

Hive product metagenomics: a promising window into honey bee genomics and bee-associated ecosystems

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Abstract

Through their pollination services, bees are essential components of ecosystem functioning, supporting biodiversity and contributing to global food production. Among them, honey bees are particularly important, both for their ecological role and their widespread contribution to many agricultural systems and beekeeping. Honey, beeswax and propolis, among other beehive products, have played a central role in human societies for millenia and remain highly valued for their societal and economic importance, as well as their growing scientific interest. In this *Perspectives* article, we explore the largely untapped potential of these beehive products for studying honey bee genomics and characterizing honey bee-associated ecosystems through metagenomic approaches. We organized these ideas along a temporal perspective, illustrating how hive products can serve both as biological archives of past biodiversity and as genomic and metagenomic matrices for monitoring future ecosystem changes. We discuss how these materials can provide unprecedented access to fundamental knowledge across time and space, thereby opening new avenues for reconstructing history of bee populations and biodiversity, characterizing species interactions and investigating the ecological complexity surrounding honey bee colonies. We hypothesise that applying metagenomics to beehive products could help address current challenges in the beekeeping sector, including bee health monitoring, assessing ecotoxicological impacts and other major human-driven pressures on bees and their environments, evaluation the effects of agricultural practices on biodiversity, and detecting fraud in the beehive-product market. Finally, we argue that genomic and metagenomic analyses of hive products open up promising avenues for otherwise difficult-to-access research in honey bee genomics, ecology and evolution.

Keywords

Environmental DNA, ancient DNA, pollinators, *Apis mellifera*, conservation, ecosystem functioning, biodiversity

1 | Introduction

Bees play a major role in the health and overall functioning of ecosystems. By pollinating a large proportion of flowering plants biodiversity, they contribute substantially to the production of fruits and vegetables, which are essential components of the human diet (Katumo et al., 2022). Beyond pollination, bees provide multiple ecological and societal benefits aligned with several United Nation's Sustainable Development Goals, supporting human well-being, ecosystem resilience and biodiversity (Patel et al., 2021). However, bees are currently facing an increasing number of environmental and anthropogenic threats, considering the emergence of pathogens and other competitors, global change, pesticides exposure, habitat loss and fragmentation, placing them at the center of major concerns (Goulson et al., 2015; Roy Chowdhury and Gupta, 2026).

Large scale monitoring studies have highlighted a drastic decline in insect biomass (Wagner, 2020), with particular considerations reported for bee species. Given their crucial role in biodiversity maintenance and global food security, research on bees has considerably expanded worldwide in recent years (Dorey et al., 2026; Orr et al., 2021). The organisms studied are, however, unevenly represented, with a clear bias toward generalist and commercially important pollinators, such as bumblebees (*Bombus* spp.) and the western honey bee, *Apis mellifera* (Nesbit et al., 2026). These species are particularly used in the pollination of economically significant crops, including tomatoes, apples and sunflowers (Divekar et al., 2024; Osterman et al., 2021). *A. mellifera* provides furthermore important economic value through bee products, particularly in food, beverage, medicine, pharmaceutical, and cosmetics industries (Puranik, et al., 2023). Taken together, these circumstances have driven a rapid expansion of 'omics' studies investigating bees and their environments, including genomic and metagenomic approaches (Brenman-Suttner and Zayed, 2026).

2 | Genomics and metagenomics in the era of alarming pollinator decline

2.1 | Advances in genomic and metagenomic approaches for bee research

Bee genomics has entered a new era, although it still reflects only a small fraction of global bee diversity. Two decades after the release of the first bee reference genome (*Apis mellifera*; The Honeybee Genome Sequencing Consortium, 2006), and one decade after the publication of the *Bombus terrestris* reference genome (Sadd et al., 2015), the number of available bee reference genomes has rapidly increased. To date, around 140 bee species, belonging to 47 genera, have been sequenced, thus corresponding to about 0.7% of all described bee species and 9.4% of described genera (Brenman-Suttner and Zayed, 2026). In parallel, very large population genomics projects are becoming available for a few Apinae

species, with hundreds or even thousands of resequenced individuals or pools of individuals (Wragg et al., 2022; Heraghty et al., 2023; Parejo et al., 2023; Eynard et al., 2025). Recent studies show that modern population genomics methods can detect the precise genetic makeup of honey bee subspecies and breeds, as well as impact of modern beekeeping practices on their genomic diversity (Leroy et al., 2024). Additional genomic studies were able to reveal strong population contractions associated with various factors, including pesticide use, the decline of wild flowering plants and habitats, and the effects of global environmental change (Espregueira Themudo et al., 2020; Tsvetkov et al., 2021).

At the same time, the development of environmental DNA approaches has deepened our understanding of both wild and managed pollinators, as well as their surrounding environments. Most research in this field has focused on describing biodiversity through molecular barcode-based approaches, commonly referred to as DNA barcoding or metabarcoding (Harper et al., 2023; Marquisseau et al., 2026, Marquisseau et al., 2025; Ollivier et al., 2025). These methods have proven particularly effective for species inventory and monitoring. They have also been increasingly used to characterize plant-pollinator interactions, as well as pollination services (De Vere et al., 2017; Newton et al., 2023; Pepinelli et al., 2025). Furthermore, they have opened up new avenues for characterizing bee-associated microbial ecosystem, ranging from the study of core microbiomes involved in biological functions and bee adaptation to the study of microbial communities within nests as indicators of bee ecology, specialization and fitness (Christensen et al., 2024; Gardein et al., 2025; Kwong and Moran, 2016; Mazel et al., 2025).

