Conflict and Cooperation amid Host-Parasitoid Interactions

When host organisms, notably insects, acquire microbes, they also acquire new genes that may lead to adaptive changes

Julien Varaldi

The presence of heritable morphs, or heritable phenotypic variants, within populations enables those populations to evolve. Hence, if one morph is more adapted to the local environment, then a selective process favoring that morph ultimately should lead all members of the population to display this particular phenotype.

The primary source for variation is allelic, involving some genes in the organism of interest. By virtue of the selective process, the frequency of good alleles increases through many generations and, ultimately, leads to a change in the overall population. However, in addition to this primary source of variation, microorganisms that infect other organisms may provide an unexpected source of heritable phenotypic variations, particularly among insects and other arthropods.

Much as a mutation may arise in the genome of the macroorganism, possibly leading to new traits, the macroorganism may acquire a microorganism. The arrival of this microorganism, carrying a full set of coadapted genes, may have a strong impact on the phenotype of the host. Because those genes may be transmitted from parent to offspring, usually through the maternal lineage, they can provide additional raw material that affects the evolution of the macroorganisms that carry those genes.

Researchers generally pay close attention to pathogenic bacteria or viruses, and devote less time to chronic infections that inflict no evident harm on their hosts even though such infections can be found everywhere among eukaryotes. This supernumerary compartment importantly may contribute greatly to the evolution of organisms. Several nice examples of their influence are found affecting insects.

Symbiotic Bacteria and Phage Can Affect Dynamics between Insect Species

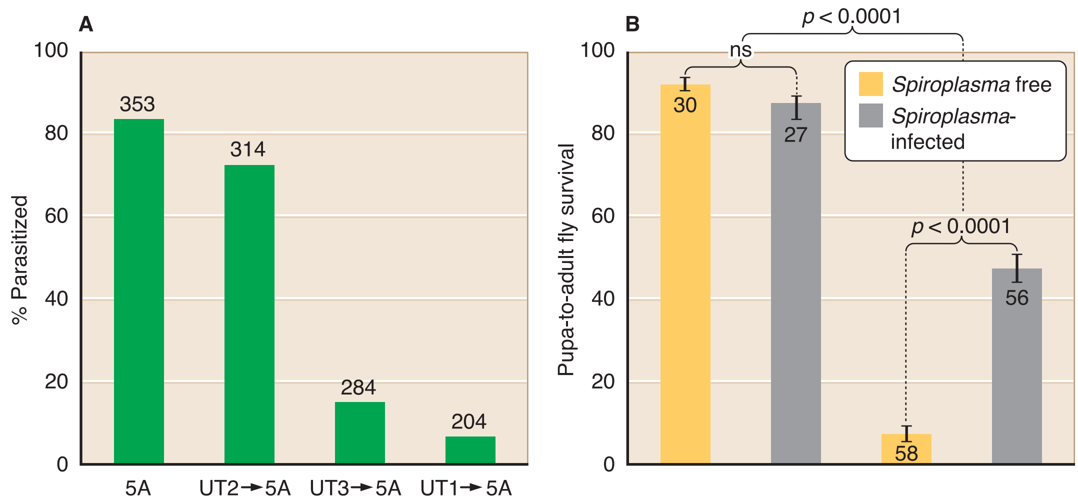
Some parasitic insects attack other parasitic insects, with the former depositing their eggs in or on the bodies of their hosts. If the parasitic insect, called parasitoid, is not eliminated by the immune system of its insect host, it will usually kill that host sooner or later. Consequently, parasitoids are important regulators of insect densities. Due to this property, parasitoids have been used for a long time as biological control agents to protect crops. In the intense antagonistic interaction between insect hosts and insect parasitoids, coevolutionary processes are at play. The hosts may develop resistance to get rid of the parasitoids, while the parasitoids may develop virulence that counteracts host resistance.

