



Conserve the germs: the gut microbiota and adaptive potential

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Abstract

Although the diversity of microbial communities (microbiota) inhabiting body niches are of proven importance to health in both humans and non-human animals, the functional importance of these collective genomes (microbiome) to the adaptive potential of their hosts has only recently been considered within a conservation framework. If loss of gut biodiversity threatens the health (and therefore the fitness of individuals), and this loss can be correlated with the adaptive potential of a species in changing environments, measuring functional composition of the microbiota from non-invasive samples, such as faeces and skin swabs, could provide a useful and practical tool for determining conservation priorities. This article reviews the evidence for adaptive potential of microbiota in wild species, and proposes future directions. While there is ample indication of inter- and intra-specific variation in microbiota diversity, there is little evidence that diversity per se confers fitness. However, there are convincing examples showing that microbiota flexibility, composition and function may well be sources of adaptive potential, although case studies are relatively few, and the analytical approaches needed to demonstrate the mechanisms underlying host–microbiota interactions have only recently been developed.

Keywords Conservation · Fitness · Host health · Metataxonomics · Microbiodiversity · Microbiome

As this volume explores in depth, in conservation genetics, attention has turned from the near-exclusive use of neutral genetic variation, to the more challenging prospect of estimating adaptive genetic variation, essential for the survival of endangered organisms, especially in rapidly changing environments. Such progress in our understanding is thanks to advancements in next generation sequencing (NGS), allowing markers to be characterized across the genome or even whole genomes to be sequenced. Even more recently, NGS technology has allowed the characterization of whole communities of microorganisms from various sample types using taxa-specific markers ('metataxonomics'; Marchesi and Ravel 2015), with rapid parallel development of appropriate field collection methods (Hale et al. 2016; Song et al.

2016) and bioinformatic analyses (e.g. Callahan et al. 2017; Jiménez and Sommer 2017; Mendes et al. 2017).

It has been recognized that the bacteria inhabiting body niches (e.g. skin, gut) of wild animals may be important to maintaining individual health and resilience as has been shown extensively for humans, laboratory models and livestock (Cho and Blaser 2012; Pascoe et al. 2017). While the conservation implications of an intact microbiota have started to be explored (e.g. Roggenbuck et al. 2014; Stumpf et al. 2016; Jiménez and Sommer 2017; West et al. 2019), fewer than 100 article titles, abstracts and/or keywords contain both 'microbiota' and 'conservation' in a literature search of public databases. In addition, evaluation of available literature on wildlife microbiota reveals that most articles are dedicated to simply cataloguing the composition of these bacterial communities (Pascoe et al. 2017). Thus, whether microbiota influences the adaptive potential of wild species has rarely been specifically addressed up to now (Bahrdorff et al. 2016). This review explores the evidence relevant to this potential, with the aim of establishing whether 'microbiodiversity conservation' should be considered concomitantly with conservation of host genomic variability to improve the management and survival of species at risk. Such evidence will mainly be derived from wild species, since these

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are more likely to possess intact microbiota demonstrating the natural relationships between host and commensal flora (e.g. Amato 2013; Pascoe et al. 2017). Since the majority of studies thus far have focussed on the effect of bacterial composition and not that of their collective genomes as such, this review will be limited to discussions of the microbiota, not the microbiome, as a source of adaptive potential.

The importance of commensal bacterial communities to host physiology, nutrition and immune health has resulted in some authors declaring that microbiota should be considered a new ‘organ’ (Baquero and Nombela 2012) or that all genomes of an individual, including that of the individual and the microbiome, should be considered as a single evolutionary unit, or ‘holobiome’ (Zilber-Rosenberg and Rosenberg 2008; Shapira 2016). However, given the complexity of the microbiota and the multiplicity of organisms that it encompasses (including symbiotic, commensal and potentially pathogenic organisms) other authors including ourselves consider this an unnecessary and possibly erroneous simplification, instead promoting the use of well-established ecological theory to analyse the relationships between the microbiota and host (Moran and Sloan 2015; Douglas and Werren 2016). In any case, relevant to the argument here is that microbiota has an effect on a host’s phenotype, and therefore, on fitness, affecting natural selection and evolutionary trajectory (Redford et al. 2012; Sharpton 2018). Essentially, in order for these bacterial communities to be a source of adaptive potential for their respective host species, intraspecific variation in microbiota composition and function must be (i) present; (ii) heritable, and (iii) have an effect on individual host fitness for natural selection to be able to act.

