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Chapter

Food Webs

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Abstract

Ciliates are important elements of the trophic networks of aquatic and terrestrial environments, they can be primary producers (myxotrophs), consumers of bacteria, algae, flagellates, even other ciliates and can serve as food for metazoans, for all the above they are the link between different levels of food webs. The structure of the ciliates varies according to the seasons of the year and depending on the trophic conditions of the aquatic systems. Ciliated communities have modifications and adaptations in response to environmental perturbations. The objective of this chapter is to describe the importance of different trophic groups of ciliates in different ecosystems, including anthropogenic perturbations and their impact on trophic webs.

Keywords: ciliates, trophic groups, food webs, perturbations

1. Introduction

Trophic relationships between organisms are the mechanisms responsible for most of energy and nutrient transfers; they allow the functioning of the ecosystem. These relationships, known as food webs, caught the attention of naturalists before the concepts of evolution and ecology were about to be determined.

Initially, the diet of a species and its skills to obtain it were recognized as the leading factors for the prevalence of the fittest. Additionally, it is one of the main forces leading to evolution of that species in the long term [1]. Furthermore, competition for food became one of the favorite hypotheses to explain species exclusion; it states that when two species seemed to feed on the same resources, the best suited ultimately leads its competitor to extinction in the long term [2]. This idea has been around for many years and has not been completely discarded or proved [1].

Examining phototrophs, also known as primary producers, is the dominant starting point to analyze food webs. They use the incoming sun's energy and inorganic nutrients to generate their biomass. This is the most important mechanism, as it initiates the cycling of nutrients and energy flux in aquatic food webs. There is primary productivity involving chemolithotrophs dominating in places devoid of sun's light [3]. These places were mostly known to be, until recent times, around underwater volcanoes more than 1000 meters deep [3, 4].

Primary production is at the base of all consumers concurring in the environment. However, macroscopic food webs tend to be very short, with few levels of consumers because these organisms dissipate matter and energy efficiently [5]. All metazoans invest their energy looking for food, ingesting it, digesting,

repairing themselves, mating, and reproducing. These activities make multicellular organisms to get around 10% of biomass fixation efficiency. Thus, 1,000 kgs of the primary producer will be needed to produce 100 kgs of herbivorous animals, only 10 kgs of small carnivores, 1 kgs of medium-sized carnivores, and only 0.1 kgs of top carnivores, following a pattern known as pyramid of productivity [5]. Adding a predatory species at any level would destabilize the food web, as this will consume higher amounts of biomass [6]. Energy dissipation is even larger, meaning that the entropy produced during the functioning of the food web is very high. However, only 1% of the incoming sunlight is used for primary production, stressing the importance of the environmental factors limiting biomass productivity to sustain food webs.

Primary productivity varies along seasons. When it reaches its peak, productivity is controlled by the top predator's consumption (top-down), and when it reaches its lowest level, productivity is controlled by phototrophs (bottom-up). There are places that are permanently bottom-up controlled such as the deep ocean communities depending on the "organic matter rain" from dead organisms living in the photic zone in places near the equator are almost always top-down controlled, where productivity may be at its peak for most of the year. All other places experience top-down/bottom-up controls alternatively, depending on the productivity seasons.

Unicellular algae lead primary productivity in marine environments, sustaining the great diversity of organisms, especially in places receiving nutrient inputs from lands. Heterotrophic unicellular organisms forage on algae and both phototrophs (phytoplankton) and heterotrophs (zooplankton) conform to the plankton. However, unicellular organisms span in sizes less than 1 µm to hundreds of micrometers, and the species' diversity of plankton, including microbial eukaryotes and bacteria, ranges in the order of thousands. Species of microorganisms are much more numerous than the metazoans. With such a great diversity of microorganisms, it become apparent that the microbial food webs may function differently from the macroscopic food webs.

It was believed that food webs would get destabilized if the number of species increases at any level above the primary producers. However, microbial food web seemed to get more stability with the increasing number of species, contradicting what was observed in macroscopic food webs [7]. Thus, the higher number of species of bacterial and microbial eukaryotes in aquatic food webs seemed to contradict that assumption; this phenomenon was named as "The paradox of microbial loop." It was paradoxical that productivity and efficiency of nutrients and energy transformation is increased by adding more species, promoting the stabilization of the food web [8].

It's been a long road since the recognition of the "paradox of the microbial loop" in the aquatic food webs. Nowadays, it is referred only as the "microbial loop," after being integrated into the food web conceptualization in both terrestrial and aquatic environments [7].

The complexity of microbial food webs needs to be approached from the analysis of different functioning capacities and nutritional needs of the participating species. It has been normal to assign very general feeding habits to protists and metazoans, like bacterivores for example. This nomenclature implicates that a single species of protist can feed on any one or indistinctly on all the thousands of bacteria species. However, observation of feeding habits has revealed that protists and metazoans prefer feeding on specific kind of bacteria while avoiding other species. Pigmented bacteria [9], for example, has fewer predators than non-pigmented ones. On the other hand, there are several species of protists, mostly amoebae, small flagellates and *Colpoda steinii* that feed on pigmented ones [10].

One explanation for pigmented bacteria to have fewer predators relied on the toxicity or poisonous effect of those pigments for many protists, pointing out the importance of the biochemical warfare that bacteria must synthetize to defend themselves. However, chemicals used for evading enemies attract other ones looking for those same compounds, putting bacteria in a situation where there is no way out for bacterial preys. Indeed, there is no way out of being preyed upon, as every living being has predators, or at least other species which may feed on them or use them as a resource.

