

Letter

Microbial Genomes as Extension Packs for Macroorganismal Diversity: A Reply to Morimoto and Baltrus

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We thank Morimoto and Baltrus for their attention to our paper, 'The extended genotype: microbially mediated olfactory communication' [1]. We agree with Morimoto and Baltrus that the genotype has been classically defined as the genes that are vertically inherited and we do not dispute this definition. However, we use the term 'extended genotype' to mean just that: an additional set of genes that extend the diversity and functionality of the vertically inherited genome. Much as extension packs may be purchased to customise almost any consumer product, such as a car, electronic gadget, or children's building set, the extended genotype concept proposes that individual organisms may access additional genetic diversity by co-opting microorganism genomes. The extension pack is not the core product, much as the microbial genome is not part of the organism's core genome; rather, it allows the genome to be extended as required, a key distinction between the extended genotype and the holobiont concept. We used the term extended genotype to refer to this concept, in deliberate homage to Dawkins' 'extended phenotype', a trope that is likely familiar to all readers of *Trends in Ecology and Evolution*.

Comments on our paper by Morimoto and Baltrus focus solely on the use of the phrase extended genotype and are

largely based on semantics. However, we appreciate the opportunity to clarify the core concept. We agree that 'precise and clear language' is important and therefore offer our understanding of the key terms under discussion. The 'genotype' is the collection of genes vertically transmitted by host cells, although we would note that in the vast majority of organisms, there is no germline. The 'holobiont' is the assemblage of species that comprise what is loosely thought of as an 'individual' organism. The 'hologenome' is the combined genetic information of host cells and microbiota in such an individual. In contrast, the extended genotype is the collection of diverse genes potentially available to an individual via acquisition of specific microbiota. Hence, the extended genotype is not a property of an individual; consequently, it is not equivalent to an extended phenotype and is not a unit of selection. The extended genotype could also be called the 'panhologenome', but we think the former term is more elegant.

The concept of the extended genotype generates important questions of relevance to adaptation, phenotypic diversity, and evolutionary processes. We have focused on its potential contribution to odour and communication, but other phenotypes such as metabolism, detoxification, and behaviour can also be modified by changing the composition of the microbiota [2]. Importantly, the resulting phenotypic changes are beneficial only to the individual, in a particular time and place, and are not vertically inherited. Thus, an organism's offspring may co-opt a different set of microorganisms to better suit their needs, resulting in a different phenotype to the parent. While some microbes may be directly transmitted from parents to offspring, it is the 'ability' to co-opt microbial genomes to suit the individual organism's

requirements that is under selection, and vertically inherited, not the microbiome itself. This idea in itself raises interesting conceptual arguments about the unit of selection in such systems, how to define an individual, and which genes are passed between generations. The extended genotype concept opens up a world of nuanced and subtle potential interactions and evolutionary trajectories in line with current discussions in the broader literature (e.g., [3–6]).

The central idea in our paper is that the vertically inherited genotype may not generate sufficient diversity for reliably identifying individuals, for rapid responses to environmental perturbations, for the complexity of communication required in a certain space and time. By co-opting microbial genes, macroorganisms can rapidly change their phenotypes in a way that would not be possible using only the nuclear genome, simply because of the vast genetic complexity available in the microbial world. This is what we mean by an extended genotype.

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