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Opinion

Into the microbial niche

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The environmental niche concept describes the distribution of a taxon in the environment and can be used to understand community dynamics, biological invasions, and the impact of environmental changes. The uses and applications are still restricted in microbial ecology, largely due to the complexity of microbial systems and associated methodological limitations. The development of shotgun metagenomics and metatranscriptomics opens new ways to investigate the microbial niche by focusing on the metabolic niche within the environmental space. Here, we propose the metabolic niche framework, which, by defining the fundamental and realised metabolic niche of microorganisms, has the potential to not only provide novel insights into habitat preferences and the metabolism associated, but also to inform on metabolic plasticity, niche shifts, and microbial invasions.

Highlights

Microorganisms present biogeographical distribution patterns and defined environmental niches.

Community complexity and methodological limitations have hindered investigations of the environmental niches of microorganisms and the associated ecological applications.

As a step forward, multi-omics can now help define the metabolic niches of microorganisms.

The proposed metabolic niche framework opens new ways to investigate metabolic plasticity, assess niche shifts, differentiate specialist from generalist phylotypes, evaluate the impacts of microbial invasions, and contribute to culturing efforts.

The microbial niche so far…

The **realised environmental niche** (see Glossary) describes the distribution and performance of a taxon in an **environmental space** and can be used to predict species distribution in a geographic space (Box 1). It has been used in ecological studies of macroorganisms to understand biotic interactions [1], community dynamics [2], geographic range limits [3], biological invasions [3–5], and species response to climate change [6,7], and to develop conservation plans [3,8]. The niche is an essential concept in ecology, biogeography, and conservation, and it matters for any type of organisms, including for microorganisms. Yet, fewer studies have investigated the niche of microorganisms, and the associated applications are still restricted in microbial ecology.

Evidence of microbial niche differentiation

While **niche differentiation** across different biomes, ecosystems, and hosts, and among microorganisms with different functions might appear evident [12,13], only the development of **high-throughput amplicon sequencing** has provided overwhelming evidence that microorganisms do display specific habitat preferences [14–17]. There have been reports of differentiated taxonomic distribution across all domains of microbial life and in all ecosystems, suggesting that different microorganisms have distinct realised environmental niches [18–23]. An interesting example is the niche differentiation of ammonia-oxidising archaea (AOA) and ammonia-oxidising bacteria (AOB). These prokaryotes belong to different domains of life, yet both contribute to the oxidation of ammonia [24]. While AOA are primarily found in marine and terrestrial ecosystems, they have been identified in many other habitats, including hot springs and animal guts [24]. By contrast, AOB live primarily in freshwater environments and wastewater treatment systems [24]. However, they not only present an environmental niche differentiation at the domain level (between AOA and AOB), but also have different niches at the **phylotype** level, with some AOA living exclusively in alkaline soils and others living in acidic soils [25]. They also differentiate along other gradients, such as salinity [26], temperature [27], depth, and altitude (as influenced by the associated environmental parameters) [28–30], providing overwhelming evidence of environmental niche differentiation between

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closely phylogenetically related microorganisms. These findings suggest the speciation and adaptations of phylotypes to local environmental conditions over evolutionary timescales, implying not only some conservatism, but also divergence of environmental niches across phylogenetic trees, depending on the clades [16,31,32]. Beyond the evidence of environmental niche differentiation, likely resulting from **sympatric speciation**, these findings also highlight the multidimensional complexity of the microbial niche with the different types of factor influencing its size and shape. The main challenge is to move beyond the observations of differences based solely on taxonomy (e.g., using amplicon sequencing) or functional genes, and leverage niche theory as a framework to actively quantify the realised niche of microorganisms and assess metabolism-based relationships to the environment.

From the environmental niche to the metabolic niche

Few studies have attempted to quantify the environmental niche of microorganisms by calculating the **niche position** (average position along environmental gradients) and the **niche breadth** (amplitude of tolerance along environmental gradients) or **niche hypervolume** (integration of niche breadth along all niche axes) [33,34]. These studies have shown differences in mean niche breadth and position along environmental gradients, at the phylotype level, highlighting the importance of abiotic factors in defining the environmental niches of microorganisms. For soil microorganisms, niche differentiations were clear along gradients of soil pH, water content, phosphorus content, temperature, and snow cover duration [33,34]. Yet, many microbial studies have investigated the environmental niche along a single dimension (e.g., only pH), although calculating the niche as a multidimensional hypervolume, as defined by Hutchinson, is important (e.g., using principal component axes). Doing so opens new ways to characterise the niche hypervolume, but still poses challenges [34,35]. The environmental niche includes all the environmental conditions, be they regulators or resources, constrained or not by biotic interactions and dispersal, and, therefore, requires numerous measurable variables, some of which may be unavailable. Furthermore, because the shape of the niche may be asymmetrical, rugged, or contain holes [36], the calculation of the niche position and breadth across multiple dimensions could

Box 1. What niche?

