SYMPOSIUM ARTICLE

Ciliates and the Rare Biosphere—Community Ecology and Population Dynamics

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ABSTRACT

Application of deep sequencing technologies to environmental samples and some detailed morphological studies suggest that there is a vast, yet unexplored rare ciliate biosphere, tentatively defined in terms of operational taxonomic units. However, very few studies complemented molecular and phylogenetic data with morphological and ecological descriptions of the species inventory. This is mainly because the sampling effort increases strongly with decreasing species abundance. In spite of this limited knowledge, it is clear that species that are rare under certain environmental conditions (temporal rare biosphere) may become abundant when the physical, chemical, and biological variables of their habitat change. Furthermore, some species may always be present in low numbers if their dispersal rates are exceedingly high (accidental rare biosphere). An intriguing question is whether there are some species that are always rare, i.e., in every suitable environment. This permanent rare biosphere is conceptually different from the temporal rare biosphere. This review characterizes typical aquatic habitats of the rare ciliate biosphere, portrays different scenarios under which some or even many species may be permanently rare (background fauna), and identifies some fundamental questions that need to be addressed to achieve a better understanding of the population dynamics of the rare ciliate biosphere.

BOTANISTS and zoologists have known for centuries that there are many rare species, which can be found only in particular habitats or under specific environmental conditions. In contrast to the more conspicuous macroorganisms, most microorganisms lead a hidden existence from the human eye and their diversity must be inferred from applying technical tools such as microscopy and molecular methods. For approximately three decades, the application of PCR-based molecular methods detected consistently a large number of uncultivated novel but not necessarily rare taxa in most terrestrial and aquatic microbial assemblages (e.g., Fuhrman et al. 1992; Liesack and Stackebrandt 1992; Olsen et al. 1986; Ward et al. 1990); however, these techniques were applied to protistan ecology only during the last decade (summarized by Dunthorn et al. 2014). Application of high-resolution phylogenetic, genomic, and the most recent “omic” analyses (metagenomics, metatranscriptomics, metaproteomics, and community metabolomics) (Wilmes 2012; Zarraonaíndia et al. 2013) to environmental samples suggests that the number of rare taxa usually by far exceeds that of the few dominant ones (Dawson and Hagen 2009; Galand et al. 2009; Lepère et al. 2013; Sogin et al. 2006; Stoeck et al. 2013). Not only due to the increased application of high-throughput sequencing (HTS), which has largely replaced fingerprinting techniques (e.g., DGGE, T-RFLP) in the last decade but also with the raising concern that major losses of (microbial) biodiversity may currently pass unnoticed, this “rare biosphere” (Sogin et al. 2006) received wide attention in recent years. This is because rare taxa could play significant roles in microbial community dynamics and biological interactions. For instance, they may carry out yet unknown physiological functions, may be useful agents for future biomedical applications, or serve as a reservoir of genetic resources (seed bank) that may alleviate adaptation to changing environmental conditions, as they are currently experienced under the global change scenario.

It is clear that some taxa that are rare in one environment may be abundant in others; similarly, species that are rare under certain environmental conditions may become abundant when the physical, chemical, and biological variables of their habitat change. However, it is not known whether there are some species that are always...
rare, i.e., in every suitable environment. Recent analyses from 454 pyrosequencing of 16S rRNA genes of the microbial assemblages in the Arctic Ocean provided conflicting evidence; in one study, 99% of the rare (i.e., abundance in the sample < 0.01%) bacterial phylotypes were never detected as abundant, although the community was sampled in summer and winter (Galand et al. 2009; Kirchman et al. 2010). Conversely, 81 of 106 phylotypes that were abundant (> 1% in the sample) in some samples were rare in others (Galand et al. 2009). These authors concluded that their results argue against the “seed bank” hypothesis (Pedrós-Alió 2006). This hypothesis assumes that rare taxa can be promoted from the seed bank to the core zone of active, abundant taxa if environmental conditions become adequate. A similar conclusion has been drawn for core, respectively occasional fish species in relation to climate change (Magurran and Henderson 2003). In contrast to Galand et al. (2009), Zeng et al. (2013), using comparable methods and investigating a similar geographic area, reported that some bacterial phylotypes that were rare in one area were the most abundant ones in other Arctic regions, thus supporting the “seed bank” hypothesis.

It is an open question if evolutionary mechanisms maintain a rare biosphere of highly diverse, low abundance microbial populations (Reid and Buckley 2011). The present molecular methods cannot adequately quantify the abundance of all protist taxa present in a given sample (Bachy et al. 2013; Pedrós-Alió 2006; Stoeck et al. 2013). Under-sampling in space and time and limited sample volumes are other principal problems; the sample volume of recent studies applying deep sequencing technology typically ranged from < 1 up to 5 liter (Galand et al. 2009; Lepère et al. 2013; Sogin et al. 2006; Stoeck et al. 2013). It is obvious that such a small sampling volume is inadequate to account for all rare protist species; however, even rare bacteria cannot be sampled in small sample volumes or areas. Based upon empirical evidence and theoretical considerations, Curtis et al. (2002) estimated that one individual of the least abundant bacterial species in soil would occur every 27 km².

Since both conventional microscopic techniques and novel molecular methods for species identification are biased, it is not surprising that the taxon (species) inventory depends on the method used (Fraser et al. 2009; Stoeck et al. 2013). Although molecular methods progressed enormously over the past two decades, the quest for the gold standard for species detection and identification in environmental samples remains (Boenigk et al. 2012; Stoeck et al. 2013). These context-dependent constraints and conceptual vagueness (discussed further below) have prevented an unequivocal definition of the term rareness across different taxa.

The majority of empirical investigations analyzing microbial communities has focused on prokaryotes, i.e., the domains Bacteria and Archaea. This is primarily because prokaryotes are the major drivers of biogeochemical cycling on earth, but also reflects the number of researchers being active in the field. The large majority of microbial ecologists investigates bacteria and archaeans, followed by algal ecologists. Only a tiny fraction of microbial ecologists deals with heterotrophic protists. Similar to the empirical studies, recent attempts to apply macroecological theory to microbes considered almost exclusively prokaryotes (Nemergut et al. 2013; Ogilvie and Hirsch 2012; Prosser et al. 2007). In general, the application of theory in microbial ecology is very limited (Prosser et al. 2007), and microbial ecology has been blamed recently to be driven by techniques, neglecting the theoretical ecological framework; “this has led to an almost unhealthy obsession for using the latest methodologies, typically at the expense of the research questions being asked” (Oliver et al. 2012).

The few studies that included or even concentrated on protists, the most abundant eukaryote microbes, yielded the same principal conclusions as obtained for prokaryotes, i.e., they all suggest the existence of a vast diversity that is primarily maintained by rare taxa (Amaral-Zettler et al. 2009; Medinger et al. 2010; Stoeck et al. 2010). Although some recent studies specifically addressed biodiversity of ciliates in aquatic and terrestrial environments (Foissner et al. 2002; Lara et al. 2007; Stock et al. 2013; Stoeck et al. 2013), we are far away from understanding the extent, origin, maintenance, and functional role of rareness among free-living ciliates. These general aspects have been reviewed in the first article of this section (Dunthorn et al. 2014). The present contribution focuses on the community ecology of rare ciliates, i.e., a field that is largely unexplored at present and is inevitably linked to methodological constraints and theoretical considerations. I will first summarize the existing conceptual knowledge and empirical evidence on the ecology of rare taxa among ciliates and other free-living microbes. Since the existing evidence does not allow drawing any firm conclusions on the key issues identified in the foregoing, I will then speculate about the possible mechanisms and evolutionary processes driving population dynamics of rare (ciliate) species. In this regard, this contribution is rather an opinion than a review article. Although findings from terrestrial habitats will be considered in the following, the focus of this article is on aquatic communities. Similarly, where appropriate, I will consider empirical evidence and theoretical progress that has been made recently with prokaryote microbes in this review. However, we have to be aware that for the eukaryotic ciliates and other protists the major evolutionary and ecological forces may be fundamentally different from that of prokaryotes. This is mainly because high rates of recombination and horizontal gene transfer (HGT) that result in rapid exchange of DNA between even distantly related bacteria and other organisms (Fraser et al. 2007) are believed to be unimportant in protists, except for the major endosymbiotic events that gave rise to mitochondria and plastids of eukaryotes. Although viruses also infect various protist species (Wang and Wang 1991), this is not comparable to the common viral-mediated DNA transfer (transduction) among bacteria.
**SPECIES RICHNESS RELATIONSHIPS, SAMPLING EFFORT, AND SAMPLE STATISTICS**

