

Toward trait-based food webs: Universal traits and trait matching in planktonic predator–prey and host–parasite relationships

Elena Litchman¹,^{2,3*} Kyle F. Edwards,⁴ Philip W. Boyd^{5,6}

¹Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan

²Ecology, Evolution and Behavior Program, Michigan State University, East Lansing, Michigan

³Department of Integrative Biology, Michigan State University, East Lansing, Michigan

⁴Department of Oceanography, University of Hawai'i at Manoa, Honolulu, Hawaii

⁵Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia

⁶Australian Antarctic Programme partnership, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia

Abstract

There is a growing consensus that traits offer a powerful way to examine the relationship between the environment, organismal strategies, species interactions, and ecological success. To date, trait-based research has largely been focusing on individual trophic levels and not on cross-level interactions. Looking at traits not only within but across trophic levels and identifying traits that together define trophic interactions holds a great potential for understanding the mechanisms of interactions. Here, we outline the conceptual foundation for cross-trophic trait-based frameworks, using planktonic food webs as an example. First, we compile a list of traits important within different individual trophic levels and show that there are traits that are common across trophic levels (“universal” traits), as well as trophic level-specific traits. Next, we focus on traits that characterize interactions across trophic levels, focusing on two types of interaction—grazer–primary producer and host–parasite, identifying the similarities and differences between these interactions. We outline the trait hierarchies that define possible and realized intertrophic interactions and their strengths. We then highlight the importance of trade-offs among those traits in shaping interactions and explaining general patterns in the structure and function of food webs. Finally, we discuss the environmental influences on traits, their eco-evolutionary responses to changing conditions and how those responses may alter trophic interactions. The extension of trait-based approaches from individual trophic levels to food webs and different trophic interactions should stimulate further conceptual development, enrich the field of aquatic sciences, and provide a framework to better predict global change effects on ecosystems.

Trait-based approaches to community ecology have become an influential framework to gain mechanistic insights into community assembly and functioning (Lavorel and Garnier 2002; Westoby et al. 2002; Diaz et al. 2004). Most trait-based studies so far have focused on a single trophic level, and it is less clear how a trait-based framework can be extended across trophic levels, especially to characterize diverse trophic interactions and reveal general patterns of ecosystem structure and function.

In planktonic food webs, traits for several major groups have been identified, characterized and compared across taxa. As discussed below, we have learned much about traits within major trophic levels, from primary producers to grazers to

heterotrophic bacteria (Barnett et al. 2007; Litchman and Klausmeier 2008; Edwards et al. 2012; Litchman et al. 2013; Weithoff and Beisner 2019). Despite this accumulating knowledge, the traits that are important for an organism's fitness have rarely been compared across trophic levels, and whether the same traits can be used to describe organismal responses to, or their effects on, the environment at those levels is less well known. The overlap in such traits across multiple trophic levels could point to universal underlying principles of community organization and help develop a general trait-based framework for understanding diverse food webs. Moreover, while the interactions across trophic levels are extremely important in shaping all ecological communities, a trait-based perspective is only beginning to be applied to those ecological interactions (Tirok and Gaedke 2010; Banas 2011; Record et al. 2016; Edwards et al. 2021). This knowledge gap persists despite an in-depth understanding of how predator–prey interactions are shaped by body size, a key organismal trait

*Correspondence: litchman@msu.edu

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(e.g., Fuchs and Franks 2010), and of defensive traits such as diatom silicification (e.g., Pančić et al. 2019).

In this review, we first compile and compare important traits across trophic levels and identify universal traits that transcend trophic levels, focusing on planktonic food webs, which are ecologically and biogeochemically influential across the global ocean and freshwaters. We then discuss the benefits and challenges of using traits to describe trophic interactions. We specifically focus on and compare the predator–prey (phytoplankton–zooplankton) and host–parasite (phytoplankton–virus) interactions, although other types of interactions, such as mutualism, would also need to be considered for a complete characterization of planktonic and other food webs. We discuss the concept of *trait matching* that helps improve trait-based descriptions of interactions and outline a *hierarchy of traits* needed to characterize and model cross-trophic interactions. We then identify several emergent principles that may be universal to different trophic interaction types and briefly discuss the role of trait evolution in shaping trophic interactions.

Developing a cross-trophic-level trait-focused framework should help improve our mechanistic understanding of planktonic food webs and the ability to forecast future modification of pelagic ecosystems in response to global environmental change. At the same time, key traits and the general approaches to linking trophic levels through traits that we discuss are universal to many other food webs, such as the grazer–primary producer or virus–primary producer links in benthic or terrestrial systems, and should thus provide novel insights beyond planktonic communities.

Trait and trade-off universality across trophic levels

Using traits to characterize organisms and ecological communities has become the mainstay in terrestrial plant ecology (McGill et al. 2006; Violle et al. 2007) and gained acceptance in other ecosystems, including aquatic food webs (Litchman and Klausmeier 2008; Litchman et al. 2013; Stuart-Smith et al. 2013). Traits can be defined as “any morphological, physiological, or phenological heritable feature measurable at the level of the individual, from the cell to the whole organism, without reference to the environment or any other level of organization” (Garnier et al. 2016). *Functional* traits are usually defined as traits that affect fitness (Violle et al. 2007). In addition to morphological and physiological traits, life history and behavioral traits can also be considered (Litchman and Klausmeier 2008). Another trait classification category that is becoming more relevant with the proliferation of sequenced genomes, especially for microbes, is genomic traits that include genome size, number of functional genes, 16S rRNA gene copy number and GC content (Guittar et al. 2019; Li et al. 2019). A popular framework classifies traits into “response” and “effect” traits, with traits determining an organism’s responses to and its effects on the environment, respectively (Lavorel and

Garnier 2002; Litchman et al. 2015b). Some traits can simultaneously be response and effect traits, for example, the nitrogen fixation rate, as it responds to the amount of available nitrogen (“response” trait) and, consequently, influences the amount of nitrogen in the system (“effect” trait).