Although some of the genes that confer resistance or virulence are known, they account for only a small portion of the variations observed in nature. In addition to the genes of the insects themselves, symbiotic bacteria and viruses also partake in these interactions. Thus, bacteria sometimes protect against parasitoid attack. For example, aphids may harbor the bacteria *Hamil-*

SUMMARY

- **Microorganisms that infect other organisms may provide an unexpected source of heritable phenotypic variations, particularly among insects and other arthropods.**
- **Symbionts can contribute to host adaptive evolution, especially when they are transmitted vertically from parent to offspring.**
- **The frequency of horizontal, or contagious, transmission can have an impact on phenotypic effects in the host, and may help to explain how a virus can change the behavior of its wasp host.**
- **Symbiotic interactions are intrinsically multidimensional.**

FIGURE 1



(A) Proportion of the aphid *Acyrthosiphon pisum* successfully parasitized by the wasp *Aphidius ervi*. Each treatment in these graphs represents different lineages of the same *A. pisum* clone (5A), each with a distinct *H. defensa* isolate (UT1, UT2, UT3). (B) Probability of survival for uninfected (white bars) or *Spiroplasma*-infected (grey bars) *Drosophila hydei* flies in the absence (left two bars) or the presence (right two bars) of the parasitoid wasp *Leptopilina heterotoma*. (Adapted from J. Xie et al., PLoS ONE 5: e12149, 2010, and K. M. Oliver, et al., *Proc. Natl. Acad. Sci. USA* 102:12795–12800, 2005.)

tonella defensa, or the fruit fly *Drosophila hydei* may harbor the bacteria *Spiroplasma*. Both protect their insect hosts against their respective parasitoids.

Remarkably, variations in the intensity of the *H. defensa* protective effect are ascribed to genetic variations in those bacteria instead of the insect host (Fig. 1). The issue is even deeper because bacteriophage (APSE) encoding toxins are responsible for that protection rather than the *H. defensa* bacteria themselves. These symbiotic bacteria are transmitted from mothers to their offspring, and it has been demonstrated that insect host lines bearing the protective symbiont increase in frequency in the presence of the parasitoid.

The symbiont is, however, counterselected in the absence of the parasitoid, suggesting that the bacteria can induce intrinsic costs to their hosts. Moreover, this interaction can lead to very dynamic host/symbiont interactions, depending on the ecological context.

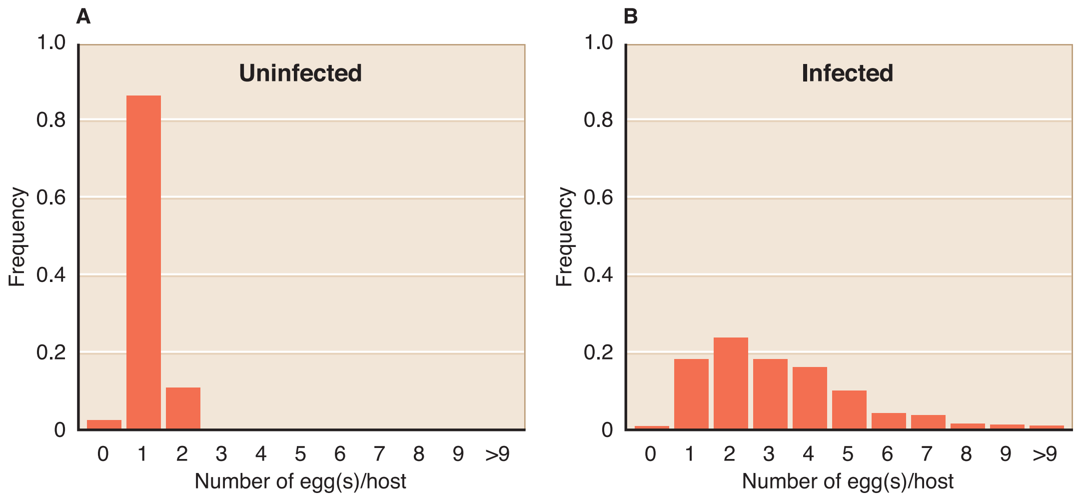
Meanwhile, the parasitoid wasp *Leptopilina boulardi* carries an inherited virus, called LbFV. This parasitoid lays its eggs inside the larvae of various species of the fruitfly *Drosophila*. The virus exerts no classical pathogenic effects on the parasitoid. On the contrary, the virus increases the virulence of the host parasitoid by protecting the parasitoid eggs from the immune response of its fruitfly hosts. Like the symbiotic bacteria, the virus is transmitted from each mother parasitoid to her offspring and may be selected for because of its immune-suppressive power.

