



The Holobiont as a Key to the Adaptation and Conservation of Wild Bees in the Anthropocene

Kevin Maebe¹, Nicolas J. Vereecken², Niels Piot¹, Sara Reverté³, Diego Cejas³, Denis Michez³, Peter Vandamme⁴ and Guy Smagghe^{1*}

¹Laboratory of Agrozoology, Department Plants and Crops, Faculty of Bioscience Engineering, Ghent University, Ghent, Belgium, ²Agroecology Lab, Université libre de Bruxelles (ULB), Brussels, Belgium, ³Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Mons, Belgium, ⁴Laboratory of Microbiology, Department of Biochemistry and Microbiology, Ghent University, Ghent, Belgium

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Chris Cutler,
Dalhousie University, Canada

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Vera Lucia Imperatriz-Fonseca,
University of São Paulo, Brazil

*Correspondence:

Guy Smagghe
guy.smagghe@ugent.be

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Ever since the development of James Watt's steam engine in 1784, and particularly after the Second World War, human societies have expanded across the world and are now acknowledged to overwhelm the Great Forces of Nature and the planetary boundaries (sensu Rockström et al., 2009). This, in turn, drove changes in the environment and the biogeochemical cycles in unprecedented ways (Gulev et al., 2021). We are experiencing the onset of a new geological epoch coined the "Anthropocene" and characterized by the overexploitation of resources (e.g., extensive soil use changes for agriculture and urbanization, and overfishing), the buildup of CO₂ in the atmosphere, massive extinctions of biodiversity, etc., all leading to major and systemic changes at the planetary scale (Crutzen and Stoermer, 2000; Crutzen, 2002; Diaz et al., 2019).

Nowadays, there is undisputable evidence that the rise of *Homo sapiens* was –and still is– sadly associated with the widespread and often-irreversible demise of multitude of life forms on the planet, including negative population trends, population extirpations and significant range contractions leading eventually to species extinctions (Dirzo et al., 2014; Wagner et al., 2021). The survival of the remaining wildlife through the Anthropocene requires the evolution of new adaptations to today's rapid and extreme changes in environmental conditions and/or biological interactions. However, the plasticity required for species to be able to adapt to the current changing conditions has grown exponentially, and the speed at which species must adapt nowadays is many orders of magnitude faster in comparison with what they have experienced in the course of their evolution (see Otto, 2018; Halsch et al., 2021).

Understanding the plasticity and adaptability of individual species and communities, and how these enable them to survive the "Anthropocene filter" is a very challenging and key issue to predict to what extent the associated shifts and/or losses in biodiversity will translate into changes in ecosystem function and services. Wild bees are often depicted as a textbook case of a *trait d'union* between biodiversity and ecological processes, as they are actively involved in the sexual reproduction of insect-dependent wildflowers and crops alike, encompassing almost 90%