Is there a single factor determining the feeding preferences? The short answer is "No." Remember that "bacterivorous" or "algivorous" are labels used to recognize the kind of food that protists and metazoans may prefer to feed on, and it involves many species. From the beginning, this was a non-exclusive way to label the category of food that may be used to group the highest quantity of species to simplify and conceptualize the food webs. Furthermore, during the first half of the XX century [11], there were many very interesting studies trying to determine the "diets" of several species of protists [11, 12], with the aim of designing a chemically defined culture media, as is the case of several recipes for culturing *Tetrahymena pyriformis, Glaucoma sp,* or *Paramecium* sp., culminating with 3 books edited by Lewandowsky and Hutner (1979), approaching the field of protists' biochemistry (at that time it was biochemistry of protozoa).

Designing a culture media for protists or bacteria was a major task, as numerous factors about their nutritional needs were unknown (and remain unknown). These attempts to cultivate bacteria and protists lead to one important conclusion: different species cannot synthesize one or several molecules needed for their metabolism and have to take those molecules, as such, from their ingested food [12] or from other microorganisms that live within the biofilm (such as the case of NAD+ **, which the bacteria has to consume from other species of bacteria for both of them to grow). Microbial biologists named this phenomenon as "auxotroph" [13]. In this way, the molecule(s) a bacterial species is auxotroph for must be added to the culture media, to keep a culture of such species [14]. The kind of molecules, their diversity, and their macro- and micronutrient composition form a universe comparable to the one containing the species' diversity on the planet.

2. Phagotrophic protists

Ecological relevant functions have been recognized in prokaryotes and microbial eukaryotes. Bacteria have been cataloged as nitrogen fixing, denitrifiers, metanogens, methanotrophs, phosphorous mobilizers, metal mobilizers, phototrophs, and chemolithotrophs as the main recognized functions in the ecosystem. On the protists' side, several trophic groups have been recognized as phototrophs and phagotrophs. The first group is strictly divided between the phototrophs and mixotrophic ones, while the second one may be divided in bacterivorous (including cyanobacteria), frugivorous (feeding on hypha and or yeasts cells), algivorous, protist consumers (raptorial protists), and metazoan predators. Parasitic bacteria, pathogenic bacteria, and microbial eukaryotes have been largely studied from the medical point of view. However, recently, they have been studied from the ecological perspective (their impact on the predator–prey relationships, the "health" of species populations protected for conservation, and their effect on the nutrients distribution along food webs [13].

Phagotrophic protists may ingest very different kinds of particles and present the capacity to eject the ones they cannot digest, or even reject particles previously ingested [15]. Even if the water current would transport a good mixture of different

bacterial species, phagotrophs may choose which particles ingest and eject the debris from their digestion together with the non-digestible microorganisms. This means that protists may show preference for the kind of food they most likely can digest (recognizing their preys by their quorum sensing signals), and, like bigger organisms, they may need a variety of food sources to get the nutrients they need [15].

A close examination of the different trophic groups allows to re-mark the unicellular phototrophs as the most productive in terms of biomass production since there is no synthesis of support or conductive structures, and, because of that, they are the base of the aquatic food webs.

The phagotrophic protists have been recognized for being the main consumers along microbial trophic networks in aquatic systems conforming a major proportion of the microbial biomass in these systems [16, 17]. These predators are also responsible for much of the recycling flow of nitrogen and phosphorus in the aquatic systems [18].

Particularly the ciliates are key elements of aquatic food webs they have several functions, they can be primary producers, predators, they serve as food for metazoans including free-living stages of metazoan parasites; there are many aquatic habitats without macro-organisms, but none without bacteria and at least few protist species [19].

2.1 Mixotrophic ciliates

One of the most interesting groups of protists are the mixotrophic ones. Some of them may correspond to the old morphological groups of ciliates, flagellates, and ameboebas. Mixotrophy is defined as the ability to combine phagotrophy and phototrophy in a single cell [20]. This group can be divided into constitutive mixotrophs, meaning they have the innate ability to photosynthesize, and the facultative or non-constitutive mixotrophs. These organisms may sequester the plastids after consuming their phototrophic preys or by harboring photosynthetic endosymbionts [20, 21]. Around 23% of planktonic ciliates species (marine and freshwater combined) perform acquired phototrophy, and this ability is present in at least 8 main ciliated taxa: Heterotrichea, Hypotrichia, Oligotrichida, Stichotrichida, Litostomatea, Prostomatea, Peniculia, and Peritrichia. Phototrophy is usually acquired from algae endosymbionts in 7 of these 8 ciliated taxa. Contrastingly, Oligotrichida usually obtains this ability by plastid sequestering [22].

The structures of the mixotrophic ciliates community varies through seasons, depending on the changing water trophic condition. Mixotrophic ciliates dominate in spring and summer, reaching from 58–100% of the ciliates in oligotrophic waters [23–25], but represent only 5% of the total community of ciliates in winter, probably due to the lower water temperatures and nutrients. These conditions restrict the growth of algae, negatively affecting the population of mixotrophic ciliates if their preferred species of algae is missing [24].