In addition to DNA barcoding or metabarcoding, which provide taxonomic information through targeted sequencing, recent years have seen the rapid development of shotgun metagenomics. Based on untargeted (*i.e.* whole-genome) sequencing of DNA from environmental samples or biological communities (Quince et al., 2017), this approach enables access to large-scale genomic information, paving the way for a broader range of investigations spanning from population genomics to functional genomics. These approaches have been particularly well developed in model species, including honey bees (Ellegaard and Engel, 2019; Prasad et al., 2025).

2.2 | Metagenomics from beehive products as a tool to unravel bee-associated biodiversity

One notable application of metagenomics for honey bee research is the characterization of DNAs present in beehive products (Soares et al., 2023). This approach has been mainly used on honey (Bovo et al., 2018, Bovo et al., 2020; Crovadore et al., 2017; Galanis et al., 2022; Paluoja et al., 2024; Wirta et al., 2021), but has also been extended to a broader range of beehive products, such as royal jelly, pollen pellets and bee bread (Bell et al., 2021; Morgil and Ecem Bayram, 2026; Standley et al., 2025), as well as processed honey-derived products (honey kefir or mead; Leech et al., 2020). These materials provide access to DNA from a wide range of organisms along the plant-bee continuum, including

plants, bees, microbiota, parasites and pathogens, and eDNA from other micro and macro-organisms present in the bee environment (Figure 1). To our knowledge, several research laboratories are at the forefront of this emerging field (e.g. University of Bologna, Italy; University of Helsinki, Finland; University of Tartu, Estonia; INRAE, Toulouse, France).

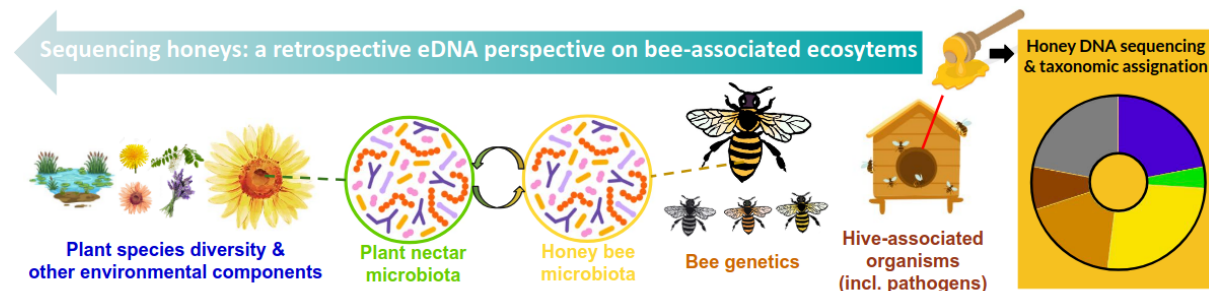


Figure 1: Sequencing beehive products provides insights into plant-honeybee agroecological continuum. Metagenomic analyses provide access to a wide diversity of species associated with bees. Bee activities, particularly foraging, transfer DNA from environmental macro and microorganisms into honey, including plants and their associated microbiota. Honey is also expected to contain bee DNA, as well as DNA from bee associated organisms, including their microbiota, parasites and pathogens. The circular representation illustrates an example of honey metagenomic characterization, inspired by results obtained in our laboratory. Each color corresponds to a different component along the agroecological continuum, ranging from blue (plant species diversity and other environmental components) to brown (hive-associated organisms). The gray section represents the proportion of sequences that remain unassigned following taxonomic assignment analyses, due to the absence of matching reference sequences in the available databases. It should be noted that the relative proportions of these components can vary considerably from one honey sample to another.

3 | The past : can ancient beehive products go beyond museum specimens ?

Unlike vertebrates, reconstructing past evolutionary changes in invertebrates remains particularly challenging, due to the scarcity of well-preserved macro-remains and the limited availability of suitable ancient DNA sources. Since the first successful extraction of ancient DNA more than four decades ago (Higuchi et al., 1984), studies have established robust methodologies and standards for the analysis of ancient DNA from well-preserved remains (Hagelberg et al., 2015). Although many other substrates have also been analysed (e.g coprolites, sediments, ice etc.) allowing research questions to be expanded (Green and Speller, 2017), the study of ancient DNA from invertebrate species has been limited to historical samples through insect museum collections. This approach, commonly referred to as museomics, successfully led informations from a relatively recent time span, allowing to study the evolution of invertebrate species, including honey bees (Cridland et al., 2018; Mikheyev et al., 2015; Parejo et al., 2020). To our knowledge, the oldest honey bee specimen resequenced to date dates back to from 1865 (Cavill et al., 2022). In the following subsections, we explore whether historical and ancient hive products could complement, and potentially extend beyond, museum specimens as sources of information on past honey bee evolution and associated biodiversity.

3.1 | Historical invertebrates museum samples as a limiting source of information

Public and scientific interest in insects is relatively recent in human history. The first organised entomological societies, dedicated to the study of insects, emerged between the late 18th and the early 19th centuries, with the oldest still active entomological society worldwide, the French Entomological Society, founded in 1832 (Carton, 2012). Many other institutional entomological societies were founded during the following decades in several countries, including the British Royal Entomological Society (1833) and the Netherlands Entomological Society (1845), among others. As a consequence, and despite the intrinsic interest of paleogenomics and museomics, ancient insect collections provide only a quite narrow temporal window for studying insect evolution. In addition, these collections are often limited in their spatial and temporal coverage, restricting the possibility of performing population-level inferences (Davis et al., 2023). As an alternative, we hypothesize that the sequencing and analysis of historical honey and other beehive products could substantially extend the temporal and geographical window over which bee evolution and changes in ecological interactions can be investigated.

