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COMMENTARY

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Applying the core microbiome to understand host–microbe systems

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Abstract

1. The host-associated core microbiome was originally coined to refer to common groups of microbes or genes that were likely to be particularly important for host biological function. However, the term has evolved to encompass variable definitions across studies, often identifying key microbes with respect to their spatial distribution, temporal stability or ecological influence, as well as their contribution to host function and fitness.
2. A major barrier to reaching a consensus over how to define the core microbiome and its relevance to biological, ecological and evolutionary theory is a lack of precise terminology and associated definitions, as well the persistent association of the core microbiome with host function. Common, temporal and ecological core microbiomes can together generate insights into ecological processes that act independently of host function, while functional and host-adapted cores distinguish between facultative and near-obligate symbionts that differ in their effects on host fitness.
3. This commentary summarizes five broad definitions of the core microbiome that have been applied across the literature, highlighting their strengths and limitations for advancing our understanding of host–microbe systems, noting where they are likely to overlap, and discussing their potential relevance to host function and fitness.
4. No one definition of the core microbiome is likely to capture the range of key microbes across a host population. Applied together, they have the potential to reveal different layers of microbial organization from which we can begin to understand the ecological and evolutionary processes that govern host–microbe interactions.

KEYWORDS

core microbiome, host-associated microbiome, host-microbe interactions, microbiome, symbiosis

1 | INTRODUCTION

One of the aims of the Human Microbiome Project when established in 2007 was to identify a human 'core microbiome', defined as a group of microbial taxa or genes that are shared by all or most humans (Hamady & Knight, 2009; Turnbaugh et al., 2007). These pioneering studies found that a universal taxonomic core rarely exists across groups of humans, even at the scale of the

family unit (Yatsunenko et al., 2012), yet most shared the same set of core microbial genes. This pattern appears to be similar for most host species studied to date, with variable microbial composition often underpinned by similar gene context across individuals (Burke, Steinberg, Rusch, Kjelleberg, & Thomas, 2011; Louca et al., 2018). Nevertheless, most ecologists aim to understand host–microbe interactions at the organismal level, accounting for microbe functional traits where possible; therefore, within this field, the core microbiome has been largely applied to taxonomically defined microbial communities with an aim to identify groups of microbes that are particularly widespread across the host population (e.g. Ainsworth et al., 2015; Grieneisen, Livermore, Alberts, Tung, & Archie, 2017; Hernandez-Agreda, Gates, & Ainsworth, 2017; Kembel et al., 2014; Lundberg et al., 2012; Muletz Wolz, Yarwood, Campbell Grant, Fleischer, & Lips, 2018).

The major motivation for identifying a universal 'common core' is to define a component of the microbiome that may be particularly important for host biological function (Parfrey, Moreau, & Russell, 2018; Shade & Handelsman, 2012; Turnbaugh et al., 2007, 2009). This assumption has been challenged over the years by increasing evidence that rare taxa are likely to be just as important as widespread taxa to various components of host and microbial ecosystem function (Jousset et al., 2017; Lynch & Neufeld, 2015). For example, rare taxa are implicated in human resistance to *Salmonella* infection (Velazquez et al., 2019), in the reproductive success in Black rhinos (Antwis, Edwards, Unwin, Walker, & Shultz, 2019), and for driving nutrient cycling in free-living microbial communities (Jousset et al., 2017). In response, the 'core microbiome' is increasingly measured by traits beyond how common they are, including their temporal stability ('temporal core'; Caporaso et al., 2011), their ecological influence on microbial communities ('ecological core'; e.g. Toju et al., 2018) and their functional properties ('functional core'; Turnbaugh et al., 2007), in order to more accurately infer their potential impact on host phenotype. However, while microbial functional properties (e.g. gene content) can directly affect host physiological and behavioural phenotype (Davidson, Cooke, Johnson, & Quinn, 2018; Sanna et al., 2019; Turnbaugh et al., 2009), there is either limited or conflicted evidence that traits such as occupancy frequency or ecological keystoneness are reliable indicators of importance to host function. This conflicted evidence has led to calls to end our reliance on such traits to indirectly infer function because taxonomic (but not necessarily functional) composition can be heavily influenced by regional abiotic conditions (Lemanceau, Blouin, Muller, & Moënne-Loccoz, 2017; Vandenkoornhuyse, Quaiser, Duhamel, Van, & Dufresne, 2015).

