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Discussion

Incorporating microbiome analyses can enhance conservation of threatened species and ecosystem functions

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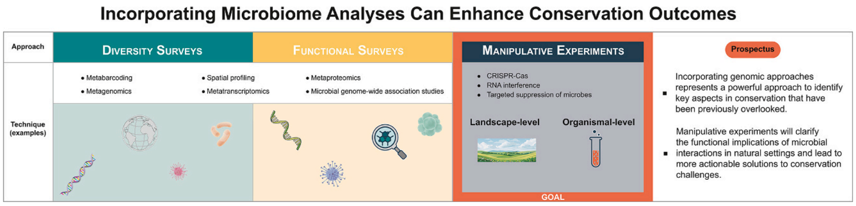
GRAPHICAL ABSTRACT



- Incorporating genomic approaches represents a powerful approach to identify key aspects in conservation that have been previously overlooked.
- Manipulative experiments will clarify the functional implications of microbial interactions in natural settings and lead to more actionable solutions to conservation challenges.

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ABSTRACT

Conservation genomics is a rapidly growing subdiscipline of conservation biology that uses genome-wide information to inform management of biodiversity at all levels. Such efforts typically focus on species or systems of conservation interest, but rarely consider associated microbes. At least three major approaches have been used to study how microorganisms broadly contribute to conservation areas: (1) *diversity surveys* map out microbial species distribution patterns in a variety of hosts, natural environments or regions; (2) *functional surveys* associate microbial communities with factors of interest, such as host health, symbiotic interactions, environmental characteristics, ecosystem processes, and biological invasions; and (3) *manipulative experiments* examine the response of changes to microbial communities or determine the functional roles of specific microbes within hosts or communities by adding, removing, or genetically modifying microbes. In practice, multiple approaches are often applied simultaneously. The results from all three conservation genomics approaches can be used to help

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design practical interventions and improve management actions, some of which we highlight below. However, experimental manipulations allow for more robust causal inferences and should be the ultimate goal of future work. Here we discuss how further integration of microbial research of a host's microbiome and of free living microbes into conservation biology will be an essential advancement for conservation of charismatic organisms and ecosystem functions in light of ongoing global environmental change.

1. Introduction

Conservation biology (bolded words are defined in Box 1) is a discipline that aims to preserve and protect diversity at all levels of biological organization, from genetic and functional diversity within and among populations of species, to diversity in the processes carried out by communities, ecosystems, and biomes (Allendorf et al., 2022; McNeely et al., 1990). From its inception, much of conservation biology has focused on genetic theory to address concerns that stem from the small population sizes of many threatened species (Frankel, 1974; Frankham, 1995; Allendorf et al., 2022). These include questions regarding minimum viable population sizes, inbreeding depression in isolated populations, selection pressures in captive environments like zoos and botanical gardens, and ecological and evolutionary sustainability within the context of each species of concern (Brown, 1994; Lacy, 1994).

As in other fields of biology, conservation genetics adopted and applied advances in molecular techniques, which transformed a largely theoretical field into an empirical one (Ouborg et al., 2010). Early molecular methods such as allozymes and single-gene sequencing revealed the structure of molecular variation within and among populations providing insights into past ecological and evolutionary processes (Sunnucks, 2000; Pearse and Crandall, 2004; Schlötterer, 2004; Recuero et al., 2014). The development of next-generation sequencing methods has further transformed conservation genetics into conservation genomics, providing higher resolution of variation across the genome than previous methods with the potential to identify functional variants in many species (Matz, 2018; Narum et al., 2013; Allendorf et al., 2022). These developments are particularly important for conservation action because they provide more details about how selection, inbreeding, or hybridization affect specific regions of the genome, which can translate into **function** (Allendorf, 2017). Such genomic approaches have been successfully applied in a variety of conservation scenarios for charismatic macrofauna and flora or those with high economic value, such as crocodiles (Chattopadhyay et al., 2019), Sicilian fir (Valle et al., 2024), seaweeds (Mamo et al., 2021), or salmon (Waples et al., 2020). However, the microbes associated with these organisms, and their habitat, are often overlooked despite lessons learned from the vast study of the implications for human health (Ma et al., 2023).

