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Editorial: Impact of anthropogenic environmental changes on animal microbiomes

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Editorial on the Research Topic

Impact of anthropogenic environmental changes on animal microbiomes

Introduction

Human activities are now recognized as being the main drivers of contemporary environmental change. While consequences of anthropogenic change at population and species levels are well-documented, effects on interspecific interactions are less understood. The interaction between animal hosts and their associated microbiomes has recently received increasing attention within the context of global change. This focus is driven by the widely recognized importance of the microbiome for host fitness, adaptive potential, and by the accrued evidence that such microbial communities are at least partly shaped by the host's environment (Macke et al., 2017). In support of this, host-associated microbiomes have recently been shown to vary with several key components of global change such as habitat degradation and fragmentation (e.g., Amato et al., 2013), urbanization (e.g., Teyssier et al., 2018), climate change (e.g., Bestion et al., 2017; Houwenhuyse et al., 2021), and pollution (Lear et al., 2021). However, studies investigating such effects in natural populations are still scarce and our understanding of the processes involved remains limited. The aim of this Research Topic was to bring together a collection of articles examining the response of animal microbiomes to different anthropogenic perturbations, in a range of host taxa and environmental contexts. A further underlying aim was to examine the role of the microbiome in mediating host responses to environmental perturbations.

Types of anthropogenic perturbations impacting animal gut microbiomes

The articles in this Research Topic collectively addressed the response of the gut microbiome of different animal taxa to a range of anthropogenic stressors, which fall within four main categories: habitat alteration, exposure to agrochemical pollutants and antibiotics, climate change and environmental changes associated with captivity. Habitat

alteration comprises one the most radical forms of anthropogenic disturbances inducing many potential changes to the microbiome. In this context, Martínez-Mota et al. investigated the impact of anthropogenic forest disturbance and fragmentation on the gut microbiota of black howler monkeys (Alouatta pigra). They more specifically accounted for feeding tree diversity and biomass to examine anthropogenic changes in food availability. Alpízar et al. addressed gut microbiota responses to changes in foraging habitat in relation to agricultural practices by comparing the gut microbiota of bats (Glossophaga soricina) feeding in natural forests, conventional monocultures and organic plantations. Urbanization is another form of habitat alteration that may impact food availability, behavior and physiology and therefore gut microbiota composition. Obrochta et al. thus explored the influence of urban environments on the gut microbiota of Canada geese (Branta canadensis) in relation to migratory behavior. Other articles examined the gut microbiota responses to exposure to pollutants, and in particular agrochemicals. Changes in the gut microbiota of honeybees (Apis mellifera) were examined following experimental exposure to several types of pesticides (Cuesta-Maté et al.) and to an antibiotic (Soares et al.). Bornbusch and Drea investigated the impact of exposure to antibiotics on the gut microbiota of ring-tailed lemurs (Lemur catta) by studying populations along a gradient of increasing exposure (undisturbed, domestic animal presence, human presence, direct human contact and antibiotic treatment) and also considered variations in environmental soil microbiota. Jaramillo and Castañeda explored the influence of heat stress in the context of climate change in Drosophila subobscura flies. Coone et al. investigated experimentally gut and body microbiomes of Daphnia and its surrounding bacterioplankton upon hypoxia, which is assumed to increase in freshwater ecosystems upon increased temperatures and the more frequent occurrence of harmful algal blooms. Lastly, Trevelline and Moeller examined the impact of exposure to human microbiota (termed microbiota humanization) due to captivity in seven mammalian families, while Jiang et al. examined seasonal variations in the gut microbiota of captive musk deer (Moschus spp.).

Effects of anthropogenic perturbations on the gut microbiome

The articles within this Research Topic examined the response of the gut microbiota to different perturbations by considering several metrics including alpha-diversity, beta-diversity, taxonomic composition, network complexity and function. A majority of these studies reported a negative effect of the considered perturbation on gut microbiota alpha-diversity (monoculture, Alpizar et al.; pesticides, Cuesta-Maté et al.; antibiotics, Soares et al.; heat-stress, Jaramillo and Castañeda; hypoxia, Coone et al.). Such a loss in diversity in gut microbial communities following anthropogenic perturbations seems to be a common pattern across many hostmicrobiota associations and contexts (Flandroy et al., 2018). Two other studies conversely reported an increase in gut microbiota in animals present in disturbed habitats (resident urban individuals, Obrochta et al.; disturbed forest fragments, Martínez-Mota et al.).

All of the studies in this Research Topic reported shifts in composition associated to perturbations, highlighting the

sensitivity of gut community structure to environmental stressors. In the context of captivity, Trevelline and Moeller reveal a compositional convergence between captive mammal and human gut microbiota in four out of the seven families examined. When considering microbiota dispersion (i.e., inter-individual microbial heterogeneity), Cuesta-Maté et al. found a homogenizing effect of pesticides on bee gut microbiota, whereas environmental alterations conversely increased beta-diversity in bats (Alpizar et al.) and geese (Obrochta et al.) thereby illustrating the Anna Karenina Principle according to which stressors induce stochastic changes and increase inter-individual heterogeneity (Zaneveld et al., 2017).

