Trends in Microbiology

CellPress

Opinion

Thank you for biting: dispersal of beneficial microbiota through 'antagonistic' interactions

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Multicellular organisms harbor populations of microbial symbionts; some of these symbionts can be dispersed through the feeding activities of consumers. Studies of consumer-mediated microbiota dispersal generally focus on pathogenic microorganisms; the dispersal of beneficial microorganisms has received less attention, especially in the context of 'antagonistic' trophic interactions (e.g., herbivory, parasitism, predation). Yet, this 'trophic transmission' of beneficial symbionts has significant implications for microbiota assembly and resource species (e.g., prey) health. For example, trophic transmission of microorganisms could assist with environmental acclimatization and help resource species to suppress other consumers or competitors. Here, we highlight model systems and approaches that have revealed these potential 'silver-linings' of antagonism as well as opportunities and challenges for future research.

Trophic transmission: microorganisms on the move

Virtually all multicellular organisms harbor symbiotic communities of microorganisms, including bacteria, single-celled eukaryotes, and/or viruses, which affect their health and performance. Given the pivotal roles of microorganisms in host function, it is important to understand the processes that disperse microbial symbionts in the environment, making them available to prospective hosts [1–3]. Trophic transmission is one potentially important dispersal mechanism in which microorganisms are distributed throughout the environment and among hosts via **consumer–resource** (see Glossary) interactions (Box 1). However, based on a thorough literature search, few studies of trophic transmission examine the dispersal of beneficial microbiota (10%, 26 of 268 studies, blue bars in Figure 1; for more information see Box S1 and Tables S1 and S2 in the supplemental information online). In our search results, the dispersal of beneficial microorganisms was relatively more frequently documented in studies of **mutualistic** and **commensal trophic interactions** (Figure 1). For example, bacteria and yeasts that might increase the fitness of flowering plants are dispersed by nectar-feeding pollinators [4,5]. Similarly, microbiota that increase the digestive capacity of their pitcher plant hosts are dispersed by midges and mosquitoes, which live as commensals in pitcher plant leaves [6,7]. Instead, most trophic transmission studies focus on the dispersal of harmful organisms via **lethal consumption** and **nonlethal consumption**, which span predation, herbivory, and parasitism (red bars in Figure 1 and Figure 2A,B); this is likely due to the direct negative impacts these microorganisms have on the health of humans, domesticated animals, and agricultural crops. In our literature search, only ~3% and ~7% (three of 90; seven of 96) of studies on lethal and nonlethal consumption reported the dispersal of beneficial microorganisms (blue bars in Figure 1; examples discussed in the following text).

We posit that consumer-mediated dispersal of beneficial microbiota is more common than reported across the full spectrum of trophic interactions, including lethal and nonlethal consumption (Figure 1, but see Box 1). We hypothesize that antagonistic consumers can indirectly benefit resource species in various ways. For instance, trophic transmission may promote resource

Highlights

Trophic interactions, from predation to pollination, can disperse microorganisms throughout natural systems and built environments.

Accounting for consumer-mediated dispersal of microbiota across the spectrum of trophic interactions will advance theory and experimentation in key areas of microbiology and ecology, including community assembly processes and food web theory.

Predation, herbivory, and parasitism are generally considered to be antagonistic in their effects on resource species (e.g., prey). Yet resource species can indirectly benefit from these interactions via increased access to symbiotic microbiota, suppression of competitor species, and potentially, acclimatization to changing environments.

Traits of microorganisms and consumers mediate successful trophic transmission in space and time and can be leveraged in applications from medicine to agriculture to ecosystem restoration.

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Box 1. Dead-end consumers: when trophic transmission of microbiota does not occur

