

Review

This Gut Ain't Big Enough for Both of Us. Or Is It? Helminth–Microbiota Interactions in Veterinary Species

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Gastrointestinal helminth parasites share their habitat with a myriad of other organisms, that is, the commensal microbiota. Increasing evidence, particularly in humans and rodent models of helminth infection, points towards a multitude of interactions occurring between parasites and the gut microbiota, with a profound impact on both host immunity and metabolic potential. Despite this information, the exploration of the effects that parasite infections exert on populations of commensal gut microbes of veterinary species is a field of research in its infancy. In this article, we summarise studies that have contributed to current knowledge of helminth–microbiota interactions in species of veterinary interest, and identify possible avenues for future research in this area, which could include the exploitation of such relationships to improve parasite control and delay or prevent the development of anthelmintic resistance.

Gut Microbiota and Macrobiota: Cooperation or Competition?

The gastrointestinal (GI) tract of vertebrates is inhabited by a vast array of organisms, that is, the **microbiota** and **macrobiota** (see [Glossary](#)). The former is composed largely of commensal microorganisms, which play a vital role in host nutrition and maintenance of energy balance, in addition to supporting the development and function of the vertebrate immune system [1–3]. By contrast, the macrobiota includes parasitic helminths, which are mostly considered detrimental to host health via a range of pathogenic effects that depend on parasite size, location in the GI tract, burden of infection, metabolic activity, and interactions with the host immune system [4]. Sharing the same environment within the vertebrate host, it is plausible that the GI microbiota and parasitic helminths interact with each other, and that the results of such interactions may impact, directly or indirectly, on host health and homeostasis [5–7]. For instance, parasitic helminths and microbiota compete for host nutrients while, in parallel, the known immunomodulatory properties of a range of parasites may translate into modifications of mucosal and systemic immunity to the resident bacteria [8]. The complex relationships occurring between parasitic helminths and microbiota have long been neglected; however, recent studies pointing towards a role for these interactions in the overall pathophysiology of helminth disease [5–7,9–28] are drawing attention to this little-known area of research. Nevertheless, current knowledge of helminth–microbiota interplay relies heavily on studies of helminth-infected humans or rodent

Trends

Increasing evidence points towards a complex network of interactions occurring between gastrointestinal helminth parasites and the gut commensal flora, which translate into fluctuations in host metabolic potential.

While multiple reports suggest that populations of Lactobacillaceae are expanded upon infections with a variety of gastrointestinal helminths, other changes in the composition of the gut microbiota and relative abundance of bacterial species are linked to specific host–parasite systems.

There is evidence that manipulation of helminth–microbiota interactions in veterinary species, either through manipulation of diet, and/or administration of prebiotics or probiotics, can sway host immune responses to helminth infections.

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models [5,7,11–15,18–22,25,26], while the impact that parasites exert on the commensal flora of species of veterinary interest is still poorly understood. Given the production losses and the considerable morbidity and mortality associated with a range of helminth diseases in livestock [29–33], as well as the global threat of emerging anthelmintic resistance [34–36], the exploration of the complexities of host–helminth–microbiota interactions in species of veterinary interest is timely and relevant. The implications of this newly acquired knowledge will be multiple, from a better understanding of the systems biology of parasites to the collection of information that could form a solid basis for the development of novel intervention strategies against GI helminths. In this article we provide an overview of current knowledge of helminth–microbiota interactions in species of veterinary interest, suggest potential applications of this knowledge in veterinary clinical medicine, and outline avenues of future research that, in our view, will be pivotal to translate research findings into practice. Given that mice are, in principle, a veterinary species, and that mouse models of infection are often used in veterinary research [37–39], data available for these hosts will be considered here alongside those from other animal species.

Matter of (Animal and Helminth) Species

Current studies of helminth–microbiota interactions in veterinary species involve a range of animals and parasites, and are characterised by a vast heterogeneity in experimental designs and techniques which, taken together, lead to a variety of findings (Table 1). In spite of these variations, a small number of specific changes in the composition of the host gut microbiota have been consistently observed in helminth-infected animals, irrespective of (host and parasite) species. Such changes are therefore likely to represent genuine helminth-associated alterations to the resident commensal flora. For instance, populations of Lactobacillaceae – Gram-positive bacteria of the phylum Firmicutes with an important role in carbohydrate metabolism [40] – are frequently expanded in the presence of helminths in the GI tract of animals, including mice infected with the roundworm *Heligmosomoides polygyrus* [5,6,12,14], the whipworm *Trichuris muris* [15], and the hookworm *Nippostrongylus brasiliensis* [13]. Interestingly, Lactobacillaceae were also increased in the biliary ducts of hamsters infected by the trematode *Opisthorchis viverrini* [26], and in the faecal microbiota of cats with patent infections by the roundworm *Toxocara cati* [17]. Members of the Lactobacillaceae are known to exert immune-modulatory functions in the host gut, primarily by promoting an expansion of T regulatory cells, which underpins their use as a probiotic supplement for GI inflammatory diseases [41]. In particular, in a recent key study, Reynolds and coworkers [5] not only demonstrated that experimental infections of mice with *H. polygyrus* were accompanied by a marked expansion in populations of Lactobacillaceae, but also that increased worm burdens could be observed following administration of *Lactobacillus* species to mice prior to experimental parasite infection [5]. This finding led the authors to hypothesise the occurrence of a form of mutualism between Lactobacillaceae and selected GI helminths, whereby each promotes the activation of T regulatory mechanisms, thus reducing the effect of the host immune response on the counterpart. Unlike for the Lactobacillaceae, knowledge of the impact of GI helminth infections on populations of other microbes is inconsistent, being largely dependent on species of hosts and parasites under consideration. For instance, members of the Enterobacteriaceae are increased in *H. polygyrus*-infected mice [5,14]. As these bacteria are able to tolerate oxidative stress [42,43], their expansion is linked to the onset of intestinal inflammation following parasite infection. In addition, a marked increase in bacteria of the genus *Mucispirillum* (family Deferribacteraceae) has been associated with infections by *T. muris* and *T. suis* in mice and pigs, respectively, likely as a consequence of the increased production of host mucin in response to helminth colonisation [11,15,24]. Conversely, the microbiota of *T. muris*-infected mice displays a marked reduction in abundance of genera of the phylum Bacteroidetes, for example, *Prevotella* and *Parabacteroides* [11,15], which results in an overall decrease in **microbial richness** and diversity (i.e., **alpha diversity**) in the GI tract.

Glossary

Alpha diversity: in ecology, the mean species diversity at the local, within-site, or within-habitat scale. It is dependent on both the number of species making up a population (richness) and the relative abundance of each species in a population (evenness).

Diet manipulation: a targeted feeding approach that is aimed at inducing a specific physiological effect.

Macrobiodiversity: the macroscopic flora and fauna of a region.

Microbial evenness: microbial species similarity in abundance within an environment or population.

Microbial metabolism: the chemical processes that occur within a microbe in order to maintain life.

Microbial richness: the number of microbial species present in a given sample.

Microbiota: the microscopic flora and fauna of a region.

Prebiotic: dietary supplements that allow specific changes in the composition and/or activity in the gastrointestinal microflora.

Probiotic: live microorganisms which, when administered in adequate amounts, confer a health benefit to the host.

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