Does intra-specific variation in microbiota composition exist, and is it heritable?

There is a wealth of evidence to confirm that intra-specific variation in the microbiota of healthy adult individuals exists for the same body niche. For example, individual variation in gut microbiota composition has been noted in the gorilla *Gorilla gorilla* (Frey et al. 2006), chimpanzee *Pan troglodytes* (Degnan et al. 2012), koala *Phascolarctos cinereus* (Alfano et al. 2015) and kākāpō *Strigops habroptilus* (Waite et al. 2012), and in skin microbiota in the bottlenose dolphin *Tursiops truncatus*, killer whale *Orcinus orca* (Chiarello et al. 2017), and several marine fish species (Chiarello et al. 2015). In addition, variation in gut microbiota composition between sexes has been noted for the black howler monkey *Alouatta pigra* (Amato et al. 2014), Verreaux’s sifaka *Propithecus verreauxi* (Springer et al. 2017), Namibian cheetah *Acinonyx jubatus* (Wasimuddin et al. 2017) and largemouth bronze gudgeon *Coreius guichenoti* (Li et al. 2016).

The heritability of microbiota is, by comparison, much less studied, especially in wildlife (but see review on humans by Koskella et al. 2017, including successful experimental approaches). Despite the complexity of these microbial communities, stable, measureable species-specific differences in composition are evident, suggesting that these may be ‘heritable’; that is, passed on to future generations by vertical transmission, and co-evolve with their hosts (Baldo et al. 2017). Phylogenetic analyses of the gut microbiota of humans and chimpanzees (Moeller et al. 2012), 59 mammals (Ley et al. 2008), eight species of lagomorphs and rodents (Li et al. 2017b), 25 *Cephalotes* ant species (Sanders et al. 2014), and *Nasonia* parasitoid wasps (Brucker and Bordenstein 2012) are consistent with evolutionary relationships estimated from host genomes. Specifically, Sanders et al. (2014) used an innovative analysis to show that vertical transmission was the most likely factor affecting microbiota stability of host-microbiota co-evolution. In addition, composition of the gut microbiota distinguishes host species, even when there is convergence in specialized diets and some microbial gut taxa, as is the case for bamboo-feeding (Li et al. 2015; McKenney et al. 2018), piscivorous (Soverini et al. 2016), 18 folivorous (Amato et al. 2018) and 15 myrmecophagous (Delsuc et al. 2014) mammals (but see Baldo et al. 2017 for cichlid fishes). Microbiota composition is also preserved across geographically separated populations, e.g. in tunicates (Cahill et al. 2016).

Does intra-specific variation in microbiota composition or diversity affect individual fitness?

Although core microbiota composition may be stable and heritable for a particular species, animal microbiota composition may also change within an individual in association with extrinsic and intrinsic factors. For example, as for humans and livestock, diet is a common driver of composition (Muegge et al. 2011; Pascoe et al. 2017), as illustrated by studies of the black howler monkey *A. pigra* (Amato et al. 2015), giant panda (Xue et al. 2015; Williams et al. 2016; Wu et al. 2017), Tasmanian devil *Sarcophilus harrisii* (Cheng et al. 2015), American bison *Bison bison* (Bergmann et al. 2015), American pika *Ochotona princeps* (Kohl et al. 2017), and birds (Waite and Taylor 2015; see also discussion of captive species below). Several authors have noted that habitat also appears to be a critical factor determining surface microbiota in corals (Kelly et al. 2014; Roder et al. 2015), plethodontid salamanders (Muletz Wolz et al. 2017) and various carp species (Eichmiller et al. 2016), as well as the gut microbiota of the Namibian blackbacked jackal *Canis mesomelas* (Menke et al. 2017) and ring-tailed lemurs *Lemur catta* (Bennett et al. 2016). Other authors have noted