At present, most trait-based studies have focused on organisms within a single trophic level, such as phytoplankton (primary producers) (Litchman et al. 2007; Litchman and Klausmeier 2008; Edwards et al. 2012, 2013a,b, 2016), fish (Block et al., 1993, Galarza et al., 2009) or heterotrophic bacteria (secondary producers) (Mulder et al. 2005; Green et al. 2008; Wallenstein and Hall 2012). Traits at other trophic levels, such as grazers, including microzooplankton and mesozooplankton (Barnett et al. 2007, Litchman et al. 2013; Vogt et al. 2013; Pomerleau et al. 2015), and viruses (Record et al. 2016; Edwards and Steward 2018) have also been explored. Hence, in pelagic food webs there is now a growing body of knowledge of traits and the relationships between traits and environment within different trophic levels, from heterotrophic bacteria to mesozooplankton. For example, Edwards et al. (2013b) found that nutrient and light utilization traits, as well as maximum growth rates predicted seasonal dynamics of individual species of phytoplankton in the English Channel. Prowe et al. (2019) found that feeding strategies in mesozooplankton exhibit a latitudinal pattern, with ambush-feeding species dominating at high latitudes and an active feeding strategy more prevalent in low latitudes, which in part is explained by the energy availability to higher trophic levels at different latitudes. However, studies that combine traits across trophic levels to identify *common* and *unique* traits and how they respond to environmental drivers are rare. Several recent studies have tested whether species interactions in terrestrial and aquatic predator–prey and plant–pollinator networks can be predicted from a matching of species’ traits, with varying degrees of success: traits either were or were not good predictors of interactions (Olito and Fox 2015; Crea et al. 2016; Cirtwill and Eklöf 2018; Laigle et al. 2018; Brousseau et al. 2019). A few studies have also quantified how traits across multiple trophic levels covary spatially across environmental gradients, and whether patterns of trait covariation are consistent with hypotheses about food web structure, such as trophic interactions shaping trait distributions (Brousseau et al. 2019; Kenitz et al. 2019).

Comparing key traits, trade-offs, and community trait structure across trophic levels

A trait synthesis across different trophic levels should help ecologists understand the mechanisms of trophic interactions and the responses of ecosystems to environmental drivers, including global change stressors. We have identified traits that are common across decomposers (heterotrophic bacteria, which can also be secondary producers), primary producers (phytoplankton), consumers (zooplankton) and parasites (viruses), and highlight traits that are unique to certain

Table 1. Summary of traits for planktonic food webs from marine microbes to mesozooplankton. Traits relevant for a given trophic level are shaded. Not all possible traits are listed, and shading decisions can be debated. Traits in bold directly mediate trophic level interactions. Many other traits at each trophic level may affect other trophic levels indirectly.

Trait type	Trait	Viruses	Heterotrophic bacteria	Phytoplankton	Microzoo plankton	Mesozoo plankton
Genomic	Genome size and organization (proportion of functional genes and number of copies, introns, transposons, DNA methylation, GC content)					
	Nucleic acid type					
	Mutation rate					
	rRNA gene copy number					
Morphological	Virion/cell/body size					
	Cell/body shape (surface area to volume ratio or volume to biomass in gelatinous forms)/ capsid morphology (helical, isometric, other)					
	Lipid envelope/cell wall					
	Coloniality					
Metabolic/ physiological	Max growth rate (population or individual)					
	Photosynthesis rate					
	Respiration rate					
	Food assimilation efficiency					
	Metabolic versatility (generalists vs. specialists)					
	Nutritional strategy (autotrophic, heterotrophic or mixotrophic; omnivory, herbivory, carnivory)					
	Max resource acquisition/ grazing rate (can be multiple resources)					
	Environmental factor tolerances—optimum and niche width (temperature, pH, UV, salinity, oxygen, organic/inorganic toxins)					
	Stoichiometric requirements (C : N : P ratios; high P demand in fast growing organisms, min cellular nutrient requirement $Q_{\min}$ for different nutrients) and other food quality requirements (e.g., fatty acids, protein)					
	Excretion rate					
	Allelochemical/toxin/antibiotic production					
	Nitrogen fixation (including symbiotic)					
	Prey size range/host range/specificity					
	Prey selection strategy					
Life history/ behavioral	Motility (e.g., active swimming, buoyancy)					
	Chemotaxis					
	Dispersal mode/distance/rate					
	Resting stages/dormancy/lysogeny					
	Resource storage/reserve form and capacity					
	Sexual/asexual reproduction					
	Reproduction strategy (burst size, offspring size/number)					
	Timing of reproduction/latent period					
	Defense strategy (behavioral)					

trophic levels. Table 1 provides a collation of over 30 traits that are divided across four categories—genomic, morphological, physiological, and life history. This synthesis reveals that many traits are universal across trophic levels, some can be viewed as key traits that control multiple aspects of organismal functioning and, thus, should be better characterized (Table 1). One such trait is cell/body size that often determines values of many other physiological, morphological, life history and, possibly, behavioral traits through allometric relationships (Chisholm 1992; Edwards et al. 2012) and plays a role in trophic interactions (Fuchs and Franks 2010; Heneghan et al. 2016). Maximum growth rate is another such universal trait that determines different ecological and life history strategies in most organisms (Litchman and Klausmeier 2008; Gibert et al. 2016; Malik et al. 2020). In contrast, some traits are limited to one (e.g., nucleic acid type in viruses) or several (coloniality in phytoplankton or filamentous bacteria, Pernthaler et al. 2004) trophic levels. It is also evident that another key distinction between traits is that some directly mediate interactions between trophic levels (denoted in bold in Table 1) whereas in other cases the influence of traits on other trophic levels is less direct. Many traits are not independent from each other but correlated, either positively or negatively (e.g., cell size in phytoplankton is often negatively correlated with maximum growth rate, Edwards et al. 2012 but see Marañón et al. 2013), and some of those correlations represent trade-offs that may be important for inter-trophic interactions (Edwards et al. 2011; Kiørboe 2011; Litchman et al. 2015a; Våge et al. 2018). Trade-offs among traits define different ecological strategies, allow species coexistence and diversity and play an important role in shaping interactions across trophic levels (Tilman 1990; Litchman et al. 2015a). It is possible that not only some traits but trade-offs and trait relationships that arise from basic metabolic and physical constraints may be universal across trophic levels as well (Litchman et al. 2015a). For example, actively searching for food and mates trades off with vulnerability to predation in zooplankton (Kiørboe 2011; Litchman et al. 2013). A similar trade-off may be present in motile bacteria and phytoplankton that move to search for patches of higher nutrients or detritus (González et al. 1993), although prey motility may increase predator encounter rates while decreasing capture efficiency of the most motile prey (Matz and Jürgens 2005). Some trade-offs may be more specific to an individual trophic-level due to physiological/life history differences across levels (Table 1). Small cell sizes in phytoplankton confer better resource competitive abilities due to the surface area to volume considerations and diffusion properties, but may render such cells vulnerable to predation (Chisholm 1992; Edwards et al. 2011; Edwards et al. 2012). In contrast, in heterotrophic bacteria, which exhibit a smaller size range and smaller minimum size than phytoplankton, smaller cells may be less vulnerable to predation (Gonzalez et al. 1990; Batani et al. 2016).