Although this review discusses the understudied cases in which interactions considered 'antagonistic' may disperse beneficial bacteria, it is important to recognize that trophic transmission does not always result from antagonistic interactions. Consumption can benefit resource species when harmful microorganisms are removed from their diseased tissues (or the environment) and rendered nonviable. Many integrated pest management efforts, in fact, rely on consumers removing pathogenic microorganisms from a given system and rendering them inert. In agricultural systems, predators such as ladybird beetles (Coccinellidae) are an important form of natural pest control that is used to reduce aphid populations [69]. Consumption of aphids can secondarily benefit plants by limiting the extent to which aphids vector *Pea Enation Mosaic Virus* (PEMV), by limiting herbivore pressure and reducing PEMV prevalence on plant hosts [70]. Additionally, many grasses harbor symbiotic fungi (*Epichloë* spp.) that protect their hosts from herbivory through alkaloid production. *Epichloë typhina* can be transmitted both horizontally and vertically; simulated folivory increased vertical transmission of the fungus and plant tolerance to damage [71]. This relationship may be broadly generalizable: under pressure from herbivores, symbiotic microorganisms that provide their hosts with antiherbivore defenses may be less likely to experience trophic transmission and, instead, be propagated vertically.

Most studies of trophic transmission address the spread of harmful pathogens by consumers (see Figures 1 and 2A,B in main text). Yet, antagonistic interactions can also benefit prey when they remove pathogens from a system, render them nonviable, or otherwise limit transmission. On coral reefs, white syndrome diseases among acroporid corals are potentially caused by harmful infections of *Vibrio* bacteria [72]. The crab *Cymo melanodactylus* lives on acroporid branches and often feeds on coral mucus. When acroporids become infected with white syndrome pathogens, *C. melanodactylus* can drastically diminish the spread of the disease, potentially because the crab feeds directly on damaged tissues (i.e., debridement, [73]). A similar relationship is hypothesized to exist – but has yet to be empirically demonstrated – for the coral-eating butterflyfish, *Chaetodon capistratus*, and stony coral tissue loss disease-affected corals and pathogenic microbiota [74–76]. As additional consumers that limit disease in resource species are identified within natural environments, resource managers and communities can leverage these relationships to promote ecosystem resilience and support restoration efforts.

species acquisition of beneficial microbiota (Figure 2C,D); such microbiota may contribute to host health, function, and acclimatization to environmental change. Consumers may additionally benefit resource species by dispersing microorganisms that are pathogenic to other (nonvector)
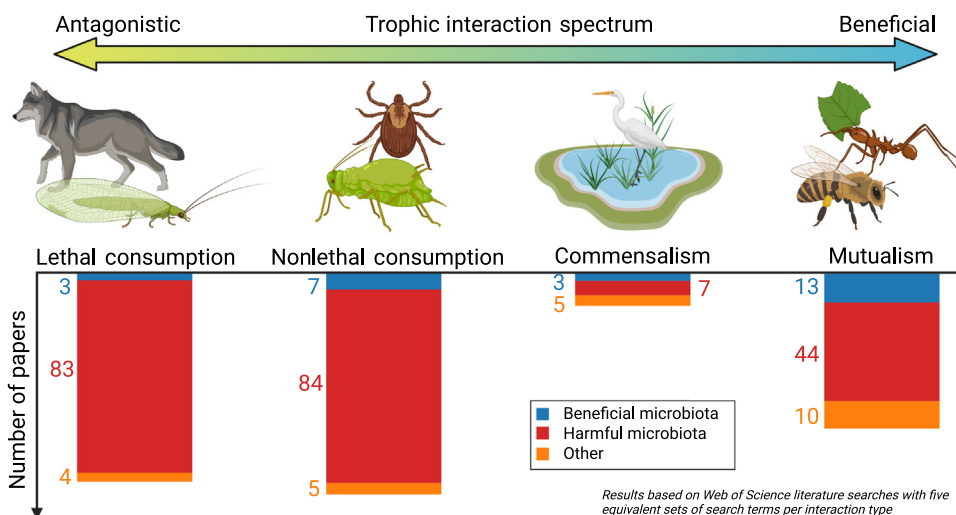

Figure 1. Consumer-mediated dispersal of microbiota across a spectrum of trophic interactions. Trophic interactions span a continuum from primarily antagonistic (lethal and nonlethal consumption) to primarily beneficial (mutualism). Based on a keyword search of the ISI Web of Science (year of publication, 1900–2021; Box S1, Table S1, S2), most studies examine the trophic transmission of microorganisms that have primarily harmful effects on hosts (red bars). Although few studies address the consumer-mediated dispersal of predominantly beneficial microbiota (blue bars), we posit that this is an important process that occurs frequently. In some studies, the hypothesized effect of the dispersed microbiota on resource species is neutral or unknown (other, orange bars). Lethal consumption includes parasitoidy and lethal predation and herbivory; nonlethal consumption includes parasitism and sublethal predation and herbivory. Organisms depicted: wolf, lacewing (lethal consumption); tick, aphid (nonlethal consumption); wading birds dispersing algal cysts (commensalism); leafcutter ant, bumblebee (mutualism). Figure made with BioRender.com.

