Protozoan Ecology

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Advanced article

Article Contents

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Protozoan ecology is the interaction in space and time of protozoa (flagellates, amoeboid organisms and ciliates) with other living organisms and the physical environment. It encompasses, among other factors, sources of food and energy used to sustain life, food web dynamics, the role of protozoa in maintaining fertility of ecosystems and adaptive strategies for survival in varying habitats. Among the physical environmental (abiotic) factors, temperature, salinity, nutrients and levels of pollutants, when present, are major sources of influence. A complex set of interactions exists among microbial biota, including the role of nutrient regeneration during protozoan predation on bacteria resulting in release of nutrients due to digestion and disruption of the bacteria during feeding. These nutrients in turn are reutilised by algae during photosynthesis. This process of cyclical nutrient uptake by algae and subsequent release by protozoan predation is known as 'the microbial loop'.

Introduction

The free-living protozoa dwelling in the open environment (as opposed to parasitic forms invading other living organisms) include flagellates, amoeboid organisms and ciliates (**Figure 1**). Only free-living protozoa will be considered here. Protozoa are heterotrophic members of the taxonomic group Protista (algae and protozoa). The Protista are eukaryotic microbes, microscopic organisms with a true nucleus and containing membrane-bound cellular organelles.

Flagellates move by a whip-like motion of one or more flagella (slender, undulating membrane-enclosed projections) protruding from the cell body. In modern terminology, the term 'cilia' is often used instead of flagella, because these motile structures are similar in internal structure to cilia, but are typically much longer. They also may be referred to as undulipodia. However in ecology, the term 'flagellate' is still used to refer to this group of organisms due to historical precedent. It is widely accepted that protozoa originated from a primitive flagellate stock and that all other groups of free-living protozoa, including amoeboid organisms and ciliates, evolved from primitive flagellated organisms. Amoeboid organisms move by cytoplasmic flow, typically using specialised pseudopodia (finger-shaped, elongated pencil-shaped or net-like cytoplasmic protrusions). Some species of flagellates (Heterolobosea) form amoeboid stages during reproduction or dispersal. The truly amoeboid protists include naked and shell-bearing (testate) amoebae. In some publications,

Figure 1 Protozoa: (a) flagellate, *Polytoma uvella* (15 μm); (b) naked amoeba, *Metachaos discoides* (400 μm) and (c) ciliate, *Phacodinium metchnikoffi* (100 μm). Reproduced with permission from Lee JJ, Hutner SH and Bovee EC (eds) (1985) *Illustrated Guide to the Protozoa*. Lawrence, KS: Society of Protozoologists.

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other psuedopod-bearing protists may also be categorised as amoeboid organisms. These include the heliozoa (the so-called sun animals with a corona of radiating axopodia), marine forms including foraminifera (with calcite shells), radiolaria (some with siliceous ornate shells) and acantharia (secreting strontium sulfate skeletons). However, based largely on modern molecular genetic evidence, only the naked amoebae and testate amoebae with lobose pseudopodia are currently included in the formal taxonomic category of the Amoebozoa. The testate amoebae with fine, filose pseudopodia are placed in the Cercozoa, a member of the Rhizaria that also includes foraminifera and radiolaria (e.g. Adl *et al*., 2005). The naked amoebae, previously called gymnamoebae, include the commonly recognised *Amoeba proteus*. Although this species is often used in teaching demonstrations, it is much larger (*c*.500 μm) than most naked amoebae, which are usually in the size range of 5–100 μm. Many are less than 30 μm. Naked amoebae lack substantial surface covering. However, some species have an organic surface coat (glycocalyx) or layer of organic scales secreted on the surface of the membrane. Testate amoebae are enclosed within an organic or mineralised shell with a terminal aperture. Pseudopodia used for locomotion and food gathering protrude from the aperture. Ciliates move by the coordinated motion of numerous hair-like cilia whose beating motion propels the ciliate through the water. Some use specialised groups of stiffened ventral cilia, called cirri, for 'walking' on surfaces. Ciliates are believed to be the most evolutionarily advanced group of protozoa. They possess two kinds of nuclei, a large macronucleus and one or more smaller micronuclei, a major taxonomic feature. They are typically particle feeders, although some prey on filamentous algae and others lack an organised feeding apparatus. The latter obtain nutrition by absorbing soluble food. **See also**: *Amoeba*; Cilia and Flagella; Protozoan Organelles of Locomotion

