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Hypothesis or Opinion

A new conceptual framework for host-microbe symbiosis

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Abstract

Host-microbe relationships are studied across biological disciplines, with unique but overlapping conceptual frameworks arising from each of them. Without a unified framework that can be applied across all host-microbe symbioses, we cannot do the interdisciplinary work necessary to understand the underlying rules that govern them. Here I present a new conceptual framework for host-microbe symbiosis, rooted in the original definition of symbiosis, across three axes: fitness effects, partner fidelity and transmission mode. The three axes make a cube where any symbiotic relationship can be placed. The position of a particular symbiosis is fluid and context-dependent, changing through evolution and throughout the lifetime of an organism. The three axes make for a simple and inclusive framework for symbiosis. We can use this framework to examine every known host-microbe symbiosis, which will allow us to understand the rules and patterns that govern them.

Keywords **symbiosis, transmission mode, partner fidelity, fitness effects**

Lay summary

Researchers from many different fields study host-microbe symbiosis using different conceptual frameworks and terminology. This makes interdisciplinary work challenging. This paper introduces a new, unified way of thinking about host-microbe relationships that anyone in the field can use. It organizes these relationships along three dimensions: how the relationship affects each partner's fitness, how reliant each partner is on the relationship, and how the microbial symbiont is passed from one host to another. Together, these three dimensions form a cube, and any host-microbe symbiosis can be placed somewhere inside it. Importantly, a relationship's position in the cube is not fixed. By using a shared framework, we can compare all known host-microbe relationships and start to uncover the common rules that shape them all.

Introduction

Symbiosis is a commonly used and contentiously argued term. It was first coined by De Bary in 1879, often quoted as "the living together of unlike organisms" but in the English translation by Oulhen *et al.* [1] "the living together of differently named organisms". Regardless of the exact wording, one important point is that, within this definition, symbiosis ranges from mutualistic interactions where both partners benefit, to parasitic ones, where one partner benefits while the other is harmed. It has long been accepted that these relationships exist on a spectrum rather than in discrete categories [2–5]. This shift in thinking has allowed us to see that there are commonalities and contrasts in how parasites, commensals and mutualists interact with their symbiotic partners [6]. It also allows us to think about how these relationships change: besides a few notable symbioses that abruptly transition between categories, generally, symbioses shift along the fitness continuum with a changing ecological context. Examples of changing ecological contexts that can affect the position on along the fitness continuum (and other axes) are resource availability, stress gradients, frequency of disturbance, other members of a community, population density, age, drugs or other chemicals, and many others.

In addition to the spectrum of fitness effects [2, 5], other axes have also been considered on continua: how the interactions between spectra of dependency and transmission mode shape mutualisms [7], or how the host response can affect transitions between pathogens and commensals [8]. In this new framework, I combine the fitness effect axis with two other axes, partner fidelity and transmission mode, allowing us to compare different symbiotic relationships in multidimensional space. My hope is that this conceptual framework can be used across disciplines to provide a unified definition and framework for host-microbe symbiosis, making us better equipped to understand patterns in how symbioses occur and change in nature.

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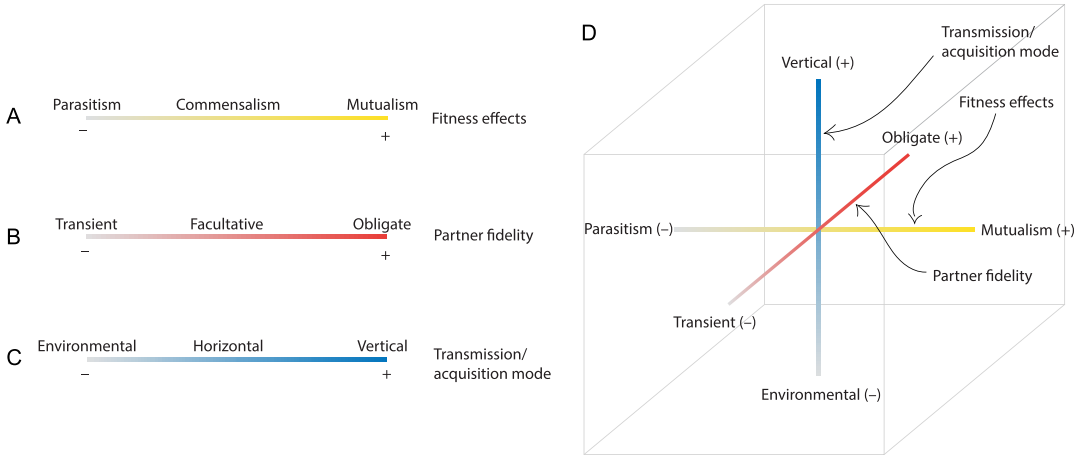