One drawback of defining the core microbiome purely with respect to host function is that it neglects the numerous facets of host-associated microbiomes that act (and are of interest) independently of host function. The concept of the core microbiome has been applied to advance our understanding of diverse ecological and evolutionary processes, including applying the common core to estimate rates of microbiome divergence across vertebrates (Moeller et al., 2014; Nishida & Ochman, 2018), the temporal core to understand community stability (Bjork, O'Hara, Ribes, Coma, & Montoya, 2018; Caporaso et al., 2011; Shade & Gilbert, 2015) and the ecological core to identifying groups of keystone taxa that disproportionately influence community structure (Toju et al., 2018). An alternative solution is to formally expand our definition of the core microbiome to encompass groups of microbes that are important or notable across multiple facets of host–microbe dynamics, including, but not limited to, host function.

Expanding how we think of and define the core microbiome can also help distinguish between the different types of function carried out by host-associated microbiomes. The functional core can be divided into two categories depending on whether the investigated function is a 'causal role' (CR) function, which refers to the change in system function when a microbe is removed, and/or a 'selected effect' (SE) function, which describes the evolutionary rationale for a microbe to be maintained within the host population (Klassen, 2018). A microbe may have a CR function in that its removal affects a phenotypic trait, yet this function will also be a SE function only if this trait is under selection in the host population and the function is not readily performed by other taxa. Such SE taxa are selectively maintained in the host population via various mechanisms (e.g. vertical transmission or specific immune or morphological mechanisms; Donaldson et al., 2018; Fisher, Henry, Cornwallis, Kiers, & West, 2017; Lanan, Rodrigues, Agellon, Jansma, & Wheeler, 2016), and make up the fifth core microbiome: the 'host-adapted core' (Shapira, 2016). The difference between functional and host-adapted cores could therefore be considered to represent different ends of the host–symbiont dependence spectrum, spanning from facultative to obligate symbionts (Fisher et al., 2017).

Here I describe five broad definitions of the core microbiome that have been applied in the literature (Figure 1), with an aim of summarizing their strengths and limitations for advancing our understanding of host–microbe systems and their potential relevance to host function. Three of these cores relate to patterns in spatial, temporal and ecological dynamics of microbiomes, while two (the functional and host-adapted core) deal directly with host function and fitness. These five definitions are flexible and can be carried out at variable spatial, temporal and taxonomic scales depending on the specific aims of the study, yet they attempt to capture the major conceptual differences between types of core and how they may be applied to understand host–microbe communities. While each of the core categories is conceptually distinct, this does not preclude that microbial taxa may meet the criteria of multiple definitions, and I highlight cases where types of core are likely to overlap. Applied together, they can identify a collection of microbes that may be particularly important for driving separate ecological and evolutionary processes within a host population.

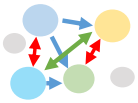
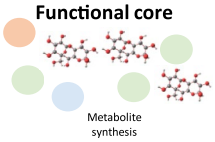
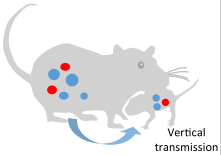
Term	Definition	Criteria
Common core 	The component of the microbiome that is found across a considerable proportion of hosts within a defined host population or species	• High prevalence/occupancy frequency across host population/species • Can be identified using occupancy-abundance curves • (Optional) Common in host species of interest but not in other closely related species • Rare (non-prevalent) taxa cannot be core
Temporal core 	A temporally stable or predictable component of the microbiota	• Taxa that demonstrate stable or predictable dynamics over time, either within a single host or across host population/species • Within individuals, rare (non-prevalent) taxa can be core
Ecological core 	The component of the microbiome that is disproportionally important for shaping the organisation and diversity of the ecological community	• Removal or introduction results in large cascading effects on ecological structure and diversity • May form interaction hubs in ecological networks • May increase community stability • Rare (non-prevalent) taxa can be core (e.g. predators or ecosystem engineers)
Functional core 	The component of the microbiome that performs essential biological functions to the host, usually in respect to their biochemical, physiological or ecological services to the host	• A set of genes or taxa that are linked to a measureable facet of host function • Natural variation in host function does not affect host fitness OR • Natural variation in function does affect host fitness but phylogenetically distinct taxa can perform function • Likely to represent facultative symbionts • Can be horizontally or vertically acquired • Rare (non-prevalent) taxa can be core
Host-adapted core 	A set of microbes that has co-evolved with the host species or sub-population and whose presence increases host fitness in at least some ecological contexts	• Taxa that are linked to a measureable facet of host function • Natural variation in host function affects host fitness in at least some ecological contexts • Are not functionally redundant (other taxa cannot perform same function) • Are expected to be vertically transmitted • Likely to represent obligate or near-obligate symbionts • Very rare (non-prevalent) taxa unlikely to be core, but host-adapted cores be restricted to certain populations or ecological conditions