The mixotrophic ciliates are mainly from the genera *Mesodinium rubrum* (*Myrionecta rubra*), *Strombidium* spp., *Laboea*, *Lohmaniella*, and *Tontonia.* All of them represented by small species (30–50 μm) [23, 25, 26]. Even *Mesodinium rubrum* and other functionally photoautotrophic ciliates can sometimes contribute significantly to primary production in lakes and oceans [27]. Other species of mixotrophic ciliates are larger; for example, the genus *Stentor* is a "large" cell ~200 μm and is contributed between 49% and 68.8% of the total biomass of zooplankton in the oligotrophic lake at the Northern Patagonia of Chile [28]. *Stentor niger* represented 90% of the total ciliates biomass in Lake McCloud [29] and was the dominant protist of acidic oligotrophic lakes [30]. Some species

of the genus *Stentor* also contributed with more than 50% of the plankton's photosynthesis of oligotrophic Australian lakes [31]. Dominance of this trophic group may be influenced by the limiting conditions for phototrophs, to achieve the same productivity that mixotrophs may obtain by feeding both ways. Grazing allows mixotrophs greater flexibility for balancing the supply and demand of scarce nutrients [32], a clear advantage in times of scarcity [19]. Due to their flexible nutrition, mixotrophic protists dominate in mature or more stable systems (e.g., during mild summer, in established eutrophic systems, and in oligotrophic systems). Furthermore, climate change can be expected to favor mixotrophs in the more stable water columns [32].

Ward and Follows [33] performed a global simulation of the ocean-surface food web, revealing that mixotrophy enhances the transfer of biomass to larger organisms at higher trophic levels, which in turn increases the efficiency of oceanic carbon storage through the production of larger and faster sinking conglomerates of organic molecules. It follows that mixotrophic protists play a key role in modulating the primary production that underlies the food web in aquatic systems [21, 22, 32]. However, their importance has not been fully appreciated because traditional field and laboratory studies focus on strict classifications as phototrophs or phagotrophs [32] because incorporating this flexibility to acquire food is difficult to modelize. Mixotrophy is known to be common in all aquatic systems but its contribution to net community production is difficult to quantify, and the integration of their impact on the global biogeochemical cycles remains to be incorporated.

2.2 Bacterivores

Ciliates and flagellates are the most dominant bacterivores among the phagotrophic protists in most aquatic systems [16, 34], consuming between 25–100% of the daily production of marine phytoplankton together with large quantities of bacterial biomass [18]. Bacterivores and algivorous protists are the core consumers of microbial biomass in aquatic food webs [16, 17] regulating these groups in two apparently contradictory ways: by feeding on the abundant food source, they keep in check their further expansion, that in turn gives other less preyed species the opportunity to become more numerous, and at the same time, the release of cellular wastes (from protists) enhance the reproduction of the species being predated. The combined effect of these two processes enhances the nutrient cycling and fuels biomass productivity. By performing this activity, ciliates and flagellates increases their own biomass, attracting metazoan predators and functioning as linkage of lower and upper trophic levels in aquatic food webs [16, 35, 36].

The size of the ciliate determines the sizes of preys they can feed on. Thus, bacterivorous ciliates ingest a different particle size range; the preferred size spectrum for each species is a function to cytostome size and morphology. For example, small ciliates usually bacteria eat <3 μm [18, 37, 38]. Ciliates that feed on the smallest particles (<1 μm) require relatively high densities of these bacteria as a minimum to keep their population growth [30]. Several groups of ciliates actively feed on specific bacteria species for a period ranging between 44% and 100% of the time, because bacterial densities will have variations as responses to predation intensity along time [36].

Bacterivorous ciliates are present in all aquatic environments, from oligotrophic to eutrophic, in both freshwater and oceans. The diversity of bacterivorous ciliates and their contribution to the flow of energy in trophic networks depend on the dynamics of the systems in which they are living. Therefore, food resources are probably the main regulators of ciliated communities (diversity, abundance, and

biomass) [30]. For example, bacterivorous ciliates contribute very little for the direct transfer of bacterial production to the trophic networks of metazoans in oligotrophic environments. Ciliates consume less than 11% of bacterial productivity in these waters [39–41]. Perhaps the heterotrophic bacteria that are very small in these lagoons (0.035 to 0.4 μm) are grazed by bacterivorous ciliates at a very low rate [41], or the number of bacteria is not enough to support larger ciliate communities feeding on smaller bacteria (<1 μm), as they require high densities of bacteria to maintain their populations [30]. Then, productivity of oligotrophic systems function most of the time as bottom-up (availability of substrate and nutrients) controlled [42]. This functioning will remain until seasonal pulses of nutrients (or human subsidies) arrive, busting primary productivity and changing the system into top-down control, and it will keep functioning the same way until the pulse of nutrients (or subsidy) is completely metabolized, returning the system to the bottom-up dynamic.

Contrastingly, densities of heterotrophic bacteria in eutrophic environments are sufficiently higher to also keep a higher diversity of active bacterivores [43], fueling ciliates biomass productivity and allowing the intervention of metazoan predation. Top-down control (predation) seems to be in function all the time for regulating the abundance of heterotrophic bacteria in eutrophic systems [42]. Normally, communities of bacterivorous ciliates of small sizes (~ 30 μm) are found as dominant in eutrophic environments [30, 38]. The most abundant ciliates in these environments are small oligotrichs (*Halteria*), scuticociliates (*Cyclidium*), and Peritrichs (*Vorticella*) [30, 38, 44, 45]. *Halteria grandinella,* for example, is one of the most important bacterivores due to its high consumption rate of bacteria [38], the genus *Halteria* is very important in meso-eutrophic lakes because they prey on a large spectrum of sizes, from bacterial cell measuring just around 0.4 μm to up to 5 μm; they have a high potential growth rate, because of its efficient nutrient absorption, and show defensive strategies reducing their vulnerability to predation by metazooplankton in comparison to other common pelagic ciliates [45].