Figure 1 The three axes of symbiosis separately (A, B and C) and as a cube (D).

Fitness effects

As I briefly introduced above, the first axis of symbiosis to consider is that of fitness effects, namely, how two organisms in a symbiotic relationship affect each other's fitness (Fig. 1A). A mutualistic relationship is one where both partners benefit. Some classic examples of mutualism include aphids and *Buchnera* bacteria [9], bobtail squid and *Vibrio fischeri* [10], humans and *Bifidobacteria* [11], algae and fungi in lichens [12] and legumes and nitrogen-fixing rhizobia [13].

Parasitism exists at the opposite end of the spectrum of fitness effects, where one partner benefits at a fitness cost to the other partner. These relationships include those that are traditionally grouped under the category of medical parasitology, such as tape worms, lice, and *Giardia* [14], but also any organism that is considered a pathogen, such as HIV [15] and pathogenic *Salmonella* in humans [16] chytrid fungi that cause chytridiomycosis in amphibians [17], and *Escovopsis* in the fungus gardens of leaf-cutter ants [18].

Between mutualism and parasitism lies commensalism, where one partner benefits and the other experiences no fitness effects. Many examples of phoresy, where a smaller organism uses a larger organism for dispersal, are considered commensal [19].

Every symbiotic relationship lies somewhere on the axis of fitness effects. However, its position along the axis is not static and can change through evolution and across ecological time and space [5]. There are countless examples of instances of change across the fitness effects axis: commensal microbes becoming opportunistic pathogens when the host's immune system is compromised [8], the breakdown of the mutualism between corals and Symbiodiniaceae during coral bleaching [20] and mutualistic endophytes evolving from latent pathogens [21]. Some relationships are less context-dependent than others (Box 1). For example, the relationship between fungus-growing ants and their cultivar is always a mutualism. This relationship has co-evolved for tens of millions of years, and there is very little that can move the relationship from this position [22]. But even within the mutualism space, one ant colony may serve as a more effective disperser and so would provide greater fitness benefits to the fungus compared to a colony with less effective dispersal. In this case, the relationship would not switch from being a mutualism to a parasitism, but if we compared the two ant colonies across the axis, one would be further toward the extreme end of mutualism than the other. This variation in symbiosis-related fitness effects between members of a population, along with the variation in the environment in which the relationships exist, are the fodder for evolutionary change across the axis.

Partner fidelity

Symbioses are often categorized as falling into one of two discrete levels of partner fidelity: obligate or facultative. Classically, obligate is the case when at least one partner cannot survive without the other, and facultative is when there may be fitness effects in a symbiosis, but the partners can still survive without the other. I argue that the concept of a facultative symbiosis is just a way to capture the inherent context-dependency of partner fidelity. We see this in the relationship between legumes and their root symbiont rhizobia bacteria. This symbiosis is used as a classic example of a facultative mutualism (Box 2). If a legume plant is grown in nitrogen-rich soil, the number of root nodules that it produces is reduced because this function is not necessary for the plant [23]. One could argue that *when nitrogen is present* in the soil, this relationship is facultative. However, what happens if you grow this plant in soil with no nitrogen at all? I argue that this plant can no longer survive without its mutualistic partner, and so the relationship would become obligate. In this case, the partner fidelity depends largely on resource (nitrogen) availability in the local environment.

