

Microbiota of bee gut and bee products

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The biosphere is dominated by microorganisms and contains about $4-6 \times 10^{30}$ prokaryotic cells (Whitman et al., 1998). This number represents at least two to three orders of magnitude more than all of the plant and animal cells combined. Thus, microorganisms are highly diverse group of organisms and constitute about 60% of the Earth's biomass (Singh et al., 2009). In aquatic environments, such as the oceans, the number of microbial cells has been estimated to be approximately 1.2×10^{29} , while in terrestrial environments, soil sustains as many as $4-5 \times 10^{30}$ microbial cells (Singh et al., 2009). Owing to such enormous numbers, microorganisms are essential components of the Earth's biota and represent a large unexplored reservoir of genetic diversity. Understanding this unexplored genetic diversity is a high-priority issue in microbial ecology from perspectives such as global climate change and the greenhouse effect (Rastogi and Sani, 2011).

Microorganisms are key players in important ecological processes such as soil structure formation, decomposition of organic matter and xenobiotics, and recycling of essential elements (e. g., carbon, nitrogen, phosphorous, and sulfur) and nutrients. Thus, microbes play a critical role in modulating global biogeochemical cycles and influence all lives on Earth (Garbeva et al., 2004). In fact, all organisms in the biosphere either directly or indirectly depend on microbial activities. In soil ecosystems, microorganisms are pivotal in suppressing soil-borne plant diseases, promoting plant growth, and in promoting changes in vegetation (Garbeva et al., 2004). An understanding of microbial dynamics and their interactions with biotic and abiotic factors is indispensable in bioremediation techniques, energy generation processes,

and in biotechnological industries such as pharmaceuticals, food, chemical, and mining (Rastogi and Sani, 2011).

The three fundamental questions that exist while discovering and characterizing any natural or artificial ecosystem are the following: (1) what type of microorganisms are present; (2) what do these microorganisms do; and (3) how do the activities of these microorganisms relate to ecosystem functions (e. g., energy flow, biogeochemical cycling, ecological resilience)? Microbial ecology aims to answer these central questions and deals with the study of microorganisms and their interactions with each other and with their environment. Many biochemical and molecular methods have been applied to reveal the microbial community composition over time and space in response to environmental changes. These new approaches allow linkage between ecological processes in the environment with specific microbial populations and help us to answer important questions in microbial ecology such as what factors and resources govern the enormous genetic and metabolic diversity in an environment (Rastogi and Sani, 2011).

Many challenges to honey bee (*Apis mellifera*) health, including dramatic colony losses due to Colony Collapse Disorder (CCD) and the introduction of pests and pathogens into managed colonies, have negatively affected honey bee stocks worldwide (vanEngelsdorp et al., 2011; Potts et al., 2010)..

Several studies attributed these alarming losses to the overlapping of multiple honey bee pathogens with chronic stressors, such as poor nutrition, increased pathogen loads, and a lack of genetic diversity among colonies' work forces (vanEngelsdorp et al., 2011; vanEngelsdorp et al., 2009;

vanEngelsdorp et al., 2008). One factor that is likely shaped by colony genotype and is crucial for reducing nutritional stress—but has not yet been fully characterized—is the composition and function of honey bee microbiotas. The breadth of bacterial flora (and other microbes) which are present in honey bee colonies may play a role in the health and vitality of these organisms, like what they do in our own bodies (Dillon and Dillon, 2004). Host-associated microorganisms contribute enormously to the development of their host's immune system, digestion, and general well-being (Martin et al., 2008; Ley et al., 2006; Mazmanian et al., 2005).

Honey bees have a diet that consists entirely of foods that are derived from plants: nectar and pollen. Bees have the ability to convert nectar into honey, which is considered the primary source of carbohydrates for the colony and contains only very small amounts of amino acids and vitamins (Gheldof et al., 2002; Roulston and Cane, 2002; Haydak, 1970). Pollen provides honey bees with virtually all of their remaining nutrients, including amino acids, lipids, vitamins and minerals (Roulston and Cane, 2000; Herbert, 1992).

However, the cytoplasmic nutrients in pollen are not readily available to bees because each pollen grain has a cell wall that is chemically difficult to degrade (e. g., an extremely resistant sporopollenin outer layer underlain by a layer of cellulose). Honey bees are one of the few insects known to have genes that encode cellulases (Kunieda et al., 2006), but their persistent difficulty with pollen digestion is evidenced by the substantial proportion of pollen grains that are not fully broken down in the guts of workers (Crailsheim et al., 1992). Furthermore, most pollen sources do not provide a complete complement of the nutrients that honey bees require or may

contain only trace amounts of some essential amino acids (Human and Nicolson, 2006; Cook et al., 2003; Day et al., 1990), which means that bees must collect a mix of pollen types when they can. To alleviate some of these nutritional challenges, honey bees typically do not consume raw pollen. Instead, workers process pollen that they collect by packing it into honeycomb, adding glandular secretions to it, and sealing it with a drop of honey (Gilliam, 1979a).

Pollen processed in this way is matured into bee bread after several weeks, presumably due to the activity of microorganisms that are found in bee bread, but are absent in unprocessed pollen (Vasquez and Olofsson, 2009). Bee bread is chemically different from pollen: it has a higher vitamin content (Haydak and Vivino, 1950), lower amounts of complex polysaccharides, a shift in amino acid profile (Standifer et al., 1980), and lower pH (Loper et al., 1980; Herbert and Shimanuki, 1978). It is routinely suggested that these changes in nutritional composition are a result of the metabolic activity of the microflora that is present in stored pollen (Vasquez and Olofsson, 2009; Gilliam, 1979a; Herbert and Shimanuki, 1978), although the organisms that are actively involved in this metabolic transformation have never been definitively identified.