Sessile ciliates such as *Vorticella* and *Epistylis* are typical members of protists' community in aquatic environments [34, 45–49]. They heavily graze on bacteria having even higher ingestion rates than free-swimming bacterivorous protist and can account for 66% of total bacterivores. Even in small numbers, epibiotic ciliates can have a great grazing impact on bacteria [34]. For example, *Vorticellides aquadulcis* had the highest grazing rates of all the ciliates from a meso-oligotrophic lake community [38]. Some common bacterivorous ciliates are found in **Table 1**.

2.3 Feeding on phototrophs

There is a difficulty in assessing a proper name for the kind of food protists feed on when they become predators of phototrophs, as this group consists of both eukaryotic and procaryotic members, and neither of these primary producers may be considered as "plants" or "herbs". Feeding on them cannot be considered as herbivory. On the procaryotic part, cyanobacteria are a phylum comprising many species that, besides being phototrophs, can also produce toxic molecules, compromising the fresh water supplies for human consumption when growing unchecked in oligotrophic waters [50, 51]. From the eukaryotic part, there is an extra complication when trying to separate the permanent phototrophs from the mixotrophs.

Moving the sizes up, ciliates are one of the most important groups feeding on phytoplankton in marine and freshwater environments [18, 41, 52]. They may consume up to 74% of the daily phytoplankton production [53], becoming the key controllers of phytoplankton biomass [54]. On the other hand, ciliates mobilize the

Trophic groups	Examples	References
Bacterivores	Colpodida (*Colpoda*), Peritrichia (*Carchesium*, *Epistylis*, *Vorticella*), Scuticociliatia (*Cyclidium*, *Parauronema*, *Pseudocohnilembus*), Stichotrichia (*Halteria*)	[34, 46, 48, 114, 116]
Feeding on Phototrophs	Choreotrichia (*Codonella*, *Strobilidium*), Oligotrichia (*Pelagostrombidium*) Heterotrichea (*Linostomella*), Peniculia (*Frontonia*), Tintinnida (*Helicostomella*, *Ptychocylis*, *Tintinnidium*, *Tintinnopsis*)	[54, 56–58, 60]
Predators of predators	Heterotrichea (*Fabrea salina*) Litostomatea (*Didinium*, *Lacrymaria*, *Lagynophrya*, *Loxophyllum*, *Mesodinium*, *Monodinium*, *Phialina*) Prostomatea (*Balanion*, *Holophrya*, *Tiarina*), Stichotrichida (*Halteria*)	[62, 64, 66, 68, 72, 108]
Omnivorous	Choreotrichia (*Rimostrombidium*), Hypotrichia (*Euplotes*), Prostomatea (*Urotricha*, *Coleps*), Scuticociliatia (*Pleuronema*), Stichotrichida (*Oxytricha*, *Stylonychia*)	[49, 66, 69, 73, 79]
Mixotrophos	Litostomatea (*Mesodinium rubrum*), Oligotrichia (*Laboea*, *Strombidium*, *Tontonia*), Choreotrichia (*Lohmanniella*), Heterotrichea (*Stentor*)	[23, 25, 26, 28, 29, 31]

Table 1.
Trophic groups free-living ciliates in aquatic environments.

highest proportion of organic carbon and nutrients in oligotrophic waters dominated by cyanobacteria, playing the fundamental role of linking the productivity of microbial food web with the metazoans [41, 53]. It has also been noticed that the flux of carbon up to metazoans is not interrupted when the density of bacterivores ciliates falls, but it is compensated by predation on ciliates feeding on phototrophs [41]. Some of the ciliates that feed on phototrophs are in **Table 1**.

Ciliates feeding on phototrophs represent between 30–65% of the total biomass of all functional groups of ciliates thriving in eutrophic lakes [55]. However, this dominance is not permanent. Ciliates feeding on phototrophs become very numerous on the blooming season [56], and even dominate the entire ciliate community for short periods between seasons [57].

Tintinnids tend to feed on small-cell-sized phytoplankton (2–20 μm) [58]. They are voracious phytoplankton feeders that may consume over half the quantity of these kind of phototrophs in marine waters [54] and over 69% of these primary producers in lakes [59]. Species like *Helicostomella subulata*, *Ptychocylis* spp., and *Parafavella* spp. make a significative contribution to biomass of ciliates feeding on phototrophs in marine environments [60].

Selective feeding has been observed in several species of ciliates. However, feeding on a wider spectrum of sizes and kind of phototrophs (non-selective feeding) allows them to take advantage of the productivity in hypereutrophic environments rich in small particulates [49]. The genus *Tintinnidium* groups species that dwell very well in these kinds of waters and may be used as model organisms to study the ciliates' adaptation to excess of organic matter [61].

2.4 Predators of predators or raptorial feeders

There are several species of ciliates and flagellates that feed on bacterivorous protists and on protists feeding on phototrophs. These are predators of predators. These predator species may feed temporarily on bacteria but cannot survive by just this consumption; they are attracted to them as they offer clues to discover their preferred preys: ciliates, flagellates, or amoebae feeding on bacteria.

Most of predator ciliates feed on preys around 10 times smaller than them [62, 63], although raptorial feeders may consume bigger preys, comparable to their own size or even bigger [64]. This capacity is due to their very flexible cytostome as is the case in protostomatids genera *Tiarina*, *Balanion,* and *Holophrya,* and in the litosto-matid genus *Didinium* [62]. Ciliates select their food based on prey's size, motility, and biochemical composition of cells' surface [62]. Raptorial ciliates exert strong pressure on populations of small phototrophic and heterotrophic flagellates [65], imprinting some velocity to nutrient cycling in environments where productivity allows them to develop large populations.