3.2 | Ancient beekeeping and beehive products, a long time relationship with the human kind

Honey hunting is a long-standing human activity. The earliest known representation associated with honey bees and honey collection dates back to approximately 8000 years ago (Cuevas de la Araña at Bicorp, Spain; Figure 2). Humans likely began collecting bee swarms and keeping them in rudimentary containers to harvest honey between 5,000 and 7,000 years BP (Crane, 1999). Since then, honey bees and beehive products have contributed to the development of numerous human societies, not only through the diverse services and uses they provide (e.g. food, lighting, medicine, etc), but also through their broader cultural and symbolic roles (Boukraâ et al. 2013; El-Didamony et al., 2024; Kieliszek et al., 2023; Papa et al., 2022; Prendergast et al., 2021).

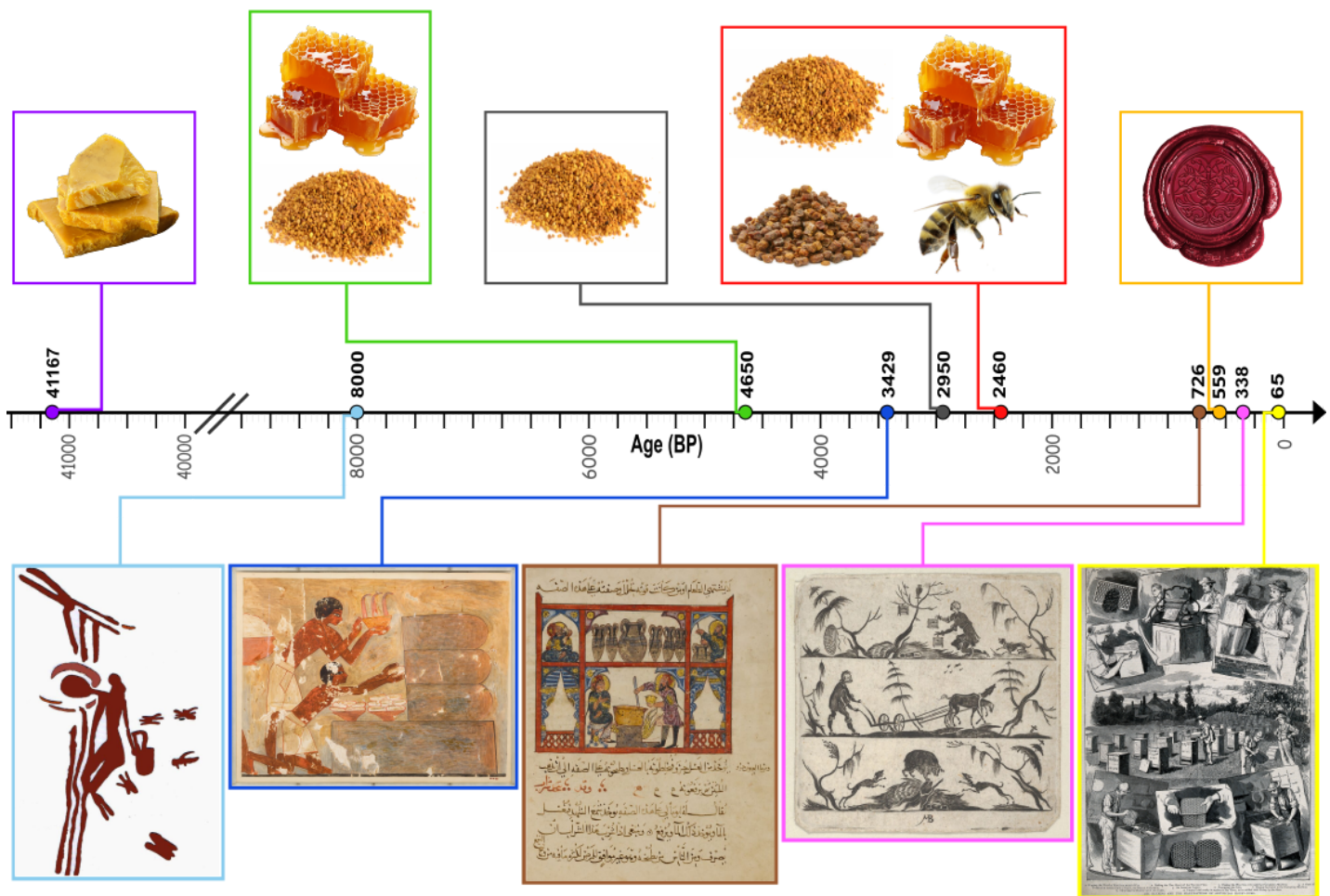


Figure 2. Timeline of ancient hive products and historical representations of the harvesting or use of hive products throughout the ages. The dates shown above the timeline correspond to the estimated age of the products or to the time of creation of the bee-related representations. Ancient hive products are indicated as follow: violet, the oldest beeswax found to date (41,167–39,194 cal BP, South Africa; d'Errico et al., 2012); green, the oldest honey found to date (4,650–4,450 BP, Georgia; Kvavadze, 2006); grey, one of the oldest large-scale apiary known to date (2,950–2,850 BP, Israël; Weinstein-Evron and Chaim, 2016); red, one of the oldest bee-breads and melted honeycombs known to date (2,460–2,445 BP, Italy; Castellano et al., 2017); and orange, a beeswax seal, a material widely used for civil and administrative purposes in medieval Europe (e.g. the 559 year-old sample DA177, United Kingdom; Kasso et al., 2023). Historical representations are indicated as follows: light blue, the oldest known representation of bees and human honey gathering (8,000 BP, Spain; Image reproduced from Achillea, “Cueva arana.jpg”, Wikimedia Commons, licensed under GNU GPL v2 or later); dark blue, Gathering Honey, Tomb of Rekhmire (3,429–3,375 BP, Egypt; reproduction by Nina de Garis Davies), depicting a person collecting honey from a wild or managed bee colony; brown, Preparing Medicine from Honey, from a dispersed manuscript of an Arabic translation of De Materia Medica by Dioscorides (Abdullah ibn al-Fadl, 726 BP, Iraq), showing the preparation of a medicinal remedy using honey; pink, Blackwork Design for Goldsmithwork with a Bee-Keeper, a Farmer and a Boar (Mathias Beittler, 338 BP, Germany), an ornamental design depicting a beekeeper alongside a farmer and a boar, illustrating the presence of beekeeping within a broader rural and agricultural context; and yellow, Bee keeping and the manufacture of artificial honey-comb (The Illustrated London News, 65 BP, United Kingdom), illustrating beekeeping practices and the human manufacture of beeswax comb used to guide or support bees in constructing the hive.

Given the widespread use of beehive products throughout human history, a large number of historical beehive samples may be available for study. Such materials have

already been identified across different regions and periods worldwide, reflecting the long-standing relationship between humans and bees (Baales et al., 2017; Buckley and Evershed, 2001; Carvalho et al., 2025; Chasan et al., 2021; Dunne et al., 2021; Garnier et al., 2002; McGovern et al., 2004; Rösch, 1999; Roffet-Salque et al., 2015; Rusch, 2020). To date, the oldest known traces of honey have been reported from Georgia and date back to around 4600 BP (Kvavadze, 2006; Figure 2). Similarly, propolis has been used for millenia, notably by ancient Egyptians, Greeks and Romans, for mummification purposes and in traditional medicine (Kuropatnicki et al., 2013). Beeswax, have likewise been found in various archeological contexts (Analytical Methods Committee Amctb No. 103, 2021). Among hive products, beeswax seems to be particularly promising for investigating bee evolution and their associated ecosystem over the last millennium and, potentially, much further back in time. Indeed, the presence of beeswax has been suggested in samples dating as far back as 41,000 years (Rusch, 2020; Figure 2).

3.3 | Beeswax, a promising resource for ancient DNA analyses

