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Perspective

Microbiomes are integral to conservation of parasitic arthropods

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ABSTRACT

Parasitic arthropods have not typically been included in conservation and management strategies, possibly because the most well-known blood-feeding arthropods are associated with human and livestock disease. However, the vast majority of parasitic arthropods pose no threat to human health and instead contribute to the overall stability of communities to which they belong. The loss of parasitic arthropod biodiversity likely has repercussions for host health, population density, and community structure. The need for parasitic arthropod conservation is urgent given they represent the majority of parasitic animal biodiversity and environmental change is expected to pose a significant threat to their survival. We urge that microbial associations of host–parasitic arthropod assemblages be considered in conservation efforts. Parasitic arthropods are dependent on their microbial associates for development, nutrient acquisition, immune function, and reproduction. The microbiome also mediates the interactions between a parasitic arthropod and a host, and the role of a parasitic arthropod in vectoring pathogens to its host. The microbiome may therefore represent a “weak link” that increases the susceptibility of parasitic arthropods to environmental change. Fundamental knowledge is missing, precluding assessment of this complex association between microbes and parasitic arthropods. We highlight broad areas of future research that focus on building primary knowledge, developing experimental protocols and novel statistics, and leveraging new techniques to increase the resolution at which we can examine microbial communities of parasites. Conservation of parasitic arthropods that accounts for microbiota will likely be more effective at maintaining parasite biodiversity and at controlling arthropod-vector disease emergence.

1. Introduction

Though often overlooked, global parasite biodiversity is threatened by environmental change and declining host biodiversity (Gómez et al., 2012; Rocha et al., 2016; Carlson et al., 2017). Indeed, all species are hosts for parasitic organisms, supporting a remarkable diversity of parasitic species, and the loss of these parasite species from ecosystems may have unforeseen negative consequences (Gómez et al., 2012; Stringer and Linklater, 2014; Wood and Johnson, 2015; Dougherty et al., 2016). Climate change-induced habitat alteration alone is expected to cause a global loss of 5–10% of parasite diversity by 2070, with ectoparasites experiencing greater extinction risk than endoparasites (Carlson et al., 2017). Parasites with high host specificity, a complex life cycle, or narrow environmental preferences will be

impacted most severely (Cizauskas et al., 2017). As arthropods comprise the majority of classified animal life on earth (Giribet and Edgecombe, 2012) and the majority of parasitic animals are arthropods (Weinstein and Kuris, 2016), extinction of parasitic arthropod species represents a significant threat to biodiversity.

Parasites are most commonly viewed as hurdles along the path towards conservation of free-living host species, rather than the target of conservation efforts themselves (Stringer and Linklater, 2014; Dougherty et al., 2016). However, increasing evidence shows that parasites contribute to healthy host immune response, host population regeneration, ecological network stability, and nutrient cycling (Gómez et al., 2012; Hatcher et al., 2012; Wood and Johnson, 2015; Dougherty et al., 2016). For example, in humans, infection with some helminth parasites modulates the immune response and eases the effects of

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autoimmune diseases, like Crohn's disease and multiple sclerosis (Summers et al., 2005; Correale and Farez, 2007; Maizels, 2019). Mussels parasitized by endoliths are better able to survive bouts of extreme heat stress than non-infected individuals (Zardi et al., 2016). The trematode *Cryptocotyle lingua* (Plagiorchiida; Heterophyidae) decreases grazing rate of the common periwinkle snail (*Littorina littorea*), allowing greater macroalgae abundance for other marine herbivores (Wood et al., 2007). While parasites by definition harm their hosts to varying degrees, the net effect on populations and communities can be beneficial through the ecological functions they contribute.

A community of organisms is more than what meets the eye. If we follow the concept of the holobiont, where an individual organism is actually a composite of itself and associated microbes, and extend it to the scale of communities, then a community is a reflection of the millions of microscopic interactions that occur between the macro and microorganisms occupying a shared space. Even the interactions between hosts and parasites in a community, which are seemingly governed by their own evolutionary associations, are impacted by microorganisms (Dheilly, 2014; Kemen, 2014; Dheilly et al., 2015). The role of parasitic arthropods as hosts of microbes, vectors of microbes, and drivers of free-living host–microbe interactions has not been examined in the context of parasite conservation. Microbes are necessary to the development, immune response, and reproduction of parasitic arthropods (Engel and Moran, 2013; Narasimhan and Fikrig, 2015; Contreras-Garduño et al., 2016) and must be considered an integral part of efforts to stem global biodiversity loss.

