


OPINION

How has horizontal gene transfer shaped the evolution of insect genomes?

Chao Liu^{1,2} | Yang Li¹ | Yun Chen¹ | Xue-xin Chen¹ | Jianhua Huang¹ |
 Antonis Rokas³ | Xing-Xing Shen^{1,2} 

¹College of Agriculture and Biotechnology and Centre for Evolutionary & Organismal Biology, Zhejiang University, Hangzhou, China

²Zhejiang Lab, Hangzhou, China

³Department of Biological Sciences and Evolutionary Studies Initiative, Vanderbilt University, Nashville, Tennessee, USA

Correspondence

Xing-Xing Shen, College of Agriculture and Biotechnology and Centre for Evolutionary & Organismal Biology, Zhejiang University, Hangzhou 310058, China.

Email: xingxingshen@zju.edu.cn

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Abstract

As the most diverse group of animals on Earth, insects are key organisms in ecosystems. Horizontal gene transfer (HGT) refers to the transfer of genetic material between species by non-reproductive means. HGT is a major evolutionary force in prokaryotic genome evolution, but its importance in different eukaryotic groups, such as insects, has only recently begun to be understood. Genomic data from hundreds of insect species have enabled the detection of large numbers of HGT events and the elucidation of the functions of some of these foreign genes. Although quantification of the extent of HGT in insects broadens our understanding of its role in insect evolution, the scope of its influence and underlying mechanism(s) of its occurrence remain open questions for the field.

Insects are a highly diverse lineage comprising >50% of all described animals, with about 30 orders (Chapman, 2009; Forister et al., 2019; Novotny et al., 2002). Insects are found in most terrestrial and aquatic environments (Gullan & Cranston, 2014; Scudder, 2017) and are key for ecosystems' health in a variety of ways, such as by acting as decomposers, prey, predators, and pollinators (Gurr et al., 2003; Majeed et al., 2022). In addition, their relatively small sizes and their high reproductive rates allow them to occupy diverse ecological niches that larger creatures cannot (Berger et al., 2008; Gullan & Cranston, 2014).

Insects also interact extensively with microorganisms, such as bacteria and fungi, enhancing insects' abilities to adapt to different environments. Microorganisms are found in the exoskeleton, gut, and blood of insects, as well as inside insect cells. The insect gut microbiota contributes to the host's digestion and

provides essential amino acids and vitamins. Some microbes can also synthesize specific toxins that boost insect immunity and protect the insects against pathogens (Douglas, 2015; Engel & Moran, 2013). In addition, several chemical signal molecules produced by microbes can even regulate insect social behaviour such as courtship and kinship recognition (Engl & Kaltenpoth, 2018).

Horizontal gene transfer (HGT) refers to the transmission of genetic material between organisms by means other than sexual reproduction (Dunning Hotopp, 2011; Keeling & Palmer, 2008; Ochman et al., 2000). HGT overcomes the mating barriers between organisms and can be an important source of genetic innovation (Burmeister, 2015; Fitzpatrick, 2012; Husnik & McCutcheon, 2018; Keeling & Palmer, 2008; Wisecaver & Rokas, 2015). HGT is very common in bacteria but occurs more