Anthropogenic perturbations also modified gut microbiota taxonomic composition, with changes in the relative abundances of various bacterial taxa according to the host and perturbation considered. In particular, habitat alterations seem to increase the proportion of Proteobacteria (generally considered as being mostly "environmental" bacteria) and decrease that of Firmicutes (generally beneficial and present in high proportions in vertebrate guts; Alpizar et al.; Martínez-Mota et al.; Obrochta et al.). The studies on the gut microbiota of honeybees revealed that agrochemicals induce a decrease in key honeybee gut taxa, including Bombella apis and Lactobacillus kunkeii (oxalic acid, Cuesta-Maté et al.) and Bombella, Fructobacillus, Snodgrassella, Gilliamella, and Apibacter spp. (tetracycline, Soares et al.). The studies that performed microbiota network analyses showed contrasting results. Alpizar et al. showed increased network complexity in the gut microbiota of bats in altered habitats whereas exposure to a pesticide lead to fewer network interactions due to the disappearance of key taxa in honeybees (Cuesta-Maté et al.). In Daphnia, it was found that hypoxia induced expelling of gut microbial strains reflecting stronger differences in the microbial communities in the Daphnia gut in comparison with its surrounding bacterioplankton community upon hypoxia vs. control treatments (Coone et al.). Last, in contrast to the above studies, Bornbusch and Drea did not consider taxonomic composition and diversity but rather focused on the influence of antibiotics exposure on metagenome function and more specifically on the abundance, alpha- and beta-diversity of antibiotic resistance genes (ARGs), also called the resistome, and found an increase in abundance of such genes in highly exposed lemur populations.

Consequences of anthropogenic microbiome shifts on host fitness

All the microbiota changes following perturbation reported above are likely to have consequences for host health and fitness. There is increasing evidence that the microbiome may mediate host responses to environmental stressors, which leads us to ask the following question: do the induced microbial changes further worsen their effects on host health (i.e., dysbiotic effect, Flandroy et al., 2018) or do they, on the contrary, mitigate or buffer their effects (i.e., the microbiome as a driver of host acclimation/adaptation to anthropogenic change, e.g., Alberdi et al., 2016; Houwenhuyse et al., 2021).

The majority of the articles in this Research Topic seem to indicate a dysbiotic effect of anthropogenic perturbations. In

monoculture bats, the overall loss of microbiota diversity and in particular the decrease in bacterial taxa associated with better host condition may indicate adverse effects for the host (Alpizar et al.). Likewise, in resident urban geese, the reduced abundances of bacterial genera involved in key metabolic functions related to host digestion could have negative health consequences (Obrochta et al.). In honeybees, the loss of bacterial taxa that play a key role in nutrient metabolism and pathogen defense following exposure to agrochemicals (Cuesta-Maté et al.; Soares et al.) and the increase in bee mortality in the case of oxalic acid (Cuesta-Maté et al.) suggest implications for bee immunity, longevity and fecundity. The humanization of the gut microbiota of captive mammals shows evidence of a mismatch between hosts and their gut microbiota (Trevelline and Moeller) with potential adverse consequences for animal health, paralleling those observed in humans with "industrialized" gut microbiota (Sonnenburg and Sonnenburg, 2019).

Jaramillo and Castañeda did not test the impact of heatinduced gut microbiota changes on fly fitness, which does not allow us to directly answer our above question. However, the gut microbiota significantly increased heat tolerance of conventional flies as compared to axenic flies, which suggests that the microbiota could play a role in host acclimation to heat and climate change. The genotype dependent effects detected in the Daphnia microbiomes suggest host genotype x microbiome x environment interactions, which could induce acclimatization (modified phenotypes) and adaptive responses upon environmental stress (Coone et al.). Martinez-Mota et al. provided interesting evidence that the microbiome response to forest disturbance is mediated by physiological stress in monkeys. They further show that low food availability and increased stress lead to an increase in SCFA-producing bacteria which could support energy availability for hosts in averse environmental contexts. This suggests that the gut microbiota may indeed mitigate the negative effects of anthropogenic disturbance and play a role in host adaptation to such changes.

Conclusion

The articles within this Research Topic explore the impact of a wide range of anthropogenic environmental changes on the gut microbiome of various host taxa. They collectively show that anthropogenic stressors systematically induce alterations in the gut microbiome, although the specific nature of these changes depends on the type of perturbations and context. Although most

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of the evidence in this Research Topic points toward dysbiotic changes in the microbiota with likely adverse effects on host fitness, certain results suggest that the microbiota may contribute to host acclimation or adaptation to anthropogenic stressors. We encourage further studies directly measuring the impact of humaninduced microbiota changes on host fitness in order to gain a better understanding of the role of the microbiome in mediating the response of organisms to global change.

Author contributions

JW organized the Research Topic together with KA, ED, and VM. All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

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