We suggest that a holistic understanding of community structure and how it relates to ecosystem function will be enhanced if the cross-trophic level comparisons outlined in Table 1 are used to develop research, focused on (1) trait distributions across environmental conditions for multiple trophic levels, and (2) whether traits common to multiple trophic levels are shaped by similar trade-offs and other constraints. These comparisons will help reveal whether similar mechanisms underlie the maintenance of functional diversity and shifts in community composition across multiple trophic levels, and whether changes in trait distribution at one trophic level are coupled to or cascade to other trophic levels (e.g., Kenitz et al. 2017).

For example, do phytoplankton, heterotrophic bacteria, and zooplankton exhibit similar patterns in body size, maximum growth rate, or maximum clearance rate/uptake affinity as resource supply increases? One might expect that across trophic levels, a lower supply of energy or nutrients to an ecosystem would select for smaller body sizes, higher affinities and clearance rates, and lower maximum growth rates (if this trait trades off with others), and vice versa as resource supply increases. Kenitz et al. (2019) compared a variety of plankton traits across an oceanographic gradient from oligotrophic to coastal upwelling environments in the northeastern Pacific. They found that size distributions changed most for protists (i.e., microzooplankton), driven by a relative increase in auto-troph size in upwelling waters, while changes in mesozooplankton size distributions along the productivity gradient were more subtle and exhibited a greater proportion of small ambush-feeding copepods in more productive systems. Making similar comparisons for traits that reflect physiological rates, such as maximum growth rates, will be challenging due to the paucity of trait data, but may be essential for understanding drivers of community structure and ecosystem functioning. When comparing traits across trophic levels, it may also be useful to consider that universal patterns or trade-offs may only be evident when traits are defined at a suitable level of abstraction. For example, uptake affinities for dissolved nutrients and maximum clearance rates for prey ingestion are clearly not identical traits (Table 1), but both define the efficacy of resource capture at low resource concentrations, and therefore may be under similar selective pressures across gradients of resource supply (Kiørboe et al. 2018b). Likewise, defense strategies may differ for different kinds of organisms, but productive conditions that lead to greater biomass within all trophic levels may select for increased defense across trophic levels, due to greater encounter rates between predators and prey, and pathogens and hosts. Therefore, more productive environments may simultaneously select for greater resistance to viral infection, morphological defenses against grazing such as diatom silicification, and behaviors that minimize encounter with predators. Resource pulses (Yang et al. 2010) may also cause nutritional and metabolic traits to shift across trophic levels in similar

ways, because of similar underlying constraints. For example, transient high availability of dissolved nutrients and sufficient irradiance tends to select for rapidly growing species of taxa such as diatoms, which are autotrophic specialists, compared to more generalized mixotrophic taxa (Barton et al. 2013; Edwards et al. 2013b; Berge et al. 2017). Blooms of diatoms can select for heterotrophic microbes that are rapidly growing copiotrophs and/or specialize on utilizing algal polysaccharides such as laminarin (Teeling et al. 2012; Unfried et al. 2018). The grazers and viruses that respond rapidly to diatom blooms may also be specialists with high maximum growth rates, such as heterotrophic dinoflagellates with feeding structures that allow them to consume diatoms larger than themselves (Saito et al. 2006). Because an entire suite of traits may undergo selection to change values as environmental conditions are modified, with potential trade-offs among traits, and concurrent trophic interactions may cause top-down driven trait selection to differ from bottom-up trait selection, there is the potential for significant complexity in multi-trophic trait dynamics over time or space (e.g., Kenitz et al. 2017). This complexity is one reason why trait-based approaches to community structure may be more successful when viewed in a multi-trophic context.

Trait matching and trait hierarchy in cross-trophic level interactions

A key question for developing a trait-based framework for trophic interactions is whether a defined set of traits can adequately describe the food web topology (i.e., presence or absence of interactions and their strength), thus increasing the predictive power of trait-based framework, and whether such traits are the same for different trophic levels and different interactions. Here, we identify the suite of traits that define cross-trophic coupling for two examples of trophic interactions, predator–prey (zooplankton–phytoplankton) and host–parasite (virus–microbe) interactions. The degree of alignment in paired traits can influence the interaction network structure (i.e., who interacts with whom) and the strength and the direction of natural selection. How well the traits that define these relationships can be generalized appears to be different for predator–prey interactions vs. host–virus interactions, which has implications for how useful and applicable/generalizable trait-based approaches could be for different types of interactions. Moreover, as explained below, the traits that are important for an organism’s performance in the absence of cross-trophic interactions may not be as relevant for characterizing interactions. To explore the concept of how traits must be framed to describe the coupling between two trophic levels we first map out our framework using the illustrative example of a primary producer and herbivore.

Predator–prey relationships are among the most influential interactions in most food webs, including planktonic food webs. The phytoplankton, major primary producers, are

consumed by zooplankton, leading to a trophic coupling between these major planktonic groups. There is a hierarchy of relevant traits that belong to different trait types, from morphological, to physiological and life history traits, involved in the coupling (Fig. 1; Table 1). First, we catalogue the relevant traits, next we attempt to categorize the traits, and finally we assess how readily we can rank the importance of the traits with respect to how influential they are in setting the trophic coupling.