Given its long-standing history, the term 'niche' has been used in many different contexts, making it necessary to clarify what concept of the niche one considers in a given context [9]. Two key definitions of the niche were given by Hutchinson, who provided a framework for niche quantification in the context of species interactions through distinguishing the **fundamental environmental niche** [the set of environmental conditions in which a species can theoretically (i.e., physiologically) live and reproduce in (e.g., as defined experimentally)] and the realised environmental niche [the restricted set of conditions a species actually occupies *in situ* when accounting for biological interactions (e.g., competition, predation), thus a subset of the fundamental niche] [9]. Hutchinson defined both environmental niches as 'n-dimensional hypervolumes', where the dimensions are the set of abiotic conditions that define the requirements of an individual or a species for its population to persist, constrained or not by biotic factors.

The realised environmental niche concept was further conceptualised to include the three main classes of factor influencing the geographical distribution of species and determining where a species is found [9]. The first and primary set of factors are the abiotic conditions [(A) in Figure I] (such as climate, and other physicochemical properties of the environment), which impose the physiological limits on the ability of the species to persist in an area. The second set of factors are the biotic factors [(B) in Figure I], or the set of interactions with other species, which further refines the ability of the species to maintain populations, thereby also affecting the geographical distribution. These interactions can be either positive (such as mutualism) or negative (such as competition or predation). The third set of factors include the accessibility by the species to the sites to be colonised by the species [(M) in Figure I]. This accessibility dimension is extremely useful in distinguishing the actual range of a species from the one that is suitable based on abiotic and biotic conditions only. It relies on land configuration (e.g., oceans or mountains as barriers) and on the dispersal abilities of the species. Soberón and Peterson [10] summarised these three interacting sets of factors in the Biotic–Abiotic–Migration (BAM) framework (Figure I). As a result, the overlap of these three sets of factors represents the envelope of conditions that are actually occupied by the species, and correspond to an expanded definition of the realised environmental niche, which is most often used in ecology and evolutionary biology [9,11].

Glossary

Accessory gene: gene shared by some microorganisms but absent in others.
Bioaugmentation: addition of microorganisms to accelerate the degradation of a contaminant.
Core gene: gene shared by all (analysed) microorganisms, generally essential for survival.
Environmental space: multidimensional space of environmental variables.
Fundamental environmental niche: set of environmental conditions in which a species can live and reproduce.
Fundamental metabolic niche: this term is introduced for the first time. It refers to the range of genes necessary for an organism to function and reproduce, defining where an organism can theoretically survive.
Genome: complete set of DNA in an organism.
High-throughput amplicon sequencing: amplification of a specific gene loci using PCR and subsequent deep sequencing.
Horizontal gene transfer: transmission of DNA between organisms from an organism that is not a parent and is typically a member of a different species.
Invader: inclusively defined as an organism that is not currently part of the resident community.
Metabolic plasticity: ability of organisms to adapt their metabolic status to specific needs.
Metagenome-assembled genome (MAG): genome that was constructed from a metagenomic data set and corresponding to one phylotype (not always the case: MAG quality can be highly variable). MAGs are generally named or numbered and referred interchangeably as a phylotype. MAGs are useful to shed light on nonculturable, novel, unannotated microbes in metagenomic data.
Metagenomics: study of DNA recovered from a complex sample (i.e., environmental samples). The DNA is extracted from a sample of interest and sequenced, resulting in millions of DNA sequences. These sequences provide taxonomic and functional information on the sample of interest. The sequences can also be assembled to produce MAGs.
Metatranscriptomics: technique used to study gene expression of

