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Editorial: Host Manipulation by Parasites

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Editorial on the Research Topic

Host Manipulation by Parasites

Host manipulation by parasites is a widespread phenomenon by which parasites alter the phenotype of their hosts to increase transmission success. Alterations can range from subtle to profound traits modifications, and can occur across a wide range of host and parasite taxa (Moore, 2002). This topic has generated much interest among researchers of different disciplines, and has evolved from simple descriptions of new cases to a full integration of the complexity of the phenomenon at different levels of biological organization. However, although substantial advances have been made in the last years, there are still important knowledge gaps and new challenges to face. Here we aim to provide an integrative overview of current lines of research at both the mechanistic (proximate) and functional (ultimate) levels.

While the number of examples reporting this phenomenon is growing, the proximate mechanisms are still poorly understood. Herbison's review, identifies four main pathways by which parasites can manipulate host phenotype at proximate level: immunological, genomic/proteomic, neuropharmacological, and symbiotic. After a literature review on these mechanisms, four major weaknesses emerged: (1) there are limited studies showing a direct connection between molecular and phenotypic changes; (2) the multidimensionality of molecular mechanisms (the ability of parasites to alter multiple molecular routes to alter the host phenotype) is rarely taken in an integrated manner; (3) most of mechanistic studies have been performed on few host-parasite systems; (4) the lack of general principles due to the many host-parasite systems that remain uninvestigated.

"Omic" technologies provide opportunities toward understanding the mechanistic processes behind parasite manipulation. Pradit et al. provide here new insights by studying the interactions among plant pathogens, host plants, and vector organisms. They performed transcriptome analysis to decipher phytoplasma-induced alterations in gene expression in cranberry displaying the false blossom disease. Infection enhanced the expression of genes associated with nutrient metabolism and suppressed genes associated with defensive pathways, which increase host quality for insect vectors, thus promoting phytoplasma transmission (Pradit et al., 2019). Further research is needed to explore how general are these observations in other plant-parasite systems, where studies are particularly scarce. Convergence between unrelated parasite lineages with respect to manipulative mechanisms will progress the field from hypotheses to theories. As stated before, most studies have focused on individual trait modification, while increasing evidence support that manipulative parasites alter multiple characteristics of their host. A promising research avenue is to assess the way different traits interact. Park and Sparkes approach this question by studying multiple traits modification in the freshwater isopod *Caecidotea intermedius* infected by the acanthocephalan

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parasite *Acanthocephalus dirus*. Results of the study show that traits were modified independently, which suggests different mechanisms were involved in trait manipulation.

Multidimensional manipulation is a complex phenomenon, so one single model cannot totally describe it. An essential step is to identify other systems in which multidimensional manipulation occur and to assess the correlations among traits to explore *how they are mechanistically related*.

Symbiont-mediated host manipulation is another area that deserves future attention. A well-known example is Wolbachia, the most widespread symbiont of arthropods and nematodes. While many studies exist on the effects of Wolbachia on host fitness (feminization of males, parthenogenesis, male mortality), there is a general lack of information on its role on mating preference. Richard provides some insight here studying how this endosymbiont influenced the odor and mating preference of their hosts, the terrestrial isopod *Armadillidium vulgare*. This author revealed that reproductively manipulated (feminized) males were less selected by males than uninfected females based on volatile cuticular compounds, which act as an honest signal of parasitic status. Thus, this model is interesting to study how parasite manipulation act as evolutionary force promoting changes in its hosts. Up to now few studies have considered how to deal with the impact of parasite manipulation in species of economic interest. Honeybees (*Apis mellifera*) are susceptible to the infection by the microsporidia *Nosema ceranae*, a manipulative parasite involved in honeybee decline worldwide. *N. ceranae* induce behavioral fever in honeybee colonies to enhance its development and fitness (Campbell et al., 2010). El Khoury et al. present here a pioneer study demonstrating that inoculation of gut microbiota can provide benefices as probiotics against this highly pathogenic parasite. Studying and selecting microorganisms with probiotic properties is a promising applied line of research to develop adequate strategies to cope with important diseases on honeybees.

Most often, manipulative parasites (particularly trophically transmitted parasites, e.g., those which depend on predation to reach the definitive host) are not very pathogenic for the final host. In their opinion paper, Øverli and Johansen explore the hypothesis that an evolutionary driver for this pattern is the energetic/nutritional benefit for the final host, and argue that increasing the fitness of the host may be an overlooked but important driver in shaping the host immune response. It can explain many apparently benign associations where infection appears to be beneficial for the host.

Finally, a central question that still drives current research on host manipulation by parasites is whether changes in host phenotypes are truly adaptive manipulation or side-effects of infection (Poulin, 2010). While manipulation implies that parasites alter host traits in a purposive manner to increase its transmission success (see Poulin, 1995), changes in host phenotype can be also a by-product of chronic infection. Changes in behavior and personality associated with toxoplasmosis in humans have been considered as a classical example of adaptive manipulation. Here Šebánková and Flegr provide new data that support the hypothesis that some toxoplasmosis-associated changes in humans are by-products of the infection based on N-70 and anamnestic questionnaire. As stated before more mechanistic studies bringing empirical causative evidence (and not correlations) are needed to discern between true adaptive manipulation and pathological side-effects of infection. Moreover, elucidation of host-parasite molecular crosstalk during the manipulative process is important to define novel therapeutic targets against these parasites and to decipher their molecular impact on biodiversity and on food webs in ecosystems.

This Research Topic represents an overview of current trends in research on parasite manipulation. New questions have emerged and promising research avenues are proposed. We hope that it will inspire new further investigations and promote interactions between different disciplines to better understand complex processes behind parasite manipulation.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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