Glossary

Aposymbiotic: when two organisms that are typically found in symbiosis live separately from each other (e.g., plants without mycorrhizal fungi).

Bleaching: the loss of endosymbiotic dinoflagellate (family Symbiodiniaceae) populations from marine invertebrate hosts, resulting in the whitening of host tissue and diminished host health.

Commensal: an organism that is positively affected from interacting with another type of organism; the latter organism is not affected positively or negatively by the interaction.

Consumer: a heterotrophic organism that intakes and digests resource species (or components of them) for energy. Examples include herbivorous and predatory organisms, as well as parasites and nectar-feeding pollinators.

Corallivores: animals that consume corals.

Facultative symbionts: microorganisms that may or may not engage in symbiosis with a given host organism; a symbiotic partnership with these microorganisms is not required by the host.

Foundation species: habitat-forming organisms that have an important role in structuring ecosystems. Can be any trophic level. Examples include kelp, corals, and trees.

Generalist: an organism that has a broad niche and can use a wide range of resources.

Horizontal transmission: acquisition of microorganisms by individuals from an external (nonparental) source.

Lethal consumption: interactions in which the consumer benefits but the resource species typically dies, including parasitoidy, lethal predation, and herbivory.

Mutualistic: refers to interactions in which both participating species benefit, such as in plant-pollinator interactions.

Nonlethal consumption: interactions in which the consumer benefits and the resource species incurs a fitness cost but typically survives, including parasitism, partial predation, and herbivory.

Rhizosphere: a layer of soil that is influenced biologically, chemically, and physically by the growth of plant roots and associated organisms.

Resource: organisms consumed by consumers for energy. Includes many plants and some animals and microorganisms.

consumers (Figure 2E). Although we posit that indirect benefits due to microbial dispersal are a common outcome of antagonistic trophic interactions, research effort on this topic has been relatively diffuse and is rarely incorporated explicitly into ecological theory. Integrating the transmission of microbiota into traditional food webs (Figure 2) and microbial metacommunity models can improve our understanding of relationships among hosts, their microbiota, consumers, and the environment, with implications for ecological processes (e.g., host-associated microbiota assembly) and phenomena (e.g., trophic cascades). Accounting for these interactions can thus advance theory and experimentation within the fields of microbiology and ecology, and support objectives in applied fields, such as agronomy, medicine, and ecological restoration.

Indirect benefits of microbial dispersal during antagonistic trophic interactions