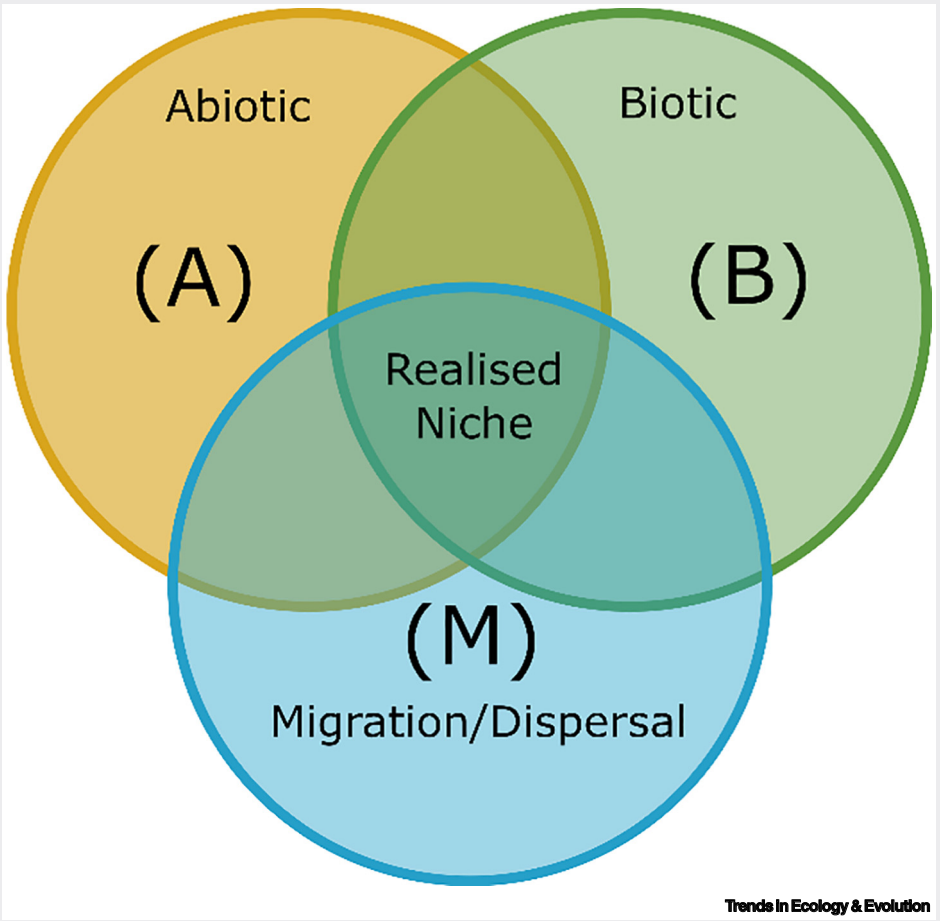

Figure I. Representation of the Biotic–Abiotic–Migration (BAM) conceptualised by Soberón and Peterson [10] to describe species distributions.

overestimate the niche breadth or result in an assumed centroid position that is shifted or even outside the actual niche. Today, however, multi-omics applied to microbial communities offers a great opportunity to go beyond the observation of realised niche differences at the taxonomic level. Thus, defining a clear framework to quantify the niche of microorganisms is an essential step to advance ecological studies beyond the taxonomic and functional characterization of microbial communities, toward a more mechanistic understanding of the drivers of microbial phylotypes in time and space. Here, we propose using multi-omics methods to expand the standard environmental niche framework used in ecology and biogeography of macroorganisms to define a new concept: the metabolic niche of microorganisms.

The metabolic niche framework

The observed differences in realised environmental niche, even for closely related phylotypes, poses the question of the mechanisms leading to these differentiations. There has been increasing momentum to use multi-omics approaches to investigate these environmental niche differences in microorganisms based on their genomic content [37–40]. As a result, we propose the metabolic niche framework (Figure 1). At the origin, the microbial **genome** hosts

microbes within natural environments. The total RNA is extracted from a complex sample of interest and processed for sequencing. The resulting millions of sequences provide information of the gene expression profile of the samples investigated.
Microbial invasion: establishment of a microorganism in a microbial community where it was not previously present. In microbial ecology, an invasion is not required to have negative impacts on the resident community and ecosystem.
Niche breadth: range of environmental conditions included within the niche.
Niche differentiation: process by which selection drives competing species into different niches.
Niche hypervolume: region defined by more than three dimensions. The environmental niche is often described as an *n*-dimensional hypervolume.
Niche position: mean environmental conditions across all areas occupied by a species.
Niche shift: change in the niche envelope in an environmental space.
Phylotype: DNA sequence sharing a high degree of similarity, often used as equivalent to microbial 'species'.
Realised environmental niche: refers to the restricted set of conditions a species actually occupies *in situ* when accounting for biological interactions.
Realised metabolic niche: this term is introduced for the first time as the range of genes transcribed defining where an organism can realistically survive.
Resident community: any community investigated for potential invasions.
Sympatric speciation: evolution of a new closely species with the same geographic range (no geographic barriers).
Unique gene: gene generally absent from most microorganisms and present in a selected few.