Symbionts Affect the Adaptability of their Hosts

Symbionts can contribute to host adaptive evolution. In these cases, the genes of the symbiont and of its host are being selected in the same direction because the symbionts are transmitted vertically from parent to offspring. Thus, any increase in the reproductive output of the host directly translates into an increase in the reproductive output of the symbiont.

However, some cases of horizontal, or contagious, transmission may occur. For the LbFV virus that infects the parasitoid wasp *Leptopilina boulardi*, horizontal transfers are frequent, and this high frequency makes a big difference. The parasitoid is a solitary species of wasp, and only one parasitoid emerges from each *Drosophila* host. Accordingly, parasitoid females usually do

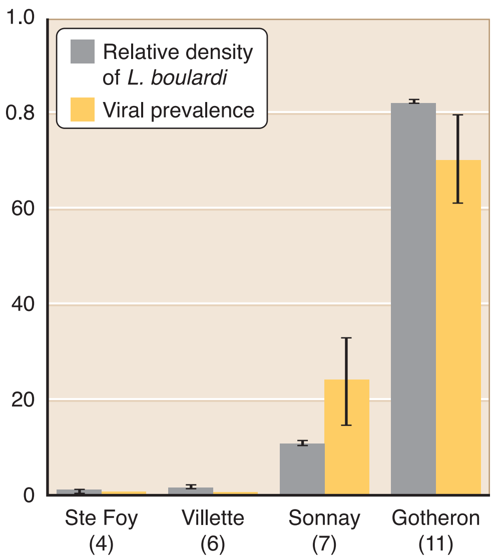
FIGURE 2



Distribution of the number of parasitoid eggs/*Drosophila* larva for two *L. boulardi* lines either infected or uninfected by the virus LbFV. Females were isolated on 10 *Drosophila* host larvae.

not lay eggs in *Drosophila* larvae that are already parasitized, thus preventing a situation of intense competition for offspring.

FIGURE 3



Relative density of the parasitoid *L. boulardi* (indicative of the competition intensity among parasitoid females) and prevalence of the virus LbFV in four localities of South-Eastern France. The numbers in parenthesis are codes for the localities. (Adapted from S. Patot et al., Mol. Ecol. 19:2995–3007, 2010.)

Unlike uninfected females, the parasitoid females infected with the LbFV virus frequently lay eggs in parasitized *Drosophila* larvae, following a behavior called superparasitism (Fig. 2). This surprising effect of the virus is better understood when one realizes that the virus is horizontally transmitted under these conditions. The virus can then jump from one parasitoid lineage to another within the superparasitized *Drosophila* larva. By inducing this behavior, the virus ensures that it propagates in wasp populations. On the basis of theoretical modeling, a viral strain that induces such a behavioral change would outcompete a viral strain that would not do so, suggesting that this change is selected for in the genome of the virus.

Inducing superparasitism is costly to the parasitoid wasp because it leads the female to waste eggs and also to spend time laying supernumerary eggs—staying in the oviposition takes more time than it does to reject a host. This phenomenon is thus beneficial for the virus and detrimental for the parasitoid. Consequently, this extended-phenotype can be viewed as the virus manipulating the behavior of the wasp.

Examining How Viruses Change Behavior in Their Insect Hosts

How does a virus manipulate the behavior of an insect? This question is being addressed by com-

AUTHOR PROFILE

Varaldi: from Parasitic Wasps and Viruses to Brazilian Percussion and Saxophone

"Nobody in my family is in the field of science, but my parents gave me lots of opportunities to develop my curiosity for science," says Julien Varaldi. "I think I soon had an interest in science in general, thanks to this favorable environment." Later, that general interest shifted to microbiology and parasitic wasps. "I had never been a naturalist, passionate with insects or any other organism," he says. "This interest for [insect] biology was constructed much later on, based on the education I received at the university, mostly crystallized around the theory of evolution."

Today Varaldi, 36, is associate professor in biometry and evolutionary biology at the University of Lyon in Lyon, France, the city where he grew up. "The general focus of my work is to understand how symbionts contribute to the evolution of insects," he says. "In particular, I am interested in the role played by inherited viruses in shaping the phenotype of parasitic wasps."