In their natural realm, all organisms occur along a continuum reaching from very rare to usually present. The conceptual framework describing species community dynamics in space and time was developed 50 yr ago for terrestrial communities. Species-area curves and the Theory of Island Biogeography (MacArthur and Wilson 1967) are the cornerstones of species richness dynamics (Ma et al. 2012). From analyses of terrestrial animal and plant communities, Preston (1962) reported that the number of species \( S \) is usually related to the area \( A \) investigated by a power function (Fig. 1A):

\[
S = \alpha A^z
\]

where \( \alpha \) and \( z \) are parameters derived from the sample data set; \( z \) is the slope of the species area relationship (SAR) in the log–log plot (Fig. 1B). The higher \( z \) is, the more species will be found in a given new area. For aquatic organisms, the volume investigated can replace \( A \) in the SAR. Preston (1960) also noted that time is similarly related to species richness as area is, since the total number of species increases both with the area (respectively, sample volume) investigated and the time of the investigation. This connectivity between species richness, area, and time is also inherent in the Theory of Island Biogeography (MacArthur and Wilson 1967). This seminal theory attempted to predict the number of species that would exist on a newly created island and explained how distance, area, and time combine to regulate the balance between immigration and extinction in an island population. Another closely related concept that was developed at approximately the same time is species turnover that describes how species communities change in space (\( \beta \)-diversity) and time (\( \gamma \)-diversity) (Whittaker 1960, 1972).

Samples with rare species usually follow a (symmetrical) log-normal distribution for the core species and a (skewed) log series distribution for the occasional species (Magurran and Henderson 2003), with a few dominant species contributing most to total abundance and many less abundant species contributing the rest (the long “tail” of the curve, Fig. 1C).

The sampling effort is nonlinearly related to the abundance of the study organisms (Fig. 1C); since small species are more frequent than larger species, a relatively small sampling volume or area may suffice for the former, but may be inadequate for the latter. The question “what is an adequate sample size” is a statistical problem. It is a truism that precision to estimate unknown parameters such as, e.g., average abundance of a given species in a community, increases with sample size. Several mathematical tools are available to estimate the required sample size for hypothesis testing. In particular, it is possible calculating the sample size required to yield a certain power for a statistical test, given a predetermined Type I error rate \( \alpha \) (i.e., the risk of rejecting a true null hypothesis – \( \alpha \) is usually set at 0.05). Several sample size calculators are available in the internet (e.g., http://www.surveysystem.com/sscalc.htm, http://www.nss.gov.au/nss/home.NSF/pages/Sample+size+calculator, http://www.ncss.com/software/pass/?gclid=ClnevNGx0LOCFanjwgodSZoAsQ). The details of the respective statistical methods are beyond the scope of this review. However, it is important to note that if, for instance, the goal is to estimate the abundance of a population of a rare marine ciliate species that occurs with < 1 individuals/l, the sample size necessary to calculate the mean abundance with a reliable statistical power should be calculated a priori. This is opposite to the common practice how rare species have been identified in the past. Most ecological studies conducted during the past decades focused on abundant or dominant protist species, because those are assumed to act as primary drivers of ecosystem functions such as production, predation, and nutrient regeneration. This is primarily because the significance of the aquatic microbial food web for biogeochemical cycling is a...
relatively recent detection (Azam et al. 1983; Pomeroy 1974; Williams 1981). However, most of the studies conducted between 1970 and 1990 used methods of sampling and fixation that turned out to be too broad or too selective to identify rare species correctly. It is generally difficult to separate the sampling effect from real ecological and evolutionary processes causing the species accumulation over space and time (Ma et al. 2012).

WHAT IS THE RARE BIOSPHERE?

The molecular approaches unequivocally revealed the presence of a large number of rare microbial taxa or OTU’s (operational taxonomic units) in a range of aquatic and terrestrial environments (Amaral Zettler et al. 2002; Amaral-Zettler et al. 2009; Lara et al. 2007; Medinger et al. 2010). HTS of small, variable regions of the ribosomal rRNA in environmental samples has largely replaced the traditional full-length PCR amplification of the SSU rRNA gene, followed by cloning and Sanger sequencing, in recent years. Although deep sequencing technologies produce artifacts that may grossly inflate the number of rare taxa if read quality filtering (data denoising) and low clustering thresholds are not applied carefully (Bachy et al. 2013; Kunin et al. 2010), they have led to the detection of many novel taxon groups, including the ciliate class Canacotrichaea (Orsi et al. 2012). A recent study that pyrosequenced the hypervariable V4 region of the SSU rRNA of ciliates from a freshwater lake revealed large discrepancy between species identification based upon the molecular data and conventional microscopic techniques (Stoeck et al. 2013). The authors concluded that “cell losses after fixation, cryptic morphotypes, resting stages, insufficient sequence data availability of morphologically described species and the unsatisfying resolution of the V4 SSU rRNA fragments” might all have prevented accurate taxonomic assignments. Furthermore, the highly variable SSU rDNA copy number in different protist taxa is a major reason for biased protist abundance data obtained from HTS (Dunthorn et al. 2014; Medinger et al. 2010; Stoeck et al. 2013). Variable gene copy number is particularly important for ciliates, resulting in spurious abundance estimates of ciliates from uncorrected HTS data. In their recent review, Dunthorn et al. (2014) pointed out that differential processing of macronuclear chromosomes can lead to hundreds of DNA copies in some ciliate taxa within the Colpodea, Litostomatea, and Oligohymenophorea, while leading to 1,000s of copies in other taxa (e.g., Phyllopharyngea and Spirotrichea). These authors suggest as a preliminary solution to this problem the use of incidence-based statistics (presence/absence data) for more robust analyses of environmental HTS amplicons. Stoeck et al. (2013) recommend intensifying group-specific barcoding efforts for an improved analysis of the rare ciliate taxa in natural samples.

In addition to the potentially large technical bias, the principal but as yet unresolved question is if the major fraction of the rare biosphere consists of dead cells, molecular debris, and/or nonactive resting stages such as cysts (Caron and Countway 2009). Future analyses of RNA sequences and protein expression may help solving this issue. Further, a significant fraction of the rare taxa may result from continuous dispersal into new environments. Dispersal rates of microbes including protists are generally high, relative to macroorganisms, and for many species assumed to be global (Finlay 2002; Finlay and Clarke 1999; Finlay and Fenchel 2004). However, it has been demonstrated that a restricted geographic distribution of protists occurs in limnetic, marine, terrestrial, and fossil ecosystems (Foissner 2006, 2007, 2008). If a species thrives in a given habitat with specific environmental conditions and is easily and continuously dispersed into less favorable environments, the result is a gradient consisting of a dense population in the center and increasingly lower abundance toward the edges of the possible distribution (Fig. 2). At the far end of the dispersal range, this species may always be rare. However, it is important to note that there is a conceptual difference between invasion and immigration (also called migration, Nemergut et al. 2013). Invasion is defined as colonization that impacts other species already inhabiting an area (Bohonak and Jenkins 2003); in contrast, immigration is the result of successful invasion, i.e., the propagules of an invader must have reproduced and survived over many generations, thus establishing a new (meta)population within the new habitat (Weisse 2008). In contrast to colonization, invasion will be successful only if, among the flow of invaders, there are some cells better adapted (i.e., with a higher fitness) to the specific local environment than those already present. Accordingly, (im)migration events are the
result of dispersal, followed by selection and possibly genetic drift (Nemergut et al. 2013). It now seems clear that this effective dispersal (Weisse 2008) is distinctly lower than the (almost) unlimited potential dispersal (Weisse 2008) of many microbes (Fontaneto and Hortal 2012). Other authors ignoring this difference (Finlay 2002; Pedrós-Alió 2006) equate immigration with dispersal to a new habitat.

In most cases, dispersal is a nonrandom process, depending on vectors such as water currents, prevailing wind directions, routes of migrating birds, etc. (Weisse 2008). If there is directional dispersal, it appears unlikely that the relative abundance of a species in a terrestrial area declines directly with distance from its center. This is because the environmental conditions in the invaded habitats represent a continuum of more or less favorable conditions for this species. Accordingly, immigration may be possible in some habitats but not in others (Fig. 2B). Only if dispersal primarily regulates the population density of a species, a pattern as depicted in Fig. 2A will emerge. In the ocean, changes in environmental conditions are much more gradual if dispersal is mediated via water currents. As long as a given water mass acts as the vector of dispersal, any change in the environmental conditions that an organism entrained in this water mass experiences will be buffered. In freshwater environments, connectivity via rivers is a major factor of dispersal.