Beeswax has been extensively used across time and space for a wide diversity of purposes. In recent history, it has been employed in many civil, political and religious contexts (e.g candles, tablets, ointments, glue, cream), constituting an important corpus for very large-scale studies. A remarkable example traces its use back to the Neolithic period for medicinal purposes (Bernardini et al., 2012). It should be noted that bee products, in general, were already used by prehistoric communities for various technological and artistic applications. The widespread use of beeswax from the medieval period in Europe (11th–15th centuries) through the early 20th century for the authentication and sealing of documents (wax seals) provides access to a large number of samples. These wax seals are especially valuable because they are often well-documented, with precise dates and locations. However, such information is only relevant if the wax was produced locally, ensuring that the date of the document provides a reliable indication of the age and origin of the wax. Finally, beeswax naturally tends to become brittle over time. As a result, museum and archive collections may contain numerous degraded seal fragments with limited conservation value, which could potentially be made available for analysis purposes.

To our knowledge, at least four laboratories worldwide have attempted to extract DNA from modern (Weis et al., 2022; Teixido et al. 2024) and ancient beeswax (Kasso et al., 2023; Szulc et al., 2020). So far, however, the amounts of DNA recovered from both modern and ancient samples have been too low to allow detailed analysis. This limitation can be explained by technical challenges related to the physicochemical properties of beeswax properties, particularly its strong hydrophobicity. Nevertheless, this methodological barrier may be overcome in the near to medium term, opening new avenues for the study of past

insects and their associated environments.

3.4 | Ancient hive products : a window into the past bee ecology and evolution

If ancient DNA recovery from hive-product matrices proves successful, it could not only provide a unique opportunity to investigate honey bee evolution and adaptation over time, but also pave the way for ancient DNA characterization from other non-bee insect products, such as silk (silkworms) or dyes (e.g. cochineal). In vertebrates, ancient animal by-products have already proved valuable for accessing historical genomics information (Brandt et al., 2011; Rawlence et al., 2009; Teasdale et al., 2017) and similar approaches may increasingly be extended to invertebrates over the coming decades.

In addition to studying honey bee genetics and evolution, the analysis of ancient hive products could allow a broader metagenomic characterization of DNA preserved in these materials. The development of methods for analysing genomic and metagenomic data from ancient samples (Der Sarkissian et al., 2021; Orlando et al., 2021; Pochon et al., 2023) offers promising prospects for deepening our understanding of past microbial communities and pathogens (Bozzi et al., 2024; Poinar et al., 2006; Slon et al., 2017; Warinner et al., 2015). We therefore argue that ancient hive products could represent a unique source of information on the genomic diversity of past honey bee populations and its evolution over time, at temporal scales that are difficult to access through other sources. More broadly, this approach could also make it possible to explore changes in the biological communities associated with bees and their surrounding environments, thereby contributing to the reconstruction of past honey bee-associated ecosystems.

4 | The present : DNA analyses of hive products, a new answer to beekeepers and consumers concerns ?

The sequencing of modern beehive products offers numerous opportunities for non-invasive monitoring of bee health, characterization of bee-associated ecosystems and assessment of genetic diversity. It can also enable the authentication of beehive products by detecting fraud and adulteration, ultimately benefiting both consumers and beekeepers. In this section, we provide a non-exhaustive overview of applications for which genomic and metagenomic analyses of beehive products could be of interest.