In cataloguing the traits, we hypothesize that some traits may be more relevant to processes within a single trophic level (within-guild traits) and would not be directly involved in the trophic interaction but could still have indirect effects (Fig. 1). For example, dormancy may help prey escape grazing but would not directly determine the physical interaction of grazers and prey. Other traits, such as the cell size of the prey (primary producer) and the size of the herbivore may be more directly involved in trophic coupling (cross-guild traits) but do not alone fully characterize the interaction, and other traits, such as feeding strategy or selectivity must be included to describe the interaction (Fig. 1). Hence the “struts” of the scaffolding point towards each other but are not necessarily linked as just pairs. To complete the trophic coupling and better understand its multi-faceted functioning, the traits at two trophic levels must be matched to form linkages, often with individual traits at one level linked to multiple traits of the other trophic level (Fig. 1). Boukal (2014) also proposed that zooplankton and phytoplankton traits are linked through size matching and spatiotemporal overlap. Some phytoplankton–zooplankton models incorporate such trophic linkages, for example, prey edibility and predator selectivity jointly determine grazing (Tirok and Gaedke 2010; Kiørboe et al. 2018b; Serra-Pompei et al. 2020).

The inventory of traits reveals that in the case of the primary producer–herbivore linkage more than a dozen of morphological, physiological, behavioral, and life history traits are needed to describe the many facets of this trophic coupling (Fig. 1). Clearly, we need some criteria to categorize the roles and the relative importance of each trait to better describe how they perform within the trophic coupling. Prey size is jointly set by cell size (in turn influenced by environmental properties such as temperature and nutrient supply; Chisholm 1992; Marañón et al. 2012) and coloniality (driven by life history but also by nutrient supply, turbulence, grazer presence, etc.; Beardall et al. 2009). In turn, the grazing “window” or a feeding kernel width of a grazer will be set by its body size and feeding strategy, with more active feeding strategy resulting in a smaller size range compared to the more passive, filter-feeding strategy (Wirtz 2012; Heneghan et al. 2016).

Based on the knowledge of what underpins a trophic coupling, the traits that set the grazing “window,” that is the compatibility of the prey (i.e., size range, determined by cell size, shape and coloniality of prey) and the grazer (its

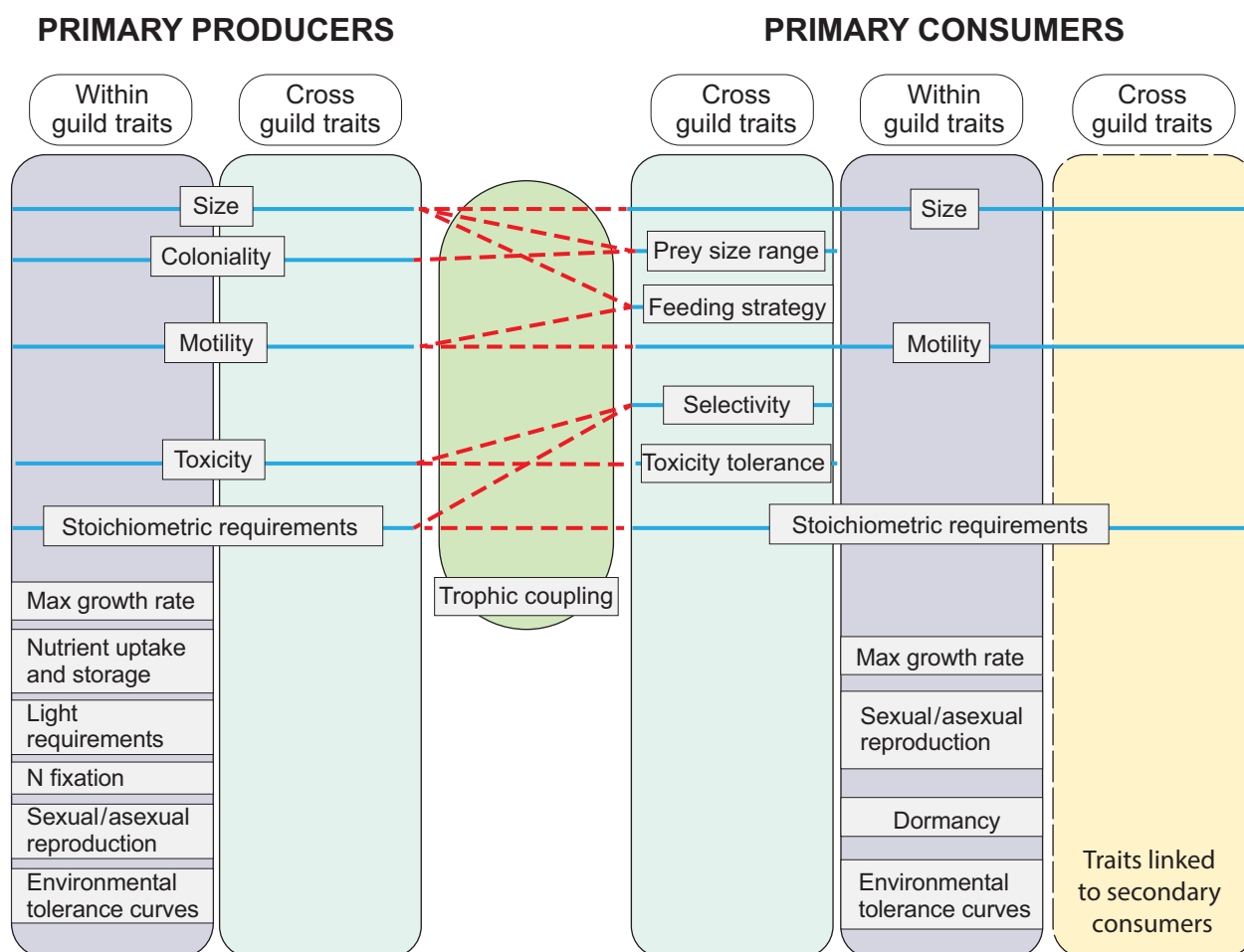


Fig 1. Trait matching and hierarchy within a planktonic predator–prey trophic interaction. Within each trophic level, there are traits that directly define the trophic coupling between primary producer (phytoplankton) and primary consumer (zooplankton), with some example traits shown as extending struts (termed cross-guild traits). They contrast with traits that may be more important for competitive interactions within an individual trophic level (within guild traits) but do not directly affect predator–prey interactions, such as nutrient uptake rate. Some traits, such as size, are important for both the individual trophic levels and for trophic coupling and are shown as extending through an individual trophic level towards the other trophic level (denoted by the dashed lines). Several traits involved in the cross-trophic interaction correspond to a trait of the other trophic level (e.g., phytoplankton toxicity and the zooplankton toxicity tolerance, or phytoplankton stoichiometry vs. zooplankton stoichiometric requirements) and others do not match but contribute jointly with other traits to the trophic coupling (e.g., phytoplankton cell size and coloniality) and pairing with several zooplankton traits (e.g., grazing “window”). The traits within this trophic coupling form a hierarchy, where traits in the upper portion of the figure determine if a trophic coupling is possible (size matching, in red). Zooplankton also interact with higher trophic levels and some traits are involved in such interactions, shown as extending to the right.