Predatory ciliates are present in small numbers along seasons in oligotrophic waters, showing surges in population numbers, in synchrony with the increase of primary productivity during the spring, reaching up to 55% of the total ciliates' abundances in temperate waters [64, 66]. However, they only reach between 24.6% to 28.7% in freezing oligotrophic waters of the Arctic and Antarctic [67].

On the other hand, predatory ciliates become important top-down controllers of microbial food web productivity in eutrophic and hypertrophic waters [68]. Eutrophic waters have the conditions to sustain high productivity rates of phototrophs and heterotrophic bacteria, sustaining, in turn, large populations of their grazers, promoting the increase of predatory ciliate population [69]. Biomass of raptor ciliates may reach almost an order of magnitude higher in eutrophic compared to the one obtained in meso and oligotrophic lakes, suggesting that they are effectively controlling the primary productivity [70]. This assumption is supported by the covariance of predatory ciliates and their preferred food. For example, the increasing population of predatory ciliates bigger than 100 μm is related to a simultaneous shrinkage of abundance of smaller ciliates (<20–40 μm), mostly phototrophs and bacterivorous [71]. Big and voracious ciliate raptors like *Monodinium* sp. and *Lagynophrya* sp. have stronger impact than rotifers on populations of small ciliates [68]. However, quantity of prey is not the only important factor, and species diversity is needed to sustain more raptorial species of ciliates. For example, only *Monodinium* remained abundant when diversity of preys falls below a limit [72].

Several species of oligotrichs feed on bacterivorous flagellates, showing an efficiency of 45% biomass transformation, also fueling the bacterial productivity by releasing essential nutrients for heterotrophic bacteria to keep their population growth [65]. Some predatory ciliates are shown in **Table 1**.

2.5 Omnivorous

Omnivorous protists are an important group to look for when assessing the stability of a food web because their very presence means productivity is enough to non-specialists, to feed on a variety of resources. Omnivores strengthen the resilience of planktonic communities by regulating the trophic dynamics [73]. Omnivorous ciliates may have a preferred prey but can easily move to other kinds of prey, which may be more abundant or easier to catch [74]. This variety of resources for true omnivorous ranges from bacteria, algae, other ciliates of different sizes to fungi [73]. This versatility gives them an advantage to withstand a resource limitation by having alternative prey [70]. Additionally, omnivorous ciliates increase the stability of planktonic communities by feeding on species that may pass undetected from their specialized predators, by having densities small enough to get an advantage of the elimination of their competitors and increase their numbers. In this situation, omnivores would prevent them to reach high densities too fast, giving time for their specialized predators to increase to population levels that may effectively control the newly abundant prey.

Omnivorous ciliates are present in any kind of environment allowing the stability of protist communities. They are elements of marine and freshwater ecosystems, both oligotrophic [66, 75] and eutrophic [69, 76], as well as in polar waters [67].

As with the other trophic groups, omnivores show seasonal bursts of abundances in the communities they are part of, especially in oligotrophic waters where they are scarce most of the time, except for occasional bursts [77, 78]. Omnivorous ciliates are commonly found in lakes throughout the year, normally with low species richness, representing between 2–12% of the ciliates species [67, 79]. Their low contribution to the number of individuals makes them reach a peak of 35% during productivity bursts [66, 79]. However, this proportion may steadily increase in the proportion the environment is turning into the eutrophic condition, increasing the species richness, although the densities of omnivorous ciliates may momentarily diminish with the eutrophication [69] as result of the species increase (more species and lower number of individuals by species). Once the eutrophication reaches a steady state, the biomass of the omnivorous ciliates will reach high values and even dominate among ciliates [76].

The numbers of small omnivorous ciliates usually dominate in meso oligotrophic environments, feeding on dominant bacteria (<2 µm) and algae (2–20 µm) [49]. Food concentration is a very important factor, strongly affecting an easily detectable feeding behavior of omnivorous ciliates [73]. Several of the most common omnivorous ciliates are shown in **Table 1**.

3. Boundaries among trophic webs. Is that possible?

Functionality alone has its own complexity in food webs because, for example, mixotrophs would be functioning as phototrophs or as heterotrophs along different hours during the same day (How long do they function as phototrophs? How long do they the function as heterotrophs?). An extra dimension in this world comes from the different sizes of preys corresponding to the predators' sizes and the number of cells each individual predator must get to produce another individual [80]. This is one of the reasons why plankton has been divided in microplankton, nanoplankton, and picoplankton. Each category corresponds to the range sizes of microorganisms. The smaller ones like picoplankton and nanoplankton, performing primary productivity (chemolithotrophs or phototrophic [3], can sustain their corresponding predator's size and be up to ten times bigger, namely nanoflagellates and microflagellates. These are the two groups of protists related to their size and morphology rather than their taxonomic affiliation [81], since very few information is known about them apart from 18S SSU rDNA sequences; they have been recognized performing predatory activity on phototrophs of the smaller sizes.