4.1 | Exploring bee population genomics

Sequencing beehive products provides a non-invasive way to study bee genetics. This approach has already been shown to be effective for analysing the population structure

of honey bees populations using honey samples (Bovo et al., 2020). Broadly speaking, it offers an alternative to the direct sampling of living bees, which can be challenging in the field, particularly in isolated or geographically inaccessible locations. In addition, honey and other beehive products are widely traded on global markets, which may facilitate exchanges between countries and support international collaborations, while reducing the need for field sampling and its associated carbon footprint. The use of beehive products could also help address ethical concerns associated with insect research by providing an alternative to destructive sampling or the killing of insects (Barrett and Fischer, 2024; Lövei and Ferrante, 2024). This may be particularly relevant for studies of wild colonies of *Apis* species, where sampling can require nest disturbance or destruction. Such an approach would support replacement, one of the three principles of the 3Rs (replacement, reduction, and refinement; Russell and Burch, 1960), governing the ethical use of animals in research, a topic increasingly debated in the context of invertebrate species.

In addition to population structure, more complex population genomics investigations, such as monitoring genome-wide levels of genetic diversity, relatedness and mutation load are expected to become accessible through beehive products, as has commonly been done using individual sequencing over the past decade (Leroy et al., 2024; Wragg et al., 2022). However, a key challenge of this approach arises from the specific mating system of honeybees, in which a queen mates with 10-20 drones. As a result, the workers contributing to hive products represent a mosaic of maternal and multiple paternal genetic backgrounds, observable at different scales depending on the nature of the sample (Figure 3).

Recent statistical methods now make it possible to analyse genetic data from pooled workers samples (Eynard et al., 2022), a situation that may be comparable to the analysis of bee DNA from hive products originating from a single colony (Figure 3). Such an approach allows to statistically reconstruct queen genotypes which may be of interest for identifying the genetic bases of traits at the genome scale, as recently demonstrated for *Varroa* mite resistance traits (Eynard et al., 2025).

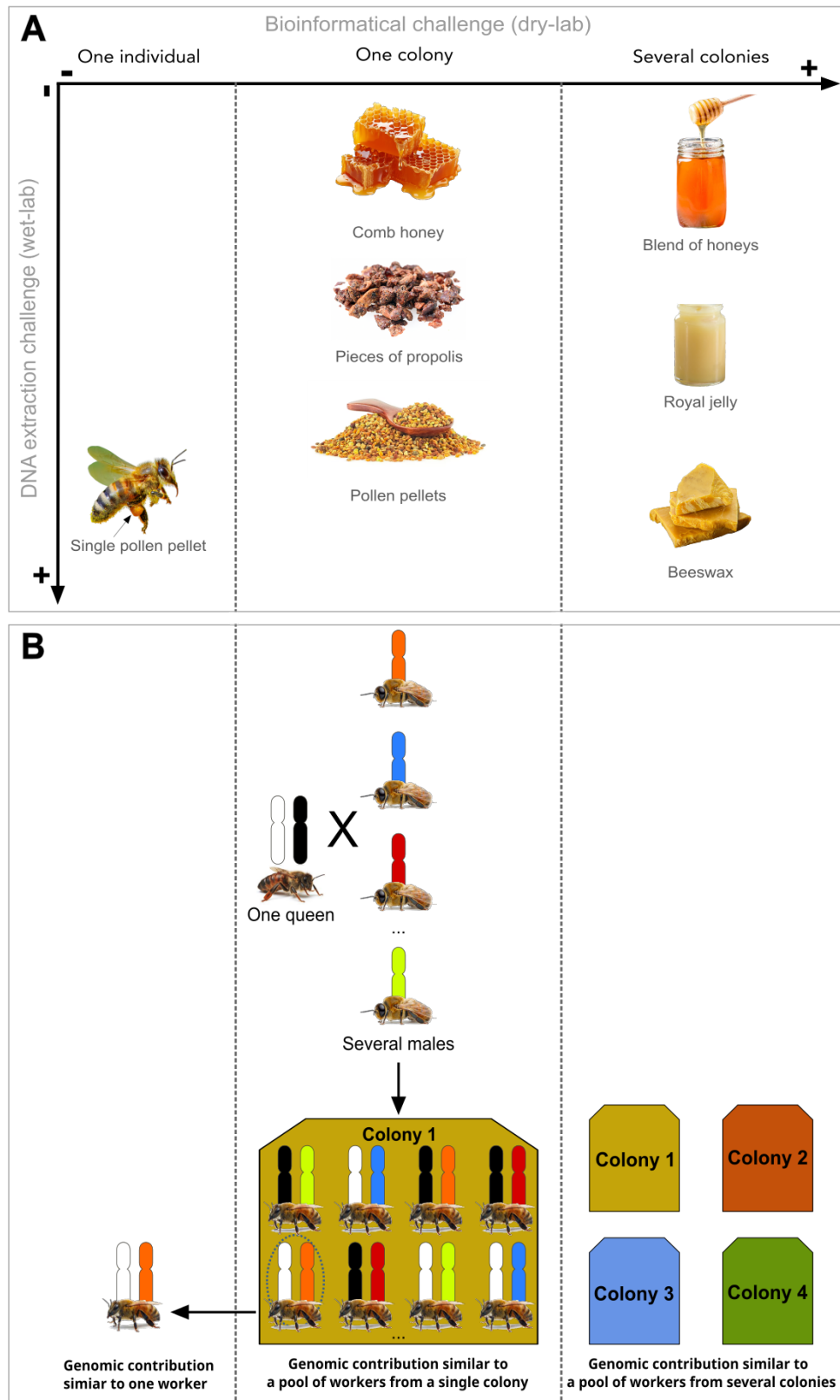


Figure 3. Advantages and disadvantages of beehive products for honey bee genomic characterization. A) Overview of the challenges associated with genomic analyses of different hive products, considering both DNA extraction and laboratory processing (wet lab) and subsequent bioinformatic analyses (dry lab). B) Expected genomic diversity recovered from each beehive product, illustrating the gradient in bioinformatic challenges associated with the analysis of the resulting genomic data.