If dispersal is of overwhelming importance for regulating microbial population structure (Finlay 2002), we will encounter an “accidental” rare microbial biosphere virtually everywhere. The actual community then is primarily a result of stochastic processes, as predicted by the Neutral Theory of Biodiversity and Biogeography (Hubbell 2001). If dispersal is less important, and nonneutral biotic interactions matter (violating the assumption of fitness equivalence among all species of the neutral theory), we still may find two types of principally different rare species. The first one comprises species that are rare under most environmental conditions but may become abundant if the environment changes, i.e., they are not fundamentally different from abundant species. The second type is the temporal rare biosphere. This is currently the prevailing hypothesis that the rare biosphere comprises species that are functionally similar but temporarily competitively inferior to the more abundant species (Caron and Countway 2009). Even subtle changes in the environmental conditions may cause changes in the community composition, turning formerly rare into abundant species and vice versa. Since dominant and rare species in a functional guild (e.g., photoautotrophs, bacterivores) are principally similar, the rare species represent ecological redundancy and provide biological buffering capacity allowing relatively stable community functions (e.g., primary production, nutrient cycling) in spite of taxonomic changes (Caron and Countway 2009). This concept was already expressed by Preston (1960), who concluded that the rarer species are not essential (“merely adventitious”) for the community. Evidence for this view emerged primarily from culture enrichments (Lim et al. 1999), microcosm experiments (Sharon 1993), and seasonal succession of natural communities, i.e., the regular and recurrent sequence of species communities (Sommer 1985; Sommer et al. 1986). Seasonal succession is typical of polar and temperate habitats with pronounced seasonal changes in temperature. In tropical and subtropical habitats, precipitation (dry vs. rainy season) can be a major driver of seasonal succession. The plankton ecology group (PEG) model (Sommer et al. 1986) verbally described physical (light, temperature, stratification), chemical (nutrients), and biological (grazing, predation, competition) factors driving the seasonal wax and wane of phyto- and zooplankton communities in lakes. Seasonal phytoplankton succession has also been documented for coastal marine areas (Karentz and Smayda 1984). A recent review considered novel interactions that have become apparent since the PEG model was published (e.g., the role of the microbial food web, parasites, and food quality), but concluded that the overall patterns of gross seasonal biomass fluctuations of phyto- and zooplankton in eutrophic and oligotrophic lakes are still valid (Sommer et al. 2012). One prominent feature of the PEG model is that phytoplankton biomass can virtually collapse due to excessive zooplankton (mainly Daphnia) grazing in temperate (eutrophic) lakes. Stimulated by the PEG model (Müller et al. 1991) demonstrated that the abundance of planktonic ciliates in Lake Constance can decline within a few weeks by a factor > 10, turning abundant species into rare ones. The opposite effect, rapid increase of ciliate cell numbers, occurs when small, edible nano- and microplankton food is abundant and biomass of ciliate predators is low (Smetacek 1981; Weisse et al. 1990). Relatively rapid temporal shifts in the dominant algae and protists have also been reported from coastal marine areas (Karentz and Smayda 1984; Smetacek 1981, 1985).

An intriguing question is whether there is a “true” or permanent rare biosphere composed of “chronically rare” organisms (Fuhrman 2009), which is partially or even fundamentally different from the common biosphere. In other words, does “rareness” represent a trait, an evolutionarily conserved way of life (Holt 1997)? Strong evidence for a chronically rare ciliate biosphere was provided by Foissner (1998) for soil ciliates. He found in 1,000 soil samples from all continents about 700 new species, half of which occurred in only one sample each. Many new species such as the giant (~250 μm) hypotrich Australothrix alwinae or the middle-sized (~60 μm) colpodid Cosmoclopo da naschbergeri, with a unique cortical ornamentation, have a distinct morphology, i.e., they can hardly be overlooked or misidentified. At the end of this article, I will explore the chances that such a true rare biosphere exists among free-living aquatic ciliates. Ignoring that there are three different scenarios of rare species is probably the main reason why an exact definition of the term rare biosphere has been elusive (Caron and Countway 2009). In the following, I will first try to quantify ciliate rareness and then qualify rareness in terms of ciliate habitats.
HOW ABUNDANT IS A RARE CILIATE SPECIES?

Classifying organisms into categories such as “very abundant”, “abundant”, and “rare” is an arbitrary decision, depending on the organisms under study and the methods used. Relative abundance can be measured in terms of frequency of occurrence, i.e., in how many samples a given species is found, respectively how many of the possible suitable sites are occupied (Bartošová and Tirjaková 2008; Foissner et al. 2002). Alternatively, the abundance of this species can be related to total abundance in the sample (Curtis et al. 2002). Taxonomists who are primarily interested in qualitative aspects (species composition and richness) prefer the first measure. Ecologists, who want to quantify species occurrence in terms of abundance and biomass, prefer the latter measure. It is important to note that these two measures of relative frequency may yield different results. For instance, if a certain species occurs frequently, but in low numbers in a certain area, a taxonomist may call this taxon a common species. An ecologist, analyzing the same samples, may conclude that this is a rare species if its contribution to total abundance is less than a few percent. The seemingly easy solution to combine both approaches is often not a practical one, because quantifying ciliate populations with high taxonomic resolution is not only time consuming but also requires profound taxonomic expertise. Unfortunately, worldwide there is only a handful of alpha taxonomists, i.e., researchers accurately describing new ciliate species based upon morphological, ultrastructural, and molecular characters, currently active (Chen et al. 2013; Foissner et al. 2004, 2014; Xu et al. 2013). Often, a compromise has to be made between analyzing more samples with limited taxonomic resolution and a few samples with high taxonomic resolution (“breadth” vs. “depth” tradeoff). The conceptual difference is that the quantitative approach also considers the evenness of the sample.

We are left with the fact that relatively few studies are currently available that assessed abundance and taxonomic composition of aquatic ciliates reliably. Tintinnids are relatively robust and conspicuous ciliates that may be considered model organisms for planktonic marine protists (Dolan et al. 2013). The mean abundance of tintinnids in oligotrophic shelf and oceanic environments is 21 individuals/l (McManus and Santoferrara 2013). In the “miniature oceans” of the Laurentian Great Lakes, the mean ciliate abundance in 0–20 m depth ranged from <1.0 to >14,000/l (Munawar and Lynn 2002). As in other studies, the abundance was lowest at the most oligotrophic sites, supporting the earlier notion that there is a general positive relationship between (lake) productivity and ciliate abundance (Beaver and Crismann 1982). An inventory of the species community in Lake Baikal revealed 102 species with total abundance ranging from 500 to 6,000 cells/l at offshore stations (Obolkina 2006). Similar ranges of ciliate density have been recorded at offshore stations in tropical Lakes Malawi (minimum abundance 200 cells/l) and Victoria (minimum abundance 500 cells/l) (Yasindi and Taylor 2003). Table 1 lists some more examples from

### Table 1. Typical habitats, dominant taxa, and total ciliate abundance of the (globally) rare ciliate biosphere. Species that are globally rare may be highly abundant in their specific habitat

| Habitat                          | Examples                                      | Dominant taxa                                      | Total ciliate abundance (ml⁻¹) | References                                                                 |
|----------------------------------|-----------------------------------------------|---------------------------------------------------|--------------------------------|---------------------------------------------------------------------------|
| Oligotrophic ocean               | Central Pacific Gyres, Indian Ocean, Mediterranean Sea | Aloricate oligotrichs and choreotrichs             | <0.1–2                         | Claessens et al. (2008); Strom et al. (1993) and references therein       |
| Ultraoligotrophic lakes          | Andean lakes                                  | Ophrydium naumannii, Stentor araucanus, S. amethystinus | 0–6                            | Corno et al. (2009); Modenutti et al. (2000, 2008); Woeifli (2007)         |
| Deep anoxic hypersaline basins   | Cariaco Basin (Caribbean Sea), DHABs in eastern Mediterranean Sea | Cariacotricha caudata, Cariacotrichia, Spirotrichea | 0.2                            | Orsi et al. (2012); Stock et al. (2013)                                    |
| Solar salters                    | Yellow Sea, Mediterranean Sea                 | Fabrea salina, Strombidium styliferum, Euplotes minuta | 0–211                          | Elloumi et al. (2006); Lei et al. (2009)                                   |
| Intertidal rock pools            | French coast                                  | Strombidium oculatum                               | <0.1 to >300                    | Jonsson (1994); Montagnes et al. (2002)                                   |
| Extremely acidic lakes and rivers | Acid mining lakes, Rio Tinto                  | Oxytricha spp. and other hypotrichs, Urotricha spp., Vorticella sp. | 0.01–0.04, max. 14 (355?) | Moser and Weisse (2011); Weisse et al. (2013b); Packroff (2000)           |
| Alkalophilic lakes (pH ≈ 10)     | African soda lakes                            | Cyclidium spp., Acineria sp., Lagynophrya sp., Spathidium sp., Frontonia sp. | <400 to >1,000                 | Finlay et al. (1987); Ong’ondo et al. (2013)                              |
| Phytotelmata                     | Tank bromeliads                               | Bromeliolothrix metapoides, Glaucomides bromelicola | 0–200                          | Carras et al. (2001); Foissner et al. (2003); Weisse et al. (2013a)       |
ultraoligotrophic Andean lakes. Accordingly, if we define that a rare species contributes < 1% to total ciliate abundance, the typical abundance of rare ciliates in marine and fresh waters should range from < 1 to 3 cells/l. This estimate is in accordance with theoretical considerations. Assuming a log-normal species abundance curve, the abundance of the least abundant species in a community ($N_{min}$) is related to the number of individuals in the most abundant species ($N_{max}$) and the modal abundance ($N_c$) according to $N_{min} = N_c^2/N_{max}$ (Curtis et al. 2002). Therefore, the above tintinnid example (with $N_0 = 21$ cells/l) may yield typical $N_{min}$ ranging from 0.1 to 1 cells/l if $N_{max}$ ranges from 440 to 4,400 cells/l.