Tremendous effort and resources directed towards human health have revealed the important role of microbes in human biology that can be applied to understanding wild animals as well (Jin Song et al., 2019; Supple and Shapiro, 2018). Humans and their **microbiome** constitute a symbiotic relationship. Microbes help regulate metabolism and the nutritional state of their hosts, impacting human health and disease outcomes. Exploring this relationship provides insight into disease etiology and potential treatments (Hou et al., 2022). For example, association studies have shown how early development is a crucial time for shaping the microbiome signature of a healthy individual, which is only established after weaning through exposure to maternal and environmental microbiomes (Lozupone et al., 2012). Gut microbes occupy functional niches and integrate into more extensive metabolic exchanges, preventing opportunistic pathogens from colonizing (Eberl et al., 2021; Osbelt et al., 2021). In contrast, the microbiome can also play a vital role in a variety of metabolic, respiratory, digestive diseases, and cancer (Hou et al., 2022; Jain et al., 2021). As such, microbiome information can now be important to diagnosis of human disease and effective treatment (Hou et al., 2022).

Similarly in wild systems, potential exposure to pathogens, toxins, or chemically-defended plants could pose health or even survival challenges to protected or reintroduced captive-reared animals. In these cases, surveys of the gut microbes or microbial communities are relevant to address those challenges. Because all organisms harbor microbiomes, they can be considered '**holobionts**', necessitating an understanding of how microbes influence holobiont performance and evolution (Nyholm et al., 2020; Gordon et al., 2013; Bordenstein and Theis, 2015; González-Pech et al., 2023). The early conservation success of the Andean condor (*Vultur gryphus*; Wallace and Temple, 1987), which paved the way for the recovery program for California condors (*Gymnogyps californianus*), highlights the potential importance of the holobiont. A critical undetermined limitation for their initial reintroduction was that animals raised in essentially pristine captive environments would be exposed to

Box 1
Definitions

Conservation biology: a discipline that aims to preserve and protect diversity at all levels of biological organization, from genetic and functional diversity within and among populations of species, to diversity in the processes carried out by individuals, populations, communities, and ecosystems

Function: role that living or nonliving entities provide for individuals, the community, or ecosystem in which they exist

Microbiome: a community of microorganisms and their immediate micro-scale environment

Holobiont: a symbiotic unit consisting of an organism and its associated microbes (e.g. bacteria, archaea, fungi, algae, protists, and viruses)

Landscape: mosaic of patches (where a patch is a relatively homogeneous area that is distinct from its surrounding) whose size, shape, and spatial configuration regulate how they interact by exchanging organisms, information, matter, and energy

Gnotobiotic: reduction in microbial organisms living within or on a host many pathogens and toxins in the wild upon reintroduction (personal communication with S.A. Temple). Subsequent research found that vultures and condors possess adaptations, including microbiomes, that allow them to consume a diet that would be lethal to many other species (e.g., Apanius et al., 1983; Zepeda Mendoza et al., 2018; Ohishi et al., 1979; de la Lastra and de la Fuente, 2007). As with the release of captive-reared scavenger bird species, researchers should ensure that the gut microbiomes of other captive-reared animals would not compromise survival if released into the wild.

There is growing recognition that interactions with microbes are functionally important in several other vertebrates (Redford et al., 2012; Alberdi et al., 2022; Leonard, Earth Hologenome Initiative Consortium, and Alberdi, 2024), but also in invertebrates (Bahrndorff et al., 2016; Douglas, 2019), and plants (Bulgarelli et al., 2013; Hawkes et al., 2021). A variety of studies have demonstrated that microbes influence organismal responses to the biotic and abiotic environment (Hawkes et al., 2021; Shaffer et al., 2018), the health of the combined holobiont (Pitlik and Koren, 2017), and ecosystem functioning (Wagg et al., 2019; Sokol et al., 2022). Therefore, an important goal of conservation biology should be to protect interactions (e.g., symbioses) and processes (e.g., biogeochemical cycles) that involve the microbiome (Cavicchioli et al., 2019; Limborg et al., 2024). Habitat degradation or other **landscape** level changes can also alter the microbiome associated with any particular habitat, animal, or plant. Hence, functional surveys of microbial communities can inform practitioners that manipulating microbial community composition may improve host health or preserve ecosystem function (Mueller and Sachs, 2015; West et al., 2019). In pursuit of this goal, conservation genomics represents a multi-disciplinary and multi-scale challenge.

Conservation genomics aims to understand how variation in the genome and genome function can contribute to the success or failure of conservation efforts. This objective requires interpreting how genomic information translates into ecologically important traits. Investigations of the microbiome have been designed to address similar questions by association of microbes with environmental conditions or specific functions (including *diversity surveys* and *functional surveys;* Fig. 1). Fewer studies have manipulated communities to yield robust causal inferences (referred to herein as *manipulative experiments;* Fig. 1). *Diversity surveys* typically involve basic genetic fingerprinting to identify which organisms can be found in a location and to quantify their levels of molecular diversity (e.g., Rusch et al., 2007; de Vargas et al., 2015; Flemming and Wuertz, 2019). These surveys are used to correlate microbial communities or microbiome composition and diversity with aspects of their environment, such as habitat or host type and physical/chemical conditions. By mapping organisms, establishing baseline distributions, and generating hypotheses, these diversity surveys set the stage for subsequent functional investigation.