One alternative to conceptually reduce the complexity of microbial food webs is analyzing them as nested compartments. This means that the transfers of matter and energy takes place inside each compartment corresponding with one size class of producers and its predators because these organisms function in the same time frame. Then, several of these compartments may get integrated in a bigger one by predation of the next size class. Time frame for this bigger class is also bigger than the previous one, as the sizes of the organisms are also bigger and so on. Every compartment of bigger sizes function as concentrator of biomass and disperser of energy. However, the wastes generated in each compartment releases the nutrients once fixed in the biomass fueling the nutrient cycle in compartments of all sizes. Up to here, it looks like the aquatic food web is functioning as a continuum along and

through the water column and surface. However, there is a chance of recognizing boundaries to help a better understanding the food webs dynamic.

When hearing the word "boundary", immediately, the existence of physical barriers delimiting something in space comes to mind. Because of that, it is hard to imagine an aquatic food web being physically limited because our experience has shown us the big animals feeding on all planktonic organisms at once, which could be in thousands or even millions. However, it just represents a small appetizer for a whale.

A careful examination reveals that very small organisms live faster than ones at the immediate upper-sized scale and intuition tells us that time may be experienced in different ways, depending on the size of organisms involved. The size ranges occupied by ciliates in the microbial food web spans from less than 10 μm to more than 4500 μm [82]. Comparatively, their pool of size ranges would be like the pool of sizes from small fishes to whales. Why are these sizes important? Because it can be argued that the velocity of nutrient exchange is faster in the smaller organisms and the nutrients may be "sequestered" for long periods by the bigger and long-lasting animals. In this way, a complication of time arises when trying to diagram the nutrient cycle in the microbial food web. Time becomes another varying feature rather than a constant in food web dynamics. In this way, time may draw the boundaries between compartments and, at the same time, could be avoiding contradicting the nested compartment proposal in the physical limitless aquatic system.

4. The soil system

It is easier to recognize physical boundaries in terrestrial ecosystems as the environment changes at slower velocities than the very dynamic aquatic environment. Soil is a heterogenic environment, the opposite to the aquatic ones. It is an environment that cannot be seen through and be dived in. Soil matrix is composed of a very complex mixture of mineral particles, organic matter and living organisms. This mixture is organized in aggregates that may facilitate or resist water and air passing through it but, most importantly, these aggregates proportionate spaces where all living beings can move through soil.

At a microscale, soil aggregates divide the open spaces in two types, the fast water passing by (the space between aggregates) and the slow motion of water in the space inside the aggregate, and consequently of slow-moving air too, as air and water move through the same spaces). These are the soil's physical boundaries, and this is the environment where roots move and look for hotspots of nutrients, as well as places where microbial symbionts may be found (normally inside soil aggregates). Water reaching soil aggregates dissolved salts and polar molecules that may contain nutrients that will be taken by roots, mycorrhiza, or bacteria. This is a complementary start of plants primary productivity, because plants have to take water from soil together with other nutrients to produce a wide range of molecules, from non-protein forming amino acids to scents and pheromones, as result of what is known as the "secondary metabolism." Plant primary productivity comprises both photosynthesis-respiration (primary metabolism) and secondary metabolism, irrespective of being vascular or nonvascular.

Soil productivity is dependent on the nutrient exchange velocity rather than the gross amount of bioavailable nutrients. Nutrients used and released very fast means energy is being captured, transformed, and degraded very fast, implying the activities of all participating organisms are taking place so fast that production

of biomass at all levels is gaining momentum and its control may come only from consumption (top-down) no matter that nutrients exist in limited quantity. This feature also explains why the smaller organisms can sustain productivity of the biggest ones. In other words, aerial part of plants are very important for primary productivity because it is the place were light, inorganic carbon, and water are used to produce organic molecules that are at the base of primary productivity (Sun's energy fixation in organic molecules).

Without diminishing photosynthesis' importance, most of terrestrial plants gather a "productivity teamwork" inside and around their roots, involving mycorrhizal fungi and mutualistic bacteria, a functional place known as the rhizosphere. Almost 80% of the known terrestrial plants need the association with a mycorrhiza, to appropriately complete their life cycle, but all plants need mutualistic bacteria to grow. Microbial partners are indeed an important part of primary productivity, as they actively participate in the acquisition, modification, and metabolization of many organic molecules containing the elements we call "Nutrients." For example, it has largely been demonstrated that mycorrhiza translocate phosphorus to plants. At present, very few people challenge this. However, what form of phosphorus is translocated from mycorrhiza to plant? Surely, it is not the phosphorous as molecule, but organic molecule where P is forming part of the structure. Plants can take up P from inorganic molecules in general or from phosphoric acid. Why do they need mycorrhiza to supply P? It is still an open question, but the degree of specificity of the plant-mycorrhiza association allows to conjecture that plant and mycorrhiza share metabolites containing nutrients (not just P) for metabolic complementation, and the same could be true for mutualistic bacteria. This would explain why one species of mycorrhizal fungi is mutualistic to several plant species but functions as pathogenic or parasite to other ones.

Contrary to what happens in waters, soil fungi and bacteria are scattered through soil and physically constrained to available surfaces. If they keep growing unchecked, bacteria may become effective nutrient competitors to plants, as nutrients forming bacterial biomass are non-available to plants. Mycorrhiza may move farther away from the root than bacteria and can establish a mutualistic relationship with other roots (whether they are from the same plant or from a different species, it does not matter) to avoid becoming competitors. Absence of bacterivores is a needed condition for bacteria to become a plant competitor in the rhizosphere [83, 84]. Bacterivores ciliates, flagellates, and amoebae release nutrients trapped in bacterial biomass, stimulating both plant and bacterial growth. In the first case, nutrient release allows roots to take them in and bacteria microcolonies may grow again in the root surfaces, already cleaned out, and obtain nutrients from predators' wastes [84].