Here, we provide a brief review of the importance of microbes to parasitic arthropods and outline areas of future research necessary to preserving parasitic arthropod biodiversity. Weinstein and Kuris (2016) define a parasite as a consumer that feeds on a maximum of one host individual during at least one life stage. We build on this definition to also include organisms that obligately feed on a single host species, regardless of the number of individuals, during at least one life stage. This definition excludes some micropredators like mosquitoes and tsetse flies, but includes others like louse flies, bat flies, and fish mites. Our current knowledge is biased towards insect parasites in the Order Diptera and arachnid parasites in the Subclass Acari, the two clades that contain the majority of parasitic arthropods (Weinstein and Kuris, 2016) and are therefore the focus of this review. However, we encourage the scientific community to investigate the role of microbes in the biology and ecology of other parasitic arthropods (c.f. Agany et al., 2020).

2. Parasite microbiomes are central to parasite health and reproduction

The microbiome is composed of archaea, bacteria, fungi, protozoa, and viruses. The sources of microbes found within parasites are not completely known, but likely include the broader environmental microbiome, the host microbiome, and the microbiomes of other parasite individuals within the same population (Fig. 1A). Primary and secondary bacterial symbionts share close evolutionary histories with their hosts and are typically maternally inherited (Moran et al., 2008). These bacteria provision nutrients missing from the arthropod's diet, leading to a mutually dependent relationship (Moran et al., 2008; Wernegreen, 2017). Arthropods may also interact with additional facultative and sometimes parasitic or pathogenic bacteria, fungi, viruses, and protozoa. The function of facultative microbes is not well understood, but there is some evidence that they contribute to arthropod health through nutrient provisioning and by modulating immune response (Gibson and Hunter, 2010; Feldhaar, 2011; Chaisiri et al., 2015; Narasimhan and Fikrig, 2015; Bonnet et al., 2017).

Parasitic arthropods have extremely narrow diets and missing nutrients have to be synthesized, often by microbial associates (Douglas, 2009; Douglas, 2017). For instance, in blood-feeding arthropods, symbiotic bacteria provision B vitamins missing from bloodmeal but

necessary for development and survival (Douglas, 2017; Husnik, 2018). One of the best-studied examples of this interdependence comes from human and chimpanzee lice (Pthiraptera) that depend on their symbiotic bacteria, *Candidatus Riesia*, to synthesize or transport the entire complex of B vitamins (Alejandra Perotti et al., 2008; Kirkness et al., 2010; Boyd et al., 2014). Without these symbionts, human and chimpanzee lice experience high nymphal mortality (Puchta, 1955; Alejandra Perotti et al., 2008). Obligate bacterial symbionts are common across blood-feeding arthropods, including non-parasitic groups like tsetse flies (Diptera: Glossinidae) that host *Wigglesworthia glossiniade* (Michalkova et al., 2014); kissing bugs (Hemiptera: Reduviidae, *Rhodnius prolixus*) that host *Rhodococcus rhodnii* (Hill et al., 1976; Beard et al., 2002); and Lone star ticks (Ixodida: Ixodidae, *Amblyomma americanum*) that host a *Coxiella*-like bacteria (Smith et al., 2015). Herbivorous parasitic arthropods similarly rely on symbiotic and commensal bacteria to access necessary nutrients (Engel and Moran, 2013; Hansen and Moran, 2014; Gutzwiller et al., 2015). By enabling parasitic arthropods to survive on limited resources, microbial associates in part define the suitable habitat occupied by parasitic arthropods.