As the legume/rhizobia example illustrates, instead of defining obligate and facultative as discrete categories as we have always done, I think we should describe partner fidelity along a context-dependent axis (Fig. 1B). At one end we have obligate relationships where the partner pair is always together, at the other end we have transient relationships where the pairing happens by chance, and everything in the middle is facultative. What is a transient pairing? A host may acquire any number of members of the microbiome that just end up living on or near the host for a time. The relationship between host and a transient symbiont is ephemeral but presents an opportunity for the symbiont and host to interact. For example, when any animal eats food, it will ingest some microorganisms—if they do not die immediately, they can turn out to be mutualists, commensals, or parasites/pathogens. They may have no partner fidelity and pass quickly from the system, but they can still potentially have fitness effects on the host. Regardless of the fitness effects, these transient relationships provide a novel niche for the symbiont, where the relationship may change to one with more fidelity in the future.

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Table 1 Categories and subcategories of transmission modes from most intimate (top) to least intimate (bottom). The categories in the first column of the table correspond to the transmission mode axis in Fig. 1C.

Traditional category	Subcategory	Real-world examples	Citations
Vertical transmission	Intracellular endosymbiont passed to daughter cells	Prophage during binary fission; *Chlamydia* during mitosis	[26, 27]
	Endosymbiont transmitted through germ line	*Buchnera* housed in bacterio and passed to egg; *Wolbachia* housed in ovaries and passed to egg	[28, 29]
	Symbiont transferred during birth, hatching, eclosion or germination	Infant acquiring symbionts during vaginal birth; Stinkbug gut symbiont transferred to egg capsule	[30, 31]
	Symbiont transferred from parent after birth, hatching, eclosion or germination	Infant acquiring symbionts during breast-feeding; fungus-growing ants acquiring protective actinobacteria from queen after eclosion	[30, 32]
Horizontal/ vertical transmission	Symbiont transferred from conspecific after birth, hatching, eclosion or germination	Infant acquiring symbionts during allomaternal care; fungus-growing ants acquiring protective actinobacteria from a nestmate after eclosion	[32, 33]
Horizontal transmission	Direct contact between conspecific hosts	Sexual transmission of Hepatitis C virus	[34]
	No contact between conspecific hosts	Transmitting an infectious virus by coughing directly onto a conspecific	[35]
Horizontal/ environmental transmission	A symbiont remains in the environment in dormant form for an extended time	SARS-CoV-2 remaining suspended in aerosols for many hours; acquisition of a long-dormant virus from thawing permafrost	[36, 37]
Environmental or vector transmission	A symbiont has free-living generation(s) or associates with another host	*Vibrio fischeri* environmental acquisition by bobtail squid; Malaria parasite transmission by a mosquito vector; dietary acquisition of symbiont from the food source	[38–40]

Where a relationship lies on the spectrum from obligate to transient will depend on context, and the position can change across ecological and evolutionary time scales. Like the fitness effects axis, the flexibility of the position along the partner fidelity axis will vary for symbiotic partners. There are some relationships in nature that we could classify as strictly obligate. *Chlamydia* and many other intracellular parasites can only reproduce inside of host cells, and so context dependency is low for the position of the relationship between *Chlamydia* and its host along this axis [24] .

Finally, the position along this axis will depend on which partner we are considering in the relationship. In the case of *Chlamydia* (and other parasites), the relationship for the symbiont can be obligate, but clearly, the host can and does survive without the symbiont. Therefore, the relationship is obligate for the parasite, but there is no fidelity from the perspective of the host, making this a one-sided symbiotic relationship. Even for mutualisms, we can have one-sided symbioses. Corals have an obligate relationship with Symbiodiniaceae, but the algae can be free-living in the water column. These asymmetrical relationships will be discussed further in the "three axes make a cube" section.

Transmission mode

Transmission mode of a symbiont can vary widely, having important effects on the nature of the relationship. Traditionally, transmission modes have been placed into discrete categories that vary in their level of intimacy [25]: Vertical transmission is the most intimate and is where a symbiont is transmitted from parent to offspring. Horizontal transmission occurs when a symbiont is shared between two conspecifics, and is at an intermediate level of intimacy. And finally, environmental transmission occurs when the symbiont comes from the environment. Within each of the traditional transmission categories, there are already existing gradations, and they fall nicely on a spectrum (Table 1).