Functional surveys involve associating genetic or organismal diversity with host health, specific community level roles or ecosystem level processes (e.g., Jin et al., 2016; Fuller et al., 2020; Bragg et al., 2015). However, connecting genomic variation to traits or functions is not always straightforward. Many traits relevant to fitness (and, therefore, to conservation) are complex and polygenic (Wellenreuther and Hansson, 2016). Genome-wide association studies correlate variation in individual genetic loci with particular traits in a specific environmental context, but such associations cannot be considered causal without further experimental evidence (Ellegren and Galtier, 2016). Additionally, sequence variation alone does not always determine differences in ecological function or the potential of a given organism to acclimate to change (Funk et al., 2019). Instead, complex interactions of genomes with other cellular processes, the abiotic environment, and the biotic community can also shape genotype-phenotype dynamics (Moran and Sloan, 2015; Nyholm et al., 2020).

Manipulative experiments can provide direct mechanistic support for the functional roles of specific taxa or groups. Typically, whole microbial communities or individual community members are added, removed, or genetically manipulated. Then, responses of individuals, communities, or ecosystems are observed (e.g., Przybyla and Gilbert, 2022; Cano-Gamez and Trynka, 2020; Garnica et al., 2022; Garces et al., 2025). Such experiments may integrate multi-omic and functional genomic techniques (Table 1). Although functional genomic approaches have been widely used in model organisms, such as *Drosophila* (Viswanatha et al., 2018), *Arabidopsis (*Bai et al., 2015*)* or yeast (Giaever and Nislow, 2014), they have rarely been applied to non-model organisms. To achieve conservation goals, it will be important to develop such approaches to understand the impacts of non-model taxa on ecosystem function. An important follow-up to these approaches will be to develop and implement management interventions based on research findings.

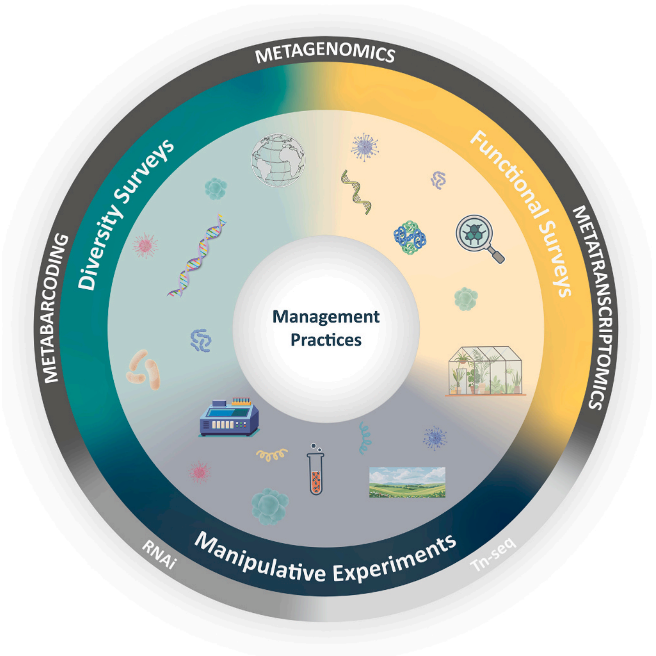

Fig. 1. Visual representation of the three key approaches to microbial research that can be used to enhance conservation management practices. *Diversity surveys* and *functional surveys* yield correlational inferences, while *manipulative experiments* can yield causal inferences. Most approaches overlap in the application of genomics techniques (e.g. metabarcoding, metagenomics, metatranscriptomics, RNAi, Tn-seq shown in outer ring). Combined, these approaches can be performed separately and in different orders, yet they complement each other for a more comprehensive understanding of the study system.

Here, we discuss several microbial studies that have included one or more of the conservation genomic approaches described above, and summarize promising techniques for all three approaches (Table 1). In particular, we highlight the need for more experiments that allow for causal inference, and advocate for greater inclusion of the microbiome in conservation research and practice.

2. Part A: Association studies (diversity and functional surveys)

Diversity and functional surveys of microbes can establish conservation targets by finding correlations between microbial communities (defined by taxa or by function) and host health or distinct ecosystem processes. Although the results may only be correlational, diversity and functional surveys can lead to more informed conservation policies and positive outcomes for imperiled species or ecosystems.