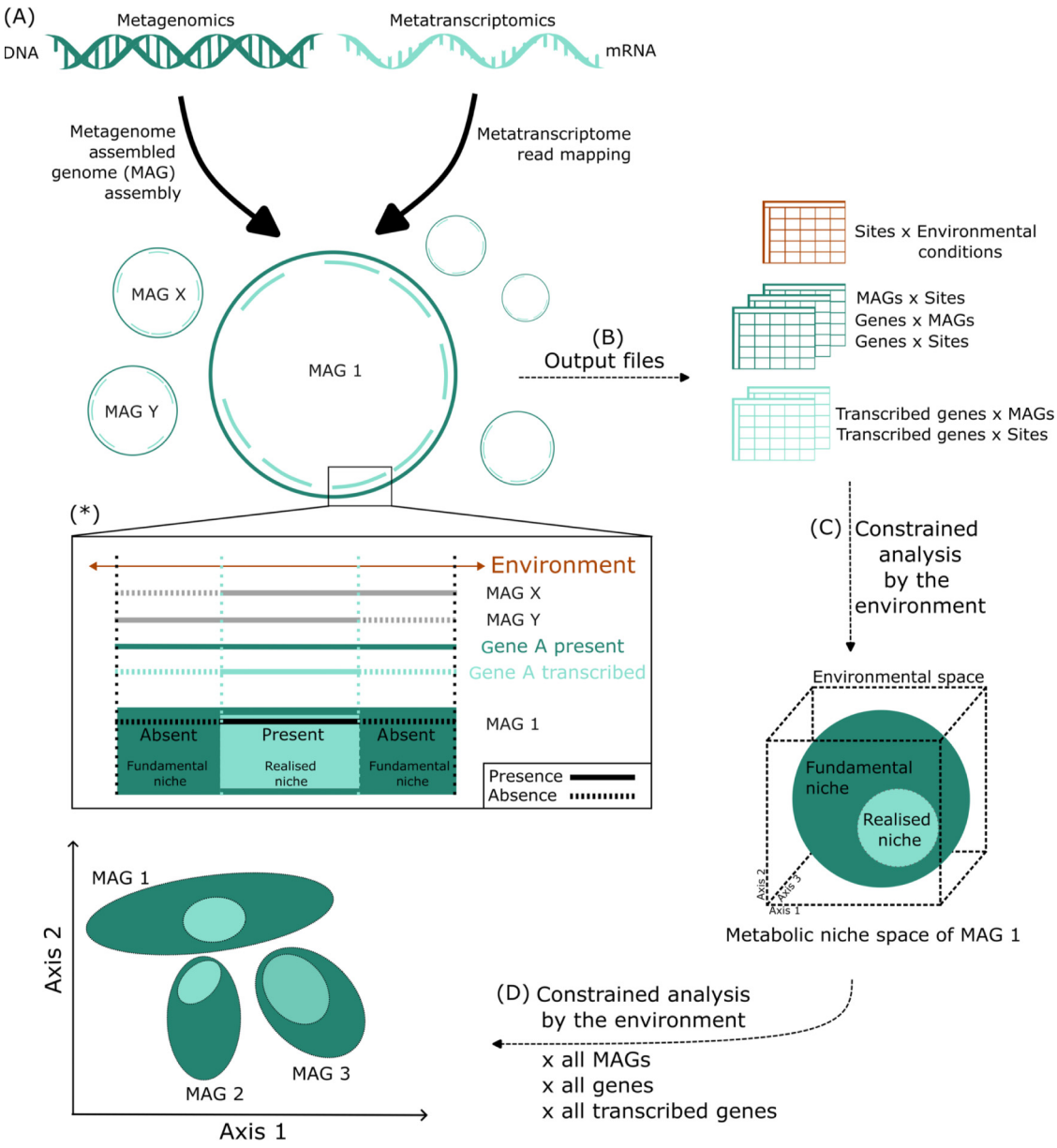

Figure 1. The metabolic niche framework. A framework to define the fundamental and realised metabolic niche of metagenome-assembled genomes (MAGs) within the environmental space. (A) Assemble MAGs from shotgun metagenomics. Metatranscriptomic reads can be mapped onto these MAGs to identify actively transcribed genes. (B) A set of output matrices are obtained and can be used to define the fundamental and realised metabolic niches of each MAG. (*) First, to understand the concept, we can look at the single gene level (gene A) under three environments. The orange arrow represents an environmental gradient. The full lines indicate the presence of a MAG or gene along that gradient. The broken lines indicate the absence of a MAG or gene along that gradient. First, by looking at all the MAGs in a sample, we know that MAG X, MAG Y, and MAG 1 all have gene A. By mapping their presence in the environment, we can identify the presence of gene A within the environment. Then, using metatranscriptomics, we can define the environmental circumstances in which gene A is transcribed (along the environmental gradient). Finally, by mapping the presence of MAG 1, we can define its fundamental metabolic niche (specific to gene A, using metagenomics): although MAG 1 is absent from the 'left' and 'right' environment, the presence of gene A in these 'left' and 'right' environments indicate where MAG 1 could theoretically be found in these environments. We can also define its realised metabolic niche (specific to gene A, using metatranscriptomics): MAG 1 is present and gene A is transcribed. (C) Scaling up to all the genes identified in MAG 1, we can comprehensively define its fundamental metabolic niche and realised metabolic niche within the environmental space. The environmental space is defined by orthogonal environmental axes that represent combinations of environmental descriptors of the niche. (D) By repeating such constrained analysis for all the genes identified, all the MAGs, and all the transcribed genes, we can delineate the fundamental and realised metabolic niche of each MAG (phylotype) in a sample, as well as the community.