FIGURE 1 Description of five types of core microbiomes found within the literature and their criteria for inclusion

2 | THE COMMON CORE

The common core microbiome identifies the most widespread microbial taxa within a host population. The common core is usually defined as microbial taxa that occur with hosts above a particular occupancy frequency threshold, often between 30% (Ainsworth et al., 2015) and 95% (Huse, Ye, Zhou, & Fodor, 2012), although biological justifications for such thresholds are rare. A more standardized approach that applies occupancy–abundance curves and rank contribution to beta diversity to prioritize core membership has been proposed (Shade & Stopnisek, 2019). Spatial distributions may also be explained by a 'gradient core', which aims to identify correlations between microbial taxa frequency and abiotic factors (Hamady, Lozupone, & Knight, 2010; Thomas, Vandegrift, Roy, Hsieh, & Ju, 2019). Taxa are often grouped by phylogeny before being filtered by occupancy frequency to generate a common phylogenetic core (Ren & Wu, 2016; Stephens et al., 2016), under the assumption that functional traits are phylogenetically conserved. While there is substantial evidence that functional traits do group by phylogeny to some extent (Amend et al., 2016; Andersson, Riemann, & Bertilsson, 2010; Lu et al., 2016; Martiny, Jones, Lennon, & Martiny, 2015; Morrissey et al., 2016; Philippot et al., 2010), high levels of horizontal gene transfer (HGT) mean this assumption should be made cautiously (Soucy, Huang, & Gogarten, 2015).

Microbial species can have high occupancy frequency within the host population for a number of reason; for example, they are common in the environment or diet (David et al., 2014), they are highly competitive against other microbes (Bauer, Kainz, Carmona-Gutierrez, & Madeo, 2018; Coyte & Rakoff-Nahoum, 2019), or they are vertically transmitted and encouraged to colonize by the host (Funkhouser & Bordenstein, 2013). In most cases, identifying the underlying reason why some microbes have high frequency is difficult, and a microbe's occupancy frequency is not necessarily linked to its function or evolutionary history with the host (especially where host dependence on its microbiome is low; Hammer, Sanders, & Fierer, 2019). While frequent microbes may indeed have a functional or adaptive role, many rare microbes are essential for host function (Jousset et al., 2017; Velazquez et al., 2019), and demonstrated host-adapted microbes can have relatively low frequency across the host species range (e.g. the root fungal symbiont *Colletotrichum tofieldiae*; Hiruma et al., 2016). As such, links between the common core and measures of host function are sparse, and the underlying assumption that the common core is functional should be discarded.

Although the common core is not necessarily a good measure of function, it does allow us to better understand how microbiomes are structured across host populations and species. The common core has been applied to advance our understanding of broad patterns in host–microbe associations across phylogenetic trees, such as linking species' ecology with microbiome structure and composition (Amato et al., 2019; Mendoza et al., 2018; Muegge et al., 2011), and calculating rates of microbiome divergence across vertebrates (Moeller et al., 2014; Nishida & Ochman, 2018). These studies do not require

an underlying assumption that common microbes are functional, but rather use common microbes as species-specific microbial fingerprints to understand large-scale patterns in microbiome composition across the phylogenetic tree. Within a study species or population, identifying patterns in microbial frequencies across sites or populations provides a critical foundation from which to build a deeper understanding of the ecological and evolutionary processes acting on host–microbe systems, and may provide potential candidates for further investigation with regard to microbe ecology and function.