2.1. Diversity surveys: Understanding patterns of natural microbial diversity

Many conservation genomic investigations of high-priority organisms begin with molecular diversity surveys, often across the species'

Table 1
Promising modern approaches in microbiological research with application to conservation genomics.

Approach	Promising technique	Relevance	Example
Metabarcoding	Full-length amplicon sequencing	Targeted sequencing of genetic markers of taxonomy in full length using long-read technologies to resolve taxonomic diversity at species and strain levels (Johnson et al., 2019).	A comprehensive diversity survey of microbial eukaryotes in soil samples and mock communities (Tedersoo et al., 2021).
	hamPCR	Modified PCR protocol to survey diversity and quantify absolute abundances of microbial communities (Lundberg et al., 2021).	Detection of protective microbes against pathogens from the host, as in plants (Shalev et al., 2022).
Spatial profiling	SEER-FISH	Imaging based on sequential fluorescence in situ hybridization that allows the creation of spatial maps of complex microbial communities (Cao et al., 2023).	Quantification and biogeographic mapping of bacterial taxa from plant rhizospheres on roots (Cao et al., 2023).
Meta-omics	BONCAT-FACS-seq	Amino acid tagging to identify newly synthesized proteins, followed by fluorescent cell sorting of active cells and metagenomic shotgun sequencing to identify metabolically active and inactive members of a microbial community and/or proteins being synthesized under specific conditions (Trexler et al., 2023).	Detection of the active microbial fraction of biocrusts after wet-up events (Trexler et al., 2023).
	Metatranscriptomics	The characterization of actively transcribed RNA to survey cellular processes in the concerted response of all members of the microbiome to conditions of interest (Shakya et al., 2019).	A metatranscriptomic assessment of the active microbiome in acid mine drainage, revealed key functions in drainage generation and in adaptation to extreme environments, which, in combination with metagenomic data, were traced back to rare taxa (Hua et al., 2015).
	Metaproteomics	The characterization of actively translated proteins by a microbial community to survey cellular processes implicated in the concerted response of all members to conditions of interest; can also be used to quantify species biomass and identify carbon sources and substrate uptake (Kleiner, 2019).	Identification of key proteins that may serve as indicators of soil quality based on their biochemical properties and role in degradation of pollutants (Bastida et al., 2009).
	Microbial Genome-Wide Association Studies (mGWAS)	Analysis to assess how variation in microbial genomes may affect host phenotypic traits (San et al., 2019).	Discovery of root microbes associated with agronomic phenotypes contingent on host genotypes (Wang et al., 2022).
	Paleometagenomics	Combination of ancient DNA (aDNA) and metagenomic techniques to reconstruct biogeochemical processes and predict ecosystem responses to environmental perturbations (Capo et al., 2022).	Identification of a proliferation of phototrophic and mixotrophic microbial eukaryotes in lakes associated with environmental changes in the Anthropocene (Keck et al., 2020).
Experimental manipulation	CRISPR-Cas genome editing	Molecular engineering tool that can be used to modify gene expression or organisms of interest (Selle and Barrangou, 2015).	The engineering of microbes for sustainable agricultural practices (Shelake et al., 2019).
	Gnotobiotics	The establishment of hosts free of microbes or with a simplified known microbial community for experimental manipulation (Williams, 2014).	Establishment of plant systems for functional assessment of microbial assemblages in the root (Ma et al., 2022).
	RNA interference (RNAi)	The use of RNA molecules to suppress gene expression to explore host-microbe or microbe-microbe gene expression interactions (Qiao et al., 2023).	Gene expression silencing of crop pathogens induced by other microbes (Wen et al., 2023).
	Targeted suppression of microbes	The use of phage consortia to selectively suppress microbes in a community (Federici et al., 2022).	Treatment for inflammatory bowel disease by eliminating associated bacteria (Federici et al., 2022).
	Tn-Seq	Transposon-insertion sequencing and mutant screening to identify and quantify genetic interactions between microbes or between microbes and host (van Opijnen, van Opijnen et al., 2009).	Determining that interactions between genes in the chromosome and accessory replicons are important for fitness of a bacterial species (diCenzo et al., 2018).

range or in specific regions of interest (Wan et al., 2024; Nigenda-Morales et al., 2023; Miller et al., 2011). Measuring the distribution of diversity makes it possible to estimate effective population sizes, determine diversity sources and sinks, detect population bottlenecks, and resolve population structures for management (Frankham et al., 2002). Genomic investigations of microbial communities in nature also begin with diversity surveys, though the goals are somewhat distinct from those for larger organisms. Given the complexity of the microbial communities, microbial surveys are often completed using molecular methods such as metabarcoding or metagenomics (Table 1; Dong et al., 2023; Rosenberg et al., 2021; Williams et al., 2022).

