranges compared to most other bees, as bumblebee diversity worldwide peaks in high altitudes, far from the actual hotspots of solitary bee diversity in Mediterranean areas (Michener, 2007; Orr et al., 2020; Boustani et al., 2021; Wood et al., 2021a) where *Bombus* are poorly represented (Rasmont et al., 2021). This contrast can be explained by the origin of bees themselves, likely to have radiated from the xeric regions of the highly seasonal interior of the old continent of Gondwanaland (Michener, 2007). Well-beyond being a simple evolutionary difference, the tendency of bumblebees to be cold-adapted now constitutes a special disadvantage in a context of global warming. While their especially hairy body displays interesting metabolic assets to overcome cool to freezing conditions, resisting to heat stress at the individual level is much more arduous. Several studies have shown the dramatic impact of heat stress in bumblebees across multiple subgenera, highlighting their global tendency to be sensitive to the heat (Pimslers et al., 2020; Zambra et al., 2020; Maebe et al., 2021a; Martinet et al., 2021a). Nevertheless, the temperatures tested by these studies are not especially uncommon in areas hosting a large diversity of solitary bees (Baldock et al., 2018; Lhomme et al., 2020). On the contrary, the remarkable resistance of bumblebees to cold climates, including areas where the ground is frozen for much of the year, allows them to take advantage of an ecological niche that is unoccupied by virtually all other Apoidea Hymenoptera. Although a few species

of solitary bees are also capable of endothermy (Stone, 1990), insects mostly remain classic ectotherms forced to strictly cope with the outside temperatures. This trait has eventually led bumblebees and most wild bees to occupy rather distinct climatic niches that do not respond similarly to the current climate change (IPCC, 2019) and that are not either expected to do so in long-term future (Spinoni et al., 2018), making comparisons of projected population trends under different climate change scenarios arduous.

## The Bigger, the Better?

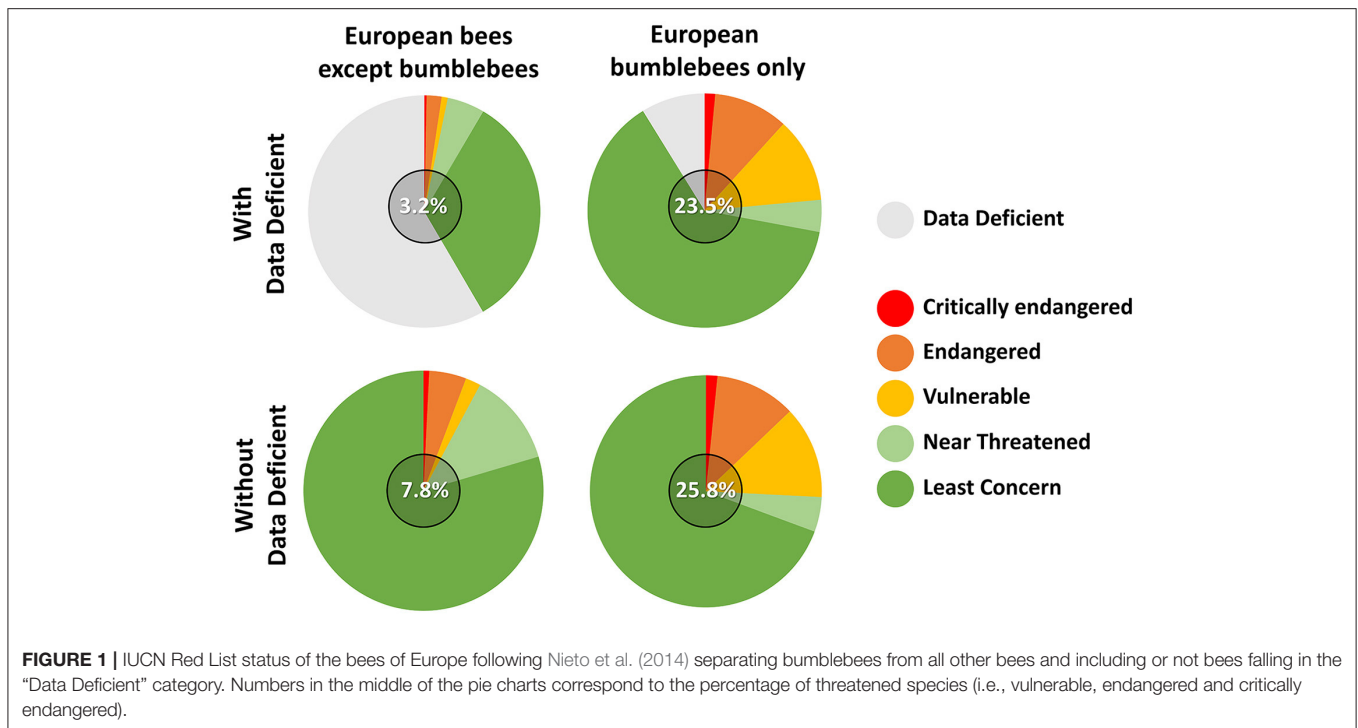
Because heat production is more efficient in larger bees (de Farias-Silva and Freitas, 2021), it is not surprising that cold-adapted animals like bumblebees display a comparatively big body size. In addition to thermoregulation, the fact that larger animals present lower rates of water loss might favor bumblebees against the issue of hydric stress (cf. Gérard et al., 2020; Maebe et al., 2021b). In addition, recent research found bumblebee body size to be correlated to habitat fragmentation, which suggests that larger bees such as bumblebees could be better selected in fragmented landscapes as they are able to reach adequate habitats at a longer distance (Theodorou et al., 2021). Finally, the comparatively large size of bumblebees could make them relatively more resilient to pesticides, as pesticide vulnerability could be negatively correlated with body size in bees (Arena and Sgolastra, 2014).