differences in microbiota diversity and composition for various life stages suggesting that early exposure to many sources of microbiota could have important consequences for host health later in life (e.g. howler monkeys: Amato et al. 2014; kittiwakes: Van Dongen et al. 2013; 212 amphibians: Vences et al. 2016; bees: McFrederick et al. 2014), as has been demonstrated in humans (Odamaki et al. 2016). The fact that changes in microbiota composition are associated with available food and other resources suggests that microbiota flexibility may affect an individual's resilience to changes in the environment throughout its lifetime (including resistance to pathogens), and therefore, could impact individual health, survival and, consequently, fitness; in other words, such plasticity could act as an adaptive trait, as has been suggested for host phenotypes (Fusco and Minelli 2010). However, the causes and effects of specific changes in taxa have rarely been verified. Only a few very careful studies thus far have come close. Kohl et al. (2017) have shown that the gut microbiota of the American pika is particularly well-adapted to their specialized moss diet, being enriched with fibre-degrading *Melainabacteria*. Sommer et al. (2016) noted changes in microbiota composition in the brown bear *Ursus arctos* during active and hibernation seasons and investigated further: by transplanting specific summer and winter microbiota from bear to germ-free laboratory mice, Sommer and colleagues were able to show that changes in gut microbiota composition were directly related to fat accumulation and metabolism, both related to individual fitness.

From human studies, we know that low bacterial diversity is associated with 'western' diets (De Filippo et al. 2010), and dysbiosis with bowel disease (Gonçalves et al. 2018 and references therein), but also other health issues (e.g. Battson et al. 2017 for cardiovascular disease; Moran-Ramos et al. 2017 for metabolic disease). Therefore, if microbiota diversity affects individual fitness, low microbiota diversity resulting in microbiota dysfunction would be expected in circumstances where adaptive capacity is compromised. For wild species, such circumstances might be predicted in captivity, where individuals are often fed high energy or other inappropriate diets, are highly stressed and/or have little contact with natural environments (which provide a reservoir of taxa from which host microbiota are normally maintained). Microbiota studies on captive and wild populations provide some evidence that microbiota diversity decreases in captivity, but the pattern is not straightforward. In a recent review on wild versus captive mammalian microbiota, McKenzie et al. (2017) concluded that many primates, canids, and equids have a lower gut microbiota alpha diversity in captivity than in the wild. Carnivorous marsupials such as the Tasmanian devil also suffer a decrease in microbiota alpha diversity in captivity (Cheng et al. 2015), as do the mainly herbivorous Andean bear *Tremarctos ornatus* (Borbón-García et al. 2017) and red panda *Ailurus fulgens*

(Kong et al. 2014), and piscivorous Yangtze finless porpoise *Neophocaena asiaorientalis asiaorientalis* (Wan et al. 2016). However, many other herbivores and myrmecophagous mammals show no changes to their microbiota in captivity. Perhaps surprisingly, given their apparent sensitivity, some frog species also appear to maintain their natural skin microbiota diversity in captivity (Flechas et al. 2017), but not all (see Antwis et al. 2014 for red-eyed tree frog *Agalychnis callidryas*). Other species even show an increase in microbiota diversity in captivity, including rhinoceros (see McKenzie et al. 2017), and some birds (red-crowned crane *Grus japonensis*; Xie et al. 2016). Based on studies of rodents, Kohl et al. (2014) concluded that specialist feeders may be more sensitive to captive conditions, but this does not always appear to be the case (e.g. myrmecophagous mammals, mentioned above). Occasionally, a loss of diversity has been linked directly to a specific component lacking in the diet of captive individuals (such as carotenoids for frogs; Antwis et al. 2014); however, in most studies diet does not appear to be the only factor affecting changes in microbiota diversity, but a more complex combination of diet, phylogeny, and living conditions. Several recent studies suggest that it may be informative to look for potential impacts of captivity on gut health in microbiota composition, rather than simply measuring diversity; for example, in the microbiota's capacity to resist pathogen invasion. For example, the Namibian cheetah shows no change in diversity between captive and wild conditions, but captive animals have a higher abundance of potentially pathogenic microorganisms in their gut microbiota (Wasimuddin et al. 2017); a similar pattern is reported for captive versus wild forest musk deer *Moschus berezovskii* (Hu et al. 2017; Li et al. 2017a), rock ptarmigan (Ushida et al. 2016), swan geese *Anser cygnoides* (Wang et al. 2016) and crocodile lizards *Shinisaurus crocodilurus* (Jiang et al. 2017).