In addition to supporting the nutrient acquisition of arthropods, microbes can decrease arthropod susceptibility to parasites and pathogens. This interaction may occur both directly through production of anti-pathogen compounds or competition, and indirectly through regulation of arthropod immune response and immune priming (Cirimotich et al., 2011; Weiss and Aksoy, 2011; Sasser et al., 2013; Dennison et al., 2014; Narasimhan and Fikrig, 2015; Contreras-Garduño et al., 2016; Saldaña et al., 2017). Competition between endogenous microbes and invading pathogens has been difficult to study, because quantifying microbe–microbe interactions requires the microbes be cultured outside of their host or that their gene products are sufficiently well known that they can be detected using transcriptomics and genome skimming. The few examples available come from arthropod vectors of human pathogens, where symbiotic bacteria impede the transmission of these pathogens by protecting the arthropod from becoming infected. Defensive symbionts in the Rocky Mountain wood tick (Ixodida: Ixodidae, *Dermacentor andersoni*) impede replication and invasion of pathogenic *Rickettsia* species (reviewed in Bonnet et al., 2017). Similarly, the absence of a maintained midgut microbiome in the deer tick (Ixodida: Ixodidae, *Ixodes scapularis*) may make them more susceptible to *Borrelia burgdorferi* – the causative agent of Lyme disease (Ross et al., 2018). *Wolbachia*, the most common facultative and obligate symbiont in arthropods, often conveys protection against pathogen invasion (Martinez et al., 2014). Recent evidence suggests that *Wolbachia* directly interferes with viral invasion and replication (Moreira et al., 2009; Rainey et al., 2016). *Spiroplasma*, another broadly distributed bacterial symbiont of insects, appear to display similar defensive properties (Ballinger and Perlman, 2019). To successfully conserve parasitic arthropods, we may also need to conserve their defensive symbionts.

Indirect defensive effects of microbes can also affect arthropod susceptibility to pathogens by aiding in the development of physical barriers, or by modulating the arthropod immune system (Gross et al., 2009; Tidbury et al., 2011; Cirimotich et al., 2011; Weiss and Aksoy, 2011; Dennison et al., 2014; Narasimhan and Fikrig, 2015; Contreras-Garduño et al., 2016). Little research on immune function is available for parasitic arthropods, but from non-parasitic model organisms, like tsetse flies (Glossinidae), there is evidence that bacteria in the midgut indirectly protect the fly by initiating development of a peritrophic matrix during fly development (Fig. 1B). The peritrophic matrix is a chitinous barrier between the gut contents and epithelium common in insects (Hegedus et al., 2009). When aposymbiotic tsetse flies are reared in the lab, the structure of the peritrophic matrix is compromised and these flies are more susceptible than wildtype flies to invasion by trypanosome parasites, the causative agent of African sleeping sickness (Weiss et al., 2013). Evidence suggests that microbes can also facilitate immune priming of arthropods (Weiss and Aksoy, 2011; Contreras-

