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The power and promise of applying genomics to honey bee health Christina M Grozinger¹ and Gene E Robinson²



New genomic tools and resources are now being used to both understand honev bee health and develop tools to better manage it. Here, we describe the use of genomic approaches to identify and characterize bee parasites and pathogens, examine interactions among these parasites and pathogens. between them and their bee hosts, and to identify genetic markers for improved breeding of more resilient bee stocks. We also discuss several new genomic techniques that can be used to more efficiently study, monitor and improve bee health. In the case of using RNAi-based technologies to mitigate diseases in bee populations, we highlight advantages, disadvantages and strategies to reduce risk. The increased use of genomic analytical tools and manipulative technologies has already led to significant advances, and holds great promise for improvements in the health of honey bees and other crucial pollinator species.

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Introduction

The winter of 2006–2007 ushered in a new era in bee biology, with the simultaneous discovery of the devastating effects of Colony Collapse Disorder on US honey bee populations [1] and the culmination of a multi-year, international effort to sequence and analyze the *Apis mellifera* honey bee genome with a large series of papers in *Nature, Science, PNAS* and elsewhere [2]. As for other topics such as social behavior [3], the knowledge and tools that derived from the honey bee genome sequencing project were quickly deployed to address CCD [4^{••}]. In the following years these resources, for honey bees and soon for other bee species, have formed the basis for new approaches to the study of bee health. This review summarizes the progress and challenges associated with applying genomics to understand the mechanisms by which abiotic and biotic factors undermine bee health and to develop novel strategies to mitigate the effects of these stressors (see Figure 1).

Comparative analyses of immune genes

Over the past several years there has been a steady increase in the availability of genome sequence information for a variety of insect species, including several bee species [5]. Additional sequencing and analyses substantially improved the *A. mellifera* genome in 2014, resulting in the identification of more than 5000 additional protein coding genes [6]. Sequenced genomes were recently reported or are underway for a managed Asian honey bee species, *Apis cerana* [7], a halictid bee, *Lasioglossum albipes* [8], two bumble bee species, *Bombus terrestris* and *B. impatiens* [9], and several other bee species $[10^{\bullet\bullet}]$. In addition, transcriptomes for over ten bee species have been published (e.g., [11-13]).

Comparisons across a broad range of insect species have provided important insights into the molecular mechanisms regulating several traits of bees, including immunity. In the first such comparison, between A. mellifera and the only two other sequenced insect genomes at the time (Drosophila melanogaster and Anopheles gambiae) it was observed that though honey bees have a fully intact immune system with genes corresponding to all known branches of the immune response pathway, they appeared to have fewer of the canonical insect immune genes [14^{••}]. However, as more genomes became available, this difference was not observed and honey bees are now thought to have a typical complement of canonical immune related genes [15,16^{••}]. Comparisons across bee species suggest that these canonical immune genes are rapidly evolving, and thus may allow different species to adapt to species-specific immune challenges [13]. However, more recent studies suggest that this rapid evolution is not due to positive selection but rather relaxed selection [17^{••}]. This might be the case because bees do not rely exclusively on canonical immune genes to fight infection, but can employ other genes and mechanisms to combat diseases and parasites, such as social immunity (behavioral mechanism to reduce disease load, [18]) or increased genetic diversity [19]. Consistent with this speculation, analyses of gene expression changes in response to immunostimulation revealed that honey bees





Genomic approaches to bee health. (1) Sequencing the genome of parasites and pathogens can provide information about unique gene sequences that can be targeted by RNAi approaches, allow for the development of efficient molecular diagnostic tools, and characterize mechanisms for host-parasite interactions and virulence. (2) Genome sequences and quantitative genetic studies of bees can identify gene variants associated with resilience to different stressors, which can be used in breeding and stock improvement programs. (3) Metagenomic approaches can identify and characterize pathogenic and beneficial microbes. (4) Functional genomic studies to identify host and parasite gene expression changes (changes in the levels of RNA produced by a given gene) associated with infection or other stressors can help characterize mechanisms for host-parasite interactions and resilience. Graphical design by Harland Patch and Nick Sloff (Penn State University).

(and other insects) may employ a much broader array of genes than those identified as part of the canonical immune pathways, though the functional significance of these gene expression changes remain to be determined $[20,21^{\circ\circ}]$.

Using genomic tools to investigate the effects of biotic and abiotic stressors on bee health

Many studies have used analyses of gene expression as a way to probe effects of various stressors on bee health (see Box 1). The underlying idea is that changes in gene expression can provide a sensitive indication of effects that will eventually negatively impact a variety of physiological systems. This approach also has provided insights into the mechanisms underlying tolerance or resistance to these stressors (see also [22,23], this issue). For example, viral infections in developing honey bee pupae led to changes in expression of genes encoding ribosomal RNA and proteins, consistent with viral impacts on protein translation [24]. Changes in expression of these genes were also found in gut samples from bees collected from colonies exhibiting symptoms of CCD [25], in accordance with the possibility that CCD, at least in some cases, involves infections with multiple viruses [26]. Viral infection caused upregulation of genes in the RNAi pathway in honey bee fat body tissues [21^{••}], supporting previous studies demonstrating that the RNAi pathway plays an important role in mediating antiviral responses in insects [27]. Introduction of non-viral double-stranded RNA also can reduce viral titers in honey bees (likely by non-specific activation of the RNAi pathway, [28]), and thus may serve as a therapeutic tool to reduce viral infections in bee colonies (see below for further discussion). Exposure of young bees to neonicotinoid pesticides altered expression of a gene that regulates NF-KB-mediated antiviral immune responses, resulting in increased Download English Version:

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