

Microbial impacts on insect evolutionary diversification: from patterns to mechanisms

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Symbiosis can favor rapid shifts in host phenotypic traits, particularly through the contribution of symbionts to the host's physiology. In addition, variations in the microbiota composition between individuals can be associated with pre-zygotic and post-zygotic barriers. All together, these phenomena may contribute to insect diversification and speciation. Recent advances have also shown that the host-microbiota molecular dialog, mediated notably by host immune and developmental pathways, is critical for the acquisition and control of the microbiota, and could also contribute to reproductive isolation. While still a controversial hypothesis, adaptation through symbiosis could thus trigger host-symbiont coevolution and accelerate differentiation.

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Current Opinion in Insect Science 2014, 4:29–34

This review comes from a themed issue on **Molecular physiology**

Edited by **Angela E Douglas**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 12th August 2014

doi:[10.1016/j.cois.2014.08.003](https://doi.org/10.1016/j.cois.2014.08.003)

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Introduction

Biology is undergoing a paradigm shift. An individual should no longer be considered as a single organism, but as a chimera composed of a community of interacting organisms, including the host itself, but also a wealth of microbial partners that are associated with it. Microbial partners can be extracellular or intracellular, vertically or horizontally transmitted, beneficial or detrimental, but all contribute to the phenotype of the symbiotic individual. This phenotype is thus an 'extended phenotype' resulting from the expression of multiple genomes and their interactions [1].

At a macro-evolutionary scale, there is no doubt that symbiosis has played a major role in the evolution and diversification of entire clades of insects by allowing the exploitation and/or colonization of new niches [2–6]. For

instance, symbionts can physiologically contribute to the provision of essential nutrients to hosts that feed on unbalanced food (e.g. plant sap or blood), or to the exploitation of recalcitrant food sources (e.g. wood) [7,8**]. Nonetheless, our understanding of the micro-evolutionary processes involved in diversification is surprisingly still very limited.

The picture is however changing. First, microbiota are described in a growing number of insect species, which makes now possible the study of the biotic and abiotic factors shaping their composition. Second, the molecular dialog between hosts and symbionts starts to be deciphered, highlighting notably a crucial role of host immune and developmental pathways in the acquisition of the microbiota and its control. Third, rapid shifts in microbiota composition have recently been associated with physiological traits, potentially favoring niche diversification and reproductive isolation. After reviewing these different aspects, we propose that the mechanisms involved in the control of symbionts (immunity, development) and the effects of microbial partners on their host (niche expansion, reproductive isolation) can reinforce each other and facilitate insect diversification.

Within-species and between-species variation in the composition of microbial communities

With the development of high throughput sequencing technologies, symbiotic communities — and notably gut microbiota — have recently been characterized in a number of insect species (review in [8**]). While descriptive, these approaches constitute a first hint to elucidate factors involved in the variation of symbiotic communities and their adaptive value within and between phylogenetically related species.

Environment has a clear influence on the symbiotic composition. For instance, changes in diet during life or during development are associated with important variations in the gut microbiota composition (e.g. *Drosophila* fruitfly and *Cephalotes* ant microbiota [9,10]), but other factors, like parasite infection, can also modulate it [11]. Interestingly, a comparison of 62 insect species from various orders highlighted convergence in the microbiota composition between distantly related species sharing the same diet [12*]. This convergence could partly result from adaptation for optimal exploitation of the environment. Together with the fact that host-associated communities are highly different from environmental ones (e.g. [10,13]), and that an important predictor of the

symbiotic composition of individuals is the species they belong to (e.g. [14,15]), these host–microbiota association patterns suggest a fundamental filtering process during the stable colonization of the host. This filtering can also occur during symbiont transmission, as recently shown in beewolf wasps, where inoculation of non-native protective *Streptomyces* symbionts led to normal colonization, but to an absence of transmission [16]. Different studies have even evidenced that variations detected in the composition of the microbiota recapitulate host phylogeny, a phenomenon now referred as phylosymbiosis [17**]. For example, different species of the ant genus *Cephalotes* display a species-specific microbiota, although individuals from a single species were collected in highly different environments [18]. Similarly, a phylosymbiotic signal was found in the wasp genus *Nasonia*, albeit all species were reared on the same environment [19]. Both species-specificity and phylosymbiosis suggest an influence of the host–microbiota dialog on the microbiota composition, with possible co-divergence in the case of phylosymbiosis.