3 | THE TEMPORAL CORE

The temporal (or dynamic) core microbiome identifies temporally stable or predictable taxa within individuals (Caporaso et al., 2011) or across the host species/population (Bjork et al., 2018). The temporal core can comprise of taxa that are present relatively consistently over time (e.g. detected in 70% of sampling events; Bjork et al., 2018), but could also include taxa whose abundance fluctuates predictably with season or life-history stages. While microbiomes are naturally dynamic and shifts in composition are normal (Chu et al., 2017; Kohl, Cary, Karasov, & Dearing, 2013; Shade & Gilbert, 2015), identifying groups of taxa that are temporally predictable allows us to estimate the contribution of conditionally rare taxa to community dynamics (Shade & Gilbert, 2015; Shade et al., 2014), distinguish between normal baseline dynamics and perturbation events (Zaneveld, McMinds, & Vega, 2017), and identify members that underpin microbiome stability (Bjork et al., 2018; Kokou et al., 2019).

The most commonly described temporal variation of microbiomes is due to season (Amato et al., 2015; Gomez et al., 2016; Maurice et al., 2015; Ren et al., 2017; Smits et al., 2017; Wu et al., 2017). For example, the relative abundance of the genera *Oscillospira* and *Coprococcus* ocillate predictably with season in the gut microbiome of Red squirrels (Ren et al., 2017); *Lactobacillus*, *Alistipes* and *Helicobacter* seasonally fluctuate in wild mice (Maurice et al., 2015); and *Lactobacillus* and *Bartonella* predictably increase over winter in the gut microbiomes of Honey bees (Kešnerová et al., 2020). The extent to which such dynamics are externally and internally driven are unclear, although laboratory studies show that seasonal shifts in at least some taxa are host controlled in response to changes in temperature/light stimuli (Carey, Walters, & Knight, 2013; Ferguson et al., 2018; Segers, Kaltenpoth, & Foitzik, 2019). These examples of seasonal variation at the host population level usually identify a small number of taxa that exhibit predictable dynamics, yet the temporal core can encompass many more species if it includes taxa that persist in a stable state within individuals, because priority effects during development can generate individualized microbiomes that are highly stable and resistant to invasion (Obadia et al., 2017). The individual temporal core is a powerful tool to distinguish between strains that are characterized by either inter-individual or intra-individual (temporal) variability (e.g. Lloyd-Price et al., 2017 in humans), and provides rich information on community stability at the individual level.

The temporal core can overlap with the common core when measured at the host population level. Widespread taxa tend to be abundant where they occur (Gaston et al., 2000; Shade et al., 2018), and since abundant taxa are less likely to become locally extinct, widespread taxa are likely to be more temporally stable than low occupancy taxa (Jalanka-Tuovinen et al., 2011; Li, Bihan, & Methé, 2013; Martínez, Muller, & Walter, 2013). In Honey bee and Red squirrel gut microbiomes, common core genera either remain temporally stable across the host population or fluctuate predictably with season (Kešnerová et al., 2020; Ren et al., 2017). However, gut microbial taxa that are not categorized within the common core can still show strong seasonal fluctuations (Kešnerová et al., 2020; Ren et al., 2017), indicating they are either sourced seasonally from the environment/diet or are present below detectable levels during parts of the year (e.g. Smits et al., 2017).

While the common and temporal cores can overlap with respect to highly abundant taxa, the temporal core may be more meaningful for understanding links to host function than spatial distribution patterns alone. Community stability and resilience against disruption are proposed to be important for host health (Sommer, Anderson, Bharti, Raes, & Rosenstiel, 2017; Zaneveld et al., 2017), and temporal fluctuations of specific taxa may also hint at functionality; for example, fluctuations of some gut microbial taxa optimize energy metabolism over the hibernation cycle of Brown bears (Sommer et al., 2016) and during pregnancy in humans (Koren et al., 2012). Importantly, community stability varies: internal microbiomes tend to be more stable than external ones (Franzosa et al., 2015; Lloyd-Price et al., 2017), and variation in microbiome stability can be large even across related host species such as corals (Bjork et al., 2018). Within relatively stable microbiomes, the temporal core can help identify taxa that are particularly important for maintaining overall community stability (e.g. Kokou et al., 2019).