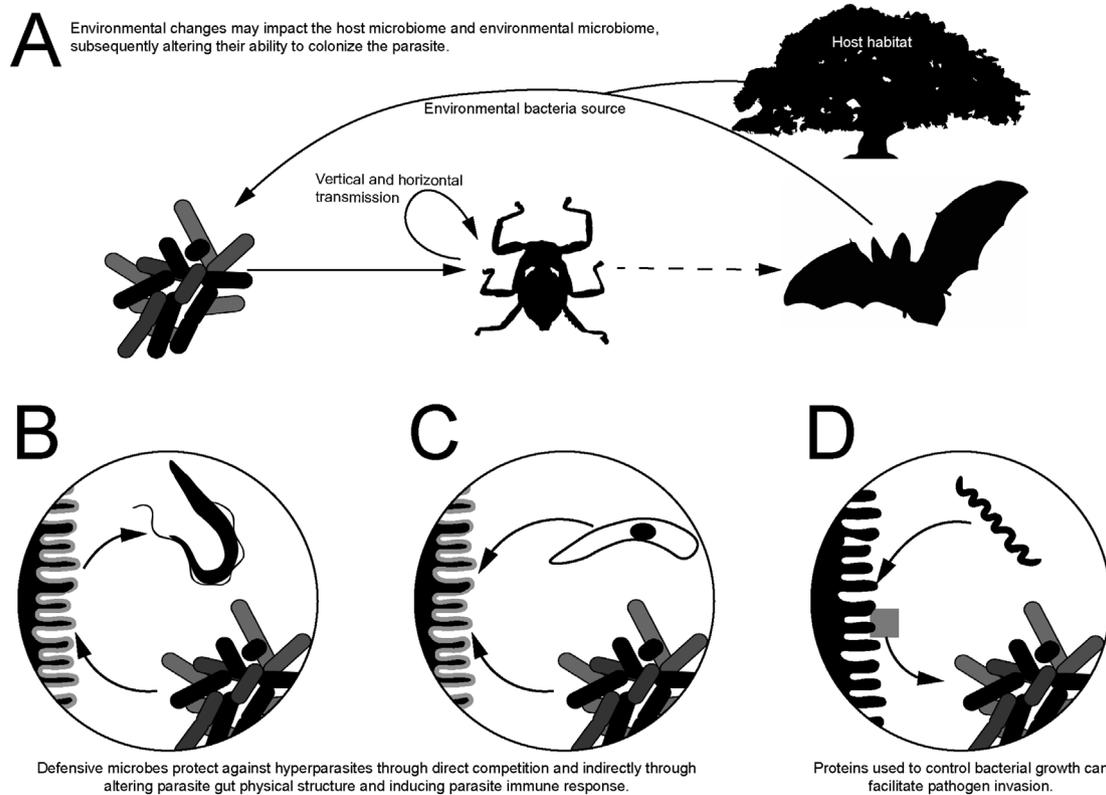


Fig. 1. Illustration of the assembly of host-parasite-microbe associations using bat flies (Nycteribiidae) and bats as an example (A). The three lower circles (B, C, D) illustrate some of the known interactions between the endogenous microbiome of a parasite with pathogenic microbes and hyperparasites.

Garduño et al., 2016). When *Plasmodium* malarial parasites break through the peritrophic matrix of mosquitoes (Diptera: Culicidae; not considered parasites here), bacteria in the midgut contact the epithelium, which stimulates a mosquito immune response (Fig. 1C). This bacteria-induced immunomodulation appears to enable the mosquito to better fight off a secondary challenge with *Plasmodium*; whereas antibacterial treatment of mosquitoes leads to higher *Plasmodium* invasion success and no immune priming to protect against secondary encounters (Rodrigues et al., 2010). The protective effects of symbionts against a pathogen not only benefits the health and fitness of the parasitic arthropod, but also decreases vector competence and reduces pathogen transmission to downstream hosts.

It should always be remembered that microbes are under selection to increase their own fitness and not that of their host (i.e., parasitic arthropod), so that interactions among microbes, and between microbes and the host can lead to diverse evolutionary outcomes that do not always benefit the host. Consider the deer tick (*Ixodes scapularis*), responsible for transmitting important human and livestock pathogens, including Lyme Disease (*Borrelia burgdorferi*) and tick-borne fever (*Anaplasma phagocytophilum*). Both bacteria elicit the upregulation of deer tick proteins (*pixr* and *antifreeze glycoprotein*) that alter the gut microbiome and make the peritrophic matrix diffuse. This allows greater invasion success by *A. phagocytophilum*, but reduces the invasion success of *B. burgdorferi* (Abraham et al., 2017; Narasimhan et al., 2017). Indeed, *B. burgdorferi* relies on a normal peritrophic matrix for invasion (Narasimhan et al., 2014) whereas the peritrophic matrix acts as a barrier to infection by *A. phagocytophilum* (Abraham et al., 2017; Fig. 1D). Interactions between microbes and the parasite can thus lead to contrasting outcomes, so that microbes can either facilitate the colonization by other microbes (e.g., *Sodalis* increases susceptibility of tsetse flies to trypanosomes; Wang et al., 2013), or provide protection of variable strength depending on the host species with which they are associated, the pathogens they interact with, small genetic variation,

and environmental factors (e.g., *Wolbachia* transinfected into non-primary host species of mosquito provide varying degrees of protection from viral pathogens; Novakova et al., 2017).

Even though the impact of individual microbes on the host lies along a continuum from beneficial to detrimental, the microbiome is without doubt essential to arthropod immune function, health and fitness, vector competence, and microbial symbionts have driven diversification in insects by facilitating changes in diet (Cirimotich et al., 2011; Weiss and Aksoy, 2011; Narasimhan and Fikrig, 2015; Sudakaran et al., 2017). Thus, microbes have enabled and are essential to maintaining the biodiversity of parasitic arthropods. We recognize that some parasitic arthropods, as vectors of disease, are responsible for significant human suffering and death (Jones et al., 2008). We do not advocate for the conservation of these extremely harmful arthropod vectors, which comprise a small portion of overall parasitic arthropod diversity. Instead, we argue that through conservation practices that make use of microbiomes, we can impede the emergence of harmful arthropod-vectored pathogens concurrent with efforts to stymie biodiversity loss.