Antagonistic trophic interactions have a direct negative impact on the health and/or reproduction of the resource individual consumed. Yet predation, herbivory, and parasitism may drive microbiota assembly in **horizontally transmitting** resource species by transferring microorganisms to prospective hosts or distributing them in local environmental reservoirs, from which hosts can subsequently acquire them. Even for **vertically transmitting** hosts [8], consumers may sometimes influence microbiota assembly if they introduce a microorganismal strain to a naïve host population. In the following text, we discuss findings suggesting that antagonistic trophic interactions can provide resource species with a 'silver lining' by facilitating their acquisition of microbiota, which may support their acclimatization to environmental change, or by dispersing pathogens to other (nonvector) consumers.
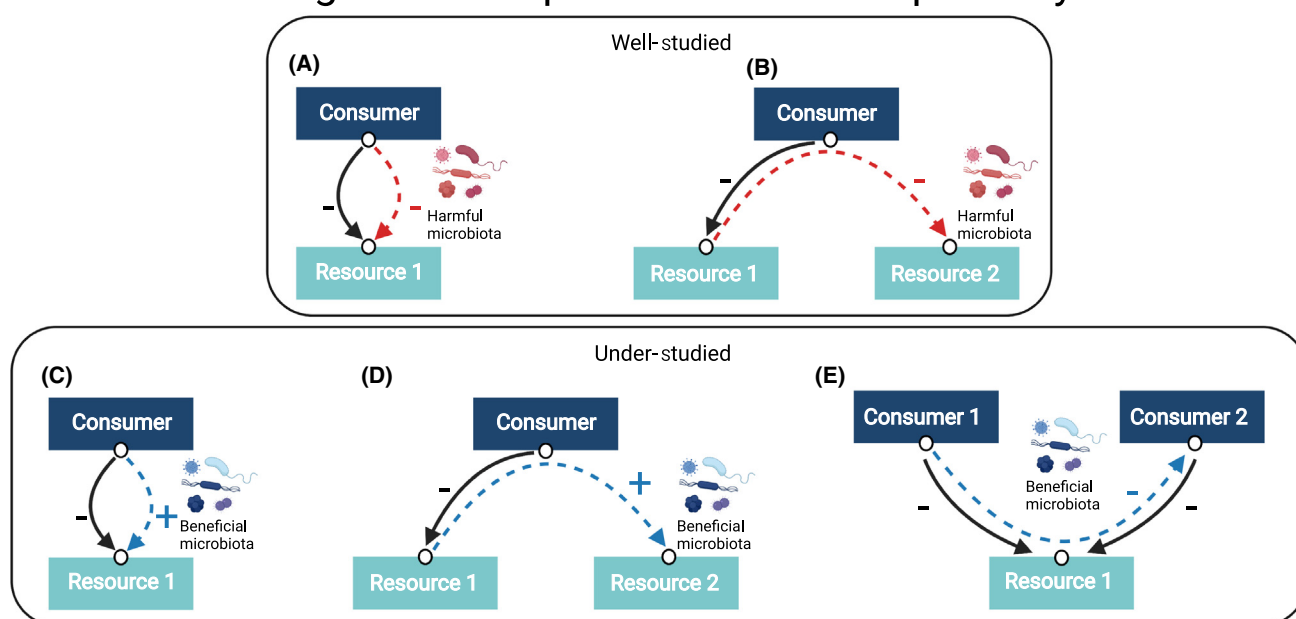
Sessile: organisms that are immobile, fixed in place (e.g., plants, corals, oysters).
Specialist: an organism that has a narrow niche and can use a limited range of resources.
Trophic interactions: interactions between organisms involving the transfer of energy.
Vertical transmission: acquisition of microorganisms by individuals from a parental source.

Antagonistic trophic transmission pathways

Figure 2. Conceptual representation of ways in which antagonistic consumer–resource interactions (unbroken lines) affect resource populations through the dispersal of microorganisms harmful (A,B) or beneficial (C,D,E) to resource species (broken lines). The process through which antagonistic consumers disperse harmful microbiota, such as viral or bacterial pathogens, either among individuals in a population of a resource species (A) or from one resource species to another (B) has been relatively well studied. By contrast, the dispersal of beneficial microbiota between individuals in a population of a resource species (C), or from one resource species to another (D), is understudied, as is the dispersal of microbiota that may benefit recipient resource species by deterring other antagonistic consumers (E). Figure made with BioRender.

Antagonistic interactions can support resource species in acquiring their microbiota

Trophic transmission of microbiota might be particularly important for **sessile** resource species, such as plants, corals, sponges, and algae, many of which are **foundation species**. For example, many plants rely on dispersal-limited, beneficial mycorrhizal fungi that enhance their ability to absorb nutrients and water (amongst other functions; [9]). Diverse invertebrate and vertebrate herbivores transport these fungi by carrying plant material or soil or by excreting viable fungi or fungal spores (Figure 2C,D; [10,11]). Mycorrhizal dispersal has been demonstrated to facilitate plant invasions [12], and dispersal by herbivores can facilitate plant colonization during primary succession [13]. In fact, some plants can successfully establish in novel regions only by coinvading with their fungi [14]. Research on the trophic transmission of mycorrhizal fungi has been facilitated by the development of cost-effective approaches specific to these microbiota, such as spore germination and staining assays [15]. 'Bait plant' approaches, in which naïve host plants are inoculated with herbivore feces, have made it possible to quantify the viability, trophic transmission, and germination of mycorrhizal spores (reviewed in [15]). Network-based approaches have also recently been used to quantify the contribution of different consumer animals to the dispersal of different types of mycorrhizal fungi [16]. Similar approaches could be used to test for the trophic transmission of other plant mutualists, such as endophytes, as well as fungal pathogens and commensals to cnidarians and bivalves (e.g., pathogenic *Aspergillus sydowii* fungi to Caribbean gorgonian corals by the coral-eating snail *Cyphoma gibbosum* [17]).