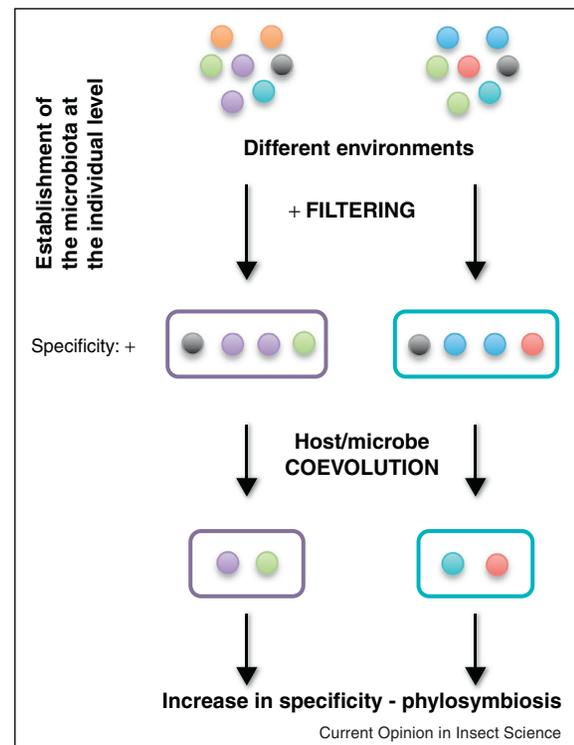
While these studies show that both environmental and host factors influence the composition of the microbiota, they also underline that host factors are of prime importance in filtering environmental bacterial communities (Figure 1). Evident directions of research are to determine the contribution of the microbiota to the host phenotype and the adaptive value of its composition, which remain unknown in most cases.

Immunity and development shape bacterial microbiota

Within the host, the microbiota resides in specific tissues (e.g. the intestine) that constitute a specific niche. This host niche is shaped by biotic and abiotic factors (e.g. temperature, pH, oxygen, metabolites, secreted molecules) that may be under the control of host and bacterial genes. Recent advances have started to elucidate the proximate mechanisms involved in the construction of this niche and how these mechanisms regulate the composition and abundance of bacterial communities.

Recent findings on *D. melanogaster* indicate that the immune system plays a central role: it does not only participate in the regulation of pathogens, but also to the regulation of resident bacteria and to the homeostasis between resident and pathogenic bacteria (review in [20*]). For instance, the repression of NFκB-dependent antimicrobial peptides (AMPs) controls the commensal microbial community in the fly gut and limits the proliferation of the pathogenic *Gluconobacter moribifer* [21]. Indeed, RNAi-silencing of the negative regulator *Caudal* (IMD pathway), specifically expressed in the posterior midgut, results in a decrease of commensal *Acetobacteraceae*. This process is followed by the overgrowth of *G. moribifer*, the induction of apoptosis, and the death of the fly [21]. Interestingly, the microbiota itself can directly

Figure 1



Processes of variation in microbiota composition. When symbionts are environmentally acquired, bacterial composition within the host depends on the microbial composition of environmental communities. A plastic composition of the microbiota may be adaptive when the environment fluctuates rapidly and without predictability. This could for example be the case in *Drosophila melanogaster*, where the local environment, among which diet, has an extreme influence on the composition of the microbiota [9,47]. Numerous examples also indicate an active filtering process, which results in the selection of a subset of the environmental community and an increase in the host/microbiota specificity. The phylosymbiotic signal observed in some instances may reflect (co)evolution of the host–symbiont interactions. Circles of different colors represent bacterial strains/species and rectangles host genotypes.

modify the niche [22]. For example, uracil produced by opportunists, but not by resident bacteria, activates the Dual oxidase that regulates the production of microbicidal Reactive Oxygen Species (ROS) [23,24**].