size and the feeding apparatus structure/feeding strategy, Wirtz 2012) are likely to be most influential. Without a match between prey size and grazing window there will be no trophic coupling, for example, if the cells are too small or the prey selection strategy excludes some cell sizes (salps vs. copepods, Michaels and Silver 1988). Next, palatability, ranging from toxicity (influential) to prey quality (stoichiometric requirements [N : P], somewhat less influential), will play a key role, determining the strength of interaction. Again, these palatability traits of the prey should have matching traits in the predator, such as the predator’s selectivity of prey items (an ability to reject unpalatable, either toxic or low quality prey; Cowles

et al. 1988, Sailley et al. 2015, Ger et al. 2019, Meunier et al. 2016), the tolerance of the prey toxicity or predator’s stoichiometric requirements (Sterner and Elser 2002; Lasley-Rasher et al. 2016; Meunier et al. 2016) (Fig. 1). If grazers are less selective, the importance of prey palatability/toxicity traits for the probability of ingestion diminishes but may still be high for grazer fitness, as the ingested low quality/toxic prey may decrease grazer growth rate and reproduction (Sterner and Elser 2002). Therefore, we can view a set of paired/matched traits that describe trophic interactions in a *trait hierarchy*, where the most general traits, such as prey size and the corresponding feeding window of the predator, define

Table 2. Comparison of predator–prey and host–virus interactions and some relevant traits involved in different interaction steps. Many of the mentioned traits in the host–virus interactions are not well characterized.

Relevant traits	Interaction steps		Relevant traits
	Predator–prey	Host–virus	
Prey and predator size, sensing (visual, chemosensory) movement speed	Initial encounter		Host and virus size, movement speed
Prey size, predator size, prey size range, feeding strategy, morphology of feeding apparatus	Size matching (prey geometry and compatibility with predator feeding apparatus)	Attachment/receptor matching	Shape and composition of virus attachment protein(s) and receptor molecule(s), host barriers to viral attachment (e.g., pore size of diatom frustules)
Prey palatability, toxicity, predator selectivity towards prey and toxicity tolerance	Sensing/manipulation/handling/ingestion	Entry into the host cell	Virion proteins that digest cell walls/glycoproteins, fuse viral envelopes with cell membrane, induce endocytosis, or inject the viral genome
Prey stoichiometry (C : nutrient), predator dietary needs, predator assimilation efficiency	Digestion	Replication/lysis	Latent period, burst size, virus and host size, host defenses, virus counter-defenses, viral genes that alter host metabolism

possible interactions and other traits, such as prey toxicity and grazer selectivity, determine whether a particular possible interaction would be realized and how strong the interaction would be.

Identification of such universal and paired traits is an important first step in building a database of measurements to examine the trophic coupling in detail. The trait pairing/matching also implies that these traits influence each other. For example, if the prey selection window (feeding kernel) of a predator changes, possibly due to evolution (see below), such change would influence the prey size distribution and vice versa. Similarly, if the prey toxicity increases, that could lead to the evolution of higher toxicity tolerance in a consumer (Hairston et al. 1999).

Host–parasite relationships, such as phytoplankton–virus interactions, are not as well characterized as phytoplankton–zooplankton (predator–prey) interactions and the traits important for this type of interaction are only beginning to be identified (Table 2). Viruses are major agents of mortality for microbes and considering virus–host interactions from a trait-based perspective is important for developing a comprehensive picture of planktonic food webs. Bulk estimates of viral mortality for bacterioplankton and phytoplankton are highly variable, with some studies finding minimal rates and others finding half or all of daily production lysed by viruses (Fuhrman and Noble 1995; Weinbauer and Höfle 1998; Jacquet et al. 2005; Tsai et al. 2013; Pasulka et al. 2015; Mojica et al. 2016). It has also been argued that viruses may terminate blooms of phytoplankton such as the coccolithophore *Emiliania huxleyi* and dinoflagellate

Heterosigma akashiwo (Bratbak et al. 1993; Tarutani et al. 2000; Lehahn et al. 2014).

To consider whether a trait-based perspective allows us to better understand or predict planktonic food webs, and host–virus interactions in particular, we can ask (1) whether focusing on a set of key traits allows us to explain who infects whom, (2) what traits can inform us about how the infection proceeds, and (3) whether universal principles relating traits, trade-offs, and diversity allow us to explain general patterns in community structure across environments.

Viruses tend to be much more specialized compared to grazers, inflicting mortality on a narrow range of hosts (host range). Usually only a single genus can be infected, and a particular virus strain will typically infect only a subset of strains in that genus. Virus host ranges likely tend to be specialized because complex traits of the virus have to precisely match or overcome complex traits of the host in order for an infection to be successful (Hyman and Abedon 2010; Samson et al. 2013). By analogy to predator–prey interactions, where prey size relative to the predator is an initial “filter” that determines whether an interaction is likely to occur, the initial step in the infection process is whether the virus can attach to the host cell. Subsequent to *attachment*, there are other potential restrictions on whether an infection will succeed, such as ability of the virion or viral genome to gain *entry* into the host cell, *host defense mechanisms* and *viral counter-defenses*, and *replication* and cellular transportation processes that rely on host machinery (Table 2).