Microbes are sensitive to local and micro-environmental conditions, whether they are free-living communities or those associated in symbiosis with larger organisms. Surveys help establish how microbial diversity varies across host diversity, different habitats, and ecosystems (Lozupone and Knight, 2007; Sarmiento et al., 2017). Diversity surveys identifying microbial members of holobionts under healthy and diseased conditions are already guiding conservation efforts. Rhinoceros are among the largest and most threatened herbivores on the planet, and establishing their baseline microbiomes in nature has been essential for their management in captivity and potential re-introduction (Burnham et al., 2023). Such efforts are based on the principle of a baseline microbiome that resembles the concept of *the healthy human microbiome* (Lloyd-Price et al., 2016).

In many organisms, microbiome differences appear to be structured by compartmentalization within the host. For example, avian gut microbial assemblages change along the digestive system, which increases microbiome spatial heterogeneity both in composition and function (Grond et al., 2020). Unlike the gut microbiome, the plumage microbiome exhibits species-specific stability in taxonomic composition (e.g., Javůrková et al., 2019), but some variation can occur depending on the ecology of the host species. Bird hosts with more similar ecological niches will share a more similar plumage microbiome even if they are not phylogenetically closely related (Musitelli et al., 2018). Such compartmentalization has also been reported for corals, where different microbial communities have been found in mucus, tissue, and skeleton. These distinct microbial compartments behave differently in response to environmental stress and exhibit different evolutionary histories from the host, with microbes in the mucus showing a stronger phylosymbiotic signal (Pollock et al., 2018).

This fine scale divergence also translates to a larger scale in coral communities. A survey of Florida's coral reef microbes found divergence of bacterial communities associated with levels of coral cover, coral species diversity, and coral disease (Becker et al., 2023). This work established that reef microbial communities reflect broader ecosystem processes (e.g. those that maintain coral health) and respond to biotic and abiotic factors that vary across biogeographic regions. In a conservation genomics framework, such information sets the stage for early detection of stress events and their sources (and thus early deployment of interventions). In addition, this can lead to identification of critical reef habitats to single out for protection, and monitoring of ecological impacts of restoration activities such as coral propagation and outplanting (Young et al., 2012). Diversity surveys can also help identify sources of stress-tolerant symbionts to use as probiotics in coral holobiont manipulations designed to improve resilience (discussed further below).

Beyond such symbionts, community divergence by habitat occurs in free living microbes at the scale of whole ecosystems. For instance, the *Tara Oceans* project collected metagenomic data to characterize the global biodiversity of microbial communities in the Earth's oceans. Among several of the measured abiotic factors, water temperature was the best predictor of microbial community composition and distribution (Sunagawa et al., 2015). Comparable surveys have been carried out in other environments, such as the Earth Microbiome Project (Thompson et al., 2017). These diversity surveys can also track simultaneous change over time in microbial communities and the environmental properties hypothesized to influence them. In a tropical rainforest, for instance, the composition of the soil microbial community and the abundance of its members varied seasonally with variation in precipitation, soil moisture and redox, and litterfall driven by canopy phenology (Buscardo et al., 2018). Likewise, the microbial community of a temperate freshwater lake exhibited phenology driven by seasonal variation in lake physical properties, the metazoan food web, and shifts in metazoan invasions (Rohwer et al., 2023).

Microbiome diversity assessments can be used as a tool to gauge the impacts of crucial changes in the environment (Angly et al., 2016; Glasl et al., 2019; Ribas et al., 2023; Ziegler et al., 2019). Climate change and rising sea levels are provoking poleward and landward expansion of mangrove forests, resulting in the loss of salt marshes (Krauss et al., 2011; Saintilan et al., 2014). The replacement of herbaceous-plant ecosystems with forests will likely entail large shifts in microbial taxa (Collins et al., 2020) given that these ecosystems possess distinct microbial communities (Barreto et al., 2018). Relative to their salt marsh counterparts, mangrove soil microbes appear to be dominated by more aerobic groups that exhibit faster soil carbon turnover (Lewis et al., 2014; Barreto et al., 2018; Lewis et al., 2021). By tracking the shift from salt marsh-associated microbes to those associated with mangrove forests, conservation practitioners can quickly recognize habitat loss and intervene to conserve ecosystem function (e.g., carbon sequestration, nursery habitat provisioning; Collins et al., 2020).