Such wasps lay their eggs inside other insects during their larval stages, which continue to develop until the parasitic wasps consume and kill their hosts. He compares this process to what happens during the 1979 science fiction movie *Alien*, in which extraterrestrial creatures similarly burrow into and attack crew members of a spaceship that is returning to Earth.

The biology of parasitic wasps, the viruses that they carry, and the insects on which they prey are all very much grounded in microbiology as well as reality, Varaldi continues. "In addition to their eggs, parasitic wasps often inject viral particles into their hosts," he says. "Some of these viruses have evolved towards a mutualistic relationship with the parasitoid, since they protect the parasitoid egg from the immune reaction of the host. Other viruses infecting these wasps may manipulate the behavior of the wasp, facilitating the spread of the virus."

Earlier during his education, Varaldi became interested in the genetics of behavior, especially after reading about the evolution of social behavior, including in several books written by the American biologist Edward O. Wilson, who is recognized as the leading worldwide authority on ants as well as an early and controversial proponent of sociobiology, the study of the genetic basis of the social behavior of animals. "I found fascinating—and sometimes scary—that part of what we are is, in fact, the consequence of genes we are carrying," Varaldi says.

Varaldi received a bachelor's degree in 1999, a master's degree in 2000, and a Ph.D. in 2003, all from the University of Lyon. He was a lecturer there from 2003–2004, left to do postdoctoral research with Laurent Keller at Lausanne University in Switzerland, and then returned to Lyon as an associate professor in 2004. In his spare time, Varaldi plays Brazilian music, mostly percussion and saxophone, and visits "this marvelous country as often as I can," he says.

Marlene Cimons
Marlene Cimons lives and writes in Bethesda, Md.

paring the way genes of infected and uninfected females are expressed. Additionally, the virus genome is being sequenced to identify possible effectors of behavior. Preliminary data from that analysis suggest that the virus can interfere with insect synapses.

Because this virus can be transmitted both vertically and horizontally, it is expected to fixate—that is, infect 100% of all individuals—within wasp populations. However, it does not fixate in the field, likely because vertical transmission is incomplete, meaning that infected females regularly produce sets of uninfected offspring. The equilibrium frequency reached by the virus in natural populations thus depends mainly on the rate of incomplete vertical transmission and on the frequency of superparasitism events.

We found that the virus frequency is extremely high, reaching as much as 90%, in populations where the competition among parasitoids for the possession of *Drosophila* hosts is high. In these populations, females are likely to encounter parasitized *Drosophila* larvae and superparasitism is frequent. That frequency is much lower in parasitoid populations with less competition (Fig. 3). Overall, the virus is responsible for about 70% of all variations observed in this behavior in natural populations. In other words, the main genetic factor responsible for this "parasitoid-trait" is not encoded by parasitoid genes but by an inherited virus.

Conclusion

The example of the parasitoid *L. boulardi* and its virus emphasizes that symbiotic interactions are intrinsically multidimensional. Specifically in this case, the virus protects the egg from the *Drosophila* immune system but manipulates the behavior of the wasp at the expense of its reproductive output. On one trait, the interacting partners agree but, on another, they completely disagree! This multidimensionality is observed in other symbiotic interactions. Some symbionts such as *Wolbachia*, known as heritable reproductive parasites, protect against natural enemy viruses.

By contrast, bacterial symbionts that confer protection against parasitoids are costly to their hosts in the absence of the parasitoid. Traditionally, symbionts were classified as mutualists because they are beneficial for their hosts, others as commensals because there is no net effect, and still others as parasites because of their negative effects on their hosts. However, the multidimensionality of these interactions render this classification scheme irrelevant, or at least makes it more complicated to find how sets of organisms fit into it.

In any case, symbionts are undoubtedly important contributors to phenotypic variations of arthropods and probably of other organisms, and should be considered important players in the evolution of organisms. Thanks to rapid DNA-sequencing technologies, investigators can access huge amounts of genetic information for many organisms, and that information will enable them to identify additional examples of symbiont-mediated traits in the future.

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Suggested Reading

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