the range of genes necessary for an organism to function. It defines where an organism can live within an environmental space and, therefore, it encodes the **fundamental metabolic niche** (Figure 1). The development of shotgun **metagenomics** and genome reconstructions to produce **metagenome-assembled genomes** (**MAGs**, a reconstructed genome) has offered the ability to identify the pool of available genes for each phylotype. As a result, using shotgun metagenomics bears the potential to define the fundamental metabolic niche of individual microbial phylotypes within defined environmental spaces, by assembling the MAG of each individual phylotype in a sample. However, not all genes in the microbial genome are transcribed because their transcription depends on the needs of the organism and, therefore, defines where an organism can realistically survive, here called the **realised metabolic niche** (Figure 1). **Metatranscriptomics** can be used to identify actively transcribed genes (with mRNA), delineating the metabolic activity of each phylotype and, therefore, the realised metabolic niche. As a result, the integration of metagenomics and metatranscriptomics will help define the fundamental and realised metabolic niches of individual phylotypes in the environmental space (or across time). While we describe this framework primarily for phylotypes, it can be adapted to investigate, compare, and identify differences in metabolic niches of diverse microbial communities.

With the growing number of studies combining metagenomics and metatranscriptomics data, the opportunities to investigate the microbial niche are increasing rapidly. To date, few studies have described metabolic niche differentiation through changes between functional potential and activity [41–45] and, to our knowledge, only Herold *et al.* [40] have considered differences in fundamental and realised metabolic niches of microorganisms. They investigated the response of the wastewater microbiome to disturbance using not only metagenomics and metatranscriptomics, but also metaproteomics and metabolomics. Metaproteomics and metabolomics could contribute to further define the realised metabolic niche of microbial communities by identifying the proteins and metabolites produced by entire communities. Overall, integrated multi-omics approaches hold the potential to resolve the fundamental and realised metabolic niches of microbial phylotypes and communities *in situ*, opening a wide range of novel applications to further develop our understanding of microbial communities.

Applications of the metabolic niche framework

Using this metabolic niche framework opens new ways to investigate the ecology of microbial phylotypes and communities with a range of applications.