Soil's physical constrains allow growth of bacteria and fungi in differentiated places. Sometimes bacteria also grow on the surface of hypha, helping fungi to mimic bacteria and somehow escape from fungal predators. It has been possible to observe protists feeding predominantly on fungi and avoiding bacteria as much as possible (*Dermamoeba granifera*, *Cochliopodium* sp.). There are also protist species feeding on soil algae (*Colpoda* sp., *Polychaos* sp., *Thecamoeba* sp.) Consequently, it is possible to recognize the existence of several functional groups of soil protists: few species of phototrophs feeders, large quantity of bacterivores, fungal feeders, raptorial feeders (*Balamuthia mandrillaris*), and omnivores (*Acanthamoeba castellanii*, *A. polyphaga*, *A astronyxis*).

This differentiation of soil's physical spaces makes it easier to visualize the small productivity compartments around roots, absorbing hairs inside small soil

aggregates, bigger compartments covering aggregates on the tip of the root and getting in contact through fungal hypha.

Motility of bigger protists are limited to litter and upper soil layer by the available spaces, restricting their abundance in the underneath layers. Testate amoeba, ciliates, and flagellates, around 100 μm, dominate in these 2 layers and actively participate nutrient recycling from litter, while smaller size ciliates like *Colpoda cucullus*, small flagellates and small naked amoebae distribute better in the underlying soil strata in and around soil aggregates.

Primary productivity in soil is restricted to the upper layers where cyano-bacteria and eukaryote algae may survive and even form thin layers known as microbial soil crusts. Both phototrophic bacteria and algae may form stable mutualistic symbiosis with other organisms, like fungi, to develop thicker structures composing soil crusts showing lichens and mosses. Beneath and into soil crusts, ciliates, flagellates, and amoebae are among the most important microbial predators, active mainly during the time of water availability [85, 86]. However, the main photosynthetic carbon input is released by roots into soil layers [87]. Roots secrete amino acids and other complex organic molecules to attract symbiotic bacteria and mycorrhiza conforming the trio of soil pro-ductivity sustaining microbial food webs deep into soil [88, 89]. Consequently, protists' species diversity may be higher around roots and the dominance of ciliates may be restricted to the sizes of soil pores [86, 90–92]. Soil protists were recognized as purely bacterivorous because fungi feeding protists may transito-rily feed also on bacteria. However more detailed studies have recognized spe-cies of soil protists feeding only on bacteria or fungi [93–95]. Among the main bacterivorous ciliates are Colpodida (*Breslaua vorax*, *Colpoda aspera*, *Colpoda inflata*, *Colpoda maupasi*, *Colpoda steinii*, *Cyrtolophosis elongata*, *Cyrtolophosis mucicola*, *Platyophrya vorax*, *Pseudocyrtolophosis terricola*, *Pseudoplatyophrya nana* [85, 96].

Fungi and bacteria normally use different kind of organic molecules, bacteria normally metabolize low molecular weight organic molecules while fungi nor-mally metabolize complex organic polymers of high molecular wight [97]. This metabolic difference allows to conceptualize two pathways for nutrient cycling: the bacterial and the fungal paths. However, this concept is being challenged because of the abundance of protists feeding on both kind of microorganisms [98, 99]. All the early recognized fungi feeding ciliates and amoebae in soil ranges from 50 microns to above 150 μm [100]. However, there are also smaller ciliates and flagellates feeding on both spores and hypha [100]. The main groups of spe-cialized fungal feeder ciliates are grouped in the family Grossglockneriidae [93]. This family of ciliates may account for mora than 2% of the protists sequences in the forest litter and grassland while may drop below 0.3% in peatland soil, prob-ably due to the reduction of soil pore sizes [100]. Although, counting techniques based in MPN calculated around 200 cells/gram soil DW in previous studies [101]. Protists have a very limited capacity to disperse throughout the soil system by themselves. However, oligochaeta disperse them as cysts farther than a few centimeters, in the range of several meters both horizontally as well as vertically into the soil system.

Soil functioning is much more variable than the aquatic systems, as it is regularly subjected to dryness and several flooding events per year. For microbial ecologists, soil is a natural stressed environment, having enormous variations of water avail-ability through seasons, especially in arid and semiarid environments. However, there is a comparable situation, although at lesser degree, in the tropical dry forests, temperate, and tundra regions. Even at the equator, the rainy forests may show an excess of soil in water, stressing microbial food webs.

5. Perturbations and food webs

Microbial communities have been evolved by modifications and adaptations in responses to natural stresses that finally allow them to get along with environmental change. The problem we are facing now resides in the velocity of environmental changes imprinted by human activities. The most important, but hardly the only one, resides in the use of fossil fuels because of the acceleration of climate change. The CO_2 released as byproduct of combustion is just one of the causes of climate modification in the short term (in historical and geological times). Internal combustion engines also produce other greenhouse gases such as NxO or NO_2, having a bigger capacity of keep heat, and this is a big problem generated only for the atmosphere. Hydrocarbons pose a permanent threat of contamination to aquatic and soil systems near the extraction zones, the transporting infrastructure to refineries, infrastructure for later transportation as fuel to expending places, and by illegal activities damaging oil ducts.

Soil microbiota react in different ways along the gradient of contamination when hydrocarbons reach soils. The plume of contamination normally eradicates the phototrophs and exert a strong selective pressure on bacteria and fungi, by killing or inhibiting the growth of sensitive species while enhancing the growth of resistant ones. These effects can be modified by the toxicity of the different compounds rupturing and/or changing the connections of the trophic networks [102, 103].