Photosynthetic (autotrophic) species occur among the flagellates, but many species of flagellates and most other protozoa are nonphotosynthetic (heterotrophic) and obtain food from the surrounding environment, either as soluble organic molecules or as particulate food ingested by the cell. Some ciliates gather chloroplasts that are segregated from ingested algae and use them as a source of intracellular photosynthesis. These chloroplasts are not permanent and are eventually lost, necessitating further replenishment from ingested algae. Species with both photosynthetic and heterotrophic modes of nutrition are termed 'mixotrophic'. These phototrophic adaptations may have been significant in supporting major evolutionary innovations that are crucial to the current ecological roles of protists in aquatic environments (e.g. Stoecker *et al*., 2009). An interesting example is the ciliate *Myrionecta* (formerly *Mesodinium*) *rubra*, which contains algal symbionts. The capacity of mixotrophic protists to adapt to widely different environmental conditions, surviving either as autotrophs or as heterotrophs, may have accounted for the evolutionary survival of eukaryotic microbes during major past catastrophic geological events such as global partial obliteration of sunlight due to atmospheric volcanic ash or other sources of atmospheric dust (e.g. Jones *et al*., 2009). Some amoeboid protists, including naked amoebae, foraminifera and radiolaria, form algal symbioses and obtain part of their nutrition from photosynthates released by the algae. Many of these symbiont-bearing species also require additional sources of particulate food (microorganismic and invertebrate prey) gathered from the surrounding environment. **See also**: Algal Symbioses; Foraminifera; Photosynthesis: Ecology; Photosynthetic Carbon Metabolism; Protozoan Nutrition and Metabolism

Highly diverse feeding strategies have evolved among heterotrophic protozoa to capture particulate food, including mechanisms for snaring and ingesting a wide variety of microorganisms and small invertebrates (see the section on General Survey). Species of free-living protozoa vary in size from a few micrometres to hundreds of micrometres, and the larger amoeboid protists (foraminifera and solitary radiolaria) reach dimensions of several millimetres. Filamentous colonial forms of radiolaria (containing up to hundreds of cells or more), with individual diameters of only several millimetres, reach lengths of a metre or more. Increasing evidence points to a critical role of protozoa in stimulating productivity of communities of microorganisms and the enhancement of the stability and productivity of food webs through mineralisation of essential nutrients that promote growth of higher organisms at upper levels of food webs (e.g. Corliss, 2004). Some of these significant contributions of protozoa in the dynamics of ecosystems are presented. **See also**: Radiolaria

General Survey

Protozoa occur in widely diverse aquatic and terrestrial habitats worldwide, spanning the dark depths of the ocean to the sun-splashed, snow-covered peaks of the highest mountains. With improved methods of detecting and enumerating some of the more delicate protozoan species (especially the small naked amoebae), we are gathering increasing evidence of their numerical importance in many habitats where they have previously been overlooked (e.g. Anderson and Rogerson, 1995; Darbyshire *et al*., 1996). Naked amoebae in highly productive ponds reach maximum abundances of over one million per litre, and in marine coastal water occur in thousands per litre. Ciliate maximum abundances reach hundreds of thousands per litre in subtropical lakes. In soils, the total number of protozoa per gram at a highly productive site was found to be 162 400, of which 123 000 were amoebae, 27 300 were flagellates and 12 100 were small ciliates (Foissner, 1987; Darbyshire, 1994, p. 52). Water column sampling in aquatic environments, using sensitive molecular genetic techniques, has uncovered sparsely abundant, but diverse populations of protists (e.g. Caron and Countway, 2009). These protists, previously undetected using conventional sampling techniques, are called cryptic (hidden) species. Although they are only sparse at certain places and times, they may bloom up when environmental conditions are favourable. Thus, it is important to more fully document their presence in varied habitats. The discovery of these rare species and the increasing evidence that many species of protozoa are cosmopolitan, distributed worldwide, have suggested that some protozoa are ubiquitous globally. This has aroused further interest in the hypothesis that protozoa, as is the case with bacteria, are present everywhere and that favourable environmental conditions determine which ones are abundant at any given time (e.g. Finlay and Fenchel, 2004). However, there may be circumstances where some populations are more restricted geographically, a moderate endemicity model (e.g. Foissner, 2008). In general, abundance and diversity of protozoa are determined by physical environmental (abiotic) and biological (biotic) factors. We examine some abiotic and biotic factors in protozoan ecology. **See also**: Macroecology; Metapopulation Ecology; Protozoan Diversity and Biogeography