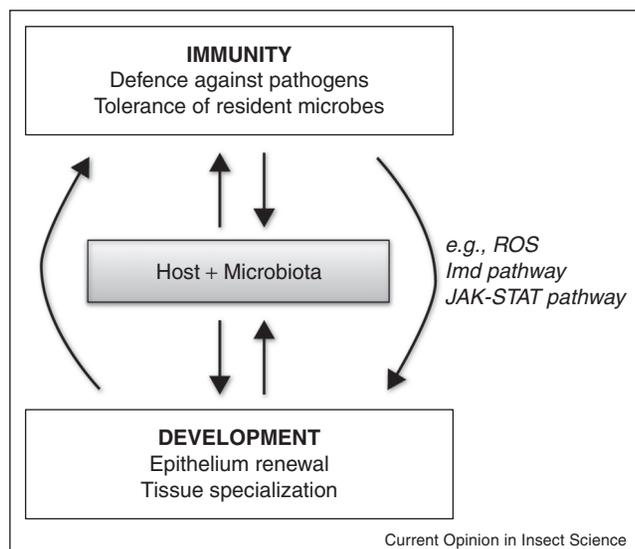
In the midgut of the majority of arthropod species, epithelial cells secrete a peritrophic membrane (PM) which constitutes a critical interface with the microbiota, protecting the host against pathogenic infections [8**,20*]. Remarkably, transcription factors and toxic molecules, by modulating immune pathways (e.g. IMD/relish, JAK–STAT or JNK), also have a pleiotropic role in host developmental processes [25–28]. Indeed, JAK–STAT or JNK pathways, which are activated by microbicidal ROS, facilitate the epithelium renewal [25]. The PM integrity is also directly impacted by gut microbiota in the tick *Ixodes scapularis*. Indeed, dysbiosed

larvae exhibit a reduced expression of STAT that lowers the expression of the peritrophin, a major glycoprotein structuring the PM [29^{*}]. In this case however, the reduced thickness of the PM limits the colonization of the pathogenic spirochete *Borrelia burgdorferi* [29^{*}].

A differential regulation of microbial populations can be supported by the development of anatomical structures where a specific immune regulation is locally triggered. For instance, the evolution of compartmentalization together with the important anatomical variation of gut structures and immune regulations between species may be the consequence of the intense selection imposed by symbiosis (reviews in [8^{**},20^{*}]). Another striking example is the confinement of *Sitophilus* primary endosymbiont (SPE) within the weevil's bacteriocytes (i.e. cells specialized in hosting symbionts) in response to secretion of AMPs. Indeed, the localized secretion of coleopteracin-A within the bacteriocytes regulates bacterial growth, initiating the development of giant filamentous endosymbionts that are not able to spread into insect tissues [30^{**}].

All these studies highlight the fundamental role of the host-microbiota dialog in shaping both immune and developmental homeostasis (Figure 2). This suggests that coevolution between partners favors the maintenance of specific microbes in a particular niche, a process which could underlie the establishment of phyllosymbiosis (Figure 1).

Figure 2



Host-microbiota dialog shapes both immune and developmental homeostasis to control the microbiota composition. Molecular pathways (italics) exhibiting a pleiotropic role in immunity and development must play a particularly important role in defining and maintaining the specificity of the interaction in a particular host niche.

Symbiont-induced mechanisms favoring diversification and speciation

While symbionts play an important role in numerous insect functions (review in [31]), only a few studies directly link the variation of the microbiota — within or between closely related species — to phenotypic traits potentially involved in diversification and speciation.

The first category of phenotypic traits relates to symbiont-mediated exploitation of the host ecological niche (review in [32]). The acquisition of symbionts has been associated with rapid niche shifts in a few cases. For instance, experimental switching of the *Ishikawaella* symbionts between *Megacopta punctatissima* and *M. cribraria* led to a complete reversal of the performances of the plataspid stinkbugs on different host plants, namely soybean and pea [33]. Another example is the evolution of a variant of the western corn rootworm *Diabrotica virgifera* in response to the pest control crop rotation (corn versus non-host soybean). This variant exhibits a shifted microbiota composition with an increase in *Klebsiella* sp. and *Stenotrophomonas* sp., which could favor tolerance to anti-herbivory defenses of the new host plant through the increase of cysteine proteases activity [34^{**}]. In these cases, provision of novel traits by symbionts can support access and/or adaptation to new environments and favor adaptive radiation.