The effect of hydrocarbon contamination and others contaminants (pesticides, heavy metals) on communities will depend on the intensity, duration, and frequency of the perturbation. Then, lower species richness and abundance, shortening of the trophic webs, and the simplification of the trophic web are among the first observable damages contamination cause on microbial and protist communities [104]. Protists must at least tolerate the presence of the contaminant to achieve this function. Protists do not feed on hydrocarbons, but their grazing activity on the microorganisms that can keep the metabolization of the contaminant as high as another limiting factor allows them to.

Greater richness and abundance of ciliates species are associated with less perturbed areas; the greater the perturbation, the lesser species richness and abundance [105], regardless of the nature of the perturbing factor. For example, a significant reduction of ciliate diversity has been found in systems polluted by high hydrocarbon concentrations [106]. Medium concentrations only reduce the quantity of individuals from dominant species [106], while low concentrations produce an increase in the numbers of heterotrophic protists [107]. Saline accumulation forces the ciliates' diversity to decrease as salinity values increase [108, 109]. In the same way, acidic pollution produces lower species richness and abundance as the environment becomes more acidic [110, 111], and the same pattern is observed with heavy metals' contamination [104, 110].

Addition of organic matter in excess suddenly changes the base of production of the microbial food web, from phototrophs' productivity to heterotrophic bacteria and yeasts' productivity. The time of reaction is also different along the different microbial groups surviving the contamination event. Bacteria may start their biological activities several hours after the pollution event, whereas yeast and protists will delay from days to weeks, depending on the size of the organism.

Changes of primary producers from phototrophs to heterotrophs scale to functional groups, accommodating species richness and abundance of bacterivores protists, followed by omnivores. This is due to hydrocarbons stimulation of bacterial growth and the consequently increase of bacterivores species [112, 113]. Some species of genera *Colpoda* and *Vorticella* dominate aquifers receiving constant hydrocarbon discharges [114]. The bacterivorous ciliates, *Parauronema virginianum,* strongly dominate sites highly polluted with hydrocarbons and are replaced by *Pseudocohnilembus*

and *Euplotes* later [115]. Additionally, organic contamination and heavy metals increase the abundance of bacterivorous ciliates in water and sediments [116].

An increase in diversity and complexity of food webs are direct effects of these perturbations. Oil spill in deep waters increase the richness of the microbial community species and the complexity of their corresponding relationships, and the oil stimulated microbial activity supports greater variety of ciliates functioning along several trophic levels [117].

Other events of enriching oligotrophic systems with organic matter produce similar changes in the community structure of ciliates. Tirjaková and Vďačný [118] analyzed the changes in the communities of ciliates before and after a windstorm hit a stream, and they found a significant increase of ciliates' species' richness and abundance after the storm. Several weeks later, the community of ciliates presented the typical values of oligotrophic sites. The increase in resources availability is the factor indirectly responsible of these changes of ciliate community, but later, communities tend to return to states similar to the initial ones after resources exhaustion, which my take place around six months [118]. However, Shabarova et al. [119] report that the microbial community recovers from perturbation to a pre-flood state within two weeks after the event.

Regarding the connections' shrinkage of the trophic networks, a gradual narrowing of the planktonic size spectrum has been reported in hypersaline lakes, correlated to salinity increases during the summer, resulting in a simplification of the community represented by the ciliated *Fabrea salina*, diatoms, and *Dunaliella* spp. [120]. Simplifications of food webs have also been described as consequence of heavy metal contamination, herbicide use, and lake acidification [104, 121, 122]. Loss of connections have consequences on carbon transfer in food webs. The decrease of bacterivores species allows an excessive increase in bacterial biomass, which may produce up to 300-fold reduction in the transfer of carbon from the bacteria to higher levels of the trophic networks [104].

Communities' characteristic of hypersaline lakes are dominated by *Fabrea salina,* which has a broad tolerance to salinity and contributes to high proportion of the biomass of ciliates in hypersaline lakes [108, 109, 120, 123]. In addition, its abundance is strongly related to the microalgae, *Dunaliella* sp. [123], and can act as a competitor to shrimp, *Artemia salina*, in saline environments [108].

Regarding the perturbances in the soil ciliated communities, similar effects have been described as in aquatic ecosystems. Exposure of ciliate communities to heavy metals induces a reduction in the biomass of ciliates and this effect lasts for 20 weeks [124]. Insecticides also generate a decrease in ciliates species immediately after contamination, they also generate a change in the dominance of ciliates, the bacterivores (*Colpoda* spp. and *Paracolpoda steinii*) and macrophage (*Grossglockneria*) considerably increased their abundance after 90 days, while that other genera of ciliates decreased [125]. In soils contaminated with hydrocarbons, a decrease in diversity and a lower functional diversity have also been observed, the ciliated communities in soils with hydrocarbons are dominated by the Colpodea class [96, 126, 127]. It has also been observed that along with the decrease in the diversity of ciliates there is a decrease in the trophic groups after an intense pulse of contamination by hydrocarbons. However, the community recovers its diversity and trophic groups after a month of contamination [127].

6. Conclusions

Protists in general, and ciliates in particular, play a key role in nutrient cycling and food web functioning in both aquatic and terrestrial ecosystems. In the world

experiencing climate change and other kind of anthropogenic menaces, protists may be useful partners to tell us how aquatic and terrestrial systems are dealing with these issues while mesmerizing the observer with their great diversity of beautiful forms.

Conflict of interest

The authors declare no conflict of interest.

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