4.2 | Tracking biotic stressors of the honeybees

Honey bees are exposed to numerous parasites and pathogens that threaten the survival of colonies (Nekoei et al., 2023). The host shift of *Varroa destructor* mite from *Apis cerana* to *Apis mellifera*, and its rapid spread across the globe has had a major impact on honey bee populations (Traynor et al., 2020). As well as causing physiological and behavioral disorders, this parasite also acts as a major vector for lethal viral diseases, e.g. Deformed Wing Viruses, Sacbrood Virus (SBV), Black Queen Cell Virus (BQCV), among others (Damayo et al., 2023). As a result, *Varroa destructor* is considered one of the main causes of colony losses. Beyond *Varroa destructor*, other parasites and competitors, such as small hive beetle (*Aethina tumida*) and *Tropilaelaps* mites (e.g. *Tropilaelaps mercedesae*) (Roth et al., 2022) have become major concerns for bee health researchers and beekeepers. Originating from South Africa and South Asia respectively, these organisms have spread to many countries worldwide, where they represent serious threats to honey bee health and colony survival.

Given the diversity of pathogenic organisms and the rapid emergence of new threats, eDNA approaches applied to hive products for detecting pathogens and parasites may become increasingly important for epidemiological surveillance in the near future (Henneken et al., 2025; Tiritelli et al., 2025). Recently, Paluoja and collaborators (Paluoja et al., 2024) demonstrated the presence of DNA sequences from many of these organisms in a large collection of honeys using shotgun sequencing. They successfully detected the DNA of several major honey bee pathogens and pests, thereby demonstrating that honey can serve as a valuable source of eDNA for monitoring and tracking of organisms affecting honey bee health. Beyond honey, other beehive products, particularly beeswax, could represent an even more promising source for monitoring bee health. Indeed, beeswax forms the brood combs, where many pathogens and parasites establish themselves and proliferate during the early stages of infection. Consequently, beeswax could prove to be particularly informative for the early detection of honey bee diseases.

4.3 | The potential tracking of eco-toxicology and agro-ecological disruptions through metagenomics?

Metagenomic approaches have the potential to reconstruct complex ecosystems associated with bee foraging activities. By providing access to a wide diversity of DNA from micro- and macroorganisms associated with bees, metagenomics could be used to assess the impacts of human activities on biodiversity and ecosystem functioning. The intensification of agriculture has indeed led to major ecological disruption in pollinator communities, not only through the loss and degradation of floral resources, but also through the widespread use of chemical pollutants, including pesticides (Goulson et al., 2015). Metagenomic analyses of beehive products could help monitor the sublethal consequences of such practices by detecting changes in ecological interactions between foraging bees and

other organisms in their environment. This approach could also contribute to monitoring ecological effects of agricultural practices at the ecosystem level, including taxonomic and functional alterations in the bee microbiota. Overall, metagenomics has the potential to provide a broader and more integrated assessment of the ecological consequences of chemical exposure than conventional ecotoxicological approaches, thereby offering new insights to support risk assessment and decision-making.

4.4 | Combating frauds in the global beehive product market

Metagenomic analyses could also be used to combat fraud in global markets for hive products. This approach is expected to prove particularly relevant for honey, which is considered one of the food products most affected by fraud worldwide, alongside milk and olive oil. Although global honey production is relatively modest in volume (2 million tons in 2024) compared to many other food products (e.g. 26, 188, 798 and 985 million tons for olives, tomatoes, wheat and milk; FAO, 2026), its high market value per kilogram makes fraud highly profitable. Honey is susceptible to various types of fraud, including the addition of sugar syrups, the mislabeling of botanical or geographical origins, among other practices (Bose and Padmavati, 2024). As methods for detecting fraud improve, fraudulent practices evolve and multiply in parallel (Zhang et al., 2023). As an example, pollen analysis of honey (melissopalynology), is a commonly used laboratory method for characterizing botanical and geographical origins of honey. However, given that pollen abundance varies considerably from one plant species to another, and that some nectar-producing plants yield little or no pollen, pollen-based honey authentication presents limitations. These limitations can be exploited by fraudsters, for instance by adding pollen to honey to mask its true origin, thereby reducing the reliability of melissopalynological approaches. In this context, metagenomic analyses offer new opportunities to overcome these limitations by potentially enabling (i) the direct detection of plant DNA derived from nectar, rather than relying solely on pollen, and (ii) the characterization of a broader diversity of organisms across the plant-bee agroecological continuum (Figure 1), providing complementary information to trace honey origin and certify its authenticity.

Such fraudulent activities are not limited to honey but also affects other beehive products, including beeswax, propolis, and royal jelly, whose market can be highly lucrative. The beeswax market is particularly important for beekeepers, as many of them partly depend on imported beeswax to meet their needs, particularly when they are first establishing their apiaries. The chemical and structural composition of beeswax shows relatively limited variation, even among different honey bee species, making traceability particularly difficult. Moreover, because of its high affinity for lipophilic compounds, beeswax can accumulate environmental contaminants, such as pesticides, which may persist for several years or even decades after their use has been banned (Albero et al., 2023). These contaminants can negatively affect adult bees and larvae (El Agrebi et al., 2020) sometimes leading to colony losses, and migrate from wax to honey, raising concerns for food safety

(Ashraf et al., 2023). If metagenomic characterization of beeswax samples were to become feasible in the future, it could offer new possibilities for authenticating the wax's origin and assessing its quality, while complementing the chemical approaches used to detect potential contamination.