Beneficial microbial symbionts can also be transmitted during antagonistic interactions involving motile resource species. For example, aphids are plant parasites that harbor obligate bacterial symbionts (*Buchnera aphidicola*) as well as bacteria that are **facultative symbionts**. The facultative bacterium *Hamiltonella defensa* helps aphids to resist mortality from parasitoid wasp attacks by disabling wasp development [18], whereas *Regiella insecticola* improves the resistance of aphids to pathogenic fungi [19]. One study used bacterial species-specific PCR assays to demonstrate that both obligate and facultative microbial symbionts of the aphids can be transmitted horizontally by parasitoid wasps that sequentially stab infected and uninfected aphids [8]. Although two-thirds of aphids died following attack by the parasitoid wasps, 4–19% of the survivors acquired facultative symbionts (horizontal transmission), which were then passed to their offspring (vertical transmission). These findings suggest that failed parasitoidy may be an important mechanism for microbial symbiont transmission in some systems (Figure 2C), and that beneficial microorganisms acquired by resource species in this way can be passed on to offspring.

Trophic transmission of microbiota may influence host acclimatization to stress

Microbial communities play a crucial role in how individuals, populations, and communities of macroorganisms respond to anthropogenic stressors, including climate change [20]. We hypothesize that, in some cases, host acclimatization to environmental stress is supported by trophic transmission of beneficial microbiota. For example, the presence of plant-growth-promoting (PGP) and drought-resistance-associated bacteria (e.g., *Bacillus* and *Pseudomonas*) in the **rhizosphere** can alleviate water stress and improve drought tolerance in their wild and domesticated plant hosts [21,22]. Inoculation of rice (*Oryza sativa* L.) with *Pseudomonas* prevented root biomass loss and improved yield by 25% during drought [23]. Similar effects were documented for corn (*Zea mays*), where inoculation with *Pseudomonas* nearly eliminated the negative effects of drought on shoot length, root length, and above-ground biomass [24]. The guts of many herbivores, including orthopterans [25] and flies [26], contain viable populations of these microbial symbionts. For instance, 16S rRNA gene sequencing of the gut microbiota of the field cricket, *Gryllus veletis*, revealed high relative abundances of *Pseudomonas* [27]. Herbivores such as *G. veletis* likely disperse these symbionts throughout the environment in their frass, making the microbiota available to prospective plant hosts (Figure 2C,D). Frass addition experiments (with appropriate controls) to confirm that plants can source symbionts

from insect waste products, and to quantify any associated changes in drought tolerance, constitute the next steps in explicitly testing whether trophic transmission influences host acclimatization to climate change stress in this system.

Trophic transmission of symbionts also likely promotes acclimatization to climate stressors in some marine ecosystems. For example, as sea surface temperatures warm due to climate change, some stony corals and other marine invertebrates may increase their stress tolerance by harboring heat-resistant populations of dinoflagellate endosymbionts (family Symbiodiniaceae) in their tissues [28]. Recent work, using a combination of targeted gene amplicon sequencing, viability stain assays, and culturing, demonstrated that coral-eating fishes (**corallivores**) disperse live Symbiodiniaceae in their feces [29–31]. Although it has yet to be empirically demonstrated that corals establish live Symbiodiniaceae cells from fish feces, this has been shown for the sea anemone *Aiptasia pulchella* – a close relative of stony corals – using infection assays [31]. Additionally, juvenile corals have been demonstrated to incorporate Symbiodiniaceae from diverse sources (e.g., water column and sediments, [32–34]), including from the feces of giant clams [35]. It thus appears likely that some stony corals can acquire Symbiodiniaceae from corallivore feces.