Metabolic plasticity

Metabolic plasticity is the capacity to alter a physiological response to environmental conditions. It is generally described based on single microorganisms grown in pure cultures at different environmental conditions to determine whether they can adapt to changes at their physiological limits [46,47]. Using the metabolic niche framework provides the possibility to not only study metabolic plasticity of individual phylotypes that are not yet cultured, but also investigate individual genes or whole changes in pathways for hundreds of phylotypes at a time. For instance, in Figure 2A, we can define the presence of gene A within the environmental space (using shotgun metagenomics) by defining the presence of MAGs with gene A. Using metatranscriptomics, we can further define the environmental circumstances where gene A is transcribed. Finally, by mapping the presence of the phylotype of interest (MAG Y), we can define its fundamental metabolic niche (gene A is present, but MAG Y is absent), its realised metabolic niche (MAG Y is present and gene A is transcribed) and the metabolic plasticity (MAG Y is present, but gene A is transcribed in some circumstances and not

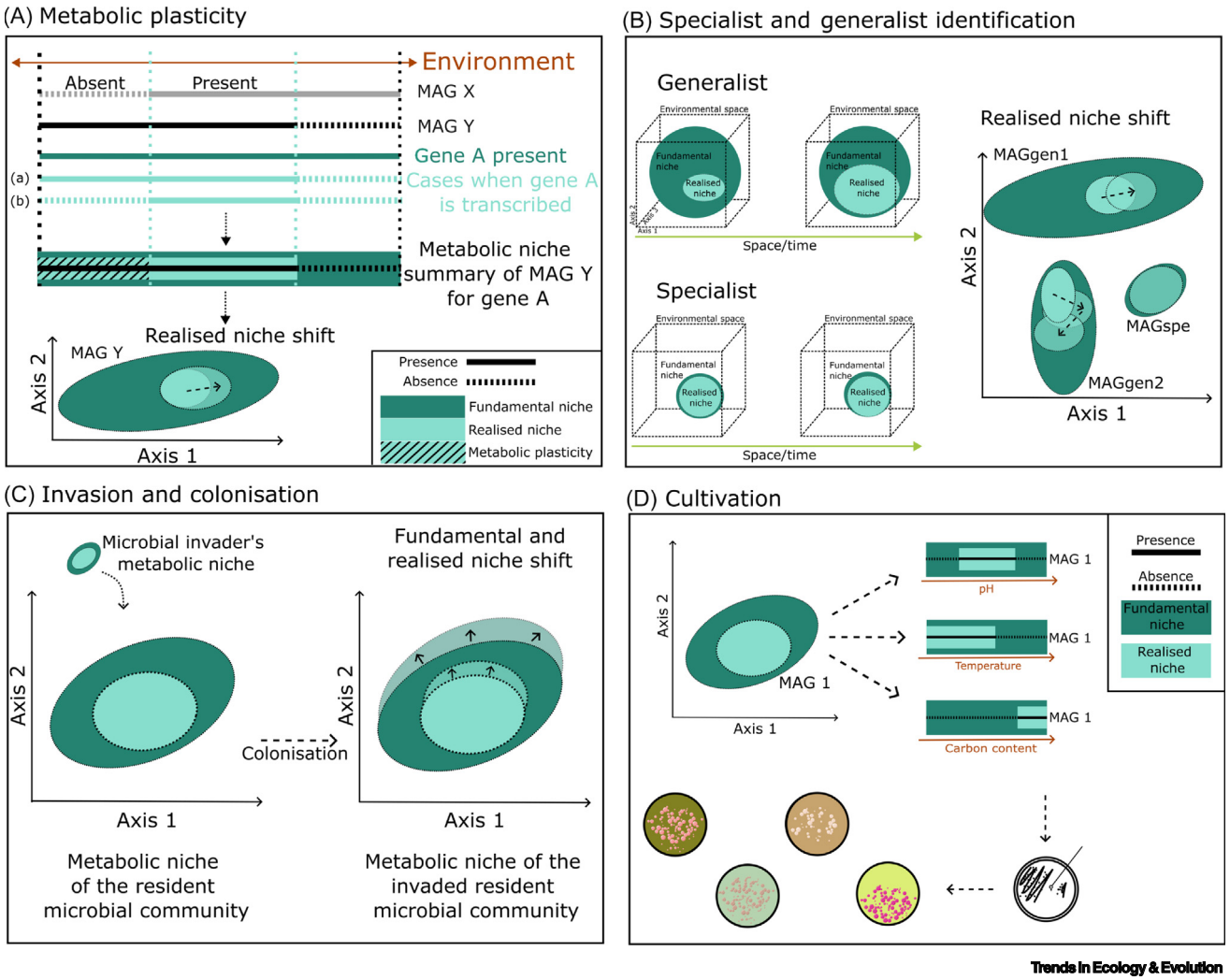

Figure 2. Non-exhaustive list of the possible applications of the metabolic niche framework to advance the field of microbiology and microbial ecology. Axis 1 and axis 2 represent axes of the environmental space (see Figure 1). (A) Using the metabolic niche framework to study metabolic plasticity. The concept is presented at the single gene level. Gene A can be transcribed or not in different environmental circumstances. (B) The framework could provide a reproducible and comparable method to identify generalist and specialist phylotypes, with generalists presenting large fundamental metabolic niches with high metabolic plasticity and specialists presenting small fundamental metabolic niches with limited metabolic plasticity. (C) By defining the metabolic niche of a resident community and of the microbial invader, we could characterise the impact of the invader on the invaded resident community. (D) The metabolic niche of uncultured microorganisms could be a useful tool to determine the optimum laboratory conditions to use for growth.

transcribed in others). As a result, we can identify shifts in the realised metabolic niche based on changing environmental conditions, opening new ways of investigation to evaluate the resistance of phylotypes (via metabolic plasticity and metabolic niche shifts) and the functional resilience of communities to global change. We should note that metabolic plasticity may also be acquired through mutations in the genome or **horizontal gene transfer** (see Outstanding questions), which could lead not only to realised metabolic **niche shifts**, but also to fundamental metabolic niche shifts. Such metabolic niche shifts could confer advantages to the phylotype [48] by providing adaptations to global change resulting in a shift in biogeographical distribution with an increase in geographic range size, for example.

Identifying specialists and generalists