5 | The future : use of metagenomics methods for ensuring sustainability of bees and their ecosystems

5.1 | Fair and global access to the hidden biodiversity

Metagenomic approaches applied to beehive products provide an unprecedented opportunity to reveal hidden biodiversity associated with honey bees and their environments. By characterizing the overall DNA content of a sample, metagenomics is a powerful tool for exploring previously undescribed biodiversity, including underrepresented microorganisms that may be difficult or impossible to cultivate under laboratory conditions. Using dedicated bioinformatic tools, reads can be assembled into contigs, annotated, and organised in a collection of Metagenome-Assembled Genomes, or MAGs. These steps generate new fundamental genomics resources that would be difficult, or impossible, to obtain using genomic methods. The bee holobiont, *i.e* the bee and its associated-organisms, is particularly worth exploring further, given the role of these communities in key biological functions (Bonilla-Rosso and Engel, 2018; Engel et al., 2012). This approach may also provide additional genomic resources from other organisms present in the environment of foraging bees (e.g macro-microorganisms related to plants, soil, water etc.). Combined with the current worldwide distribution of honey bees today, these technologies offer strong potential to generate fundamental ecological knowledge across complex ecosystems at an unprecedented spatial scale.

The production of genomic data remains highly unequal worldwide, as many countries lack the financial resources, sequencing infrastructure and bioinformatic capacity required to generate and analyse large-scale genomic datasets. As a result, many regions of the world remain largely underrepresented in public genomic databases. In the context of honey and other hive products, this imbalance is reflected in the samples currently available for metagenomic studies, to the best of our knowledge to date (Figure 4). Thus, although the honey market shows extensive trade and easy access to products from a diversity of origins worldwide (e.g shops and online purchases), the samples currently available in public databases show very large disparities in geographic representation (Figure 4). It cannot be ruled out that this disparity will widen further. Although the Nagoya Protocol was adopted to ensure fair and equitable sharing of benefits arising from the utilization of genetic resources and to address historical asymmetries in biodiversity research (Sirakaya, 2022), its complex and heterogeneous implementation create substantial administrative challenges for non-commercial research. These requirements may disproportionately affect institutions with

limited financial, legal, and administrative capacity, including those located in biodiversity-rich countries (Colella et al., 2023), and could further exacerbate the underrepresentation of global south populations and ecosystems in large genomic datasets (Maghini et al., 2025).

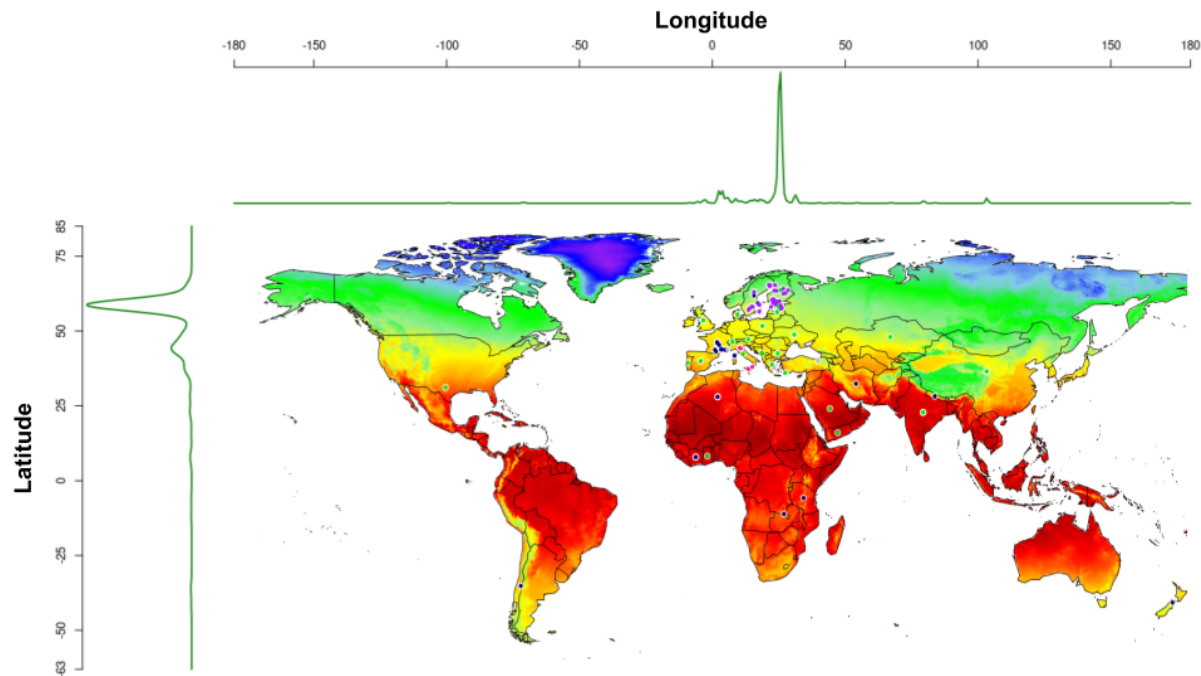


Figure 4: Spatial distribution of honey samples sequenced by shotgun sequencing techniques to date, to the best of our knowledge. The map is colored according to average annual temperature (WorldClim v2.1, period 1971–2000, 30" resolution). Colored dots indicate the sampling locations of datasets generated by the University of Bologna, Italy (Bovo et al. 2018, Bovo et al. 2020; pink, $n=5$), the University of Helsinki, Finland (Wirta et al. 2021; purple, $n=46$), the University of Tartu, Estonia (Paluoja et al. 2025; green, $n=369$), and at INRAE, Toulouse, France ($n=68$). Other samples recovered from the literature are shown in grey (Crovadore et al. 2017; Galanis et al. 2022; Morgil et al. 2026; $n=10$). When precise sampling locations were unavailable, coordinates were approximated using the centroid of the corresponding country or region within the country. Consequently, several samples can overlap at the same location. Density distribution curves along longitude and latitude are shown, highlighting the uneven geographic distribution and coverage of the currently available samples.