When corals are stressed by high temperature anomalies (driven by climate change), they may lose their resident Symbiodiniaceae, causing them to exhibit a disease sign called '**bleaching**' [36]. To survive, bleached corals must recover their Symbiodiniaceae communities. Although the few Symbiodiniaceae cells retained by bleached hosts likely play an important role in host recovery, evidence also suggests that corals of some species take up novel Symbiodiniaceae species during or following environmental stress [37–41]. Corallivorous fish feces might be sources of relatively functional (and perhaps thermotolerant) cells during bleaching events since many corallivorous fishes preferentially feed on remaining unbleached colonies [42,43]. Using approaches similar to those described previously, tests of the extent to which trophic transmission of Symbiodiniaceae increases host temperature tolerance are critical next steps for the field – not only for corals but also for other foundation species including hydrozoans, sponges, and giant clams.

The enemy of my enemy is my friend

Microorganisms transferred during antagonistic interactions may also indirectly benefit consumed species by repelling other potential (nonvector) consumers (Figure 2E). For example, the cabbage root fly, *Delia radicum*, is an agricultural pest [44]. Laboratory experiments using green fluorescent protein (GFP) labeling demonstrated that feeding activity by *D. radicum* results in the transfer of diverse strains of the bacterium *Pseudomonas protegens*, including strain CHA0 [45]. CHA0 promotes plant growth and kills most insects [46], but not *D. radicum* [45]. Trophic transfer of CHA0 may thus decrease herbivory by other insects on recipient plants, but empirical demonstrations of this mechanism in natural plant populations are lacking. *In situ* experiments using strain-specific detection methods (Box 2) are a crucial next step to determine how commonly herbivores such as *D. radicum* transfer insecticidal bacterial strains like CHA0 between plants under natural conditions, and to what extent the transfer of CHA0 reduces feeding by other herbivores.

In a similar vein, aphids disperse *Cucumber Mosaic Virus* (CMV [47]) between plant hosts; this virus reduces plant growth and fruit production, and alters plant volatiles [47,48]. These altered plant volatiles cause aphids to preferentially feed on CMV-infected plants, thereby increasing virus dispersal – even though aphid performance on CMV-infected plants is reduced. Yet CMV can also provide its plant hosts with resistance to herbivory by other nonvector herbivores like squash bugs – a potential 'silver-lining' to aphid herbivory (Figure 2E) [48–50]. Given that squash bug feeding often results in plant mortality, infections with CMV may in some contexts increase plant survival [50–52]. Similar to

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Box 2. Challenges and approaches

Here, we summarize some challenges and approaches that will improve our ability to recognize, quantify, and evaluate the impacts of trophic transmission of microbiota.

Characterizing microbial provenance

High-throughput sequencing of 16S rRNA gene regions has been instrumental for characterizing bacterial diversity in hosts. However, such sequencing datasets often cannot resolve microbial taxa to the genus or species level. When studying the transmission of microbial genera or species to naïve hosts, long-read sequencing approaches that resolve microbiota to genus or species (e.g., full-length 16S rRNA for bacteria) should improve our ability to detect trophic transmission in natural systems. However, even strain-level differences amongst microbial taxa can have differential impacts on the host. For example, some strains of *Escherichia coli* are gut commensals, whereas others are highly pathogenic [77]. Unfortunately, some individual strains cannot be distinguished using even long-read sequencing. In these cases, higher-resolution approaches such as strain-resolved metagenomics [68] and metagenome-assembled genome (MAG) assembly [63] constitute powerful new (albeit more costly) approaches for parsing individual bacterial strains.

Assessing microbial viability

Determining microbial viability can be straightforward when foundational methods such as germination assays and culturing are applicable (e.g., [29–31]). However, routine approaches for sequencing microorganisms do not discriminate among metabolically active, metabolically inactive (dormant), and dead cells. Viability PCR [78] or cell sorting (e.g., via microscopy or flow cytometry) following application of a cell membrane permeability-based stain can be used to quantify the proportion of viable versus dead cells in a sample (with some caveats). Approaches such as epicPCR [79], that link a taxonomically informative gene with a gene of interest (e.g., indicative of active metabolism), could also be useful in confirming that target microbial groups are alive and functioning within consumer feces or the prospective hosts that acquire them.

Tracking microbial fates within prospective hosts

Following trophic transmission, a prospective host can either establish microorganisms as symbionts or digest/dispel them. The propensity of a resource species to acquire and maintain microorganisms as symbionts may vary with its taxonomic identity and/or life stage; some hosts may have more 'flexible' microbiomes than others, and may thus be more likely to establish symbionts via trophic transmission [80]. In all cases, infection assays – including careful controls (e.g., 'no addition', 'heat-killed addition') or molecular labeling approaches (e.g., [45]) – will be necessary to demonstrate successful establishment of symbiotic partnerships. Trophic transmission likely occurs more frequently in horizontally transmitting species, and may be easily identified for resource species in which aposymbiotic individuals can readily be generated (e.g., [31]).