As human activities continue to alter natural ecosystems, the dramatic effects of intensive land use must be considered when conserving soil function. Under urban land use, for instance, soil microbial communities may grow more diverse locally, but globally they become more homogenous (e.g., similar urban soil communities across cities in different climate zones) and are influenced by human factors such as land management and affluence (Delgado-Baquerizo et al., 2021). Spatial variation and temporal change in land use and water chemistry may also result in shifts in stream microbial diversity and composition (Zeglin, 2015). A study in the subtropics revealed different microbial community compositions and patterns of taxa co-occurrence in streams that have been urbanized compared to forested streams (Hosen et al., 2017). Agricultural decisions about tillage and fertilizer sources have likewise been associated with differences in diversity and composition of soil microbial communities (Lupatini et al., 2016; Kraut-Cohen et al., 2020).

Although characterizing patterns of microbial diversity in isolation may not provide a holistic understanding of the microbiome's functional role for the host or ecosystem, it can be an important first step in formulating relevant hypotheses for follow-up studies and serve as a method of environmental monitoring for conservation and restoration programs.

2.2. *Functional surveys: Associating microbial diversity with ecological processes*

In practice, microbial diversity surveys are rarely performed in isolation. Instead, they are often integrated into experimental designs that further address questions about the function of these communities and their emergent properties in ecosystems (Fuhrman, 2009). Functional surveys have led to the discovery of microbes that naturally protect amphibians from chytridiomycosis, a disease that is threatening them globally. Bioaugmentation of these beneficial microbes might be an effective mechanism to fight chytridiomycosis in susceptible amphibian communities (Bletz et al., 2013). Additionally, microbes serve important functions in various other mutualisms: fungal symbionts may alter plant responses to environmental stresses (van der Heide et al., 2012; Kivlin et al., 2013; Garnica et al., 2022), bacterial symbionts may broaden insect nutrient supplies (Reis et al., 2020; Bourtzis and Miller, 2008), and microalgal symbionts may contribute to coral thermotolerance and disease resistance (Sampayo et al., 2008; Rouzé et al., 2016). Alternatively, invasive species may introduce new microbes (Hawkes et al., 2005; O'Hanlon et al., 2018; Wang et al., 2023) or reshape the microbial community (Eberly et al., 2024; Li et al., 2022). While some changes may be benign, others may displace native microbes by releasing allelopathic chemicals (Torres et al., 2021) or reshape nutrient availability and water cycling (Hawkes et al., 2005). Thus, invasive species management plans can benefit from incorporating functional surveys of microbes.

On the ecosystem scale, many of the functional capabilities of microorganisms–including carbon fixation, nitrogen fixation, and denitrification–are broadly dispersed among taxa. For instance, the *Tara Oceans* initiative explored the global distribution of nitrogen-cycling organisms using metagenomics, finding similar functional diversity among communities from different oceans despite extreme taxonomic variation (Song et al., 2022). Ultimately, conservation practitioners are concerned with preserving ecosystem functions and services, so it may be more pertinent to address "which jobs are being performed" by a community rather than "who is doing which job."

A common approach for determining microbial function is to examine which genes are present and which of those genes are expressed in a given microbial community via metagenomics and metatranscriptomics, respectively (Table 1; Yu et al., 2021; Nakai et al., 2011). Such techniques resolve metabolic potential, often in addition to taxonomic composition or diversity. For instance, shotgun metagenomic sequencing of Florida Everglades soil was used to identify dominant bacterial taxa and the abundance of marker genes for ecosystem functions performed by bacteria, including methane production, nitrogen fixation, and sulfur reduction (Abraham et al., 2020). A global assessment of urban soil microbial communities isolated functional genes via shotgun metagenomics, finding that urban environments featured an elevated abundance of genes associated with the cycling of nitrogen and phosphorus–nutrients that regulate ecosystem productivity–as well as genes associated with human pathogens (Delgado-Baquerizo et al., 2021). Clearly, city development patterns and policies can influence ecosystem processes and human health via microbial changes, demonstrating the importance of examining microbial functional diversity for conservation practices.

3. Part B: Manipulative experiments (from organismal to landscape level experiments)

Experimentation is the gold standard of causal inference and an integral part of the scientific method: this approach can be applied at all levels from organisms to landscapes. Microbiome research over the previous decades has mostly been limited to methods that can characterize microbial communities rather than methods that manipulate them. Even when (non-manipulative) experimentation has been used to study microbial ecology in a conservation context, the links between changes in the microbiome and changes in host health, organismal ecology or ecosystem processes are often correlational. The extensive diversity surveys of the past decades have produced numerous hypotheses that remain to be tested with manipulative experiments.