4 | THE ECOLOGICAL CORE

The ecological core can be defined as groups of microbial taxa that are particularly influential for shaping the ecological structure of the microbial community. In ecological theory, such taxa are termed keystones and are defined as species whose presence is disproportionally important for shaping the organization and diversity of their ecological community (Mills, Soulé, & Doak, 1993; Power et al., 1996), usually via trophic interactions, competition or due to their role as abiotic ecosystem engineers. This contrasts with the influence of dominant species, which make up the largest biomass yet may not necessarily have an overt influence of community diversity (Power et al., 1996). The keystone concept is increasingly being applied to microbiomes to identify an ecological core, in part due to the expected potential of keystones to mediate community function (e.g. nutrient cycling; Banerjee, Schlaeppi, & Heijden, 2018; Jousset et al., 2017) and/or host function (e.g. growth and pathogen resistance; Toju et al., 2018).

Identifying keystones generally requires experimental removal or introduction of taxa; therefore while many candidate keystones have been identified (Banerjee et al., 2018), validated examples of microbial keystones are rare (Röttjers & Faust, 2019). Experimental colonization of specific genera to the root microbiome of *Arabidopsis thaliana* show that some taxa have disproportionally large effects on community structure and diversity compared to others (Agler et al., 2016; Carlström et al., 2019), and such keystones may positively facilitate community diversity and stability, thereby promoting host health (Toju et al., 2018). However, pathogens can also exhibit keystone traits if they remodel a benign microbiota into a dysbiotic one (Hajishengallis, Darveau, & Curtis, 2012; Hajishengallis et al., 2011); therefore, keystone traits could identify pathogens as well as beneficial taxa. The cooperative and antagonistic interactions that underpin a keystone taxa's maintenance of community structure are still largely undocumented in microbial communities, yet there is increasing evidence that, as with macrobes, a taxa's position in its trophic network is important (Koskella & Brockhurst, 2014; Lucas, McBride, & Strickland, 2020; Wang, Goyal, Dubinkina, & Maslov, 2019). Microbial predators such as bacteriophages can significantly reduce abundances of common taxa, thereby maintaining community diversity and stability via negative density-dependent mechanisms (Morella, Gomez, Wang, Leung, & Koskella, 2018; Welsh et al., 2016).

Many keystone taxa in microbial communities have low abundance (Banerjee et al., 2018); therefore, members of the ecological core are likely to differ from those captured by the common and temporal core. Nevertheless, there is evidence that widespread and temporally stable generalist microbes can increase community stability in gut microbiomes (Kokou et al., 2019), suggesting such taxa may be important across cores. While identifying ecological keystones remains challenging, applying time-series data (Stein et al., 2013) or experimental inoculation (Agler et al., 2016; Carlström et al., 2019) are robust methods for identifying ecological interactions and keystone taxa. Co-occurrence networks are an accessible method that can shed light on (non-trophic) ecological interactions (Coyte & Rakoff-Nahoum, 2019) and potential keystones (Banerjee et al., 2018; Berry & Widder, 2014), although correlations can represent shared responses rather than direct interactions. Overall, while the ecological core (as with the common and temporal core) may indeed have indirect consequences for host function (e.g. via their stabilizing effect), the extent to which this is really the case is still unclear (Röttjers & Faust, 2019), and any correlations with function may an indirect consequence stemming from their influence on community organization and diversity.