I believe that our understanding of symbioses would be improved if we considered transmission modes along a spectrum, rather than discrete categories (Fig. 1C). Along the transmission mode axis, the symbiont will vary in its ability to persist outside of the host. Typically, vertically transmitted, or tightly horizontally transmitted symbionts will not survive outside the host, whereas at the far end of the spectrum in environmental transmission, the symbionts will either have a resilient dormant phase that can persist for a long time or can have multiple free-living generations outside the host before finding a new host.

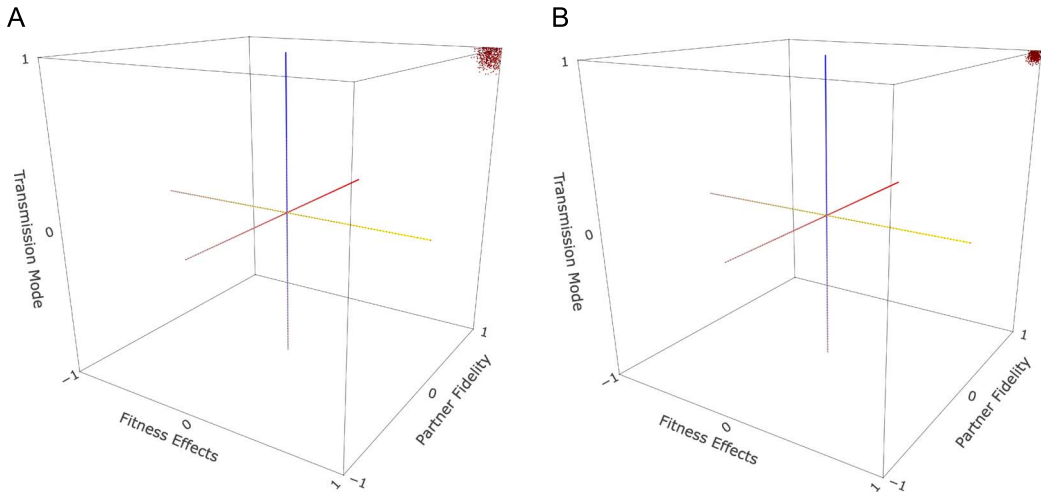
A classic example of strict vertical transmission is that of aphids and *Buchnera* bacteria, which the aphids house in specialized cells called bacteriocytes, in an organ called the bacteriome. The parent aphid uses a precise mechanism for ensuring the *Buchnera* is transmitted from its bacteriocytes into the embryo [28]. Vertical transmission can happen in a slightly less intimate way as well. For example, when a human gives birth through the vaginal canal, the infant receives its initial microbiome from the parent. But the infant also receives some members of its microbiome during the process of breastfeeding and by sharing intimate space with its birthing parent [30]. At what point do we consider transmission of symbionts from parent to offspring vertical transmission vs horizontal transmission from individuals who happen to be the child's parents? Notably, if a child acquires symbionts from breastfeeding from a non-parent individual, then this would be considered horizontal transmission even though the process of acquisition is the same [33]. These examples demonstrate that the

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Box 1. Comparing two obligate, vertically transmitted mutualisms

Atta cephalotes, like other fungus-growing ants, relies on a fungal cultivar to survive. The ants cut leaves that they feed to the fungus, and the fungus produces gongylidia for the ants to eat for most of their nutrition. Neither the fungus nor the ant can survive without the other. When an unmated queen emerges from her mother's colony, she will carry a tuft of fungus in her infrabuccal pocket and use that to start her own fungus garden. The relationship can be described as an obligate mutualism with vertical transmission and would appear as a small cloud in the symbiosis cube [22]. However, there is some variation and context-dependency in this system. There will be variation between individuals in both populations of cultivar and ants that will make it so that along all three axes, there will be some spread in the cube. Other contextual factors may vary as well. Other community members in the fungus gardens can change the relationship between the ant and the cultivar. For example, an *Escovopsis* parasite of the cultivar will cause harm to the fungus and will increase the level of partner fidelity in the relationship because the cultivar will rely on the ants to weed and groom their gardens. In the absence of the parasite, this relationship would be less obligate. While the ants have a mechanism for vertical transmission, very rare horizontal transmission events are possible, particularly during mating flights or if a colony moves into an abandoned nest [48]. To visualize this relationship in the cube, we would see a small cloud in the corner, near the extremes of all three axes.