Despite these advantages, bigger animals are also expected to retain heat more due to their higher volume/surface ratio. As bumblebees become distressed when temperature reaches 35°C (Heinrich, 2004), one could consider their larger body as detrimental as it could cause overheating when foraging in warming environments. In contrast with other wild bees however, bumblebees are generally bigger under warmer climates (Gérard et al., 2018), although substantial intraspecific and species-specific variation in size has been recently demonstrated (Lozier et al., 2021). Importantly, evidence from an analysis involving >30,000 specimens from >430 species suggests that taxa with a larger body size (including bumblebees) have been more likely to decline over a 140-y period (Bartomeus et al., 2013). Overall, more work is needed to disentangle the impacts of body size in bumblebees (Oyen et al., 2021) to assess whether larger species might be favored or not in areas particularly affected by climate warming.

## DOMESTICATING AN OUTLIER

The end of the 1980s was marked by an important event in the study of bumblebees: the commercial domestication of the buff-tailed bumblebee *Bombus terrestris* (Velthuis and van Doorn, 2006). Beyond the purely economic interest of this feat, the availability of colonies of this species on demand has allowed scientists in many countries to thoroughly study its ethology, metabolism and their resilience to different drivers of decline such as heat waves or pesticides. All in all, the domestication of *B. terrestris* has made it possible to test *ex situ* the impacts of the Anthropocene on a bee that is different from the honeybee, and with an unprecedented possibility of experimental replication.

<sup>1</sup>“bear wasp” is the literal translation of a widespread Chinese name for bumblebee.



Recent studies have however highlighted the over-performance of *B. terrestris* against global stressors (e.g., heat stress) compared to other bumblebees (Zambra et al., 2020; Martinet et al., 2021a,b), making it an exception among bumblebees in the Anthropocene (Ghisbain et al., 2021).

The metabolic and physiological performances of *B. terrestris* have been mostly discussed in the current context of geographic expansion and invasions in the Anthropocene (Geslin et al., 2017; Aizen et al., 2020; Ghisbain et al., 2021). Very quickly after its domestication began, the buff-tailed bumblebee became invasive in very many areas of the globe where it was originally absent (Rendoll-Carcamo et al., 2017; Aizen et al., 2019; Chandler et al., 2019). This expansion syndrome is relatively uncommon among bumblebees and other bees in the context of global change, being again the exception rather than the rule (Rasmont et al., 2015, 2021; Ghisbain et al., 2021). This pattern of geographic expansion in the buff-tailed bumblebee may be explained by a series of traits whose combination in a single species is relatively exceptional. *Bombus terrestris* has a large and highly flexible diet (Rasmont et al., 2008), produces larger pupae than other bumblebees even on resources of lower quality (Romain Moerman et al., 2016), copes well with a variable climate and extreme weather events (Zambra et al., 2020), is an early-emerging bumblebee with the ability to be active in winter (Stelzer et al., 2010) and seems to have an inherently high dispersal ability (Rasmont et al., 2015). Instead, numerous other bumblebee species display a more restricted diet (Wood et al., 2019, 2021b), cannot stand pronounced heat waves (Martinet et al., 2021a), are univoltine and tend to decline or remain stable rather than expand (Cameron et al., 2011; Cameron and Sadd, 2020). Overall, this drastic difference between *B.*

*terrestris* and all other bumblebees is an additional point questioning the relevance of using it as model for other wild, solitary species.