3.1. Organismal experiments: Validating microbial function through microbe manipulation

Conceptually, (micro)organismal experiments can be analogous to knock-in/knock-out genetic experiments where the impact of adding/removing a single gene can be monitored in a semi-controlled system. Microbial communities can be altered through targeted addition or subtraction of specific members (Agler et al., 2016). Such methods have revealed the importance of host-microbiome, host-gene-microbiome, and host-metabolome-microbiome interactions (Bodenhausen et al., 2014; Harbort et al., 2020b; Pfeilmeier et al., 2021; Pacheco and Vorholt, 2023; Schäfer et al., 2023). However, these approaches require prior knowledge about the taxonomic diversity and presumed functional roles of the microbial community.

Direct microbial manipulations may be limited by several factors. Many microbes of interest cannot be easily cultured, altered communities may be difficult to establish in experimental systems, and community compositions may shift rapidly. Additionally, phenotypic responses may be noisy and thus difficult to attribute to particular microbes, especially if a given microbial species performs distinct functions in different scenarios. Finally, organismal experiments are usually performed in controlled laboratory conditions, and the results may not be representative of natural dynamics. Despite these challenges, manipulative experiments are the path forward for testing the many hypotheses that have emerged from correlational diversity/functional surveys.

One common manipulation method is to indiscriminately remove some or all microorganisms in the holobiont (e.g., via filters, antibiotics, fungicides, or other sterilization methods; Parepa et al., 2013; Costa et al., 2021; Matthews et al., 2016), and then establish a specific community via inoculation (Vorholt et al., 2017; Sarmiento et al., 2017; Garces et al., 2025). In one of the most well-studied systems, whole microbial communities have been isolated from the model plant *Arabidopsis thaliana* (Bai et al., 2015). This allowed for the creation of a synthetic community (SynCom) in which specific microbes could be added back into the microbiome at different concentrations or started at equal parts. The newly constructed microbiome along with the host could then be monitored for changes over time in response to different environmental factors or stress (Castrillo et al., 2017; Toju et al., 2020; Souza et al., 2019). The SynCom approach has been used in agriculture to identify key members of the microbiome that enhance plant growth under greenhouse and field conditions (Shayanthan et al., 2022). Building a similar SynCom that achieves the minimum set of functional microbial groups that support a host or habitat could have similar conservation applications.

Gnotobiotic individuals have been established in several host organisms, such as mosquitos (Steven et al., 2021), mice (Arrieta et al., 2016), plants (Sauer, 1986; Lundberg et al., 2012; Clough and Bent, n.d.; Harbort et al., 2020a), and sea anemones (Costa et al., 2021; Dungan et al., 2022; Hartman et al., 2022). One benefit of sterilization procedures is that they reduce interactions between the original community and the experimental community, thereby increasing confidence in the mechanistic link between the target microbes and the change in host phenotype or ecosystem functioning. One set of studies used this approach to show that the presence of the full community of native soil microbes favored invasive knotweed growth over that of six native plant species (Parepa et al., 2013). Eventually, researchers were able to isolate a specific fungal endophyte (*Serendipita hermamans*) that improved knotweed performance under some conditions (Garnica et al., 2022).

This basic research has important application potential; once the function of a specific microbe or community of microbes is identified, conservationists can leverage microbes of interest to improve management of holobionts. Farmers have benefited from this approach through the discovery of probiotic bacterial strains that can be added to soil instead of fertilizer to increase crop yields (Jorjani et al., 2011). A similar probiotic bacterial cocktail has been developed to improve coral thermal tolerance at small scales (Rosado et al., 2019), and individual coral colonies can be supplied with natural or experimentally-evolved microalgal symbionts to reduce bleaching susceptibility in a laboratory setting (Nitschke et al., 2024). However, maintaining large cultures of beneficial microbes and inoculating corals across kilometers of reef remains a logistical challenge for broad implementation.

Alternatively, indiscriminate manipulations of soil microbial diversity have been used to study responses in ecosystem function. For example, serial dilution of soil suspensions can produce cultures that vary in soil microbial diversity but with similar soil microbial biomass. This design has revealed positive responses of organic carbon degradation and CO_2 production to microbial diversity (Maron et al., 2018). Soil diversity treatments have also been established by passing soil through sieves of varying mesh sizes, with the resulting inocula added to sterilized planting media. These treatments have demonstrated that greater microbial diversity fosters activity of different taxa at different times, in turn promoting temporal stability in ecosystem functions such as plant biomass production and soil carbon assimilation (Wagg et al., 2021). Taxonomic assignments from sequence information were then used to describe community composition and infer the importance of various taxonomic groups in ecosystem processes. Indiscriminate manipulations such as these preserve the natural dynamics of an ecosystem's microbiome while simulating a variety of ecologically-relevant scenarios (e.g., increased rainfall).