Abiotic Factors

Importance of water

Living cells contain as much as 80% water, which is essential for metabolic life-sustaining processes. Many species of protozoa lack substantial surface protection and depend on an abundant supply of moisture during active stages of feeding and growth. However, many are capable of forming cysts during drought or other unfavourable conditions. Many freshwater species of protozoa also occur in terrestrial environments and have become adapted to form resting stages or cysts during intermittent periods of water depletion. Terrestrial environments are particularly susceptible to unfavourable growth conditions due to lack of moisture, either through periodic drying or due to binding of the water in thin films on surfaces or within microspaces in the soil. This water is bound so strongly that protozoa cannot compete for it osmotically. In general, it has been estimated that a water film thickness of 3 μm is the ultimate lower limit for protozoan activity (Albouvette *et al*., 1981), and below this range, the protozoa die or must encyst to survive. The smaller the species, the thinner the film of water required for subsistence. The small ciliate *Colpoda steinii* (*c*.20 μm) is active only if the water film thickness is approximately 30 μm (Darbyshire, 1976), whereas small amoebae can undoubtedly tolerate thinner water films (Fenchel, 1987). The amount of water bound is expressed in pressure units, for example, bars ($1\ \text{bar} = 10^6$ dynes cm^{-2}), equivalent to the amount of suction required to remove water from a soil sample. The relation between pressure (h in bars) and pore size (d in μm) is $h = 3/d$. Temperate soils when fully moistened (field capacity) contain approximately 30–50% water (although this may vary at different geographic locations) and have a water suction of approximately 50 mbar. This corresponds to a pore size of approximately 60 μm, an amount sufficient to sustain active protozoa. By contrast, tropical soils at field capacity reach suction pressures of 350 mbar, corresponding to maximum sizes of water-filled pores of approximately 10 μm. If evaporation reduces the amount of water in these ordinary soils to approximately 20%, only fine pores are filled with water and some protozoa become inactive. Sandy soils tend to lose water rapidly by evaporation or draining by gravity. The remaining fine pores may be too small, and hold water too tenaciously, to allow protozoan activity. In aquatic environments, water salinity is one of the major factors determining the range and composition of protozoan species. Stenohaline species are adapted to rather narrow salinity ranges, whereas euryhaline species tolerate a much broader range of salinities. Marine species dwelling in coastal waters are typically more tolerant of variations in salinity than those adapted to open ocean environments. Some coastal species adjust rapidly to changing osmotic properties of the surrounding water by varying intracellular concentrations of osmolytes such as amino acids and other small organic compounds. Some protists are adapted to extreme salinities, including those found in hypersaline pools. For example, some heterotrophic nanoflagellates isolated from hypersaline environments in Korea grew and grazed on bacteria at maximum salinities of $>300‰$ (Park *et al*., 2003). Heterolobosean amoebae have been isolated that grew in salinities up to 300‰ (Park *et al*., 2009), which is close to the observed upper limit of *c*.270‰ reported for naked amoebae isolated from the highly saline Salton Sea, California (Hauer and Rogerson, 2005). **See also**: Protozoan Cysts and Spores; Water: Structure and Properties

Temperature

In addition to available moisture, temperature is a major factor determining species composition and distribution in space and time. Cryophilic species, adapted to low-temperature environments, have been identified in extremely cold environments, including polar habitats and abyssal depths of the oceans. Thermophiles occur in shallow bodies of water receiving intense solar illumination and in thermal springs. Shallow ponds in temperate latitudes sustain substantial populations of thermotolerant protozoan species. For example, free-living thermotolerant amoebae (capable of growth at 37–45°C) isolated from surface water in a shallow pond in the Piedmont region of South Carolina, United States, included *Naegleria* (64.4%), *Vahlkampfia* (17.8%), *Acanthamoeba* (13.3%) and *Hartmannella* (4.4%), expressed as percentage of total abundances (Kyle and Noblet, 1986). An extremely thermophilic amoeba (*Echinamoeba thermarum*), growing at temperatures up to 57°C, has been isolated from hot springs (Baumgartner *et al*., 2003). Aquatic amoebae in temperate climates vary in abundance seasonally. Peak abundances occur typically in spring and autumn (e.g. Anderson and Rogerson, 1995). However, deviations from this pattern may occur in some habitats due to predation by larger