The identity of viral receptor molecules is poorly understood in planktonic microbes, but the importance of

attachment in explaining host range is supported by a variety of evidence. For example, the host range of *H. akashiwo* viruses is predicted by their ability to attach to host strains (Tarutani et al. 2006), experimental evolution of phage resistance in *Synechococcus* yielded mutant strains to which the phage could not attach (Stoddard et al. 2007), and haploid cells of *E. huxleyi* are resistant to infection by a virus that infects diploid cells but does not attach to haploid cells (Frada et al. 2008). Studies of model bacteriophages demonstrate in detail how the attachment process that limits host range can operate. For example, phage λ attaches to *Escherichia coli* via the J protein at the base of its tail, which binds to the maltose porin on the outer membrane of the host cell, which is produced by the *lamB* gene. A variety of single amino acid substitutions in *lamB* can confer resistance to λ (Chatterjee and Rothenberg 2012), only some of which affect maltose transport or starch binding (Charbit et al. 1988), while single-step mutants in the J protein can overcome host resistance (Werts et al. 1994). This subtle control over trophic linkages suggests a “lock-and-key” type of mechanism that contrasts with predator–prey linkages, which are usually more generalized and less likely to be affected by single amino acid substitutions.

There is also evidence that broadening the host range of a virus comes at a cost of reduced fitness on individual hosts (Duffy et al. 2006; Keen 2014). For this reason, it may actually be adaptive for viruses to attach to only a narrow range of hosts on which they have the greatest infection efficiency (Heineman et al. 2008). This *generalist–specialist* virus trade-off is probably not as common or as strong for zooplankton grazers, as most zooplankton can consume a relatively wide range of prey (Steinberg and Landry 2017), suggesting different selective pressures for specialists vs. generalists in these two types of interactions. However, in other systems, some grazers may be highly specialized. For example, a sea hare *Stylocheilus striatus* readily grazed a toxic cyanobacterium *Lyngbya*, while other grazers, such as sea urchins and amphipods, avoided consuming it (Cruz-Rivera and Paul 2007).

In light of the specialized and intricate nature of virus–host interactions, a trait-based perspective may not be as helpful for predicting who infects whom a priori, if there is no modest set of universal traits shared by viruses and hosts which could be used to predict such linkages. Even for the initial stage of virus attachment to a host cell, we have little knowledge of the identities of the viral receptors, why the viral particle can attach to these receptors for particular virus–host pairs, and why particular host or virus mutations inhibit attachment. A general lack of understanding of the “rules” of virus–receptor interactions extends also to well-studied human pathogens (Str  h and Stehle 2014). This contrasts with zooplankton–phytoplankton predator–prey interactions that can be reasonably inferred from the size comparison between predator and prey and further defined by a limited set of other traits, such as grazer feeding strategy and prey palatability/

toxicity. This fundamental difference between the predator–prey and host–parasite interactions in how well these relationships can be described by key traits such as size may also hold true for other ecological systems. For example, Petchey et al. (2008) could predict predator–prey links based on size much better than the parasite–host or pathogen–host interactions in different aquatic and terrestrial food webs.

Although the host range of a virus is difficult to predict based on phenotypic characteristics of the virus, this does not mean that trait-based approaches are not useful for other aspects of viral ecology. In particular, the strength of host–virus interactions and the potential impact of a virus on host populations may be more amenable to a trait-based approach. Comparative analyses and experimental evolution with model bacteriophages as well as phytoplankton viruses indicate that variation in key traits across virus taxa may be explained in part by trade-offs and other constraints (Gudelj et al. 2010; Goldhill and Turner 2014; Record et al. 2016). For example, substantial variation in burst size of phytoplankton viruses (the number of virions released per infected cells) can be explained by the host genome size relative to the virus genome size, indicating that host genomic resources constrain viral production (Brown et al. 2006; Edwards and Steward 2018). Latent period (the time elapsed between infection and cell lysis) may be optimized to maximize fitness, contingent on host density and the availability of host resources for reproduction (Abedon et al. 2003; Edwards and Steward 2018). The viral decay rate (the rate at which virions decay or become noninfective) is positively correlated with replication rate across coliphages, and decay rate is negatively correlated with capsid thickness, indicating that stable, high-quality “offspring” are produced at a slower rate (De Paepe and Taddei 2006).

Importantly, viruses vary greatly in physical size and genome length (Campillo-Balderas et al. 2015), with genome size varying a thousand-fold and capsid volume nearly a million-fold. Furthermore, the greatest known range of virus sizes occurs among viruses infecting unicellular eukaryotes, and “giant” eukaryote-infecting viruses, as well as large prokaryote-infecting “megaphages” appear to be widespread and diverse in the ocean (Al-Shayeb et al. 2020; Schulz et al. 2020). Similar to cellular organisms, considerable variation in virus traits may be explained by size, because there are physical disadvantages to large size, while at the same time larger viruses with longer genomes can code for additional fitness-enhancing functions. Larger viruses should diffuse more slowly, reducing contact rates with their hosts, although observed adsorption rates are often less than the theoretical maximum (Talmy et al. 2019; Edwards et al. 2021). There is evidence among phytoplankton viruses that larger viruses have a reduced burst size, but at the same time the expected cost of increased size is mitigated by greater production of viral mass during infection (Edwards et al. 2021). In addition, larger viruses infecting marine bacteria tend to have broader

host ranges (the number of strains they can infect) compared to smaller viruses (Edwards et al. 2021).

Because viruses vary greatly in size, but the trade-offs shaping virus size are different than the trade-offs shaping the size of unicellular organisms, patterns in the distribution of virus size may differ from patterns in cell size. For example, oligotrophic environments that select for small cell size may select for giant eukaryote-infecting viruses, because oligotrophic environments with low host density and predominantly phagotrophic eukaryotes may select for broad host range, tighter control of cellular metabolism, and entry to the host via phagotrophy (Edwards et al. 2021).

Traits in models of predator–prey and host–virus interactions

Predator–prey interaction

As with most predator–prey interactions, the interaction between a phytoplankter and a zooplankter includes several processes, including prey encounter, selection, capture, ingestion and digestion (Flynn and Mitra 2016) and each of these processes are influenced by the interacting traits of both predator and prey. There are numerous modeling studies describing phytoplankton–zooplankton interactions that range in their generality and complexity (Banas 2011; Ehrlich and Gaedke 2020; Serra-Pompei et al. 2020). We provide a very brief overview here but the detailed descriptions of the different models can be found elsewhere (Tirok and Gaedke 2010; Serra-Pompei et al. 2020). The most commonly used equation to describe grazing is Holling’s type II functional response formula (Holling 1965; Kiørboe et al. 2018a):

$$I = a \frac{P}{1 + ahP},$$

where I is the ingestion rate, P is prey concentration, a is the attack/encounter rate and h is the handling time.