The metabolic niche framework also provides a novel way to differentiate habitat generalist from habitat specialist phylotypes using metabolic plasticity (Figure 2B). In microbial ecology, habitat specialists and generalists have often been defined by surrogates of environmental niche properties, such as based on their prevalence across samples: phylotypes identified in many distinct habitats are considered habitat generalists, while those with restricted distributions are considered habitat specialists [49]. While this may be applicable for global studies, this characterisation is more difficult when focused on smaller regions of the globe. Indeed, a habitat specialist phylotype in one study could be a habitat generalist when upscaled geographically [50]. Given that a habitat generalist is characterised by a large distributional range, it is likely to present a wide environmental niche breadth and, importantly, harbour a large number of genes to adapt to each environment in which it can live in. As a result, a habitat generalist will likely present a large fundamental metabolic niche with high metabolic plasticity [37], occupying different fractions of the fundamental niche as a function of the environmental conditions and potentially changing in time and/or space (Figure 2B). By contrast, a phylotype with a restricted distribution likely has a small fundamental metabolic niche because it may lack many of the genes required to adapt to other environmental conditions. In this case, the fundamental metabolic niche is likely small with limited metabolic plasticity [37] and, as a result, a specialist will always occupy the same fraction of the fundamental niche, performing the limited number of functions encoded in its genome (Figure 2B). Using the metabolic niche framework might provide a more robust, widely applicable, and comparable method to differentiate specialist from generalist microbial phylotypes [37] by assessing changes in metabolic plasticity and realised metabolic niche shifts.

Invasion and colonisation

Biological invasions are a leading cause of biodiversity loss globally [51]. They have been mostly documented for macroorganism invasions; however, although greatly underestimated, **microbial invasions** of natural ecosystem are likely common [52,53] and their impacts on local ecosystems and **resident communities** remain largely unknown [54]. Microbial invasions are frequently mediated by humans for agriculture or **bioaugmentation** [55]; nevertheless, the impacts on resident communities and ecosystems are still understudied. The metabolic niche framework could characterise some of the impacts of the **invader** on the invaded resident community by comparing the metabolic niches of the microbial invader to those of the phylotypes comprising the resident community (Figure 2C). Specifically, the framework could determine whether the invader introduces new genes and/or new functions, which could shift the (fundamental and/or realised) metabolic niche of the resident community and potentially change ecosystem functioning. This could be a major step forward to predict the probability of invasion success and the impacts of microbial invasions [38], especially in rapidly changing ecosystems.