5 | THE FUNCTIONAL CORE

The functional core microbiome aims to identify sets of microbes and their genes that are important for host biological function, and it is the ultimate goal for many studies applying the concept of the core microbiome (Burke et al., 2011; Engel, Martinson, & Moran, 2012; Luca, Kupfer, Knights, Khoruts, & Blekhman, 2018; Zhang et al., 2015). These functions may be biochemical in nature (e.g. the ability to produce metabolites or neutralize toxins), physiological/behavioural (e.g. interactions with the host that maintain physiological homeostasis) or ecological (e.g. outcompeting pathogens), and have been extensively reviewed elsewhere (Louca et al., 2018; Sampson & Mazmanian, 2015; Sommer et al., 2017; Sommer & Bäckhed, 2013). Given the importance of microbe functional traits (often measured by their collective genome, transcriptome or metabolome) to understanding the mechanisms by which microbes impact host function, as well as frequent horizontal gene transfer across microbial phylogenies, the functional core is often measured at the gene rather than taxonomic level (Shafquat, Joice, Simmons, & Huttenhower, 2014; Turnbaugh et al., 2009). However, an important point to be made here is that while up to 80% of host-associated microbes perform some manner of biochemical function (Dunham et al., 2012), the large majority of these functions are likely not under host selection (Doolittle, Brunet, Linquist, & Gregory, 2014; Graur, 2017; Klassen, 2018). Therefore, functional effects of microbes do not necessarily lead to host fitness effects.

Both the functional core and the host-adapted core (described below) aim to understand the functional relevance of host-associated microbiomes, yet I draw from Klassen (2018) to distinguish between the two types of function. The functional core can be distinguished from the host-adapted core where (a) natural variation in the microbe-mediated function is not correlated with host fitness or (b) natural variation in the function is correlated with host fitness but can be performed by diverse, phylogenetically unrelated microbes. The functional core refers to the ensuing change in host function when a microbe (or gene) is removed, while the host-adapted core refers to the change in host fitness when the same microbe (or gene) is removed. Notably, these can differ when the measured function is biochemical in nature (e.g. nutrient metabolism, immune cell induction, protein binding, cell signalling, DNA methylation, etc.), for which there is little evidence of selection (Doolittle & Brunet, 2017).

Functional core microbiomes have been associated with regulation of metabolic pathways (Turnbaugh et al., 2009), plant nutrient metabolism (Mendes, Kuramae, Navarrete, Veen, & Tsai, 2014) or plant functional traits such as leaf chemistry (Kembel et al., 2014). An example of a functional core may be members of Bacteroidetes and Firmicutes phyla in herbivorous (and omnivorous) host species, because members of these phyla commonly degrade plant polysaccharides (Zou et al., 2019). The degradation of polysaccharides is essential for animals with plant-based diets, yet genes for polysaccharide degradation are common across the entire Bacteroidetes and Firmicutes phyla (El Kaoutari, Armougom, Gordon, Raoult, & Henrissat, 2013; Zou et al., 2019), and phylogenetically diverse taxa can perform this function. In this example, the relatively broad range of microbes that can digest polysaccharides may reduce selection pressure to promote the colonization and maintenance of any particular microbial species or genus. Moreover, it is unclear whether natural variation in polysaccharide digestion is correlated with host fitness across wild herbivorous species, although

selection pressure may occur during period of low food availability, or for species such as the Giant panda which remain poorly adapted to digesting bamboo (Xue et al., 2015). Therefore, while polysaccharide-degrading genes, mainly found across Bacteroidetes and Fimicutes phyla, may be considered the functional core of animals with plant-based diets, there is not enough evidence to suggest that particular suites of microbes are under selection. Nevertheless, further investigation may identify specific microbes that are under selection for this function in herbivores; for example, two specific *Clostridiales* species have been shown to increase digestive efficiency in cows (Shabat et al., 2016).

Functional genes can be spread across the microbial phylogenetic tree; consequently many broad functions of host-associated microbiomes (e.g. digestion and production of metabolites by gut microbiomes) can be performed by rare or low occupancy taxa (Jousset et al., 2017; Lynch & Neufeld, 2015). The functional core is therefore likely to include a much larger diversity of taxa than the common, temporal or ecological cores, if measured by taxonomy, and represent loose facultative associations between the host and numerous microbial taxa. Overall, while microbiome function can be measured numerous ways, measures that incorporate host physiology or phenotype will be more pertinent to understanding downstream effects on host populations than those based on gene content alone.