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the *D. radicum*–CHA0–plant system, *in situ* experiments are a vital next step to resolve the contexts in which CMV provides benefits to plants in natural communities.

Traits influencing consumer-mediated microorganism dispersal

Recognizing general traits of microorganisms and consumers that promote trophic transmission strengthens our ability to predict when and how this process occurs, and can identify additional consumer–microorganism–resource systems that should be tested for evidence of this process.

Traits of microorganisms

Although few studies have tested how microbial traits affect trophic transmission, we highlight several possibilities below. Some microorganisms have 'life stages' especially adapted for dispersal, similar to the seeds of plants. For example, spores of mycorrhizal fungi have fortified cell walls that promote spore viability during and following ingestion [53,54]. Additionally, external hooks and spines, as well as hydrophobicity of the spore wall, assist spores in attaching to consumers [53,55]. Many members of the bacterial phylum Firmicutes, which contains plant and animal symbionts, can form endospores that are resilient to desiccation, extreme temperatures, and acidity (reviewed in [55,56]). Additionally, some freshwater and marine dinoflagellates form cysts that survive passage through the guts of migratory birds [57]. It is notable, however, that in many cases, increased stress resistance in microbiota comes at the cost of reduced growth rates [58].

Some symbiotic microorganisms can colonize and persist in consumers, facilitating dispersal to novel hosts. As described earlier (in the section 'The enemy of my enemy is my friend'), the

root-colonizing bacterium *P. protegens* CHA0 can be transmitted between plant roots by the cabbage root fly, *D. radicum*. CHA0 can switch between plant-beneficial and insect-associated lifestyles that are characterized by broad-scale changes in gene expression [45,59]. In some insect species, including *D. radicum*, CHA0 can persist in digestive tracts throughout the larval, pupal, and adult life stages, promoting dispersal to novel host plants (but note that CHA0 is pathogenic to many other insect species; [45]). Similarly, the specialized floral nectar yeast species *Metschnikowia reukaufii* can colonize the gastrointestinal tracts of bumblebee queens and survive there between flowering seasons (but note that a related nectar yeast species, *Metschnikowia greussii*, did not persist in bumblebee queen gastrointestinal tracts; [60]). The ability to persist in consumers may be especially beneficial in biological systems that are temporally disrupted, such as seasonal plants, and may also facilitate microbial dispersal over longer distances. Identifying where microorganisms persist in consumers (e.g., gastrointestinal tract), characterizing their persistence strategies (e.g., molecular mechanisms), and the extent to which persistence strategies change across host life stages may support the development of tools that promote or hinder trophic transmission in applied fields, including medicine, agriculture, and restoration.

Traits of consumers

Dispersal of microbiota by consumers can occur via a variety of mechanisms, including transmission via oral or fecal routes, contact with appendages, and/or 'messy feeding' [4,15,61,62]. Consumer traits likely affect the quantity and diversity of microbiota dispersed, as well as the resource species microbiota potentially encounter [63]. Consumers with lower digestive efficiencies are likely better dispersers of microorganisms [15,64]. In some cases, consumption may even be beneficial to consumed microorganisms: passage through the guts of some marsupials, pigs, and rodents increases germination and colonization rates of some mycorrhizal fungi, potentially because digestion degrades the protective tissues surrounding viable spores [65,66]. Conversely, consumers that are adapted to consume microbiota using digestive enzymes, such as some parrotfishes, may egest fewer viable microorganisms (Box 1; [29,30,67]).