The second category of traits potentially involved in differentiation relates to the impact of symbionts on the interruption of gene flows between individuals harboring different microbiota, that is, on host reproductive isolation. Individuals harboring similar extracellular or intracellular microbiota exhibit kin recognition and mate preferentially together in several *Drosophila* species [35–37]. For instance, the different microbiota composition of *D. melanogaster* flies fed on different food sources, and particularly the presence/absence of *Lactobacillus plantarum*, influences the sexual isolation pattern [35]. In the *D. paulistorum* species complex, infection by *Wolbachia* also influences mating preference of males and females [37]. These preferences could directly rely on the modification of pheromonal profiles through the participation of symbionts to the synthesis of cuticular hydrocarbons or volatile compounds [35], but other mechanisms, such as a modification in the neuronal integration of the signal, remain to be explored. In addition, both vertically-transmitted and horizontally-transmitted symbionts may participate to post-mating isolation by inducing hybrid sterility. In the *Drosophila paulistorum* and *Nasonia* species complexes, sterility is associated with the over-proliferation of symbionts in the testes of hybrid males [37,38]. While the mechanisms involved are not known, proliferation of symbionts in hybrids may result from the perturbation of the genetic interactions between symbionts and host genes involved in the control of the symbiotic population. Supporting this hypothesis, Brucker and

Bordenstein showed that hybrid viability is restored when gut bacteria are removed from *Nasonia* wasps [17**]. Dead hybrids show an altered microbiota, a strong melanization coupled with an activation of the immune system, suggesting that ‘control’ mechanisms may diverge rapidly between closely related species, and be involved in post-zygotic barrier to hybrid formation. This hypothesis has recently been convincingly exposed in [17**]. Finally, microbe–microbe interactions can also participate to post-mating isolation. The most studied example is the hybrid mortality resulting from bidirectional incompatibility in crosses between individuals infected with different *Wolbachia* strains (reviewed in [39,40]).

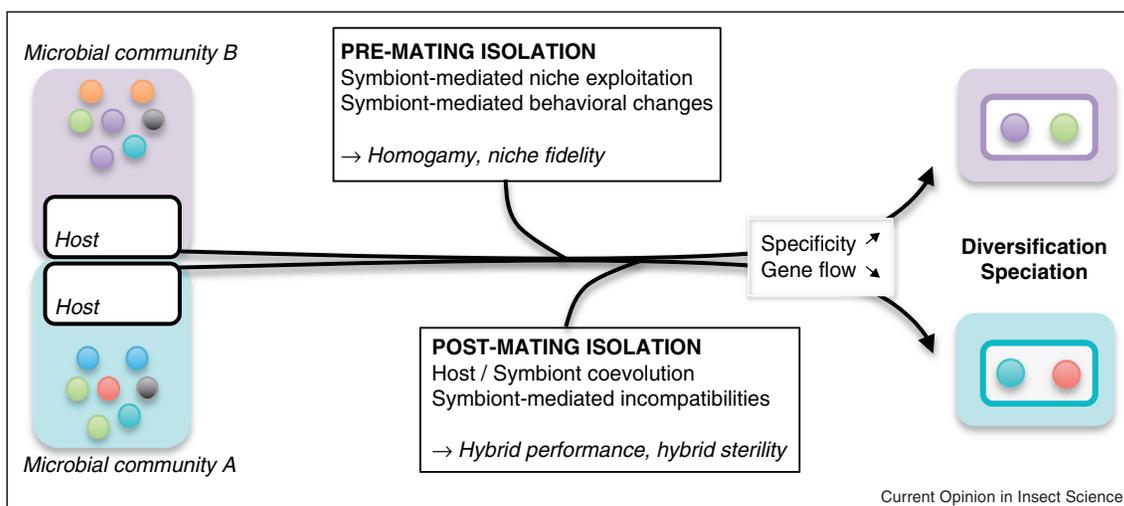
Symbiosis as a driver of insect diversification