## SIMILAR STATUS FOR DISSIMILAR BEES?

The well-established and well-studied patterns of decline experienced by several bumblebees worldwide are very often used as example to illustrate the parallel non-*Bombus* bee decline, both at local (Drossart et al., 2019) and global scales (Potts et al., 2010, 2016). As a case study, I will focus here on the comparatively well-known European bee fauna, for which assessments of both bumblebee and wild bee population changes have been thoroughly reported (Nieto et al., 2014; Michez et al., 2019; Wood et al., 2020). In the latest European Red List of Bees, ~9% were assessed “threatened” against the IUCN criteria (Nieto et al., 2014). Importantly, more than a half of all European bees could not be assessed due to an insufficient amount of available data, making them fall in the category “Data Deficient.”

Figure 1 shows that regardless of the inclusion or not of the Data Deficient category, bumblebees appear to be especially threatened when separated from all other bees at the continental scale. Although results from Red Lists at national levels and following the same IUCN criteria also highlight the particular sensitivity of bumblebees against global changes (e.g., Drossart et al., 2019; Gogala, 2019; Quaranta et al., 2019), comparisons of that type remain nebulous. Indeed, the “Data Deficient” non-*Bombus* bees could include a substantial proportion of threatened species, making threatened non-*Bombus* bee ranging from ~4 to ~60%, respectively, if none or all data deficient were considered



as threatened (Nieto et al., 2014). In addition, given that the Red Listing of Nieto et al. (2014) includes *all* historic data of European bees (including from areas where species have now vanished) and that bumblebee records have always been more represented in the last two centuries, both the EOO (Extent of Occurrence) and AOO (Area of Occupancy) calculations of the latter have benefitted from higher spatial resolution at the continental level. Overall, these fundamental sampling differences emphasize the difficulty to extrapolate trends from bumblebee to wild bee conservation, highlighting the need for an updated and more extensive sampling of the European bee fauna.

## IMPERFECT MODELS, YET BETTER THAN NOTHING

The fact that bumblebees are imperfect models for understanding wild bee conservation does not make them completely irrelevant for the understanding of the basic ecological requirements of wild bees. Research on bumblebees has provided key insight into the importance of maintaining connected habitats with an adequate supply of high-quality resources for all bees (Potts et al., 2016; Drossart and Gérard, 2020). The lessons learned from bumblebees concerning the impacts of biological pollution caused by domesticated organisms must be a warning signal to avoid such repercussions on other bees (Aizen et al., 2019; Bartomeus et al., 2020). The pathogen spillover by domesticated species is, for instance, a significant cause of decline in native bumblebee fauna and another growing concern for other native wild bees (Graystock et al., 2016). Similarly, the impacts of chemical pollution caused by plant protection products, repeatedly tested in bumblebees, should also be a cause for alarm for other bees (Sgolastra et al., 2020). Last but not least, the overall impact of climate change on bumblebees as a driving force leading to species extirpation (Kerr et al., 2015; Rasmont et al., 2015) can be used as

a preliminary understanding of how climatic variations could affect the population dynamics of bees.

## CONCLUSION

Although species-specific understanding of population trajectories would be ideal for selecting the bee species that are at greater risk, the paramount diversity of ecological traits (e.g., activity period, specialization in nesting substrate, social level, diet breadth) of wild bees at the global scale forces conservation biologists to use model species as surrogates. However, as for honeybees (Wood et al., 2020), the responses of bumblebees and wild bees to similar threats are generally not comparable. Although many aspects resulting from bumblebee sociality such as colony homeostasis, optimized food intake and broader diet breadth could make them particularly resilient under specific stressors, their overall tendency to be cold-adapted makes them especially disadvantaged in a warming environment. Overall, these results reinforce the need for conservation actions that consider a broader array of ecological diversity in wild bees, which in turn requires additional research into their biological requirements.

## AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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