The parameters that describe grazing rates are influenced by multiple traits of both the prey and the grazer. For example, in some model parameterizations, the encounter rate depends on predator and prey swimming speeds and prey concentration (Visser 2007) and handling time is determined by grazer’s selectivity, prey size relative to the grazing “window” and palatability (e.g., toxicity) (Kretzschmar et al. 1993). The differences in prey defense traits (Van Donk et al. 2011) would result in different ingestion rates in model simulations. Conversely, the same prey would be ingested at different rates by predators with different traits (Levine et al. 1999; Nejtgaard et al. 2007). Differences in prey defense traits may promote prey coexistence; the defense traits that increase predator handling time (postattack defense traits) may promote coexistence more effectively (Ehrlich and Gaedke 2018).

There are explicitly size-dependent models that define the size ratios of predator and prey, simplifying the trophic

coupling as a function of size and feeding strategy (Wirtz 2012; Heneghan et al. 2016). The models assume that the size ratio of prey to predator declines with increasing predator size because the feeding apparatus does not increase as fast as the predator size (Wirtz 2012, Heneghan et al. 2016). The different feeding strategies such as passive (filter) or active (ambush) feeding can also be included to better characterize the trophic interaction (Wirtz 2012). The ingested prey is then converted to zooplankton biomass with a certain biomass conversion efficiency which can be different for different prey but often assumed the same (Ehrlich and Gaedke 2020).

While there are many empirical studies that investigate how the coupling of the trophic traits other than size (e.g., prey palatability and grazer selectivity or resistance to toxicity) influence the grazer–zooplankton interaction, most food web models do not explicitly include them. Adding more traits to model trophic interactions makes models more complex and more difficult to parameterize but—as a trade-off—could describe the interactions more realistically (Flynn and Mitra 2016). Future modeling studies should investigate how sensitive food web dynamics are to the addition of more traits to describe trophic interactions. Such sensitivity analysis could inform the above trade-off between realism and computational expense/parameterization complexity.

Some of the models of predator–prey interactions specifically focus on how traits change as a result of such interactions (Tirok and Gaedke 2010; Banas 2011; Ehrlich and Gaedke 2020). In a strict sense, those are “trait-based” models, in contrast to models that simply incorporate traits (most models) (Klausmeier et al. 2020).

Host–virus interaction

The population dynamics of a lytic virus infecting a microbial host are often modeled with the equation:

$$\frac{dV}{dt} = bKS^{t-L}V^{t-L}e^{-mL} - kSV - dV,$$

where V is concentration of free virions, b is the burst size (virions created per infected cell), k is the effective adsorption rate, S^{t-L} is the concentration of host cells at time $t - L$, L is the latent period (time between initial attachment and lysis), m is the host mortality rate, and d is the rate at which infective virions are lost due to decay of infectivity and other processes (Levin et al. 1977). The key traits of a lytic virus are therefore the burst size, the latent period, the adsorption rate, and the decay rate. The effective adsorption rate parameter may depend implicitly on encounter rate, attachment (host/virus receptor matching) and successful entry into the host. The population dynamics of the host can be modeled as separate fractions of susceptible and infected cells (Levin et al. 1977). As with the models of the phytoplankton–zooplankton interaction, different model parameters either represent individual traits or composites of several physiological traits and processes. A potentially fruitful development of models could be a more explicit

incorporation of the key traits that define intertrophic interactions that could be determined empirically (Table 2).

This challenge requires establishing the hierarchies of traits that are relevant to individual interactions and determining the trait overlaps across interactions and the ways to reduce the number of traits without losing the ability to meaningfully characterize multiple interactions. These goals of identifying important interaction traits, reducing their number while preserving both qualitative and quantitative aspects of interactions are especially relevant to modeling studies, as including more traits could help increase the realism but would make parameterizing the models more difficult.

Unifying trait-based principles that structure trophic interactions

As there are traits and trade-offs that are universal across trophic levels and trophic interactions, it may be possible to identify some unifying principles that structure various food web interactions. One such universal trade-off that transcends different trophic interactions is the competition-defense trade-off, where investment in defense against enemies reduces the ability to compete for limiting resources. In plankton communities such trade-offs are thought to apply to both predator-prey interactions and virus-host interactions (Edwards et al. 2011; Våge et al. 2018). This trade-off is well-established for the zooplankton-phytoplankton interaction, where variation in cell size is one source of a competition-defense trade-off. Small cells are highly competitive for nutrient resources (Edwards et al. 2011; Edwards et al. 2013a) but often susceptible to grazing. For example, predation pressure on freshwater algae by cladocerans selects for larger morphologies associated with slower growth rates (Steiner 2003). Other defense-related trade-offs are orthogonal to cell size, for example, in marine diatoms their silicification reduces copepod herbivory but is associated with slower growth rates (Pančić et al. 2019).

In virus-host interactions the evolution of resistance is often associated with reduced growth rate or increased susceptibility to alternative viruses (Lennon et al. 2007; Avrani et al. 2011; Thomas et al. 2011). If competition-defense trade-offs are prevalent, then trait diversity in a guild of co-occurring species may be aligned along a competition versus defense axis, and similar diversity may also occur among genotypes within a species (Yoshida et al. 2004; Våge et al. 2018). Thus, the same trade-offs can occur at different levels of taxonomic resolution, displaying a trade-off hierarchy (Litchman et al. 2015a). Furthermore, it is predicted that increased resource supply will shift communities toward better-defended species, and better-defended genotypes within species, because the selective pressure to reduce mortality increases as greater populations of enemies are supported (Leibold 1996; Steiner 2003) (Fig. 2).