However, the challenges associated with implementing the Nagoya Protocol can be mitigated. Practical guidance is emerging to help non-commercial researchers meet the requirements of the Protocol more easily (Faggionato et al., 2026a, 2026b). Growing efforts to give researchers from biodiversity-rich countries a stronger role in deciding how their genetic resources are accessed and used have also been implemented. As an example, the Data and Biospecimen Access Committee established by the Human Heredity and Health in Africa (H3Africa) initiative provides governance and oversight for access to human genomic data and biospecimens collected in African populations (Rebai et al., 2025). Although H3Africa focuses on human health (human genetic resources fall outside the scope of the Nagoya Protocol), it offers a useful example of how researchers and institutions in the regions of origin can govern access to genetic resources and associated data. The

challenges associated with implementing the Nagoya Protocol are unlikely to disappear in the short term, and compliance will continue to require time, expertise and institutional resources. Emerging examples suggest that research can proceed through more practical approaches that reduce administrative procedure and support greater local participation and leadership (Van Daele et al., 2026).

5.2 | Monitoring and mitigating the detrimental effects of climate change on honeybees

Given the strong dependence of both wild and cultivated plants on pollination services, global environmental change poses major challenges by disrupting ecological interactions and ecosystem functioning, ranging from mismatches between plant flowering phenology and bee life cycles to direct physiological effects on bees. The detrimental effects of climate change on bee nutrition and survival are increasingly well documented, with cascading consequences for ecosystem functioning and global food security (Quaresma et al., 2025). A key question is to what extent bee associated species, and particularly the honey bee, will be able to adapt to environmental changes. Analyses of beehive products could provide a partial view into these dynamics by monitoring eco-evolutionary changes in genomes and species interactions over the coming decades. We hypothesize that such large scale spatio-temporal metagenomic data could be integrated into predictive models of maladaptation. These models could independently estimate the degree of genomic mismatch of each agroecological partner under future climate conditions (Fitzpatrick and Keller, 2015; Rellstab et al., 2021). Integrating these species-specific predictions at holobiont community-level could generate accurate predictions at the community level (Leroy and Heuertz, 2026), and provide reliable predictions of the resilience ability.

5.3 | Developing conservation strategies through genomics and metagenomics approaches

Conservation metagenomics is an emerging field that has so far focused primarily on host-associated microbiomes (Wei et al., 2019), especially gut microbiomes (Wang et al., 2025). We propose that this approach could potentially be extended beyond individual hosts to encompass entire biological communities and their interactions, in such a way that metagenomic analyses of beehive products could, in a long term perspective, open up new avenues for research in conservation biology. Considering that beehive products act as integrative biological archives, capturing information on the microbial, plant, and other biological components associated with bee colonies and their surrounding environments, establish metagenomic profiles of healthy or undisturbed beehives could therefore help define reference states against which altered or declining bee colonies and ecosystems could be compared. Subsequently, we could anticipate that metagenomic approaches could

contribute to the design and monitoring of restoration strategies at multiple scales. At the colony level, they could help identify disruptions in the bee-associated microbiome and inform interventions aimed at restoring or complementing key microbial taxa and functions. At the ecosystem level, metagenomic signatures could provide information on the availability and diversity of plant resources and other environmental components, potentially guiding habitat-restoration measures such as the planting of essential floral resources. More broadly, integrating metagenomic data from beehive products with ecological and environmental information could not only offer a non-invasive means of monitoring ecosystem integrity, but also a possibility of assessing the progress of conservation and restoration programs.

Conclusion

Metagenomics analysis of hive products offers a unique opportunity in bee biology and, more broadly, in insect biology to track evolutionary changes and human impacts. This approach is therefore expected to lead to major progress in the coming years, both in basic eco-evolutionary research and in applied research for beekeeping. We expect that sequencing beehive material will allow the scientific community to further investigate bee genetics, microbiota diversity, and other communities associated with honey bees, as well as their spatial-temporal evolution scale, as it has already demonstrated by pioneering studies. This approach may also help us understand interactions between these partners and provide ecosystem diversity and functioning monitoring. In applied research, this method can support bee health studies, including the detection of emerging pathogens and pests, and monitoring environmental contamination impacts by chemicals. Beyond these scientific applications, this approach has also strong potential to contribute to One Health strategies by providing an integrated view of bees, their associated organisms, and their environment. Furthermore, this approach has strong potential for commercial innovation, particularly for the traceability and quality control of hive products. This could support the development of certification labels that meet an important demand from consumers for honey and from beekeepers for products such as beeswax. These developments in the study of beehive products are also likely to benefit other biological models and matrices in the future. Such research aims, therefore, to open new avenues for both fundamental and applied research in invertebrates, while revealing the broader potential of metagenomics to study ecosystems and their evolution over time.

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Conflict of interest disclosure

The authors have no conflict of interest to declare.

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