**TYPICAL HABITATS OF RARE SPECIES**

Ignoring the accidental and the temporal rare biosphere, permanently rare species occur under two different scenarios: as inferior competitors of more common species at low abundance in universal environments (background fauna) or as specialists with occasionally dense populations in extreme habitats that most species cannot colonize (specialist fauna). While typical extreme habitats occur in both marine and fresh water (Table 1), they have been researched unevenly. Deep Hypersaline Anoxic Basins (DHABs), in particular, received much attention in recent years (reviewed by Edgcomb and Bernhard 2013; Edgcomb and Pachiadaki 2014). Most of the recent studies using deep sequencing technologies reported relative frequency of OTU’s but did not measure ciliate abundance. An exception is the study by Orsi et al. (2012), who found an in situ abundance of 0.2 cells/ml of cariacotrich ciliates at a depth of 900 m in the Cariaco Basin. Although Cariacotrichaea belong to the specialist fauna and do not seem to occur in habitats less hostile to life, their abundance is in the range of typical rare species of the background fauna. Saline lagoons and ponds (solar salterns) are another, but less isolated type of hypersaline environments than DHABs. Compared to the latter, the ciliate fauna in solar salterns appears to be more abundant, more diverse, and primarily composed of generalist species (Table 1). In intertidal rock pools, Strombidium oculatum is a locally adapted, specialist species that exhibits an endogenous circatidal behavior (Jonsson 1994; Montagnes et al. 2002) and may occasion species that exhibits an endogenous circatidal behavior (Jonsson 1994; Montagnes et al. 2002) and may occasion extremely high cell numbers (Table 1). Remarkably, (unidentified) species of the genus *Frontonia*, which can be dominant in alkalophilic lakes, have also been reported from AML (Packroff 2000). However, in the phylogeny based upon SSU rRNA gene sequences, *Frontonia* species from the African soda lakes clustered with *Apofrontonia* and *Paramecium* rather than with other *Frontonia* species (Ong’ondo et al. 2013). Although these authors could identify some species unequivocally in alkalophilic lakes that may be extreme generalists (e.g., *Cyclidium glaucoma*), most of the species did not match available species descriptions, suggesting that these lakes harbor a specialist ciliate fauna.

Foissner and colleagues recently described a highly specific ciliate fauna from tank bromeliads (Foissner 2010, 2013; Foissner and Wolff 2009; Foissner et al. 2003). The life cycle and some ecophysiological peculiarities have been identified as the main reasons restricting the occurrence of these ciliates to their particular habitat (Weisse et al. 2013a). For a detailed account on the morphology of rare ciliates in extreme environments, consult Hu (2014).

In conclusion, the evidence accumulated from extreme habitats (Table 1) demonstrates that species, which are globally permanently rare, may become locally highly abundant.

**WHICH FACTORS DRIVE POPULATION DYNAMICS OF PERMANENTLY RARE CILIATE SPECIES?**

Two principle scenarios allow the existence of permanently rare ciliate species in various environments. First, I will portray a scenario based upon the assumption that the environmental factors and evolutionary processes are virtually the same for abundant and rare species, i.e., that the realized abundance of any species is the result of a dynamic interplay of known processes (Fig. S1).

Spatial and temporal heterogeneity of the aquatic environment may affect our perception of the rare ciliate biosphere. Microenvironments might support rapid growth of some ciliate species that are (on average) much rarer in larger sample volumes that are more readily sampled by standard methods. Microenvironments may consist of milliliters or even microliters of water or microparticles such as marine snow and fecal pellets (Alldredge and Cohen 1987; Alldredge and Silver 1988) or lake snow (Grosshass and Simon 1993), while our routine sampling methods typically average across a few liters of water. Ciliates whose growth is associated with the microscale might become highly abundant but show up rather consistently as “rare” in the larger samples. Similarly, transient environmental conditions may alternately promote and retard the growth of some species on time scales not captured by most of our sampling approaches, keeping those species present but rare in a sample, relative to other species that are less affected by the same transient conditions (see temporal rare biosphere, above).
It appears likely that in some habitats, a few superior competitors or predators, keeping the abundance of most species low, permanently dominate the ciliate fauna. Inferior competitors may avoid being outcompeted via encystment and excystment. Recent laboratory experiments with two ciliate species from tank bromeliads demonstrated that stable coexistence can be mediated by continuous encystment and excystment of the inferior competitor (Weisse et al. 2013a). In those experiments, only the inferior competitor was able to form cysts. It has been shown that both intrinsic and external factors may determine the encystment/excystment cycle in ciliates (Corliss and Esser 1974; Gutiérrez et al. 2001; Müller 2000; Verni and Rosati 2011). However, although many free-living ciliates are known to form resting stages (Lynn 2008), the factors triggering encystment/excystment and the frequency of encystment remain unknown for the vast majority of species. For instance, among the aloricate oligotrich and chooreotrich ciliates, many of which are dominant marine microzooplankton taxa, resting cysts are known only in a few species (reviewed by Agatha 2011). Furthermore, knowledge about the dynamics of active and encysted populations is limited due to methodological difficulties. Even for comparatively well studied ciliates in soil, no method is currently available for re-activating most or all resting cysts (Ekelund et al. 2002; Foissner 1997). Assuming that the ability to form resting cysts is widespread among terrestrial and aquatic ciliates, this may allow many rare species to survive not only temporally but also permanently under presumably unfavorable conditions.

While cyst formation may or may not be density dependent, competition, predation and parasitism certainly are. It is unrealistic that in a large volume of water such as in the ocean competitive dominance completely eliminates competitively inferior taxa; similarly, extremely low abundance provides a perfect refuge from grazing mortality (Caron and Countway 2009) and parasitism. Both predation and parasitism are a function of the encounter probability between predator and prey, respectively host and parasite. The encounter probability is related to the cell size; everything else being equal, small cells suffer less from predation and parasitism than larger cells. Ciliate cell size varies primarily in relation to the nutritional state of the cell; cell volume of well-fed specimens may be more than ten times larger than that of starved congeners (Weisse 2002). Other environmental variables such as temperature and pH usually affect biovolume of planktonic ciliates by a factor of 3–4 (Weisse 2004; Weisse and Montagnes 1998; Weisse and Stadler 2006). It is also well known that bactovorous and herbivorous or omnivorous ciliates follow a typical numerical response, i.e., their growth rate is positively related to the food supply (Montagnes 1996; Montagnes and Berges 2004; Taylor 1977). The food threshold that is needed to sustain a population has been determined experimentally for a number of planktonic species (Weisse 2006). I conclude that an inferior ciliate competitor will lead a famine existence, characterized by low abundance, slow growth, and relatively small cell size. Due to density dependent feedback, low abundance and small cell size will automatically reduce mortality due to grazing and parasitism, thus stabilizing the population at low cell numbers (Fig. S1).