Another unifying principle important for traits in trophic interactions is that specialized trophic interactions tend to increase diversity. In predator-prey interactions size-structured

predation can allow larger phytoplankton to persist, because smaller phytoplankton with higher specific nutrient affinity are suppressed by relatively small grazers that cannot consume larger phytoplankton (Armstrong 1994; Landry et al. 2000). Similar dynamics are thought to be important for virus-host interactions, where superior competitors are suppressed by viral mortality, potentially allowing inferior competitors to persist (Winter et al. 2010). In both cases, trait diversity within a community is broadened beyond the strategy that would dominate in a world structured only by resource competition. Interestingly, when specialized predators are important, an increase in resource supply should allow a broader diversity of poorer competitors to persist (Armstrong 1994), while generalized predators should favor defended strategies over competitive strategies at high resource supply (Leibold 1996) (Fig. 2). Natural communities possess a diversity of predator strategies, and viruses are specialized at the community scale but may select for defense strategies within species, suggesting that a mix of the two patterns may occur over natural resource gradients.

Phenotypic plasticity and eco-evolutionary responses of traits to environmental factors and the effects on trophic interactions

Traits are not fixed but exhibit considerable plasticity and change depending on the environment. For example, phytoplankton cell size can either increase or decrease under nutrient limitation: often nitrogen limitation leads to a reduction of cell size, while phosphorus limitation may increase cell size (Litchman et al. 2002; Vanucci et al. 2012). Changing cell size may make phytoplankton more or less susceptible to herbivory by specific grazers, thus mediating the predator-prey interactions. Other phytoplankton traits, such as C:N:P stoichiometry that determines food quality for zooplankton, also depend on nutrients, as well as on light and temperature (Sterner and Elser 2002; Finkel et al. 2010; Edwards et al. 2016). Thus, environmental conditions may modify predator-prey relationships by changing relevant traits. Prey defense traits, such as increase in colonial forms or the size of the colonies, spines or cell wall structure, as well as toxicity, are also plastic and often controlled by the presence of grazers (Van Donk et al. 2011). Changes in prey traits induced by grazers can then feed back into the prey-grazer interactions.

Traits may also evolve due to diverse selective pressures, including cross-trophic level interactions. The most notable examples of evolution of traits that are involved in cross-trophic interactions are the “evolutionary arms races” between predators and prey, where selection by the predator leads to changes in prey traits and then predator traits evolve in response, creating the co-evolutionary dynamics (Smetacek 2001). Among the traits that may evolve are the traits that decrease prey susceptibility to predation, for example, defense traits, such as cell size or coloniality (Yokota and Sterner 2011), thickness of cell wall or gelatinous sheath (Meyer et al. 2006; Demott and McKinney 2015),

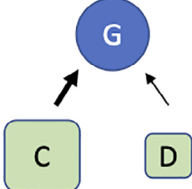
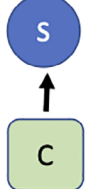
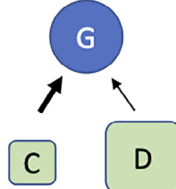
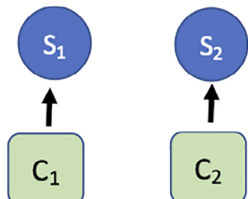
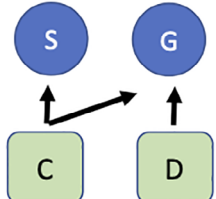
Predator/parasite type	Generalist Predators	Specialist Predators	Generalist-Specialist Spectrum
Prey trait variation	Competition-Defense Tradeoff	Competitive differences	Competition-Defense Tradeoff
Low resource supply community			
High resource supply community			
Examples	Single cells vs. colonies of <i>Phaeocystis</i> and diatoms Viral infection of different host strains	Size-structured plankton food webs Viral infection of different host species	Zooplankton with broader vs. narrower prey size ranges Viral infection of different host strains

Fig 2. Some general principles connecting traits, trade-offs, and community structure in food webs. In the first column, a generalist predator can select for multiple prey types (competition vs. defense strategies), and the prey community will shift towards better defended types under higher resource supply. In the second column, specialist predators can allow multiple prey types to coexist, even if some are competitively inferior, and the diversity of prey and predators will increase with higher resource supply. In the third column, the predator guild contains a spectrum of generalists vs. specialists, while the prey guild contains competition vs. defense strategies, and higher resource supply allows more generalized predators and better defended prey to persist. The examples listed in the bottom row illustrate how these different food web structures can be present in both zooplankton–prey and virus–host interactions. Note that some food web structures are more representative of strain-level host–virus interactions (left and right columns), while some are more representative of how host–virus interactions appear at the species level (middle column).

palatability and toxicity. In turn, predators can evolve relevant traits as well. For example, eutrophication led to dominance by toxic cyanobacteria in a lake but the main grazers *Daphnia* evolved resistance to cyanobacterial toxins over a couple of decades (Hairston et al. 1999).

The evolution of traits that define inter-trophic interactions may lead to changes in the strength of such interactions, especially if the time scales of adaptation differ between different trophic levels. Better defense traits in the prey may evolve faster than the corresponding predator's traits that allow prey consumption. In this case, the strength of interaction would weaken until the predator's traits catch up. Another consequence of trait evolution due to trophic interactions is that evolved traits may allow new interactions to arise. If prey size evolves towards larger sizes to avoid predation by a certain predator, other predators that are adapted to the new, larger prey size may become the dominant consumers for that prey and, thus, the trophic interactions would be rearranged.

Conclusions and future directions

Here we identified universal, as well as the trophic-level specific traits in planktonic food webs. We discussed traits that directly characterize two major trophic interactions, predator–prey and host–parasite interactions. When comparing different trophic interactions, the known traits may differ in their usefulness for predicting whether the interaction would happen or not. Currently, the traits underlying phytoplankton–zooplankton interaction are better characterized and more informative in predicting that interaction compared to the host–virus interaction, where we still cannot identify traits that would predict the occurrence of this host–parasite interaction.

Mutualistic interactions, such as those between bacteria and eukaryotic phytoplankton, may also be amenable to trait-based approaches, where key traits could be metabolic traits of the partners and their complementarity (Amin et al. 2015).

The examples and discussion presented here are generalizable and applicable beyond just the planktonic food webs and could provide insights into trait-based approaches to food webs in other systems as well. In particular, identifying the universal traits and trade-offs across trophic levels and determining how the distributions of such traits change along environmental gradients, as well as comparing the important traits for different interactions, can be carried out for other interaction types and for other, benthic or terrestrial, food webs.

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None declared.

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