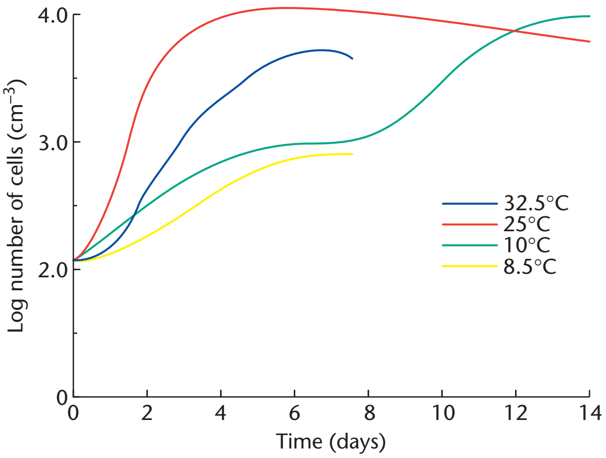

Figure 2 The effect of temperature on the population density of *Tetrahymena pyriformis*. Growth is best at 25°C, with a minimum temperature of 10°C. Adapted from Sleigh M (1989) *Protozoa and Other Protists*, p. 260. London: Edward Arnold.

invertebrates that reduce peak abundances of the protists at certain seasons of the year (e.g. Muylaert *et al*., 2000). A threshold temperature of *c*.10°C seems to be critical for a rapid increase in population densities. Growth is diminished at temperatures below 10°C. Low densities occur in late autumn and winter when the water temperature falls below 10°C. This may be attributed to low metabolic rate of the amoebae and a diminished availability of bacteria prey. On the contrary, many protozoa thrive in Antarctic and Arctic conditions where temperatures of seawater remain below 4°C. Some marine Antarctic amoebae have recently been shown to be capable of growth at −2°C. Laboratory studies of temperature tolerance in the ciliate *Tetrahymena pyriformis*, typically found in temperate environments, show that growth is diminished at temperatures below 10°C. Growth is also inhibited at temperatures above 25°C. The culture dies within a week at a temperature of 32.5°C (**Figure 2**). Further studies are needed on temperature tolerances and optimal growth conditions of major protozoan species. **See also**: Tetrahymena; Thermophiles

Nutrients

Protozoa utilise a broad range of dissolved inorganic and organic nutrients, including inorganic solutes (potassium, chloride, essential metals, etc.), nitrogen compounds (nitrates, ammonium and amino acids), inorganic phosphates and organic phosphate compounds (e.g. glycerophosphate), short-chain alcohols (e.g. ethanol) and small organic acids, including acetate, pyruvate and lactate. These organic acids sometimes accumulate in the environment as waste products of metabolism by other organisms. Many photosynthetic species of protozoa require only inorganic nutrients to support photosynthesis, but they also can utilise organic compounds in heterotrophic nutrition. The so-called acetate flagellates (including euglenids and some chrysomonads) are especially capable of using short-chain organic acids as a carbon source and subsist in relatively low pH environments. Among these are peculiar species of interest (acidophiles) because they grow in environments of extremely low pH and in some cases with heavy metal pollutants (e.g. Aquilera *et al*., 2007). These protists (extremophiles), living in extreme environments also, are studied by astrobiologists as examples of possible ways life may have adapted on other planets. Some protist species require exogenous sources of vitamins (e.g. vitamin B_{12}) and have been used in bioassays to detect the presence of the vitamins. **See also**: Acidophiles; Astromicrobiology; Protozoan Nutrition and Metabolism

Biotic Factors

Interactions among biota are significant in determining the abundance and diversity of species in ecosystems. Protozoa, as with other forms of life, exhibit complex interactions within communities of interdependent organisms. Among other factors, resource availability, photosynthetic productivity, competition for space and resources, predator–prey relations, niche specialisation and a variety of mutual supportive/inhibitory mechanisms (including release of vitamins, growth factors and exudates that either enhance or decrease environmental quality) dynamically influence the abundance, diversity and stability of protozoan communities. **See also**: Competition