If microbiota diversity is associated with species survival, we might also expect that endangered species to have low diversity if they are at a particularly low population size, and/or are forced to survive in suboptimal habitats, such as those that are highly fragmented. Waite et al. (2012) has found an extremely low Phylum-level diversity in the critically endangered kākāpō compared to other species studied thus far, but even this example of low diversity may be related to its specialist leaf-chewing habit, not conservation status (Waite et al. 2012; Perry et al. 2017). Lower diversity has also been found in fragmented populations of several primate species compared to populations in intact habitat, those of the black howler monkey *A. pigra* (Amato et al. 2013) and Udzungwa red colobus *Procolobus gordonorum* (Barelli et al. 2015), but not in disturbed populations of primates in Uganda (McCord et al. 2014). However, more specifically, Amato et al. (2013) found that the gut microbiota of howler monkeys from intact habitats were composed of higher

abundances of beneficial bacteria. Barelli et al. (2015) also reported that the lower diversity in gut microbiota in red colobus from fragmented habitats translated into a loss of microbiota function, i.e. loss of genomes conferring the ability to digest toxic plant compounds. Therefore, the effect of lower diversity on microbiota function appears to be more important than diversity alone. However, in both examples, direct evidence that this loss of diversity or function has a measureable effect on individual health or fitness still needs to be demonstrated.

Direct evidence for adaptive potential of microbiota

Does the microbiota provide adaptive potential in the long-term? In other words, does the co-evolution of the host-microbiota interaction affect host evolution? There is certainly some intriguing evidence that microbiota composition or diversity directly affects fitness. In their review, Lizé et al. (2013) brings together a number of examples of how microbiota could affect behaviour, but the most convincing case in point, providing the mechanism underlying the link, concerns the fruit fly *Drosophila melanogaster*: in this species, the gut microbiota has been shown to influence cuticular hydrocarbon profiles (sex pheromones), which determine individual scent, and therefore mate selection (Sharon et al. 2010). In another elegant study using a combination of metagenomics, transcriptomics and metabolomics, Vogel et al. (2017) show how each gut section of the burying beetle *Nicrophorus vespilloides* has a specialized microbiota with specific activity for digesting and detoxifying its ephemeral food sources, as well as providing oral and anal excretions that these beetles apply to carcasses to preserve this resource for its larvae.

For several wild species, microbiota has also been shown to confer an immune phenotype. For example, the survival of Panamanian golden frogs *Atelopus zeteki* infected with the chytrid fungus *Batrachochytrium dendrobatidis* is predicted by the composition of skin microbiota in this amphibian (Becker et al. 2015). Interestingly from a conservation standpoint, Becker et al. (2017) went on to show that such composition is maintained among populations by habitat corridors, ensuring interactions between individuals from different populations, while other authors are identifying the exact strains of bacteria responsible for the anti-fungal activity (Madison et al. 2017; Woodhams et al. 2017). Similarly, Lemieux-Labonté et al. (2017) reported that the skin microbiota of little brown bats *Myotis lucifugus* that survive infection of the fungus causing white-nose syndrome *Pseudogymnoascus destructans*, was less diverse than that of bats that did not survive, but had a higher prevalence of taxa known for their anti-fungal activity. The eggs of the sea

turtle *Eretmochelys imbricate* have been shown to have a surface microbiota with taxa showing activity against the pathogen *Fusarium falciforme* (Sarmiento-Ramírez et al. 2014). Bumblebee *Bombus terrestris* gut microbiota also protects individuals from invasion of the intestinal parasite *Crithidia bombi* (although these were laboratory studies; Koch and Schmid-Hempel 2011) and similarly, the gut microbiota of Manila clams *Ruditapes philippinarum* includes detoxifying bacteria allowing them to cope with winter water pollution (Milan et al. 2018). Lastly, in a transplant experiment, Macke et al. (2017) showed how gut microbiota (in combination with genotype) protects the freshwater crustacean *Daphnia magna* from toxic cyanobacteria.

