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Diversity begets diversity: do parasites promote variation in protective symbionts?

Nina Hafer[1] and Christoph Vorburger[1,2]

Insects commonly possess heritable microbial symbionts that increase their resistance to particular parasites. A diverse community of defensive symbionts may thus provide hosts with effective and specific protection against multiple parasites, although costs might constrain the accumulation of many symbionts. In parallel to the allelic diversity in the MHC complex of the vertebrate immune system, parasite diversity could be the driving force behind symbiont diversity. There is indeed evidence that parasites have the ability to drive frequencies of defensive symbionts in their hosts, and that these symbionts influence parasite communities, but direct evidence that parasite diversity can promote symbiont diversity is still lacking. We provide suggestions to investigate this potential link.

Addresses
[1] EAWAG, Swiss Federal Institute of Aquatic Science and Technology & Institute of Integrative Biology, Überlandstrasse 133, 8600 Dübendorf, Switzerland
[2] Institute of Integrative Biology, ETH Zürich, Universitätsstrasse 16, 8092 Zürich, Switzerland

Corresponding author: Hafer, Nina (nina.hafer@eawag.ch)

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Introduction

One of the great challenges any living organism faces is how to defend itself against a multitude of parasitic organisms such as parasitoids, macroparasites, fungi, bacteria and viruses. In addition to their own immune system, many organisms rely on microbial symbionts to help them with this challenge. Such defensive symbionts are especially abundant among insects and other arthropods (e.g. [1,2]). Different secondary symbionts, for example, provide aphids with protection against different parasitoid wasps and pathogenic fungi [3–5]. In this paper, we briefly summarize the evidence for the diversity, specificity, and costs of protective symbionts in insects and draw comparisons with the specific protection afforded to vertebrates by their adaptive immune system. We then go on to discuss the potential role of parasites in shaping and maintaining symbiont diversity.

Properties of defensive symbionts in insects

Symbiont-mediated protection has been reported from a wide variety of insects. Flies can be protected against parasitoid wasps or parasitic nematodes by bacteria of the genus *Spiroplasma* [6–8], and against viral pathogens by *Wolbachia* (e.g. [9–11]). Another example are antibiotic-producing bacteria protecting developing beewolves (*Philanthus* sp.) or the eggs of Lagriinae beetles against pathogenic fungi [12,13••]. Symbiont diversity has been studied most exhaustively in aphids with at least 9 different species of heritable facultative endosymbionts described to date, 7 of which have been shown to confer protection against entomopathogenic fungi or parasitoids [5]. These different symbionts occur in many aphid species [14], and they can co-occur within the same host species, the same host population, or even the same host individual [1,3–5,15,16]. The frequencies of infection with particular symbionts show extensive variation among aphid populations from different sites or different host plants [1,3–5,15,16] as also observed in other groups of insects [17,18]. This variation is ecologically relevant, because symbiont-conferred resistance is strong, often stronger than any innate resistance (reviewed by [3–5,19,20]), and parasite-specific. In *Drosophila*, for example, *Wolbachia* provides protection against different RNA-viruses, but not against DNA-viruses [10,11]. In aphids, the endosymbiont *Hamiltonella defensa* typically provides protection against parasitoids and *Regiella insecticola* protects against fungal pathogens (reviewed e.g. by [3,4]), although notable exceptions exist (e.g. [21,22]). This specificity even extends to variation within species. Particular strains of the symbionts protect well against some parasite genotypes but not against others (G × G interactions), such that no symbiont offers the best protection against all parasites [22–29].

Symbionts as a modular defence toolbox?

Multiple symbionts might provide a way to overcome the restrictions of this specificity by providing wider or more effective protection. Infections with more than one symbiont are regularly observed in the field (reviewed by [3,5,15,16]) and a recent laboratory study confirmed that they can be stable [30•]. Indeed, symbionts seem to maintain their protective effect in the presence of another symbiont species or strain [30•,31]. Some studies have even found indications that co-infections can enhance

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protection [26,32,33] or ensure protection even under adverse condition such as heat stress, which normally reduces the protective effect of *Hamiltonella* [34], but see [35]. On the other hand, the possession of multiple defensive symbionts might be constrained by a reduced fidelity of vertical transmission [36•,37], or by detrimental effects of symbiont infection. In flies and aphids, protective symbionts have repeatedly been found to be associated with fitness costs such as shorter lifespan or reduced competitive ability [3,4,23,25,38]. Infection with multiple symbiont species or strains can have even more severe fitness costs in aphids [26,30•,31,33], although this might depend on host genotype [31], host environment [26], and symbiont-symbiont combination [30•].