Sex is a major process of achieving and maintaining genetic variety in a given population. In ciliates and many other protists, facultative sexuality is assumed to occur in almost all major clades; in fact, it is seen as the ancestral condition for all eukaryotes (Dunthorn and Katz 2010). King and van Leeuwenhoek already observed sexuality of ciliates in the late 17th century (Bell 1988; Dini and Nyberg 1993). Contrary to daphnids and rotifers, and most other animals, sex in ciliates is decoupled from reproduction since the various sexual processes such as autogamy (self-fertilization, inbreeding) and conjugation (cell mating, outbreeding; reciprocal-fertilization typically including the exchange of nuclear material between the two partners) do not lead to an increase in cell numbers. In outbreeding ciliates, sexual recombination can be identified relatively easily by observing conjugating specimens (Fig. 3C, left insert). Similar to predation and parasitism, conjugation is density dependent; it requires a minimum abundance of

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**Figure 3** Postulated key characteristics of the rare ciliate biosphere. A, B. Substrate and prey affinity (A) and dispersal and loss rates (B) all decrease from common to rare species. C. Along this continuum, the tendency to form resting stages (cysts) increases (dashed curve), while the significance of sexual recombination declines (solid line). D. Disturbance is less important in habitats harboring the rare biosphere; the opposite holds true for interspecific cooperation and multispecies networks. The inserts in C show two conjugating Bursaridium sp. (top left; light microscopy photo provided by B. Sonntag), respectively a cyst of the rare ciliate Meseres corbisti (top right; SEM photo provided by W. Foissner).
the two partners in order to have a realistic chance to meet and mate. It has been demonstrated recently for facultative sexual rotifers that sex provides an adaptive advantage over asexual reproduction in spatially heterogeneous environments and under (rapidly) changing environmental conditions (Becks and Agrawal 2010, 2012). By implication, sex should be less important in relatively homogeneous environments with little seasonal change, such as in the oceanic central gyres or the deep sea. If asexuality and selfing reduce fitness, a decrease in distribution and local abundance will be the consequence (Kunin 1997). For these theoretical reasons and the practical considerations discussed above (low rate of encounter), I conclude that “true sex” (outbreeding) plays virtually no role in rare ciliate species dwelling in spatially and temporarily homogenous environments. Gaston and Kunin (1997) reached a similar conclusion for animals and plants; these authors identified the lack of outcrossing and sexual reproduction as a major characteristic of rare species. In ciliates, increased cyst formation may have compensated the lower reproductive investment that seems to be a general trait of rare species (Gaston and Kunin 1997; Kunin and Gaston 1993).

If gene flow is also limited due to low rates of dispersal, it follow that genetic diversity in a rare ciliate population is primarily maintained by mutation (and, possibly, by autogamy). This is supported by evolutionary theory predicting that sexual recombination has little effect in very large populations; this is because if population size exceeds $10^{12}$, recombination is not needed to escape Muller’s ratchet (Bell 1988). Although counterintuitive, many rare species may still build very large populations. In the ocean, a rare ciliate, with an abundance of 0.1 cells/l, would reach the above critical population size in a water volume of 10 km$^3$. This is a tiny volume, considering the dimensions of the oceanic provinces. The North Pacific Subtropical Gyre is the largest ecosystem on earth, located between the equator and 50° N latitude; with a surface area of 20 million square kilometers (Karl 1999), its upper 100 m of the water column comprise a volume of $2 \times 10^6$ km$^3$.

In summary, I conclude that a permanent ciliate background fauna may exist in some environments that is regulated principally by the same processes as the dominant taxa but with different emphasis (Fig. S1). A corollary from this scenario is that most of the rare species will never become abundant.

Alternatively to the above scenario, we may postulate that there are as yet unknown, respectively largely ignored interactions or processes that govern population dynamics and diversity of the rare biosphere. One realistic possibility is the existence of networks; rare ciliates may directly or indirectly require other organisms to survive. For instance, rare species may take refuge from parasites in the presence of an abundant, closely related species. Such a scenario may occur with chytrids, fungal parasites that infect a suite of freshwater and marine algae and other organisms with considerable variation in host specificity (Gleason et al. 2008; Gsell et al. 2013; Gutman et al. 2009). Among free-living ciliates, host–parasite interactions have been studied intensively in a few model systems such as several Paramecium species with their highly infectious intracellular bacteria of the genera Holospora and Caedibacter (Fokin 2004; Fujishima and Kodama 2012; Goertz 2010). Interspecific and intraspecific interactions may occur in hierarchical networks with complex positive (mutualism, commensalism) and negative (predation, parasitism) feedbacks and nonlinear processes such as chaotic population dynamics (Ma et al. 2012) or metabolic consortia (Caron and Countway 2009). Network analysis of microbial species (or OTU’s) and their physical–chemical environment, which is an emerging field in microbial ecology (Fuhrman 2009; Steele et al. 2011), may reveal such relationships. Network analysis applied to the ubiquitous marine SAR11 bacteria cluster showed that most subtypes are associated with multiple bacterial uncharacterized OTU’s and yielded multiple instances where bacteria and eukaryotes (including ciliates) were connected (Steele et al. 2011).

With their highly diverse and specific metabolism, certain prokaryotic microorganisms (bacteria and archaea) may condition the habitat for ciliates. A well-known example are microaerophilic ciliates such as several species of the hypotrich genus Euplotes and the scuticociliate Uronema filicum, which live in the chemocline of lakes, marine sediments, and microbial mats (Fenchel 2012; Fenchel and Bernard 1996; Fenchel et al. 1989). Microaerophilic ciliates are exposed to steep chemical gradients resulting from the metabolic activity of chemolithotrophic bacteria. If the prokaryotic microorganisms also benefit from the ciliates (e.g., from their release of exudates and feces), the relationship would be mutualistic. Mutualistic interactions are vital for terrestrial ecosystem function (Hirsch and Mauchline 2012) and for complex marine systems such as coral reefs (Rosenberg et al. 2007) but have received little attention in planktonic aquatic ecosystems, with the exception of symbiosis (Dziallas et al. 2012; Gast et al. 2009). Mutualism characterizes a “win-win situation”, where each partner benefits from their cooperation, i.e., increases its fitness. It represents one end of a dynamic continuum of biotic interactions ranging from antagonistic (parasitism, predation) to mutualistic. However, it may be more realistic to assume that each cooperator pays a cost, thereby reducing its relative fitness. Evolutionary explanations for cooperation have been studied in some detail (reviewed by West et al. 2007). Network reciprocity, where clusters of cooperators outcompete defectors, has been identified as one mechanism promoting the evolution of cooperation (Nowak 2006). Symbiosis is another form of cooperation between taxonomically unrelated organisms that has been studied in detail in coral reefs, resulting in the formulation of the Hologenome Theory of Evolution (Rosenberg et al. 2007; Zilber-Rosenberg and Rosenberg 2008). This theory posits that the object of natural selection is not the individual organism (i.e., the coral), but the organism together with its associated pro- and eukaryotic microbial communities. Although it may appear far-fetched at present to assume that processes known from more “solid” systems such as
coral reefs control the rare biosphere, we cannot rule out that we do not even see the tip of the iceberg of all realized abiotic and, primarily, biotic interactions in this widely unexplored realm. However, we can define major open questions that should be addressed to achieve a better general understanding of the rare biosphere.

**POPULATION DYNAMICS IN THE PERMANENT RARE BIOSPHERE—SOME FUNDAMENTAL OPEN QUESTIONS**

Let us assume the following “best guess scenario” for the existence of a permanent rare (ciliate) biosphere: Many species occur permanently at low numbers, environmental change is small, and the species turnover in space and time is rather low than moderate. It follows that there is a dynamic, but low-level equilibrium where local extinction equals immigration. The processes leading to local extinction may include senescence, parasitism, competition, and predation. **Immigration from a large (?) metapopulation may enable stable species coexistence** (open question 1). Of the four main mechanisms leading to species coexistence (frequency-dependent predation and parasitism, the storage effect, niche partitioning, and relative nonlinearity of competition (Chesson 1994, 2000a,b; reviewed by Ma et al. 2012), we can ignore the first, the second, and the last one because they all have a temporal dimension. Predator-prey cycles and host–parasite fluctuations relate to the temporal rare biosphere discussed above but play no role in the permanent rare biosphere. The storage effect postulates that a weaker competitor “stores” members of its population from a previous, more favorable period, in which its population size was larger, during less suitable times. This assumption violates the above postulates of permanently low numbers and little seasonal variation in the rare biosphere. Similarly, relative nonlinearity is a temporal mechanism caused by the highly nonlinear response of a superior competitor relative to that of an inferior competitor. We are left with niche partitioning, which is enhanced by, but does not depend on fluctuating environmental conditions. Long-term (4.5 yr) analysis from a microbial observatory site off the southern California coast revealed probably highly predictable patterns of bacterial community change and a significant subset of the bacteria exhibited low levels of functional redundancy (Fuhrman et al. 2006). This finding implies the presence of well-defined, probably narrow niches for the bacteria (Fuhrman 2009). However, if we preclude temporal mechanisms allowing species coexistence, the number of ecological niches may severely constrain the number of permanently coexisting, metabolically less versatile protist species. According to the Intermediate Disturbance Hypothesis (IDH), species richness is greatest in communities that experience some intermediate level of disturbance (Connell 1978). If we postulate environmental change is minor in the permanent rare biosphere (see above), the IDH has little explanatory power for the existence of many rare species. According to the general relationships between diversity, stability, and disturbance it is stability that allows diversity to develop (Ma et al. 2012) and, in consequence, increased connectivity in the form of hierarchical networks as outlined in the previous section. Accordingly, I postulate that because of various, as yet unknown biotic interactions the niches in the rare ciliate biosphere are much more complex than is evident from the few, easy-to-measure environmental variables (open question 2).