3. The link between host and parasite microbiomes and parasitic arthropod conservation

We cannot fully address projected parasite biodiversity loss without accounting for the multidimensional nature of hosts, parasitic arthropods, and the microbes that mediate their interactions. Microbiome perturbations may effectively limit the suitable habitat for parasitic arthropods, putting them at greater risk of extinction in the face of environmental change. Suitable “habitat” for parasitic arthropods encompasses both the host and broader environment where the host lives. The link between microbes and arthropod survival is currently successfully exploited to manage agricultural insect pests and decrease population sizes of arthropod vectors of human disease (Zabalou et al.,

2004; Douglas, 2007; Zindel et al., 2011; Liu and Guo, 2019). The same principles can be leveraged for conservation efforts of parasitic arthropods in the face of the rapid environmental change threatening their survival.

Environmental change leads to changes in the microbiome composition of free-living organisms that act as hosts for parasitic arthropods (Lau and Lennon, 2012; Amato et al., 2013; Becker et al., 2017; Ferguson et al., 2018; Kokou et al., 2018; Wu et al., 2018; Ingala et al., 2019). Environmentally induced alterations to host microbiomes could have downstream consequences for host–parasite interactions, because parasitic associations are in part mediated by host microbiomes (Koch and Schmid-Hempel, 2012; Knutie et al., 2017a). For example, host defensive microbes play an important role in determining the colonization success and virulence of parasites (Rouchet and Vorburger, 2012; McLean and Godfray, 2015; Hahn and Dheilly, 2016; King and Bonsall, 2017; Vorburger and Perlman, 2018). Climate conditions that narrow the suite of host defensive microbes may selectively impede colonization of some parasite species, while eliminating host defenses against others. Little research is available on the role of temperature in mediating the interaction between defensive microbes and parasitic arthropods. However, hints of its significance can be inferred from vertebrate systems: recent evidence from red-backed salamanders (*Plethodon cinereus*) indicates that temperature alters the skin microbiome composition and persistence of bacteria putatively protective against *Batrachochytrium dendrobatidis*, a fungal pathogen of amphibians (Muletz-Wolz et al., 2019). In this way the microbiome of the host may be just as important as the microbiome of the parasitic arthropod in determining access to habitat (i.e., the host).

In addition to climate, changes in resource availability may favor some parasitic arthropod species over others. Previous research has indicated that high resource availability enables hosts to withstand parasite infections through greater tolerance (i.e., parasites colonize successfully, but hosts are able to outlast infection), resistance (i.e., reduction in successful parasite colonization; Knutie et al., 2017b) or through greater energy allocation to anti-parasite behaviors (e.g., preening; Murray et al., 2018; Altizer et al., 2018). The host microbiome is also impacted by changes in resource availability, which subsequently impacts host tolerance or resistance to parasitic arthropods. For example, in Eastern Bluebirds (*Sialia sialis*), provisioned nestlings host a more diverse microbiome and a higher relative abundance of *Clostridium*, which was correlated with higher antibody response and lower parasitism by the fly *Protocalliphora sialia* (Diptera: Calliphoridae; Knutie, 2020). In Galápagos mockingbirds (*Mimus parvulus*), nestlings infected with the parasitic larvae of the fly *Philornis downsi* (Diptera: Muscidae) experienced greater resource provisioning than uninfected nestlings, but had microbiomes with lower diversity and lower antibody levels than uninfected nestlings (Knutie, 2018). Even though the causality of parasitism is unclear here, increased provisioning may allow nestlings to tolerate parasite infection rather than resist it (Knutie, 2018). Changes in the diets of host species in response to environmental alteration may impact parasite microbiomes and the interaction between hosts and parasites. For example, *P. downsi* larvae infecting insectivorous green warbler finches (*Certhidea olivacea*) have a different microbiome than larvae infecting finches with broader diets (small and medium tree finches, *Camarhynchus parvulus* and *C. pauper*, and small ground finch, *Geospiza fuliginosa*), possibly due to differences in the host diet (Ben-Yosef et al., 2017). Changes in host ecology may lead to changes in the host or parasite microbiome that decrease resource availability for the parasite and make the parasite more vulnerable to extinction.