Modifications of symbiotic communities can be extremely rapid both within individuals and populations. These shifts can reflect selection for symbiont-mediated traits that allow adaptation to the local environment. For example, *Spiroplasma* has rapidly spread within *Drosophila neotestacea* populations, owing to the protection it confers against sterilizing nematodes [41]. These adaptive processes can also be coupled to processes that are not adaptive for the host. For example, *Rickettsia* rapidly spread in populations of *Bemisia tabaci* in the United States as a result of the benefit it provides on some traits (e.g. fecundity, developmental time), but also because of the reproductive manipulation it induces (i.e. female-bias in the progeny) [42]. Whatever the mechanisms involved, these examples highlight that symbiont frequencies can

dramatically change over short periods of time. Importantly, these rapid changes can dramatically affect the selective pressures acting on the host to acquire, control and tolerate beneficial and/or prevalent symbionts [43*]. For example, tolerance evolution has been proposed as the fundamental force that led to the evolution of host dependence in the *Wolbachia*–*Asobara tabida* symbiosis, as a consequence of the accommodation of the host to the modification of ROS homeostasis by the symbiont [44–46]. This coevolutionary dynamics of hosts and symbionts following rapid changes in microbiota composition could have dramatic consequences on hybrid viability, as shown in *Nasonia*.

All together, symbiosis could thus trigger insect differentiation through a variety of mechanisms. Symbionts, by providing new physiological capabilities to their hosts, can allow niche expansion, a first step toward adaptive radiation. In addition, acquisition and spread of a new symbiont may be accompanied by side effects that facilitate or trigger host differentiation. First, facilitation can occur when individuals harboring the same microbiota exhibit mate preference. Second, host genes underlying local adaptation may not only encode traits directly involved in niche exploitation, but also genes involved in the adaptation to the symbiotic partner, such as immune and developmental genes. Rapid evolution of these genes may favor the emergence of post-zygotic barriers and increase host–symbiont specificity, thus allowing niche segregation and rapid differentiation (Figure 3).

Figure 3



Model for the role of symbiosis in the reinforcement of differentiation between populations. Symbionts can promote rapid adaptation to local conditions. Rapid shifts in microbiota can also generate selective pressures on the partners for optimization of symbiont acquisition and/or for tolerance. As a consequence, host–microbiota specificity should increase, leading to a reduction in hybrid performance. Furthermore, host–symbiont coevolution can lead to symbiont-mediated incompatibilities between hosts adapted to different microbiota, reinforcing specificity and thus niche segregation between hosts harboring different microbiota. This scenario can be applied when microbiota diversification occurs in allopatric populations. In the case of sympatric/parapatric populations, reinforcement mechanisms possibly mediated by symbionts, such as niche fidelity or mate choice would be required.

Conclusion

For a long time, global phylogenetic patterns have suggested that symbiosis is an important driver of insect diversification. Recent advances in symbiont-mediated behavioral modifications and in the mechanisms involved in symbiotic homeostasis now highlight proximate mechanisms through which this could occur. Studies of symbiosis diversification at a short time-scale are needed to get a better picture of the selective pressures and processes involved in the evolution of symbiotic relationships, and of their role in the diversification of insects. A full understanding of these processes requires to expand our documentation on the variations of community composition, but more importantly on the mechanisms underlying host–symbiont interactions within species, between biotypes/host races or closely related species. New methodologies are offering a unique opportunity to tackle these questions, providing a full description of the composition and the functioning of these interactions and facilitating the detection of host genes involved in local adaptation. Are those genes frequently associated with the regulation of the symbiotic compartment? How do they influence hybrid performance and viability? Studying the mechanisms of host–symbiont interactions and their micro-evolutionary dynamics is thus a crucial step for the field of insect symbiosis in particular, but more importantly for the entire field of entomology.

Acknowledgements

We apologize to our colleagues for references that have not been cited because of space limitations. FV is supported by the Agence Nationale de la Recherche (ANR-2010-BLAN-170101/ImmunSymbArt) and NK by the Marie Curie Actions (FP7-PEOPLE-2010-IOF/272684/SymbiOx).

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