The third major open question is how much of the observed genetic variability in the rare biosphere is ecologically and thus evolutionary, neutral. This relates directly to the conjecture of ecological equivalence and functional redundancy (Caron and Countway 2009; Hubbel 2001). If the vast majority of the measured variability is functionally neutral, there is no benefit for community composition and resistance to perturbation. Similarly, resilience of the rare biosphere to disturbance would be unaffected. An inherent difficulty is that it is virtually impossible to predict that what appears to be neutral now may not become functional in the future, if the environmental conditions change (see seed bank hypothesis, above). This, however, is part of a larger play of which we have at present a very limited understanding: what are the major drivers of genetic change and adaptation in the rare biosphere? From the previous discussion, I deduce that (sexual) recombination plays a minor and mutation a major role for creating genetic variation in the rare biosphere. It is plausible to assume that selection may act slower in the rare biosphere than in the “common” biosphere, but principally similar, thus mediating adaptation. Of the remaining major evolutionary forces, the significance of genetic drift and cooperation for creating and maintaining the rare biosphere needs to be explored (open question 4).

At the moment, effective population size \( N_e \), which is a key concept of population genetics (Wright 1931, 1932, 1938), cannot be determined in the rare ciliate biosphere. The effective population size is an abstract concept that accounts for the fact that most natural populations deviate from an ideal population of sexually reproducing individuals, where each member has the same chance to reproduce. In real populations, the number of individuals that actually contribute genes to the next generation is lower than the total number of potentially mating individuals. This is because a number of factors such as sex ratio, population fluctuations, nonrandom mating, and variable fertility influence \( N_e \) (Ridley 2004). **Within-species genetic diversity and mutation rate**, which can be used to calculate \( N_e \) (Futuyama 2009; Lynch and Conery 2003), are currently largely unexplored (open question 5). To my knowledge, the effective population size is not only unknown in ciliates but in any other free-living protist species. If we assume that most ciliates in the rare biosphere produce primarily or exclusively asexually, it is important to consider their clonal population structure, since clonal growth has a major impact on \( N_e \) (Campbell and Husband 2005). The selection effective population size \( (1/s_{critical}) \), where \( s_{critical} \) is the critical value of the selection coefficient at which selection becomes more important than genetic drift (Neher and Shraiman 2011), has not yet been measured for rare ciliates (open question 6).
To provide estimates related to these six open questions for the rare biosphere is a major challenge for contemporary microbial ecology and population genetics. However, if the molecular techniques progress at a pace similar to that made during the past two decades, new insight into hitherto unknown processes will be gained soon. The master-piece will consist of integrating the ever faster increasing novel information into a context combining population genetics with macroecological and evolutionary theory.

CONCLUSIONS

The foregoing discussion was speculative. However, I argue that since Lindeman’s seminal paper (Lindeman 1942) and the long debate about bottom-up vs. top-down regulation of pelagic communities in the 1970s and 1980s (McQueen et al. 1986, 1989), aquatic ecologists are trapped in a view that food webs are structured primarily vertically. Intraguild, lateral effects beyond competition (the latter received wide attention by the mechanistic resource competition theory; Sommer 1989; Tilman 1977, 1982) remained largely unexplored among eukaryotes. This is significantly different in prokaryotic microorganisms where HGT has been identified as a major driver of evolutionary change and adaptation. Although there is increasing evidence that HGT is more wide spread among eukaryotes than assumed until recently (Andersson 2005; Keeling and Palmer 2008), this has little explanatory power for the existence of the rare protist biosphere. Lateral gene transfer frequently occurs in protists with endosymbiotic or phagotrophic lifestyles, which take up genetic material from their (bacterial) food (“you are what you eat”, Doolittle 1998); however, eukaryote-eukaryote HGT appears to be rare.

We may anticipate that ciliates and other protists use their diverse chemosensory abilities for yet unknown functions and interactions in the natural realm. In the era of whole genome sequencing and the various “omics” technologies (Wilmes 2012; Zaraanaindia et al. 2013) it is a safe bet that new functional genes will be detected that will enlarge and modify our current view of the various roles ciliates and other microbes play in aquatic ecosystems.

In conclusion, I postulate the following characteristic features for permanently rare ciliate species (Fig. 3): Rare ciliates have

- lower substrate affinity (i.e., higher thresholds and less steep initial slopes in Fig. 3A)
- lower growth and loss rates (Fig. 3A, B)
- less sex (Fig. 3C)
- fewer, smaller, and less connected metapopulations and, therefore, lower dispersal rates (Fig. 3B)

and

- rely more on symbionts and cooperation partners,
- are more frequently encysted, and
- experience fewer disturbances (Fig. 3D)

than more common species.

The shape of the variables and processes along the common-to-rare-continuum illustrated in Fig. 3 remains speculative. In order to advance significantly our understanding of the rare ciliate biosphere, it is imperative that these presumed seven major characteristics will be tested rigorously, following clear and falsifiable hypotheses in the near future.

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LITERATURE CITED

Agatha, S. 2011. Global diversity of aloricate Oligotrichae (Protista, Ciliophora, Spirotricha) in marine and brackish sea water. *PLoS ONE*, 6:e22466.

Alldredge, A. L. & Cohen, Y. 1987. Can microscale chemical patches persist in the sea? Microelectrode study of marine snow, fecal pellets. *Science*, 235:689–691.

Alldredge, A. L. & Silver, M. W. 1988. Characteristics, dynamics and significance of marine snow. *Prog. Oceanogr.*, 20:41–82.

Amaral-Zettler, L. A., McCliment, E. A., Ducklow, H. W. & Huse, S. M. 2009. A method for studying protistan diversity using massively parallel sequencing of V9 hypervariable regions of small-subunit ribosomal RNA genes. *PLoS ONE*, 4:e6372.

Amaral Zettler, L. A., Gómez, F., Zettler, E., Keenan, B. G., Amils, R. & Sogin, M. L. 2002. Eukaryotic diversity in Spain’s river of fire. *Nature*, 417:137.

Andersson, J. O. 2005. Lateral gene transfer in eukaryotes. *Cell Mol. Life Sci.*, 62:1182–1197.

Azam, F., Fenchel, T., Field, J., Gray, J., Meyer-Reil, L. & Thingstad, F. 1983. The ecological role of water column microbes in the sea. *Mar. Ecol. Prog. Ser.*, 10:257–263.

Bachy, C., Dolan, J., Lopez-Garcia, P., Deschamps, P. & Moreira, D. 2013. Accuracy of protist diversity assessments: morphology compared with cloning and direct pyrosequencing of 18S rRNA genes and ITS regions using the conspicuous tintinnid ciliates as a case study. *ISME J.*, 7:244–255.

Bartošová, P. & Tirjaková, E. 2008. Diversity and ecology of ciliates (Alveolata: Ciliophora) living in the bark and decaying wood mass in Slovakia. *Acta Protozool.*, 47:173–187.

Beaver, J. R. & Crismann, T. L. 1982. The trophic response of ciliated protozoans in freshwater lakes. *Limnol. Oceanogr.*, 27:246–253.

Becks, L. & Agrawal, A. F. 2010. Higher rates of sex evolve in spatially heterogeneous environments. *Nature*, 468:89–92.

Becks, L. & Agrawal, A. F. 2012. The evolution of sex is favored during adaptation to new environments. *PLoS Biol.*, 10: e1001317.

Bell, G. 1988. Sex and Death in Protozoa. Cambridge University Press, Cambridge. p. 199.

Boenigk, J., Ereshefsky, M., Hoef-Emden, K., Mallet, J. & Bass, D. 2012. Concepts in protistology: species definitions and boundaries. *Eur. J. Protistol.*, 48:96–102.