Roles in Ecosystems

Protozoan communities can be categorised according to the plan of Hausman (1917) into five environmental types based on the ecosystem where they occur (e.g. Anderson, 1988, p. 141). Type 1 (marsh pools) with warm water and abundant decaying vegetable matter emitting a swampy odour contain bacterial predators (including *Saccamoeba limax*, *Difflugia acuminata*, flagellates such as *Oikomonas* spp. and ciliates *Coleps*, *Carchesium*, *Stylonichia*, *Stentor* and *Vorticella*). Type 2 environments (clear cold-water habitats lacking plant growth) are dominated by flagellates (e.g. *Astasia*) and some lesser numbers of ciliates (*Colpidium* and *Paramecium*). Type 3 environments (clear, flowing water with abundant plant life) contain species of *Amoeba*, ciliates (e.g. *Chilodon*, *Colpidium* and *Colpoda*) and flagellates (*Monas* and *Chilomonas*), and testate amoebae. Type 4 habitats (clear, small pools with abundant decomposing organic sediments) contain filamentous algal growth and are rich in ciliates and flagellates. The major genera include ciliates *Chilodon*, *Coleps*, *Paramecium*, the flagellate *Monas* and testate amoebae (e.g. *Difflugia*). Type 5 environments (warm-water pools with abundant algae) are especially driven by photosynthetic activity and are dominated by flagellates (e.g. *Chlamydomonas*, *Euglena*, *Monas*, *Synura* and *Peridinium*). There are lesser numbers of ciliates (*Colpoda*, *Campyla*, *Frontonia* and *Vorticella*), heliozoa and occasional testate amoebae.

Protozoa are excellent indicators of environmental health or pollution, as they are single-celled organisms living in intimate relationship to their surroundings (e.g. Foissner, 1987). They are often used as bioindicators of environmental pollution. They are also significant in water purification in sewage treatment plants, where they help to remove organic wastes and reduce mineral nutrient load in the water before it is discharged. **See also**: *Amoeba*; *Euglena*; Paramecium; *Vorticella*

Aquatic, Photosynthesis-based Communities

A general model of a photosynthesis-based protozoan community is shown in **Figure 3**. Algae, cyanobacteria and photosynthetic flagellates are primary producers providing a major source of carbon compounds and energy in protozoan food webs. Bacteria utilise organic compounds released into the environment by primary producers, or by death and decay of other biota, to form a major particulate food source for small and intermediate-sized heterotrophic protozoa. Bacterial predators include small amoebae, ciliates and some flagellates. During bacterial feeding and waste egestion, minerals and other nutrients are released into the environment, thus enhancing the availability of resources for other biota, including plants. In aquatic environments, the dynamic relationships among bacteria and protozoan bacterial feeders, resulting in replenishment of available nutrient resources, are an important component of what has been termed the 'microbial loop' model (Fenchel, 2008). Some of the resources bound up in bacterial particulates are released by protozoan predators, thus making them available for primary producers and increasing primary productivity (**Figure 3**). This enhanced primary productivity further fuels bacterial and protozoan growth, thus maintaining a vigorous and active protozoan/bacterial community. Among the protozoa, heterotrophic nanoflagellates and ciliates are commonly cited as major consumers of bacteria. However, increasing evidence also indicates that planktonic, particle-associated naked amoebae are also major consumers in some coastal locations and highly productive ponds (Anderson, 2007; Lesen *et al.*, 2010). Some larger protozoa, including amoebae, ciliates and phagotrophic flagellates, consume algae and small photosynthetic flagellates. These are primary consumers and serve a role similar to herbivores in macro-organismic communities. They provide a 'top-down' control on the abundance and activity of their prey through diverse feeding strategies and grazing rates (Weisse, 2002). There is increasing interest in ecological dynamics of harmful algal blooms caused by the over production of some algal species that also release harmful or toxic substances. These substances may disable or kill other organisms including shellfish and bony fish of commercial value. There is some evidence that top-down, protozoan predators may suppress harmful algal proliferation, especially early in the formation of a bloom (Tilman, 2004). However, if the bloom proliferates, even the top-down predators may be disabled or annihilated, thus enhancing the explosive spread of the harmful algae (e.g. Buskey, 2008). Generally in nontoxic algal communities, ciliate abundance is positively correlated with chlorophyll *a* concentrations or with flagellate prey abundances in temperate freshwater lakes, further exemplifying the trophic relation between primary producers (represented by chlorophyll *a* concentration) and ciliates as consumers (Laybourn-Parry, 1992). **See also**: Chlorophyll: Structure and Function; Cyanobacteria; Photosynthesis and Respiration in Cyanobacteria

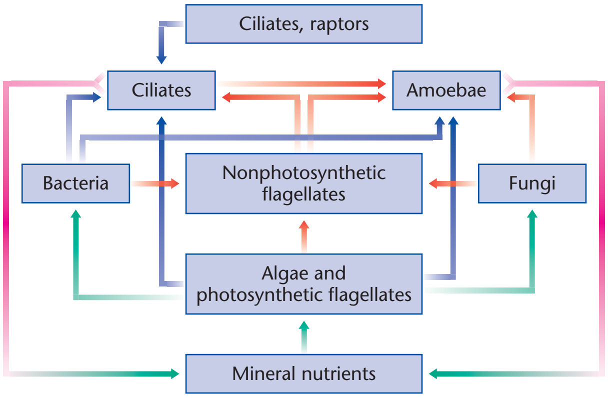

Figure 3 A photosynthesis-based protozoan food web. Green arrows show dissolved nutrient flow and orange and blue arrows indicate prey and predator relations. Feeding activity of protozoa mineralises nutrients that are available for primary production (recursive arrows).