Improving cultivation

There has been a resurgence in interest in culturing previously uncultured microorganisms [56,57] and the metabolic niche framework may help with these culturing efforts. Calculating metabolic niche properties for individual phylotypes and identifying the environmental conditions where a phylotype can live along natural environmental gradients, the range in which it is identified, as well as the conditions in which genes are transcribed, may help determine the optimum laboratory conditions to use for growth (Figure 2D). Furthermore, defining the microbial niche across multiple microbial groups or phylotypes might advance co-culturing efforts and enhance natural product discoveries [58].

Box 2. Challenges and limitations of omics data

While multi-omics present a great potential to advance the field of microbial ecology, many challenges and limitations remain.

Capturing complex microbial communities using MAGs remains a challenge, especially for rare phylotypes (i.e., low abundance taxa), or domains other than bacteria (i.e., viruses, archaea, or eukaryotes) [59], because the sequencing depth and sample type are likely to have a strong impact on the recovered community and the resulting fundamental metabolic niche. The lack of processing standardisation and pipelines is likely to influence MAG assembly, completeness, contamination, and coverage [59,60], thus influencing the accuracy of the fundamental metabolic niche evaluation. Metatranscriptomic data sets also present limitations, starting with the fact that the presence of a mRNA does not reflect the presence of the associated function because the mRNA expression can be regulated post transcription. Furthermore, working with mRNA presents inherent biases (i.e., short life span or low concentrations) [61,62] in addition to the methodological difficulties associated with RNA and sequencing [63,64]. As with metagenomic data, sequencing depth, processing pipelines, and tools are likely to influence the accuracy of the captured realised metabolic niche. For instance, a shallow metatranscriptome would likely underestimate the realised metabolic niche and, as a result, bias any application of the framework.

While these issues still represent significant challenges, the constant improvement in the methods and tools available for metagenomic and metatranscriptomic analyses is leading to the increase in the number of multi-omics studies investigating the metagenome and metatranscriptome of microbial communities [62,64] and a surge in the number of MAGs recovered [59,65,66]. As a result, this framework will be increasingly useful to investigate the microbial niche and tackle fundamental questions in microbial ecology.

Concluding remarks and future perspectives

Defining the environmental niche of organisms allows the investigation of community dynamics, biotic interactions, biological invasions, and species response to global change. Yet, we have lacked methods to define the niche of microorganisms and go beyond taxonomic descriptions of microbial communities. Here we propose the metabolic niche framework using multi-omics to define the metabolic niche of microorganisms and move toward a more mechanistic understanding of the drivers of microbial phylotypes distribution in space and time. Specifically, the integration of metagenomics and metatranscriptomics will define the fundamental and realised metabolic niche of microorganisms, opening new routes for the investigation of microbial communities. For instance, it will open new grounds to study metabolic plasticity, assess niche shifts (especially in the context of rapid ecological change), differentiate specialists from generalist phylotypes, evaluate the impacts of microbial invasions, and contribute to culturing efforts. Finally, using both the environmental niche and metabolic niche frameworks could also help improve spatial distribution models of microbes [67,68], which are usually based on amplicon sequencing and, thus, focusing on the traditional environmental niche. By predicting metabolic traits or functions in space (or time), expanded to also predict ecosystem functions and services [69–71] , it could provide major advances for microbial spatial modelling. Although some challenges (Box 2) and questions remain (see Outstanding questions), this framework is a step forward in understanding and predicting the fate of individual phylotypes, microbial communities, and ecosystems in the context of global change.

Outstanding questions

What is a prokaryotic species? There is no universally accepted species concept for prokaryote, yet the threshold of similarity chosen to define species will impact the results.

How would different methodological biases impact the accuracy of the metabolic niche evaluation?

Is it possible to differentiate the metabolic niche of phylogenetically close strains using MAGs? Using very high-quality MAGs, core genes encoding 'basic' functions that are common to all strains may be removed across all MAGs, preserving only accessory/unique genes, which may confer environmental advantages and drive niche differentiation, thus improving the metabolic niche differentiation of closely related strains.

Is it possible to evaluate the importance of horizontal gene transfer in increasing the size of the fundamental and realised metabolic niche? This could be evaluated by conducting single cell experiments; however, the identification and assignation of plasmids (key elements for horizontal gene transfers) to MAGs within complex communities remains a major methodological challenge.

How accurate would the spatial distribution models of gene or phylotype be using the metabolic niche framework and would they be improved from models using amplicon sequencing?

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Declaration of interests

No interests are declared.

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