Bohonak, A. J. & Jenkins, D. G. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecol. Lett.*, 6:783–796.
Campbell, L. G. & Husband, B. C. 2005. Impact of clonal growth on effective population size in *Hymenoxys herbacea* (Asteraeae). *Hereditas*, 94:526–532.

Caron, D. A. & Countway, P. D. 2009. Hypotheses on the role of the protistan rare biosphere in a changing world. *Aquat. Microb. Ecol.*, 57:227–238.

Carrias, J. F., Cussac, M.-E. & Corbara, B. 2001. A preliminary study of freshwater protozoa in tank bromeliads. *J. Trop. Ecol.*, 17:611–617.

Chen, X., Hu, X. Lin, X., Al-Rasheid, K. A. S., Ma, H. & Miao, M. 2013. Morphology, ontogeny and molecular phylogeny of a new brackish water ciliate *Bakuella subtrophi* sp. n. (Ciliophora, Hypotrichida) from southern China. *Eur. J. Protistol.*, 49:611–622.

Chesson, P. 1994. Multispecies competition in variable environments. *Theor. Popul. Biol.*, 45:227–276.

Chesson, P. 2000a. General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.*, 58:211–237.

Chesson, P. 2000b. Mechanisms of maintenance of species diversity. *Ann. Rev. Ecol. Syst.*, 31:343–366.

Claessens, M., Wickham, S. A., Post, A. F. & Reuter, M. 2008. Ciliate community in the oligotrophic Gulf of Aqaba, Red Sea. *Aquat. Microb. Ecol.*, 53:181–190.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199:1302–1310.

Corliss, J. O. & Esser, S. C. 1974. Comments on the role of the cyst in the life cycle and survival of free-living protozoa. *Trans. Am. Microsc. Soc.*, 93:578–592.

Corno, G., Modenutti, B. E., Callieri, C., Balseiro, E. G., Bertoni, R. & Caravata, E. 2009. Bacterial diversity and morphology in deep ultraoligotrophic Andean lakes: role of UVR on vertical distribution. *Limnol. Oceanogr.*, 54:1098–1112.

Curtis, T. P., Sloan, W. T. & Scanwell, J. W. 2002. Estimating prokaryotic diversity and its limits. *Proc. Natl Acad. Sci. USA*, 99:10494–10499.

Dawson, S. & Hagen, K. 2009. Mapping the protistan ‘rare biosphere’. *J. Biol.*, 8:1–3.

Dini, F. & Nyberg, D. 1993. Sex in ciliates. *In* Jones, J. G. (ed.), Advances in Microbial Ecology, Vol. 13. Plenum Press, New York, p. 129–144.

Dolan, J. R., Montagnes, D. J. S., Agatha, S., Coats, D. W. & Stoecker, D. K. (2013) The Biology and Ecology of Tintinnid Ciliates: Descriptions of new species. *J. Protist.*, 8:1–188.

Doolittle, W. F. 1998. You are what you eat: a gene transfer model for the evolution of eukaryotic diversity and its limits. *Proc. Natl Acad. Sci. USA*, 95:11111–121.

Edgcomb, V. P. & Bernhard, J. M. 2013. Heterotrophic protists in hypersaline microbial mats and deep hypersaline basin water columns. *Life*, 3:346–362.

Edgcomb, V. P. & Pachiaudi, M. 2014. Ciliates along oxygen and niches of permanently stratified marine water columns. *J. Eukaryot. Microbiol.*, this issue, doi:10.1111/jem.12122.

Ekeland, F., Frederiksen, H. B. & Rønn, R. 2002. Population dynamics of active and total ciliate populations in arable soil amended with wheat. *Appl. Environ. Microbiol.*, 68:1096–1101.

Elloumi, J., Carrias, J.-F., Ayadi, H., Sime-Ngando, T., Boukhirs, M. & Bouaïn, A. 2006. Composition and distribution of planktonic ciliates from ponds of different salinity in the solar salt-work of Sfax, Tunisia. *Estuar. Coast. Shelf Sci.*, 67:21–29.

Fenchel, T. 2012. Protozoa and oxygen. *Acta Protozool.*, 52:11–20.

Fenchel, T. & Bernard, C. 1996. Behavioural responses in oxygen gradients of ciliates from microbial mats. *Eur. J. Protistol.*, 32:55–63.

Fenchel, T., Finlay, B. J. & Gianni, A. 1989. Microaerophily in ciliates: responses of an *Euplotes* species (Hypotrichida) to oxygen tension. *Arch. Protistenkd.*, 137:317–330.

Finlay, B. J. 2002. Global dispersal of free-living microbial eukaryote species. *Science*, 296:1061–1063.

Finlay, B. J. & Clarke, K. 1999. Apparent global ubiquity of species in the protist genus *Paraphysomonas*. *Protist*, 150:419–430.

Finlay, B. J. & Fenchel, T. 2004. Cosmopolitan metapopulations of free-living microbial eukaryotes. *Protist*, 155:237–244.

Finlay, B. J., Curds, C. R., Bamforth, S. S. & Bafort, J. M. 1987. Ciliated protozoa and other microorganisms from two African Soda Lakes (Lake Nakuru and Lake Simbi, Kenya). *Arch. Protistenkd.*, 133:81–91.

Foissner, W. 1997. Global soil ciliate (Protozoa, Ciliophora) diversity: a probability-based approach using large sample collections from Africa, Australia and Antarctica. *Biodivers. Conserv.*, 6:1627–1638.

Foissner, W. 1998. An updated compilation of world soil ciliates (Protozoa, Ciliophora), with ecological notes, new records, and descriptions of new species. *Eur. J. Protistol.*, 34:185–235.

Foissner, W. 2006. Biogeography and dispersal of microorganisms: a review emphasizing protists. *Acta Protozool.*, 45:111–136.

Foissner, W. 2007. Dispersal and biogeography of protists: recent advances. *Jpn J. Protistol.*, 40:1–16.

Foissner, W. 2008. Protist diversity and distribution: some basic considerations. *Biodivers. Conserv.*, 17:235–242.

Foissner, W. 2010. Life cycle, morphology, ontogenesys, and phylogeny of *Bremeliolithix metopoides* nov. gen., nov. spec., a peculiar ciliate (Protista, Colpodidae) from tank bromeliads (*Bromeliaceae*). *Acta Protozool.*, 49:159–193.

Foissner, W. 2013. Description of *Glaucornides bromelicola* n. gen., n. spec. (Ciliophora, Terahymenida), a macrostrom forming inhabitant of bromeliads (*Bromeliaceae*), including redescription of *Glaucorna scintillans* and *G. reniformis*. *J. Eukaryot. Microbiol.*, 60:137–157.

Foissner, W. & Wolf, K. W. 2009. Morphology and ontogenesis of *Platyphrya bromelica* nov. spec., a new macrostome-forming colpodid (*Protists*, *Ciliophora*) from tank bromeliads of Jamaica. *Eur. J. Protistol.*, 45:87–97.

Foissner, W., Agatha, S. & Berger, H. 2002. Soil ciliates (*Protozoa*, *Ciliophora*) from Namibia (Southwest Africa), with emphasis on two contrasting environments, the Etosha region and the Namib Desert. *Denisia*, 5:1–1459.

Foissner, W., Strüder-Klappe, M., van der Staay, G. W. M., Moon van der Staay, S.-Y. & Hackstein, J. H. P. 2003. Endemic ciliates (Protozoa, Ciliophora) from tank bromeliads (*Bromeliaceae*): a combined morphological, molecular, and ecological study. *Eur. J. Protistol.*, 39:365–372.

Foissner, W., Jung, J.-H., Filker, S., Rudolph, J. & Stoeck, T. 2014. Morphology, ontogeny and molecular phylogeny of *Platy nematum salinarum* nov. spec., a new scuticociliate (*Ciliophora*, *Scuticociliatia*) from a solar saltern. *Eur. J. Protistol.*, 50:174–184.

Foissner, W., Moon van der Staay, S.-Y., van der Staay, G. W. M., Hackstein, J. H. P., Krautgartner, W.-D. & Berger, H. 2004. Reconciling classical and molecular phylogenies in the stichotrichines
(Ciliophora, Spirotrichea), including new sequences from some rare species. *Eur. J. Protistol.*, 40:265–281.

Fokin, S. I. 2004. Bacterial endocytobionts of ciliophora and their interactions with the host cell. *Int. Rev. Cytol.*, 236:181–249.