Secondary consumers include a wide range of larger amoebae, flagellates (e.g. heterotrophic dinoflagellates, some phagotrophic euglenids, chrysomonads and other large heterotrophic flagellates) and some ciliates. The latter include raptorial ciliates that actively pursue other ciliates and, through a variety of attack mechanisms, snare and subdue them before ingestion. Flagellates exhibit a range of feeding strategies encompassing osmotrophy (absorbing dissolved organic compounds) to phagotrophy (engulfing particulate food in digestive vacuoles). In the simplest form of phagotrophy, particles of food attached to the surface of the cell membrane become enclosed in a cup-like invagination and eventually are surrounded by and enclosed within an intracellular digestive vacuole. Some species have an elaborate ingestion apparatus including a gullet or feeding pouch with a specialised region where a food vacuole is formed. Some of these phagotrophic species, such as the euglenid *Peranema* spp., are capable of ingesting other euglenids nearly as large as themselves. Many amoebae snare prey by enclosing the food particle within a food vacuole formed by the flowing action of pseudopodia that gradually enclose and engulf the prey. Larger members of the amoebae (e.g. *A. proteus*) are capable of attacking and ingesting other protozoa, including ciliates. Others prey on flagellates or algae (e.g. diatoms). Ciliate species use a wide range of feeding mechanisms, including a feeding groove where beating cilia sweep prey particles (e.g. bacteria and small algae) into an oral pouch, where a food vacuole is formed (e.g. *Paramecium* spp.), or an oral pore and funnel-like cyrtos (conical array of microtubular rods) within the cytoplasm used to ingest strands of algae or cyanobacteria (*Nassula* spp.). Some carnivorous ciliates have a highly complex feeding apparatus, such as a gaping anterior oral groove to enclose prey (*Bursaria truncatella*), an elongated flexible proboscis with barbs used to strike at and impale motile prey (*Dileptus anser*) or a conical anterior region with extrusible barbs used to impale ciliate prey and, by inversion of the cone, ingest it (*Didinium nasutum*). **See also**: Ciliophora; Diatoms

Terrestrial Communities

Terrestrial protozoa include heterotrophic flagellates, amoebae and ciliates (Darbyshire, 1994; Adl, 2003). Food webs are largely bacterial-based and productivity depends on the abundance and suitability of bacteria as prey (**Figure 4**). Larger protozoan densities have been found near roots of plants compared with the surrounding bulk soil (up to 10-fold higher), probably due to increased bacterial prey sustained by organic compounds released from the roots. Current evidence indicates that increased protozoan grazing activity also promotes decomposition of organic matter and remineralisation of essential nutrients, thus promoting plant growth (e.g. Adl, 2003; Adl and Gupta, 2006). It has been estimated that in a growing season, as much as 25 kg of nitrogen per hectare can be released for plant utilisation by protozoan grazing activity. In short grass prairies, protozoa consume 1.6 g nitrogen per square metre annually and excrete 1.2 g inorganic nitrogen and 90 mg organic nitrogen (as faeces). The vast majority (98%) of nitrogen mineralised by protozoa is the result of amoebae rather than flagellates, one of the most abundant soil protozoa (Darbyshire, 1994, p. 80). Terrestrial protozoa are therefore increasingly recognised as enhancing soil fertility and plant productivity. Protozoa are also major components of terrestrial invertebrate food webs and serve as prey for nematodes that are consumed by microarthropods (**Figure 4**). With increasing concern about increasing atmospheric carbon dioxide concentrations leading to possible global warming, interest has increased in accounting for how much terrestrial respiratory carbon dioxide can be attributed to soil microbial communities. Protozoa are known to increase bacterial decomposition activity and may also contribute to respiratory carbon dioxide contributions to the atmosphere. This is particularly the case at higher latitudes (such as the Arctic) where global warming may lead to increased melting of the soil permafrost thus enhancing microbial activity and consequent substantial release of respiratory carbon dioxide to the atmosphere (e.g. Anderson, 2010a). **See also**: Food Webs