Beyond host-mediated changes in suitable habitat, environmental change may directly limit suitable habitat for arthropods through the narrow thermal constraints of symbiotic microbes (Wernegreen, 2012; Kikuchi et al., 2016; Moran, 2016; Corbin et al., 2017). For instance, microbiome communities of *Ixodes scapularis* are altered after only 10 days at 30 °C and 5 days at 37 °C (Thapa et al., 2019). The highly

abundant symbiotic bacteria *Rickettsia* decrease in relative abundance after 10 days at 30 °C and 8 days at 37 °C, while *Brevibacterium* rapidly increased in relative abundance (Thapa et al., 2019). Increasing temperatures may reduce the stability of interactions between heritable symbionts and arthropods and lead to novel associations with thermophilic microbes (Renoz et al., 2019), with unknown consequences for host–parasite interactions. Heat stress variably alters ability of the host immune system and endogenous microbiomes to combat pathogen or parasite invasion (Busby et al., 2012; Lambrechts et al., 2011; Heyworth and Ferrari, 2016; Novakova et al., 2017), making it difficult to predict how global catastrophic climate change will impact survival of parasitic arthropods and vector competence of these parasites.

4. Directions for future conservation efforts

Conservation strategies targeting free-living arthropod species are broadly used to improve agricultural and natural landscapes, and to prevent arthropod biodiversity loss (Lattin, 1993; Hartley et al., 2007; Gaspar et al., 2011; Sebek et al., 2016; Mader et al., 2017). For example, many species of butterflies and moths have had or continue to have their populations supplemented by captive breeding programs to counteract declines caused by climate change and habitat loss (Ngoka et al., 2007; Schultz et al., 2009; Gardiner et al., 2017; Ghosh et al., 2019). Conservation biological control, where reproduction, survival, and efficacy of natural arthropod enemies of crop pests (also arthropods) is aided by captive breeding and/or altering agricultural and surrounding landscapes, has been successfully implemented as an alternative to dependence on pesticides that broadly damage arthropod biodiversity (van Lenteren et al., 2018; Shields et al., 2019). These efforts to protect biodiversity of free-living arthropods provide a foundation on top of which conservation of parasitic arthropods can build. While bacteria in the genus *Wolbachia* have been studied for their reproductive manipulation in captive breeding and release programs (Nice et al., 2009; Hamm et al., 2014), microbiome research is not yet integral to arthropod conservation. For arthropod species with narrow diets, including parasitic arthropods, microbiome change in response to environmental change must be considered for successful conservation efforts.

First, our baseline understanding of the microbial associates of host–parasite assemblages is lacking. Any species extinction is associated with many more seemingly invisible extinctions; parasites disappear with their host, and microbes associated with parasites disappear as a result. Global climate change and other human alteration of the environment will have unforeseen consequences on these host–parasite–microbe assemblages, because we do not understand how they emerge, are maintained, or function in response to perturbations. In addition, most research has focused on the bacterial members of the microbiome and there is little information available on the impact of viruses, fungi, and protozoans on parasitic arthropod fitness, life history traits, ecology and evolution. The lack of information on parasite microbiomes has been recognized in the literature (see The Parasite Microbiome Project, Dheilly et al., 2017; Dheilly et al., 2019) and similar calls to arms have targeted microbiome research on free-living organisms (Trevelline et al., 2019). We cannot protect a species we do not know exists, and in the age of the holobiont, this means we cannot protect a species whose microbiome we do not know.