Parallels and differences between protective symbionts and the vertebrate MHC

The defensive symbionts of insects can be seen as a second line of defence in addition to their innate immunity. With its remarkable diversity and specificity of action, symbiont-conferred resistance shows some interesting parallels to the vertebrate major histocompatibility complex (MHC) that are worth exploring (Table 1). The MHC is part of the adaptive vertebrate immune system and MHC-encoded proteins (i.e. MHC molecules) are responsible for the specific recognition of parasites and pathogens (Box 1). As for protective symbionts, there are numerous variants of the MHC, which provide effective and specific protection against different parasites and pathogens, but each individual can only possesses a limited number of different MHC variants. Their number, however, is usually higher than the number of different protective symbionts within a single insect host and, unlike symbionts, MHC is present in each individual. Being part of the nuclear genome the MHC can change only through recombination during reproduction, albeit immune memory can improve control of familiar parasites and pathogens during an individual's lifetime. Protective symbionts, by contrast, remain organisms of their own that are usually transmitted vertically by the mother only, but can also be lost or acquired horizontally [16,36•,39]. Additionally, symbionts can change through horizontal gene transfer, such as the loss or acquisition of bacteriophages, which in *Hamiltonella* are responsible for the protection of their aphid hosts against parasitoids [40–42]. This will also alter their benefits and costs to the host.

Box 1 The MHC of vertebrates and parasite driven selection

The major histocompatibility complex (MHC) is a gene region that consists of multiple loci encoding parts of the adaptive immune system of all jawed vertebrates. For each locus there are numerous alleles making the MHC extremely diverse. The MHC molecules, i.e. antigen binding transmembrane proteins encoded by this region, contain a highly variable antigen-binding site capable of the specific recognition of pathogens. In each MHC molecule, this site binds to specific parasite-derived antigenic peptides and presents them on the cell surface where they are recognised by specific T-cells, which then activate a specific immune response. In order to prevent self-reactivity, all T-cells that bind to self-peptides are eliminated during T-cell production (negative T-cell selection). Each individual possesses only a limited number of different MHC alleles and hence is not equally effective in fighting off all parasites. Certain MHC molecules have frequently been found to be associated with resistance to particular parasites and the evidence for some relationship between protection against parasites and individual MHC diversity is convincing, but the exact shape of this relationship is less clear and selection might favour optimal rather than maximal MHC diversity (reviewed by [43,45,47,61]). Such an optimum in MHC diversity would ensue if there were a cost to high MHC diversity. Indeed, individual MHC diversity might be restricted by negative T-cell selection limiting the capability of increasing the number of parasites that can be recognised through increasing MHC diversity and the risk of autoimmune diseases that increases with increasing MHC diversity [43,45,47]. Additionally, certain MHC alleles, in addition to their protective effect, are associated with susceptibility to autoimmune diseases or parasites [43,45,62]. The MHC repertoire and its diversity differs between populations and species [47,63,64]. Frequently, populations or species co-occurring with a more diverse parasite community have a more diverse MHC repertoire [65–69]. It has been the subject of an ongoing debate whether MHC diversity is driven by heterozygote advantage and/ or frequency dependent selection, but in either case it seems clear that parasites are the driving force behind the diversity [43–45,47,61,63].

Diverse parasite communities should favour high symbiont diversity

Their many shared properties suggest that the MHC and protective symbionts are subject to similar selection pressures. Hence, parasites should be important drivers in maintaining symbiont diversity akin to the maintenance of MHC diversity (see Box 1). This could occur via balancing selection in the face of multiple parasites or via

Table 1

Comparison between properties of MHC and symbiont-conferred protection

	Symbionts	MHC
Prevalence	Intermediate, highly variable (encoded by facultative symbionts)	100% (encoded by the host genome)
Diversity between individuals	High	Very high
Differences between Populations/environments	Yes	Yes
Effective protection against pathogens/parasites	Yes	Yes
Specificity	Yes	Yes
Costs	Yes	Yes (depend on individual MHC diversity)

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