Conclusions and future directions in conservation

If microbiota confers adaptive potential, then loss of this potential could be an additional factor together with loss of genetic diversity and habitat loss leading to species extinction. Because the effects of microbiota loss, like loss of genetic biodiversity, may only become measurable at the host phenotypic or population level when loss is irreversible (e.g. gut dysbiosis leading to visibly ill individuals or negative population growth), it is important to consider the conservation implications of microbial diversity loss along with other factors threatening specific species.

This review indicates that there is now intriguing evidence in wild animal species of an association between host genotype and microbiota composition (i.e. microbiota appears heritable), combined with extensive intraspecific variation in these bacterial communities, as shown in humans. Such variation confers flexibility and adaptive ability (e.g. to diet), and could certainly be useful to individuals in periods of very rapid climate change and habitat destruction during the host's lifetime. The extent and functional significance of a flexible microbiota diversity and composition within individuals may be considered an adaptive phenotype in itself, as suggested by the pika and bear examples above, with implications for host evolution and species survival (Erkosar et al. 2017); however, more examples are needed to demonstrate a pattern of causality, and show that flexibility itself is variable and heritable. The constraints on flexibility due to physiology and phylogeny also need to be better understood (e.g. Koskella et al. 2017; Amato et al. 2018). From a conservation point of view, better knowledge of the 'intact' diversity of microbiota in wild species of interest would also be useful for identifying which biotic or abiotic factors cause loss of diversity or function (e.g. Waite et al. 2012; Barelli et al. 2015; Stumpf et al. 2016), and possibly to facilitate the restoration of the original microbial diversity if this is deemed beneficial for species recovery in what

Jiménez and Sommer (2017) term a ‘meta-organism conservation approach’ (Bahrndorff et al. 2016; see also attempts at enriching skin microbiota to combat pathogens, e.g. Küng et al. 2014, and review by Stumpf et al. 2016). The attraction of adding this potentially powerful tool to the conservation ‘omics repertoire has already inspired biologists to adopt creative and non-invasive methods of sample collection, such as using drones to collect whale blow for monitoring lung microbiota (Apprill et al. 2017).

Although an ‘unhealthy’ gut in humans has been associated with low bacterial diversity, there is little evidence from wild animals that diversity per se is associated with individual fitness, in both captive or endangered species. Instead, there are increasing indications that microbiota composition and function are more relevant, conferring, for example, immune phenotypes, the ability to detoxify food resources, behavioural traits, or resistance to pathogens, all of which are known to have direct effects on lifetime fitness. Although diversity level and microbiota composition will vary across species even with the same diet (see examples above), with data from more species, some patterns may become more evident, especially with regards function (e.g. generalist vs. specialist; common vs. rare). In fact, functional redundancy, or the ability of various bacterial compositions to provide the same function, needs to be explored, and may even provide the flexibility needed to overcome change, or evolutionary constraints, without loss of fitness (Sharpton 2018). Investigating microbiota function is still in its infancy even in human studies (Degli Esposti and Martínez Romero 2017; Moran-Ramos et al. 2017), but becoming more common even in wildlife with the advent of more powerful algorithms and adequate databases, and is essential to understanding the adaptive potential of the microbiota (Hernández-Gómez et al. 2017). Recent laboratory studies in mice using multi-‘omics data (metataxonomics, transcriptomics, proteomics) also show how it is possible to identify the exact mechanisms of microbiota function (Manes et al. 2017). Again, such comparative analyses are becoming possible thanks to the development of more sophisticated analytical tools (e.g. Callahan et al. 2017; Zhai et al. 2017). However, experimental work will also be essential to connect genotypes with phenotypes and their impacts on fitness, especially because so little is known about the function of the underlying metagenome or even how functions are defined, gained and lost.

At least one other aspect of microbiota ecology with respect to adaptive potential are also virtually unknown. Just as wildlife corridors are considered essential for maintaining or restoring exchange of individuals between isolated populations and, therefore gene flow, the routes of microbiota transmission between individuals and populations should be investigated and understood. However, at present, even in humans this process is virtually unexplored (Browne

et al. 2017), although it has been suggested that transmission mode may be critical to the role of microbiota in host evolution (Rodrigo et al. 2017), as well as to microbiota-host co-evolution (Sanders et al. 2014).

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