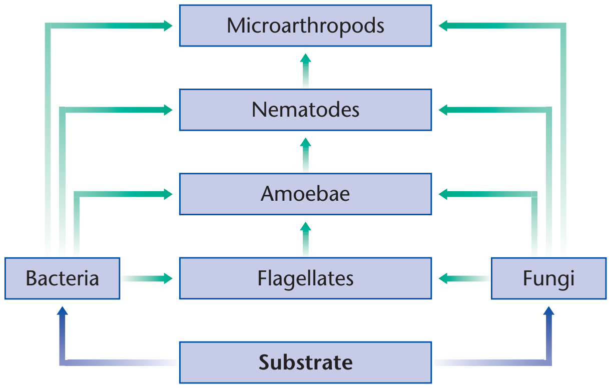

Figure 4 A terrestrial protozoan, bacterial-based food chain showing predator–prey relations. Adapted from Griffiths BS (1994) Soil nutrient flow. In: Darbyshire JF (ed.) *Soil Protozoa*, p. 80. Wallingford, UK: CAB International.

Specialised Habitats

Marine taxa of protozoa are distinct from freshwater aquatic and terrestrial protozoa. Furthermore, characteristic marine species occur among different habitats such as marshes, sandy shores, benthic locations and the water column. Each group has specialised adaptations to enhance survival within a particular habitat. Coastal, sand-dwelling ciliates, and those living along the margins of lakes, are typically elongate and slender, thus improving their movement among the fine sediment spaces (Fenchel, 1987, p. 121; Finlay *et al*., 1988; Patterson *et al*., 1989). Some species of *Remanella*, *Tracheloraphis*, *Geleia* and *Helicoprorodon* are found only within marine sediments. Hypotrichs with somewhat flattened bodies and ventral tufts of cilia (cirri) move with a crawling motion through the sediment particles. Testate amoebae often have flattened tests with marginal flanges or flared terminal apertures. This may help to anchor them within the sand and prevent detachment during water movement. Planktonic species have evolved mechanisms for flotation and capture of prey while carried within water currents. For example, some planktonic foraminifera and radiolaria have a frothy external cytoplasm and abundant lipid reserves that aid flotation. Long spines and radiating pseudopodia increase surface area and enhance capture of prey suspended in the water column. As cited in the section on Nutrients, some protists are acidophiles, capable of utilising organic acids as nutrients. They inhabit extreme acidic environments such as mine tailings (acidic streams with heavy metal pollutants) and other natural habitats with low pH. **See also**: Marine Communities

Many species found in freshwater environments are also found in terrestrial habitats. This is probably due to similarities in osmotic properties of water in soils and freshwater habitats. Moreover, cysts of freshwater species are undoubtedly blown back and forth by wind between soil and freshwater habitats, especially during periods of extended drought.

Competition, Niche Differentiation and Coexistence

Resources are limited in natural environments, and theoretically, a species that is most competitive would eventually dominate. However, competition may be reduced when protozoa occupy different niches (differentiation based on kind of food, location inhabited, season for peak activity, etc.). For example, some protozoa feed on suspended food particles, whereas others graze on particles attached to surfaces. Differences in kinds of prey also allow protozoan species to coexist in the same habitat. Planktonic foraminifera and radiolaria coexist within the same open ocean water mass. Radiolaria tend to consume more phytoplankton prey, whereas planktonic foraminifera consume more zooplankton prey, thus possibly alleviating competition through prey differentiation (Anderson, 1988). Moreover, species in both groups form algal symbioses, and this additional source of photosynthetic-based nutrition may help to reduce competition for prey. In deep, unmixed lakes, the water column is typically stratified much of the year, with warmer, oxygenated water near the surface and more anoxic, cooler water at greater depths. Different species of protozoa occur at different depths, thus avoiding direct competition for resources (e.g. Finlay *et al.*, 1988). Furthermore, in the natural environment, food particles occur in a range of sizes, allowing for different species to specialise in capturing food of a given size. For example, four different species of the ciliate *Remanella* (varying in size from 85 to 300 μm) coexist in marine sediments. Each consumes a different sized diatom, thus reducing interspecies competition (Fenchel, 1987, p. 94). **See also**: Competition; Foraminifera; Interspecific Competition; Radiolaria