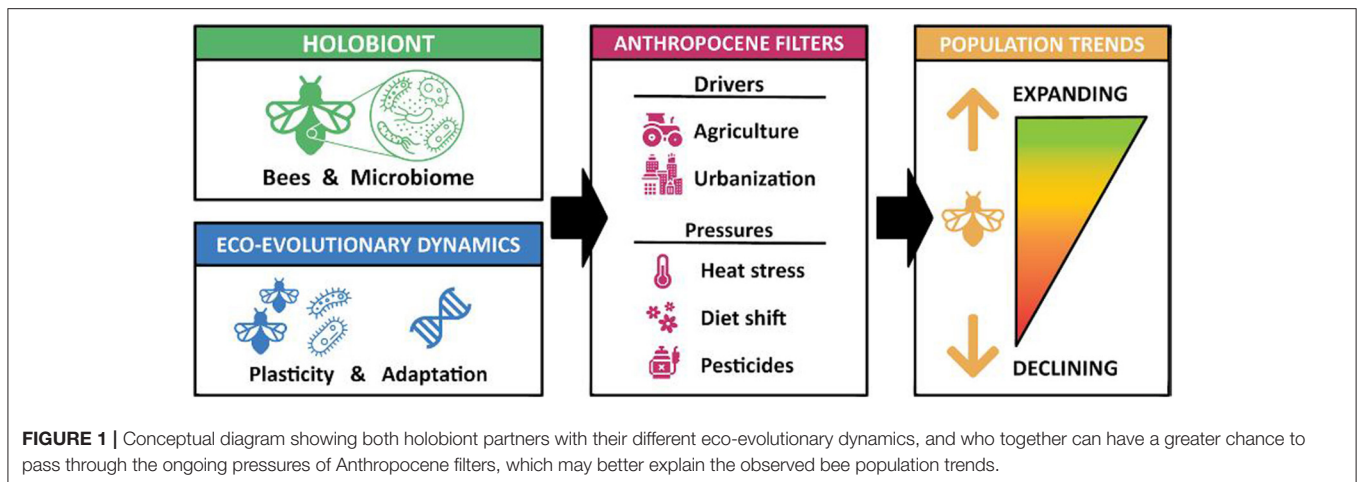
of the angiosperm plants on the planet (Ollerton et al., 2011). They represent an excellent model group to tackle these questions as they show high species diversity with over 20,000 wild bee species described at the worldwide scale (Michener, 2007; Engel et al., 2016; Ascher and Pickering, 2020), >2,000 recorded in Europe (Michez et al., 2011), all with various population trends (Nieto et al., 2014; Cameron and Sadd, 2020). Indeed, different bee species display a large variation in morphological traits (e.g., body size from 3 mm to 4 cm), and contrasting “partial habitat” requirements (Westrich, 1996) that make them more or less successful in the Anthropocene. They also include exotic species that currently thrive in many different regions of the world (e.g., *Megachile sculpturalis*; Lanner et al., 2020). Recent studies suggest that the diversity of wild bees is increasingly threatened by Anthropocene-associated processes, with reports on the decline of bees emerging in various regions of the world such as in Europe (Nieto et al., 2014), as well as in South and North America (Cameron et al., 2011; Maharramov et al., 2013; Jacobson et al., 2018). One of the core messages of these studies on pollinator decline is that spatial and temporal population trends are not consistent among species: many species are declining (e.g., 33% of species recorded in Belgium are threatened with extinction as reported by Drossart et al., 2019), while others are currently expanding their distribution range (Dellicour et al., 2014; Dew et al., 2019; Ghisbain et al., 2021). Bees are therefore a very appropriate model group to study pollinator insect plasticity and adaptability to the Anthropocene across different ecological and evolutionary contexts, with the potential to uncover key facets of the mechanisms associated with bee population trends and, consequently, to propose accurate mitigation strategies (Engel et al., 2016).

While potential mechanisms of plasticity and adaptation of bees to the threats posed by the Anthropocene are still explored, an increasing number of studies have demonstrated the importance and the key functional role of bee gut microbiome as a toolbox regulating bee nutrition and promoting bee health (Zheng et al., 2018; Steffan et al., 2019; Miller et al., 2021). Bees are characterized by a derived herbivorous diet (i.e., their ancestors were carnivorous) which can be broad (generalist) or narrow (specialist) based on the breadth of the taxonomic spectrum of host plants visited for the collection of floral resources (mainly pollen, nectar and/or oil) by the adult females to feed their larvae (Dötterl and Vereecken, 2010; Vaudo et al., 2015; Michez et al., 2019; Rasmussen et al., 2020). Recent evidence points toward the key role of the bee microbiome in their ability to process their pollen-rich diet (Steffan et al., 2019; Keller et al., 2021; Miller et al., 2021). Furthermore, growing evidence suggests that the fermenting microbial biomass itself contributes to the nutritional value for the brood: a good example is that larval stages of different bee species likely acquire bacteria essential to their development through their diet (Dharampal et al., 2019; Rothman et al., 2019; Voulgari-Kokota et al., 2019a,b). Besides its role in nutrition, the microbiota can also protect the brood cell environment against pathogens and brood spoilage by lowering the pH and producing antimicrobial metabolites, and can help detoxify plant toxins and xenobiotics (Parmentier et al., 2018; Praet et al., 2018; Cuesta-Maté et al., 2021; Keller et al., 2021).

Moreover, bees and microorganisms experience specific and contrasting modes and speeds of genetic evolution (e.g. mutation, gene loss, evolutionary pace; Kwong et al., 2014), but additional drivers of bacterial evolution can also be mediated through gene exchange via homologous recombination and lateral gene transfer. Most bees typically have one generation per year in temperate regions, although some species can have several generations per year (Santos et al., 2019); by contrast, microorganisms reproduce through several thousands of generations in the course of a “bee season” (Gibson et al., 2018). This short generation time and rapid genetic evolution of microorganisms and the possibility of pollinators to use flowers as microbial transfer hubs provide the bee host with a highly dynamic adaptive potential (Keller et al., 2021). Bees with a stable microbiota or those that were able to shift to alternative diets or which can have rapid plastic responses, are more likely to adapt to an “Anthropocene diet”.