6 | THE HOST-ADAPTED CORE

The host-adapted core, first introduced by Shapira (2016), consists of specific microbial taxa that perform a function or functions that increases host fitness, either consistently or under particular ecological contexts, and their maintenance within the host population is a product of (host) natural selection. Therefore, the major criteria for the host-adapted core is that natural variation in the measured function correlates with host fitness *and* the function is performed by specific microbial taxa (and cannot be performed by other microbes). In addition, members of the host-adapted core are expected to be transmitted vertically to progeny or by cohabitation with family members (Fisher et al., 2017; Shapira, 2016), although many symbionts use both vertical and horizontal transmission to increase their spread (Ebert, 2013).

An example of a host-adapted core microbiome can be found in burying beetles, which vertically transmit specific microbes to their offspring that demonstrably aid their larval development (Shukla, Plata, et al., 2018; Shukla, Vogel, Heckel, Vilcinskas, & Kaltenpoth, 2018). Another example comes from Hiruma et al. (2016), which combines wild and experimental *Arabidopsis thaliana* plants to demonstrate that the host-adapted root symbiont *Colletotrichum tofieldiae* provides fitness benefits in low-nutrient conditions, occurs in only one part of the host species range, and has variable prevalence across sites (40%–80%). This study provides rare evidence that host-adapted microbes may not necessarily be abundant nor detectable across the whole host population, but may be restricted to sub-populations of the host species.

The identification of host-adapted microbes and the mechanisms by which selection occurs remains a significant challenge (Klassen, 2018; Kopac & Klassen, 2016). Nevertheless, candidates for host-adapted microbes may be related to specific ecological challenges or contexts faced by the host species that act as a selective force; for example, microbes that increase adiposity prior to hibernation in brown bears (Sommer et al., 2016), or, more broadly, facilitate growth during development (Ramayo-Caldas et al., 2016; Schwarzer et al., 2016; Videvall et al., 2018). Taxa which are highly phylogenetically conserved across the host phylogenetic tree ('phylosymbionts'; Brooks, Kohl, Brucker, Opstal, & Bordenstein, 2016; Moran, McCutcheon, & Nakabachi, 2008; Yeoh et al., 2017) also suggest host-adaption, although they can also reflect shared diet and physiology of closely related species (Woodhams et al., 2020) and may not always be adaptive (Xue et al., 2015). Finally, taxa that are vertically transmitted may also point towards host-adapted microbes, since vertically transmitted symbionts have the greatest impact on host fitness (Fisher et al., 2017).

Unlike the facultative symbionts represented by the functional core, host-adapted microbes are unlikely to have low occupancy across the host population because imperfect vertical transmission may obstruct host selection. However, host-adapted microbes may be restricted to particular populations (e.g. Hiruma et al., 2016) or detectable only during particular temporal windows, therefore may not always appear widely distributed nor abundant. Moreover, it should be noted that not all species may have host-adapted microbes (Hammer et al., 2019), with birds (and perhaps bats) in particular having low levels of phylosymbiosis and vertical transmission (Song et al., 2020; van Veelen, Salles, & Tieleman, 2018; Youngblut et al., 2019), suggesting low levels of dependence on microbes in these groups.

7 | CONCLUSIONS

The core microbiome is a widely used term, yet confusion and disagreement remain regarding its relevance to both ecological and biological research. The core microbiome has evolved to have many different meanings within the literature, yet in most cases it is used to mean a group of microbes that are particularly notable or important for various facets of host-associated microbiomes, whether those be their spatial distribution, stability, ecological influence or contribution to host function and fitness. Sometimes, these definitions identify overlapping components of the microbiome (e.g. common microbes are often temporally stable, and host-adapted microbes must be functional), yet each type of core reveals different layers of organization of host–microbe systems from which we can begin to understand ecological processes. While many studies ultimately aim to identify microbes (or their genes) that are important for host function and fitness, we should perhaps aspire to first understand common, temporal and ecological cores of host study systems before integrating these concepts into host ecology. For the core microbiome to be a useful concept going into the future, there needs to be wider acknowledgement that host-associated microbes act and are of interest independently of host

function, and that this should be reflected in a more precise and well-defined lexicon surrounding the core microbiome.

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DATA AVAILABILITY STATEMENT

This commentary uses no data.

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