The pea aphid *Acyrthosiphon pisum* and its bacterial endosymbiont *Buchnera aphidicola* also have an obligate, vertically transmitted mutualism [9, 28]. Across all three axes, this relationship is more constrained and less context-dependent than the relationship between *A. cephalotes* and Leucoagaricus *gongylophorus*. Therefore, it would appear as almost a dot on the symbiosis cube. Even for the aphid/*Buchnera* relationship, there is variation between individuals in the populations of both symbiotic partners, so it will not be an exact dot, but it will be a very tightly constrained cloud compared to other more context-dependent symbioses. For a description of how these figures representing hypothetical values were made, refer to the Supplemental Methods and Supplemental Table 1.



Symbiosis cubes representing the relationships between (A) leaf-cutter ants and *L. gongylophorus* and (B) aphids and *Buchnera*.

boundary between vertical and horizontal transmission can be diffuse and that how we define transmission mode in a symbiosis is context-dependent. They support the notion that vertical and horizontal transmission should be placed on a spectrum rather than discrete categories.

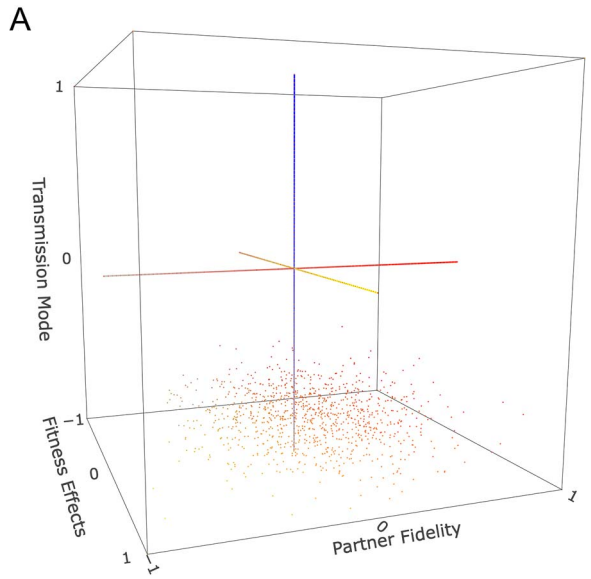
Similarly, the boundary between horizontal transmission and environmental transmission is not clear. Let's consider the example of SARS-CoV-2. If someone infected with the virus infects another person through close contact, this would be horizontal transmission. However, if someone coughs the virus out in a room and it remains suspended in the air for several hours, then another person walks in and breathes it in, the transmission mode would exist somewhere between horizontal and environmental transmission [41]. There are other symbionts, for example HIV, *Chlamydia*, or the Hepatitis C virus that cannot be environmentally transmitted—they must be either horizontally or vertically transmitted because they cannot persist outside of a host's tissues. Once again, the position of a relationship along this axis is context-dependent, but the level of context-dependency varies from one relationship to another.

Importantly, some symbionts are transmitted by vectors or intermediate hosts. This may seem to break the transmission mode axis. Instead, for the purposes of this conceptual framework, I lump vector transmission with environmental transmission. Clearly, these phenomena are very different, but if we focus on just the relationship between the two focal partners in a symbiosis, we can use a separate cube for the relationship between the symbiont and vector. For our focal species, whether a symbiont is transmitted through the environment or through a vector, it still requires some kind of adaptation that allows for it to be separate from its symbiotic counterpart, either to tolerate being in the environment or to be successfully picked up by a vector. For the sake of simplicity, environmentally acquired and vector transmitted symbionts can be grouped together on the far end of the transmission mode spectrum from vertical transmission, where the symbiont must remain in constant contact with the host.