3.2. Landscape level experiments: Validating the role of microbes through environmental manipulation

Broad-scale manipulations of environmental conditions can augment functional surveys by tracking changes in microbial diversity or associated functions after manipulation. Whole-ecosystem manipulations such as these, similar to indiscriminate manipulations, grant the opportunity to simulate future environmental conditions (e.g., different climate scenarios) and gain insight into their outcomes, including how microbiomes and ecosystem processes may recover. In a watershed-scale experiment, aerial application of pelletized calcium carbonate over both short and long time scales increased soil pH and drove changes to the soil microbial communities (Sridhar et al., 2022). The modified bacterial and fungal communities were associated with altered ecosystem respiration, primarily by suppression of biomass of key fungal decomposers. In another example, a freshwater lake was artificially mixed during peak summer stratification, exposing organisms to vastly different environmental conditions, including temperature and dissolved oxygen availability (Shade et al., 2012). The microbial community returned to a pre-mixing composition within one to two weeks even as environmental properties remained altered, demonstrating resilience to an ecosystem-wide disturbance. Further work is required to isolate the specific ecological roles of individual microbial taxa. However, such information may not be necessary to implement conservation goals in many cases (e.g. raising soil pH may facilitate more diverse microbial communities that improve overall carbon cycling for an endangered plant). In other situations, it can be critical (e.g. choosing which strains of rhizobia to include in a prebiotic mix to facilitate drought resistance in an endangered plant).

Some ecosystem-scale environmental manipulations aim to reveal consequences of anthropogenic global changes for microbial communities, microbiomes, and the functions they perform, such as increased acidification of forest soils from acid deposition caused by industrial pollution (Sridhar et al., 2022), and experimental whole-ecosystem acidification and eutrophication of lakes (Mejbel et al., 2023). As humans continue to directly and indirectly alter the environment, many organisms with known conservation value will be displaced (Gao and Reitz, 2017), non-native organisms will continue to be introduced (Dukes and Mooney, 1999), and critical ecosystem functions may diminish (Malhi et al., 2020). Microbial communities contribute to each of these factors. Understanding the functional role of these communities may contribute to supporting the health of critical species, limiting the spread of invasives, and preserving vital ecosystem processes.

4. Prospectus

The field of conservation genomics is still early in development, particularly with respect to incorporating microbial communities in management decisions. Ignoring the microbial communities associated with organisms and habitats of high conservation priority represents a missed opportunity to improve management. Just as biologists have grown to embrace the importance of the microbiome to human and wildlife health (McFall-Ngai et al., 2013), so too have conservationists recognized the need to incorporate microbiome research into conservation planning (Redford et al., 2012). The microbiome of wild individuals can often be distinct from those of captive individuals (Cheng et al., 2015; Kong et al., 2014). If hosting an inappropriate microbial community leads to adverse health outcomes in the wild, then zoos, nurseries, fisheries, and hatcheries may need to work to prevent mismatch when reintroducing animals to their natural habitats (Bahrndorff et al., 2016). Additionally, given the sensitivity of the microbiome to environmental conditions, alterations to the microbiome that lead to negative consequences for holobionts may become more prevalent under global change (Boilard et al., 2020). Consequently, conservation efforts will be improved if the causal links between microbial diversity and host fitness can be established and incorporated into management strategies (Trevelline et al., 2019; West et al., 2019). Bornbusch et al. (2024) argue, moreover, for an integration of microbiome science with environmental medicine to promote animal health and conservation.

Thus far, studies that examine microbial interactions are often correlational, highlighting how communities differ across tissues, environments, or disease contexts. These studies are valuable in generating hypotheses as to which microbes, communities, or functions may be informative for conservation purposes. Moreover, identifying the minimum set of functional microbial groups that support processes of compromised hosts or ecosystems should be a critical first step in guiding their conservation. Only through experimental manipulations, however, can causal links between particular microbes and ecophysiological functions be revealed. It is time for microbial genomics to move from a predominantly hypothesis-generating field (*diversity* and *functional surveys*) to a hypothesis-testing field (*manipulative experiments*), in which microbial communities or ecosystems are directly altered to verify microbial functions. Consequently, this direct evidence will clarify the functional implications of microbial interactions in natural settings and lead to more actionable solutions to conservation challenges.

CRediT authorship contribution statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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