Seasonal differences in abundances due to changing optimal conditions for each species, such as temperature, oxygen concentration, pH and available moisture (correlated with encystment and excystment patterns) and so on, reduce competition. Staggered cyclical peaks in populations of different species reduce interspecies competition. For example, in aquatic environments, fast-growing, flattened discoidal forms of naked amoebae (i.e. *Vannella* spp.) alternate in abundances throughout the growing season with some slower growing forms with extended subpseudopodia (e.g. *Acanthamoeba*, *Vexillifera*, *Thecamoeba* and *Rhizamoeba*) (Anderson and Rogerson, 1995). Examples of alternation of abundances of protozoa have also been reported in freshwater lakes and subtropical open ocean surface water subjected to seasonal variations in temperature. Variations in reproductive cycles and patterns of encystment and excystment can help to explain these variations in temporal patterns of abundance (e.g. Anderson, 2010b).

Life Cycles

Asexual reproduction and sexual reproduction occur among protozoa, but only asexual reproduction has been observed in some groups (e.g. most naked amoebae). Asexual reproduction includes binary fission (cell division producing two daughter cells), multiple fission (producing several daughter cells) and budding (pinching off of new cells from a cell surface). In flagellates, the cells divide longitudinally, typically by formation of a division cleft that progresses from the flagellated, anterior end to the posterior end. Naked amoebae divide symmetrically to produce two nearly equal daughter cells. Ciliates divide transversely. The division plane is through the short axis of the cell. In many of these species, periods of encystment are interposed with periods of asexual reproduction and proliferation, giving rise to cyclical patterns of abundance. **See also**: Binary Fission in Bacteria; Budding; Protozoan Asexuality

Sexual reproduction is highly diverse among various groups, and only a few examples can be given here. Some species of flagellates reproduce by gametogamy, the fusion of free-swimming gametes (e.g. *Chlamydomonas*). Fusion of the flagellated gametes yields a zygote. The zygote may undergo immediate meiosis to form haploid daughter cells, thus completing the reproductive cycle, or a resting spore may be formed and persist during adverse conditions for some time before meiotic division. In the colonial flagellate *Volvox*, numerous flagellated haploid cells are interconnected by cytoplasmic strands and enclosed within a spherical gelatinous envelope. Sperm packets are produced in one colony and swim to the egg-containing colony, where they are released and fertilise the egg cells. The resulting zygote undergoes meiosis and gives rise to daughter colonies. As a taxonomic note, *Chlamydomonas* and *Volvox* are included among the algae by botanists (phycologists) as are some other pigmented flagellates. To avoid this confusion, some modern taxonomists have proposed that all single-celled eukaryotic organisms, including the heterotrophic and autotrophic (photosynthetic) forms of protozoa, should be assigned to a kingdom called Protista. **See also**: Protist Systematics; Protozoan Sexuality

There are many different sexual reproductive strategies among ciliate species, but they all involve a basic plan of cell conjugation. Compatible individuals pair at the anterior end, where a porous membrane is formed. Sperm nuclei are exchanged across the porous membrane. Each sperm nucleus fertilises the egg nucleus of the reciprocal partner in the pair. The resulting exconjugants separate and swim away to produce additional offspring by asexual reproduction.

Some protozoa have complex life cycles with intermediate stages of highly varied form and habit. In some cases, these stages have been misinterpreted as different species. This condition of polymorphism (highly varied morphological forms within the same species) is widely encountered among protozoa. Asexual and sexual reproductive stages are interposed in the life cycle of many protozoa, usually with many asexual stages occurring between each sexual stage. Asexual reproduction supports rapid proliferation during favourable environmental conditions. Sexual reproduction allows for genetic variation, giving rise to new gene combinations in offspring and enhancing survival when environmental variations may require adaptive responses. These reproductive strategies, combined with a capacity to form cysts and resting stages, allow protozoa to inhabit diverse environments and to adapt to a wide range of habitats. Some species are cosmopolitan and are found worldwide. Their cysts are carried by water currents and wind to distant locations, and they are undoubtedly transported by waterfowl and other aquatic animals as they migrate from one location to another. Protozoa, although among the smallest of life forms, exhibit remarkably complex behavioural and physiological adaptations that have allowed them to invade and proliferate in widely diverse habitats. Their biodiversity (which includes tens of thousands of extant species), essential role in maintaining food webs and enhancing ecosystem productivity, and increasing evidence of numerical abundance and diversity in widely divergent habitats worldwide give evidence of their importance on a global scale. **See also**: Protozoan Cysts and Spores; Protozoan Diversity and Biogeography

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