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Box 2. A classic facultative symbiosis

Medicago truncatula is a model legume plant that associates with *Sinorhizobium* spp. as well as many other species of bacteria that provide nitrogen fixation to their host. Both the fitness effects and partner fidelity are highly context-dependent while the transmission mode is consistently environmentally acquired. This type of relationship would create a flattened disk in the symbiosis cube.



Symbiosis cube representing the relationships between *Medicago* and *Sinorhizobium*.

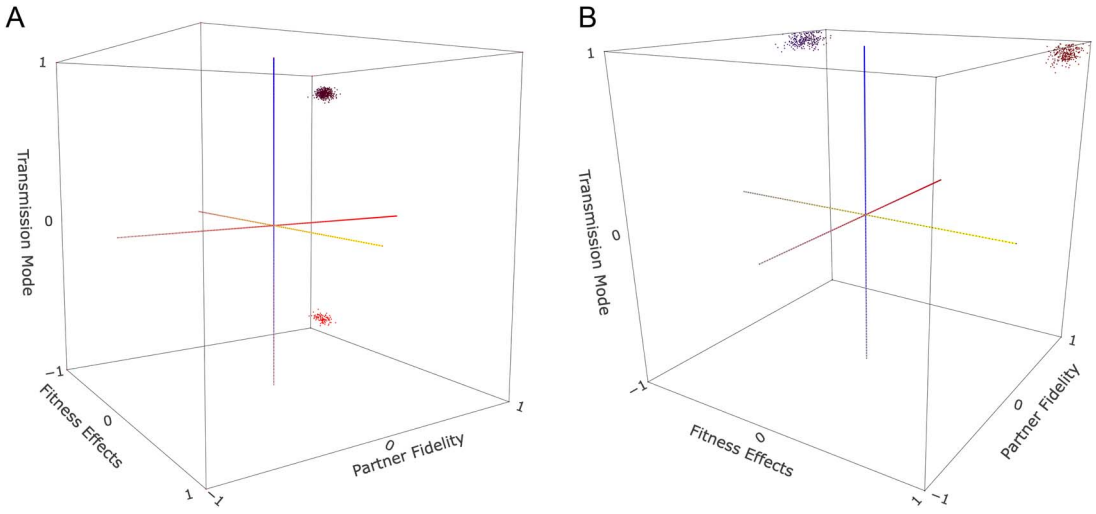
Three axes make a cube

Every symbiotic relationship can be placed somewhere in the three-dimensional space of a cube created by the three axes (Fig. 1D), occupying a cloud of probability space (Boxes 1–3). In cases where there is not a lot of context-dependent flexibility, the cloud will be small, and where a relationship is heavily context-dependent, it will be large. The cloud of possible relationship space will not necessarily be symmetrical. A relationship may be heavily context-dependent along one axis but not the others. Through either ecological or evolutionary time, many symbiotic relationships may transition gradually across the axis of fitness effects, from commensal to mutualistic or commensal to parasitic, or even from mutualistic through commensal to parasitic. However, this is not the case for all symbiotic relationships. Transitions between mutualism and parasitism can also happen abruptly [42]. In these cases, the cloud of possibilities for a symbiotic pair would not pass through commensalism. Instead, this relationship could be represented by two clouds of possibility at the extremes of the axis of fitness effects. This should be the case for the other axes as well, and indeed there can also be discrete clouds along the transmission mode axis. For example, dengue virus is typically vector-transmitted but can also be vertically transmitted through umbilical cord blood; however, it is never horizontally transmitted [43] (Box 3). Earlier, we encountered the problem of asymmetrical symbioses, particularly for the purpose of partner fidelity (obligate for one partner but not for the other). To solve this problem, when we make a cube for a symbiotic relationship, we should note for which partner the relationship is obligate. Similarly, for the transmission mode axis, we should note which symbiotic partner is being transmitted.