In the Anthropocene context of changing landscapes and fluctuating floral resources (e.g. Roger et al., 2016; Gao et al., 2020), the health and survival of bees, particularly the generalist species, which are ecological linchpin species and key for the resilience of ecological networks (e.g., Bascompte and Stouffer, 2009), are likely to be more intimately associated with the plasticity of their microbiota than previously thought. The time is ripe to embrace a “paradigm shift” where the conservation of bees is intertwined with the conservation of their microbiome (i.e. bee holobiont conservation). Both holobiont partners (i.e., bees and microbiome) contribute to its plasticity: the microbiome is primarily involved in processing food, toxins and promoting immunity, while the bee host contributes to thermal tolerance and mobility. Some bee species seem to be able to face environmental changes through plasticity in their thermoregulation (e.g., Martinet et al., 2021a,b), thermal tolerance (Maebe et al., 2021a), phenology (Duchenne et al., 2020; Gérard et al., 2020a), size (Gérard et al., 2020b, 2021), nesting behavior (Ghisbain et al., 2021) or diet (Scheper et al., 2014), which might partly explain their contrasting population trends (reviewed by Maebe et al., 2021b).

With this opinion paper, we advocate that future research should embrace and implement the “holobiont” concept (Bordenstein and Theis, 2015; Carrier and Reitzel, 2017; O’Malley, 2017) also for bees, as well as obtain and disseminate innovative and integrated insights into the plasticity mechanisms and adaptation of the bee holobiont to anthropogenic changes of the environment. This could be done by disentangling the evolutionary associations of plant-pollinator-microbiota networks, how these associations have changed in an Anthropocene context of human-altered habitats (e.g., intensive agriculture and urbanization), and by studying each holobiont partners in isolation. The latter could be achieved by (i) the development of gnotobiotic (or “germ-free”) bees to assess the adaptive responses of the bee without the bee’s microbiota, as recently performed with honeybees and bumblebees (Zheng et al., 2018; Hammer et al., 2021), and (ii) by creating an *in vitro* bee gut simulator to assess the plasticity of the microbiome *per se* (e.g., sensitivity to xenobiotics). The combined knowledge obtained from both study systems, being which microbiota has



a particular importance for a particular bee species in a specific environment, together with the effects of a specific xenobiotic on the microbiota, will provide insights into the key microbiota for the survival of a bee in a specific environment. For instance, negative effects of pesticides on the bees' microbiota – and thus the bee holobiont – may have deleterious effects for the adaptation potential of the host, and thus on a longer-term harbor a sublethal threat to bees that has received virtually no attention to date. Plant phytochemicals also have this potential to negatively impact the host microbiota: for instance, several invasive plants have a high polyphenol content – such as in honey from Japanese knotweed (*Fallopia japonica*) (Bobiş et al., 2019) or in the pollen of the Himalayan Balsam (*Impatiens glandulifera*) (Vanderplanck et al., 2019) – which has been shown to decrease the prevalence of *Apicystis bombi* in bumblebees (Vanderplanck et al., 2019), and could potentially impact also the host microbiota. In turn, this knowledge could set the base for specific new regulatory measures for the use of these xenobiotics and invasive plants, for the conservation of bee populations.

Therefore, a framework to monitor the holobiont as a part of conservation or risk assessment practices should be developed. While it remains still mostly speculative, as future research still needs to generate the essential information to produce such a framework, some general or basic ideas can already be put in place. By identifying “marker” components of the bee microbiota such as “indicator” OUT's (similar to indicator species, see e.g., Dufrière and Legendre, 1997), and their possible statistical association with function loss (e.g. in pesticide detoxification or food digestion), we will gain insights into the adaptive vs. random nature of the bee microbiota, i.e. the extent to which and how its diverse components impact the survival potential of

the bee subject to environmental stressors in a given locale (e.g., in agricultural areas). These results could also be used as a lever toward more sustainable and regenerative land use practices.

To conclude, an integrative and interdisciplinary approach as summarized in **Figure 1** will help uncover how and to what extent the bee holobiont is adapted to present-day and future Anthropocene environments. Future research should also help increase our understanding of how response diversity, through the presence of bee species with contrasting and variable microbiota, can contribute to the resilience and maintenance of ecosystem functioning, and the important ecosystem service of pollination. The “holobiont approach” has much potential to understand wild bee population trends and to provide evidence-based recommendations on hitherto overlooked aspects of bee conservation relevant to pollinator protection strategies at all scales, from regional to global.

AUTHOR CONTRIBUTIONS

KM and GS conceived this opinion paper. KM, NV, and GS developed and wrote the initial manuscript. NP, SR, DC, DM, PV, and GS participated in the revisions. All authors have read and approved the final manuscript.

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