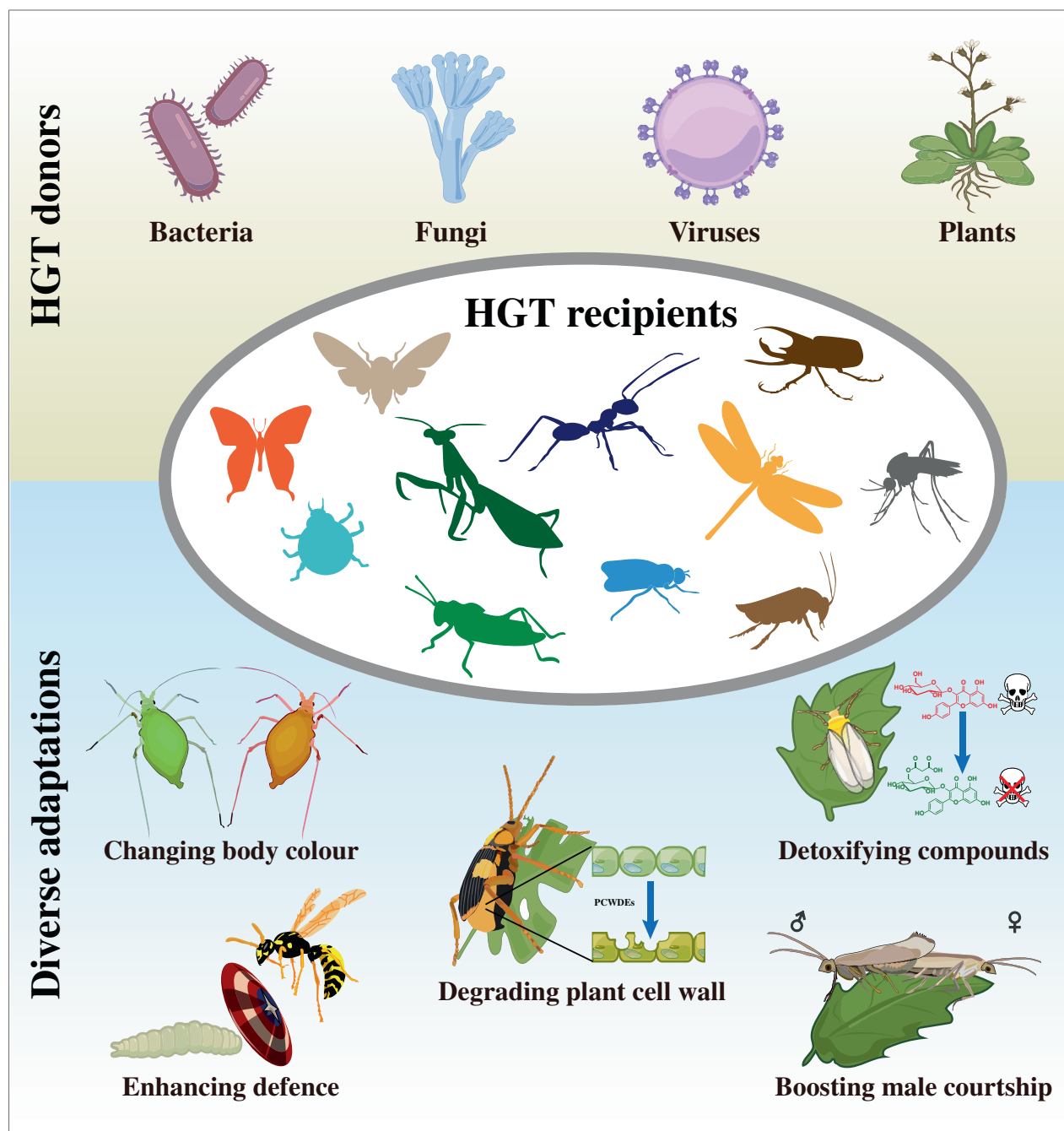


FIGURE 1 Insect genes horizontally acquired from bacteria, fungi, viruses, and plants are responsible for diverse insect adaptations. Some well-known examples of horizontal gene transfer (HGTs) are shown as follows: carotenoid biosynthesis genes transferred from fungi to pea aphids contribute to a red–green colour polymorphism (Moran & Jarvik, 2010); genes that neutralize phenolic glucosides acquired from plants contribute to the detoxification capabilities of whiteflies (Xia et al., 2021); a parasitoid killing factor gene transferred from a virus to lepidopterans contributes to lepidopteran defence (Gasmi et al., 2021); plant cell wall degrading enzymes (PCWDEs) obtained from bacteria and fungi contribute to efficient plant tissue digestion (Kirsch et al., 2022; McKenna et al., 2019); and an HGT-acquired gene from bacteria enhances male courtship behaviour in lepidopterans (Li et al., 2022).

rarely in eukaryotes. It is estimated that 1.6%–32.6% of genes in a bacterial genome has been acquired by HGT (Koonin et al., 2001). However, the small number of multicellular eukaryotic genomes makes it difficult to estimate how many genes have been acquired by HGT in eukaryotes. With the advances of

sequencing technologies, genomics and bioinformatics have substantially changed our understanding of HGT in eukaryotes. In the past two decades, large numbers of HGT events have been reported (Panoff & Chuiton, 2004; Wickell & Li, 2020). Now it appears that HGT in eukaryotes occurs more often

than what we expected and has contributed to adaptation of a wide variety of organisms.