Second, we must examine how the parasitic arthropod microbiome is assembled. The host, environment (where the host lives), and microbe–microbe interactions likely all influence the community assembly of the parasitic arthropod microbiome. However, our understanding of the impact of ecological and evolutionary processes, like heritability, selection, niche conservatism, and priority effects, on microbial ecosystems is extremely limited. If climate change results in the loss of necessary functional benefits provided by endogenous microbes, the tolerance or adaptability of parasite species to climate change will depend on whether these functional necessities can be provided by

another microbial species (see Mueller et al., 2019 for review on microbial rescue). Environmental microbial ecosystems exhibit high functional redundancy (Louca et al., 2016; Louca et al., 2018), so it is possible that the functions required by the parasite are available in other microbes, and microbial rescue might be a viable option to replace lost symbionts. The function or level of function of a microbe may change in response to microbiome community changes due to priority effects (Fukami, 2015), so the viability of microbial rescue may be context dependent. Through research on sources of variation in the assembly of parasitic arthropod microbiomes, we can identify predictors of microbiome functional variation relevant to parasite survival and reproduction.

Third, genotype-by-genotype and genotype-by-environment interactions of the microbiome are important drivers in the evolution and population dynamics of free-living organisms (van Opstal and Bordenstein, 2015), but have not been examined in parasitic arthropod microbiomes. Parasite populations may become locally adapted to different host populations or species (Carius et al., 2001). The intraspecific diversity of parasites resulting from local adaptation with host populations may facilitate functional diversity of associated microbes, but make parasite species more vulnerable to environmental change. If a microbe contributes to either host susceptibility or parasite virulence, it would influence the host–parasite co-evolutionary dynamics (King and Bonsall, 2017) and the amount of suitable habitat available to a parasite. The advent of single cell genomic sequencing and increasing use of shotgun metagenomics (compared to 16S rRNA metabarcoding) provide unprecedented insight into the genomic mosaic of microbes associated with parasitic arthropods and their hosts (Blainey, 2013; Anantharaman et al., 2016). These tools will be especially useful for examining the evolutionary history of microbes through multilocus phylogeny reconstruction, and for assessing the role of parasite and host dispersal in microbial gene flow through horizontal gene transfer. Examination of microbial genomic variation within and between parasite populations will enable us to better predict vulnerability of parasite populations due to local adaptation and isolation.

Fourth, our ability to statistically and experimentally examine whether environmental, ecological, or evolutionary variables are predictive of the protective capacity of parasite microbiomes is limited by currently available statistical tests, analysis software, and experimental methodology. Host–parasite systems can be extremely difficult to examine quantitatively due to the inherent nestedness of the system, the probability of unbalanced sampling (more than one parasite individual may infest a single host individual), and the difficulty of rearing host-specific parasites in laboratory settings. Adding information about microbial associations creates further complexity by adding an additional layer to the hierarchy, and also because of the transiency of some microbial associations. Current statistics and software only account for effects of environment and phylogeny of one or two levels of this complex assemblage (Ives and Helmus, 2011; Rafferty and Ives, 2013; Fountain-Jones et al., 2018; Youngblut et al., 2019). Refinement of analytical methods to account for environment and the phylogenies of the host, parasite, and microbiome simultaneously are necessary to rigorously test how climate change and habitat loss impact the host–parasite–microbiome assemblage. In addition, experimental methodology development (e.g. lab rearing protocols) is necessary to confirm correlation- and model-based hypotheses of microbiome function in response to environmental change and to prepare for the possibility that some parasite species will rely on captive breeding and release for survival. The unique biology of microbes may preclude them from analysis using methods developed on eukaryotic species (Koskella et al., 2017), and experimental development of null hypotheses will aid in expanding existing analyses to microbial communities. It may be that existing analyses cannot be modified to adequately account for the nuances of microbial communities, however, new frameworks are being developed through which more comprehensive analyses may emerge (Hall et al., 2018). Regardless, the tools we have available now are

limiting our ability to understand microbiome variation and therefore limiting our ability to protect parasitic arthropods and other microbe-dependent species.

5. Conclusion

Parasitic arthropod microbiomes offer opportunities for future research with implications for community ecology and evolutionary biology, conservation of global biodiversity, and disease ecology of pathogens relevant to human health, livestock, crops, and wildlife. The microbiome mediates the development, health, and reproduction of parasitic arthropods as well as the interactions of parasitic arthropods with the outside world. Through this interdependence, microbiomes must be a primary consideration for conservation of parasitic arthropods. While a minority of parasitic arthropods are extremely harmful, most species perform crucial roles in regulating host communities and represent a significant portion of all life on earth. Parasitic arthropods warrant conservation efforts and microbiomes must be central to these endeavors.

Declaration of competing interest

The authors have no conflicts to declare.

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