As it is now, we can use this conceptual framework start to think about how symbioses will fill it with hypothetical numbers based on

Box 3. Abrupt transitions across axes

While context-dependent transitions will often occur gradually across an axis, sometimes there can be abrupt transitions. Here we have two examples of how these abrupt transitions can be visualized. The first is of a plant endophytic fungus, *Colletotrichum magna*, which through a single-locus mutation can go from being a pathogen to a mutualist, which acts as a defensive symbiont for its host plant [42]. Next is the example of dengue fever, which is usually transmitted by a vector, but can also be occasionally transmitted vertically through the placenta, but never through horizontal transmission [43].



Symbiosis cubes representing the relationships between (A) humans and dengue virus and (B) a host plant and *C. magna*.

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the ecological and evolutionary patterns that we would expect, as I have done for the cubes in Boxes 1–3. However, important steps need to be taken to go from conceptual framework to comparative tool and eventual theoretical models. The next step is to create a standardized method for quantifying relationships across the axes. This is not trivial, but some attempts have been made toward this goal [25, 44]. I particularly appreciate the approach that Ollerton took in the attempt to quantify "intimacy" [25] and imagine that as we proceed, we could make subcategories for each axis (like in Table 1 for transmission mode) and provide scores depending on which subcategories a relationship occupies and how context-dependent that relationship is along the axis. Once we have this standardized method, then for each symbiosis that we study, we could produce a cube that represents it. Cubes for different symbioses can then be put side-by-side (similarly to how they are in Box 1) to be used as a comparative tool to standardize how we describe symbioses.

Another approach we can use is to populate a universal cube with every described symbiosis; then we may observe interesting patterns or even rules. I expect that we will see more symbioses toward the edges of the cube, largely because as scientists, we are drawn to striking phenotypes. But there may also be patterns that result from the realities of biology. For example, obligate mutualists will tend to be vertically transmitted, whereas parasites will be more likely to be horizontally or environmentally transmitted [44, 45]. One rule that emerges from thinking in this holistic way is that environmentally transmitted obligate symbionts must have a dormant phase. You can see this with viruses – all of them are obligate to their hosts, and all of them have a dormant particle phase when they are outside of their host cells. This rule holds for parasites such as *Giardia* and *Chlamydia* as well. There are no parts of the cube where it is impossible for a symbiotic relationship to exist, but there will be regions that will be less populated because of the interaction between the axes resulting in the types of patterns described above.

There is some debate around the bounds of symbiosis, particularly as it relates to the level of intimacy necessary in a relationship to consider it a symbiosis. For an excellent discussion of this debate, refer to the review by Martin and Schwab [46]. For this perspective, I have focused only on symbioses involving at least one microbial partner. Since microbes have rapid generation times, one can assume that their time associated with a host involves multiple generations, so we can consider all host-microbe relationships under symbiosis. If we wanted to expand this conceptual framework beyond host-microbe symbioses to include all mutualisms, parasitisms, and commensalisms, I believe that we could, but we would need to add at least one more axis to capture levels of intimacy in the relationship. However, that is a topic for future work.

I believe that by using this conceptual framework, we will have a powerful tool to understand patterns in host-microbe symbiosis more broadly by examining which parts of the cube are more commonly occupied. Specifically, we can ask questions about the tendencies and the mechanisms behind transitions between locations on the cube. Are there parts of the cube that are harder to occupy and why? Are there certain transitions that are more likely than others? Transmission mode, fitness, and partner fidelity are interrelated and, particularly as we consider evolutionary changes in symbiotic relationships, we would expect there to be feedback between the different axes [45, 47]. Does vertical transmission lead to mutualism, or does mutualism lead to vertical transmission? Given a particular ecological context, will the future positioning of a symbiotic relationship be predictable? I believe that by adopting this framework, where each factor of symbiosis is considered along three interrelated axes, we will more easily be able to answer these types of questions.

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Author contributions

Lily Khadempour (Conceptualization, Funding acquisition, Visualization, Writing—original draft, Writing—review & editing)

Supplementary material

Supplementary material is available at *ISME Host Microbe* online.

Conflicts of interest

The author declares no conflicts of interest.

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