The diet of a given consumer also likely impacts its microbiota dispersal. **Generalist** consumers feed on diverse resource species, potentially leading them to distribute a higher diversity of microorganisms among a greater variety of potential hosts (Figure 2B,D); we hypothesize that this leads to the dispersal of microorganisms among evolutionarily disparate hosts, with higher incidence of 'heterologous transfer' that might drive new combinations of microorganisms and hosts. Specialists feed on comparatively fewer resource species and may therefore disperse higher numbers of a more constrained diversity of microorganisms among fewer host species (Figure 2A,C). For example, obligate corallivores, which feed almost exclusively on corals, disperse a higher abundance of live Symbiodiniaceae cells than facultative corallivores, which feed on a combination of corals and other organisms [30]. The genetic composition of Symbiodiniaceae dispersed in fish feces also differs among **specialist** and generalist fishes; coral specialists disperse Symbiodiniaceae species that are harbored by corals, whereas generalist fishes tend to disperse both coral-associated (symbiotic) and free-living Symbiodiniaceae species [30]. In another example, fungal specialist rats generally disperse higher abundances of plant mycorrhizal fungi – and a higher diversity of plant-associated mycorrhizal species – than generalist rats [16]. Quantifying how these (and other) consumer traits affect microbial dispersal will help to generate foundational knowledge on the contribution of consumers to microbiota assembly in resource species.

Concluding remarks and future perspectives

Although antagonistic interactions have obvious negative effects on the health of consumed individuals, foundational studies (e.g., [8,16,31,45,49]) from diverse marine and terrestrial systems suggest that antagonistic interactions can also indirectly benefit resource species at the individual

Outstanding questions

How does trophic transmission of microbiota fit into our conceptual models of energy flow in ecosystem food webs?

How important/frequent is trophic transmission of microbiota for foundation (resource) species, such as corals, trees, oysters, and sea grasses?

How frequently do consumers facilitate the coinvasion of microorganisms and their resource species hosts?

To what extent do variation in consumer diet (e.g., diet breadth and dietary preferences) and behavior shape microbiota assembly processes in resource species?

How do consumer digestive system type (chemical, mechanical, or both) and efficiency influence the viability of dispersed microorganisms?

Does passage through a consumer digestive tract promote particular processes in dispersed microorganisms (e.g., infection by viruses, sexual reproduction, change in metabolic state)?

Which traits of recipient resource species/individuals facilitate (or limit) their acquisition of symbiotic microbiota?

How can we leverage the trophic transmission of microbiota for agriculture, medicine, conservation, and restoration?

and/or population levels through the trophic transmission of symbiotic microorganisms. To date, trophic transmission research has mostly focused on pathogenic and opportunistic microorganisms that can harm recipient organisms. Given the diverse examples described in this opinion piece, we posit that the dispersal of beneficial microbiota via antagonistic interactions is widespread in natural systems, and has important implications for host health and ecosystem function (see Outstanding questions).

We encourage microbiologists and ecologists to advance our collective understanding of antagonistic trophic transmission of beneficial microbiota by using diverse microbial identification, labeling and tracking approaches on consumer (oral, feces, appendages, etc.), host, and environmental samples, as well as in manipulative experiments to test (i) how antagonistic consumer-mediated trophic transmission of microorganisms contributes to microbiota assembly in resource species, (ii) how this process affects environmental acclimatization of resource species, and (iii) how trophic transmission of microbiota affects interactions among resource species and other consumers. Experimental designs such as factorial feces addition experiments, consumer exclusion/inclusion experiments (with appropriate controls), and network analysis will provide a mechanistic understanding of the roles of consumers in microbiota dispersal and subsequent microbiota assembly in resource species. In turn, common garden experiments using individuals of resource species with distinct microbial communities (or sterile/**aposymbiotic** individuals) will facilitate the identification of transferred microbiota that alter environmental sensitivity or biotic interactions. Studies that quantify links between consumer traits and the quantity, diversity, or traits of microbiota dispersed to resource species should also be prioritized.

The provenance, viability, and fate of specific microbial taxa of interest can be determined and tracked using a combination of 'conventional' approaches described previously (e.g., culturing, germination assays, fluorescent labeling, targeted PCR assays). Thanks to recent advances in sequencing technologies, researchers can additionally now also study the transmission of entire assemblages of microbiota at the strain level (e.g., strain-resolved metagenomics [68], metagenome-assembled genomes [63]; Box 2). The combination of foundational approaches and experimental designs, and powerful new tools for tracking microbial taxa, will greatly advance our understanding of the role of trophic transmission in driving microbiota assembly and, thereby, modulating abiotic and biotic interactions.

Declaration of interests
No interests are declared.

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