The mechanisms by which HGT occurs are well known in bacteria but are less well understood in eukaryotes. In bacteria, the mechanisms of HGT include transformation, transduction, and conjugation (Arnold et al., 2022). Once exogenous DNA has entered a cell, it can be incorporated into chromosomes by homologous recombination (Li & Heyer, 2008). In eukaryotes, HGT can occur through a variety of vectors, such as symbiotic microorganisms, viruses or transposons (Catoni et al., 2018; McDonald et al., 2019; Perreau & Moran, 2022). Symbiotic microorganisms are currently thought to be the main vectors of foreign DNA in eukaryotes (Li et al., 2022; Perreau & Moran, 2022). The degree of openness of the symbiotic relationship between host and symbiont largely determines the ease and frequency of HGT occurrence (Perreau & Moran, 2022). Host genetic population structure, which can be classified as open, closed, or mixed, can influence foreign gene transmission and retention. Host-symbiont genetic recombination activity is common in open and mixed symbiotic relationships.

HGT-acquired genes across different insect orders exhibit diverse functions (Figure 1). For example, in Diptera, a large amount of genetic material from *Wolbachia* bacterial endosymbionts has been integrated into the genome of *Drosophila ananassae*. This foreign DNA was involved in the evolution of metabolic pathways in *Drosophila* (Dunning Hotopp et al., 2007). In Lepidoptera, most butterflies and moths have acquired exogenous genes from bacteria; one of these transferred genes was shown to enhance the courtship of male moths (Li et al., 2022). Horizontally acquired genes could also enhance the recipient insect's defences. A parasitoid killing factor gene acquired from a virus to lepidopterans contributes to defence against natural enemies (Gasmi et al., 2021). In Coleoptera, herbivorous beetles can use plant cell wall degrading enzymes (PCWDEs), which were horizontally obtained from bacteria and fungi, to convert complex fibres of plant cell walls into simple oligosaccharides and monosaccharides (Kirsch et al., 2022; McKenna et al., 2019). In Hemiptera, whiteflies have acquired the plant-derived phenolic glucoside malonyltransferase gene *BtPMaT1*. This foreign gene enables whiteflies to neutralize toxins in plants. This suggests that herbivores use genetic material from their host plants to evolve resistance to plant defences (Xia et al., 2021). Finally, carotenoid biosynthesis genes transferred from fungi to pea aphids contribute to a red-green colour polymorphism, which influences their susceptibility to natural enemies (Moran & Jarvik, 2010).

A recent study systematically examined HGT across 218 insect genomes (Li et al., 2022), finding that HGT is widespread in insects and that the donors of the transferred genetic material are diverse; 80% of

exogenous genes originated from bacteria, with smaller proportions derived from complex eukaryotes, including fungi (11%) and plants (4%) (Li et al., 2022). Did these HGT events occur via direct eukaryotic-eukaryotic contact or is there a prokaryote that acted as an intermediate vector to assist their transfers? We do not know, but no matter which hypothesis turns out to be correct, the prerequisite of DNA material transferred into eukaryotic organisms from other prokaryote or eukaryote donors is that its transmission should occur in eukaryotic germ cells. Otherwise, these HGT-acquired genes will not be passed on to offspring in insects. In addition, Li et al. found that the number of HGT events in insects varied widely in different orders (Li et al., 2022). For example, the numbers of HGT-acquired genes in insects of the orders Hymenoptera and Diptera are relatively small, whereas the number of HGT-acquired genes is much higher in the order Lepidoptera. What factors lead to disproportional distribution of HGT across major insect orders? Although the answer to this question remains a mystery, consideration of the ecologies of insects in different orders might be helpful to answer it. Lastly, it is unclear whether microorganisms, such as symbionts, acquired foreign genes from insects via HGT.

In summary, many previous studies have found the occurrence of HGT in insects, but there are some burning questions that still are unknown:

- i. How did HGT occur between insects and their donors?
- ii. Why are microorganisms the major donors?
- iii. Why are lepidopterans more prone to HGT?
- iv. Does HGT ever occur in the opposite direction, that is, from microorganisms to insects?

AUTHOR CONTRIBUTIONS

Liu Chao: Writing – original draft (lead); writing – review and editing (lead). **Yang Li:** Conceptualization (supporting); writing – original draft (supporting). **Yun Chen:** Writing – review and editing (supporting). **Xue-xin Chen:** Writing – review and editing (supporting). **Jianhua Huang:** Writing – review and editing (supporting). **Antonis Rokas:** Conceptualization (supporting); writing – review and editing (supporting). **Xing-Xing Shen:** Conceptualization (lead); writing – original draft (lead); writing – review and editing (lead).

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

This study does not generate any new data.

ORCID

Xing-Xing Shen  <https://orcid.org/0000-0001-5765-1419>

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