Fontaneto, D. & Hortel, J. 2012. Microbial biogeography: is everything small everywhere? In: Ogivie, L. A. & Hirsch, P. R. (ed.), Microbial Ecological Theory – Current Perspectives. Caister Academic Press, Norfolk. p. 87–98.

Fraser, C., Hanage, W. P. & Spratt, B. G. 2007. Recombination and the nature of bacterial speciation. *Science*, 315:476–480.

Fuhrman, J. A., McCallum, K. & Davis, A. A. 1992. Novel major archeabacterial group from marine plankton. *Nature*, 356:148–149.

Fuhrman, J. A., Hewson, I., Schwalbach, M. S., Steele, J. A., Brown, M. V. & Naeem, S. 2006. Annually reoccurring bacterial communities are predictable from ocean conditions. *Proc. Natl Acad. Sci. USA*, 103:13104–13109.

Fujishima, M. & Kodama, Y. 2012. Endosymbionts in–paramecium. *Eur. J. Protistol.*, 48:124–137.

Futuyama, D. J. 2009. Evolution. Sinauer Associates Inc, Sunderland, MA. p. 633.

Galand, P. E., Casamayor, E. O., Kirchman, D. L. & Lovejoy, C. 2010. The structure of rare communities are predictable from ocean conditions. *Proc. Natl Acad. Sci. USA*, 106:22427–22432.

Gast, R. J., Sanders, R. W. & Caron, D. A. 2009. Ecological strategies of protists and their symbiotic relationships with prokaryotic microbes. *Trends Microbiol.*, 17:563–569.

Gast, K. J. & Kunin, W. E. 1997. Rare-common differences: an overview. In: Kunin, W. E. & Gaston, K. J. (ed.), The Biology of Rarity. Chapman & Hall, London. p. 12–29.

Gleason, F. H., Kagami, M., Lefevre, E. & Sime-Ngando, T. 2008. The ecology of chytrids in aquatic ecosystems: roles in food web dynamics. *Fungal Biol. Rev.*, 22:17–25.

Goertz, H.-D. 2010. Microbial infections in free-living protozoa. *Crit. Rev. Immunol.*, 30:95–106.

Grisebach, H.-P. & Simon, M. 1993. Limnetic macroscopic organic aggregates (lake Snow): occurrence, characteristics, and microbial dynamics in Lake Constance. *Limnol. Oceanogr.*, 38:532–546.

Gutierrez, J. C., Calejas, S., Borniquel, S., Benitez, L. & Martin-Gonzalez, A. 2001. Ciliate cryptobiosis: a microbial strategy against environmental starvation. *Int. Microbiol.*, 4:151–157.

Gutman, J., Zarka, A. & Boussiba, S. 2009. The host-range of *Paraphysoderma sedekobakensis*, a chytrid that infects Haematococcus pluvialis. *Eur. J. Phycol.*, 44:509–514.

Hirsch, P. R. & Mauchline, T. H. 2012. Mutualism: plant-microorganism interactions. In: Ogivie, L. A. & Hirsch, P. R. (ed.), Microbial Ecological Theory – Current Perspectives. Caister Academic Press, Norfolk. p. 43–55.

Holt, R. D. 1997. Rarity and evolution: some theoretical considerations. In: Kunin, W. E. & Gaston, K. J. (ed.), The Biology of Rarity. Chapman & Hall, London. p. 212–234.

Hu, X. 2014. Ciliates in extreme environments. *J. Eukaryot. Microbiol.*, this issue, doi:10.1111/jeu.12120.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton Univ. Press, Princeton, NJ.

Jonsson, P. R. 1994. Tidal rhythm of cyst formation in the rock pool ciliate *Strombidium oculatum* Gruber (Ciliophora, Oligotrichida): a description of the functional biology and an analysis of the tidal synchronization of encystment. *J. Exp. Mar. Biol. Ecol.*, 175:77–103.

Karentz, D. & Smaeyda, T. J. 1984. Temperature and seasonal occurrence patterns of 30 dominant phytoplankton species in Narragansett Bay over a 22-year period (1959-1980). *Mar. Ecol. Prog. Ser.*, 18:277–293.

Karl, D. M. 1999. A sea of change: biogeochemical variability in the North Pacific Subtropical Gyre. *Ecosystems*, 2:181–214.

Keeling, P. J. & Palmer, J. D. 2008. Horizontal gene transfer in eukaryotic evolution. *Nat. Rev. Genet.*, 9:605–618.

Kirchner, D. L., Cottrell, M. T. & Lovejoy, C. 2010. The structure of bacterial communities in the western Arctic Ocean as revealed by pyrosequencing of 16S rRNA genes. *Environ. Microbiol.*, 12:1132–1143.

Kunin, V., Engelbrektson, A., Ochman, H. & Hugenholtz, P. 2010. Wrinkles in the rare biosphere: pyrosequencing errors can lead to artificial inflation of diversity estimates. *Environ. Microbiol.*, 12:118–123.

Kunin, W. E. 1997. Introduction: on the causes and consequences of rare-common differences. In: Kunin, W. E. & Gaston, K. J. (ed.), The Biology of Rarity. Chapman & Hall, London. p. 3–11.

Kunin, W. E. & Gaston, K. J. 1983. The biology of rarity: patterns, causes and consequences. *Trends Ecol. Evol.*, 8:298–301.

Lara, E., Berney, C., Harms, H. & Chatziotis, A. 2007. Cultivation-independent analysis reveals a shift in ciliate 18S rRNA gene diversity in a polycyclic aromatic hydrocarbon-polluted soil. *FEMS Microbiol. Ecol.*, 62:365–373.

Lei, Y., Xu, K., Ki Choi, J., Pyo Hong, H. & Wickham, S. A. 2009. Community structure and seasonal dynamics of planktonic ciliates along salinity gradients. *Eur. J. Protistol.*, 45:305–319.

Lepère, C., Domaizon, I., Talib, N., Mangot, J.-F., Bronner, G., Boucher, D. & Debros, D. 2013. Geographic distance and ecosystem size determine the distribution of smallest protists in lacustrine ecosystems. *FEMS Microbiol. Ecol.*, 85:85–94.

Liesack, W. & Stackebrandt, E. 1992. Occurrence of novel groups of the domain bacteria as revealed by analysis of genetic material isolated from an Australian terrestrial environment. *J. Bacteriol.*, 174:5072–5078.

Lim, E. L., Dennett, M. R. & Caron, D. A. 1999. The ecology of *Paraphysomonas imperforata* based on studies employing oligonucleotide probe identification in coastal water samples and enrichment cultures. *Limnol. Oceanogr.*, 44:37–51.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23:399–418.

Lynch, M. & Conery, J. S. 2003. The origins of genome complexity. *Science*, 302:1401–1404.

Lynn, D. H. 2008. The Ciliated Protozoa – Characterization, Classification, and Guide to the Literature. Springer, Dordrecht. p. 605.

Ma, Z., Geng, J., Abdo, Z. & Forney, L. J. 2012. A bird’s eye view of microbial community dynamics. In: Ogivie, L. A. & Hirsch, P. R. (ed.), Microbial Ecological Theory – Current Perspectives. Caister Academic Press, Norfolk. p. 57–70.

MacArthur, R. H. & Wilson, E. O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Magurran, A. E. & Henderson, P. A. 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature*, 422:714–716.

McManus, G. B. & Santoferrara, L. F. 2013. Tintinnids in microzooplankton communities. In: Dolan, J. R., Montagnes, D. J. S., Agatha, S., Coats, D. W. & Stoecker, D. K. (ed.), The Ecology
and Ecology of Tintinnid Ciliates: Models for Marine Plankton.
John Wiley & Sons Ltd, Chichester. p. 198–213.
McQueen, D. L., Post, J. R. & Mills, E. L. 1986. Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci., 43:1571–1581.
McQueen, D. L., Johannes, M. R. S., Post, J. R., Stewart, T. J. & Lean, D. R. S. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr., 59:289–309.
Medinger, R., Nolte, V., Pandey, R. V., Jost, S., Ottenwälder, B., Schlötterer, C. & Boenigk, J. 2010. Diversity in a hidden world: potential and limitation of next-generation sequencing for surveys of molecular diversity of eukaryotic microorganisms. Mol. Ecol., 19:32–40.
Modenutti, B. E., Balseiro, E. G. & Queimadilhias, C. P. 2000. Ciliate community structure in two South Andean lakes: the effect of lake water on Ophrydium naumannii distribution. Aquat. Microb. Ecol., 21:299–307.
Modenutti, B. E., Balseiro, E. G., Callieri, C. & Bertoni, R. 2008. Light versus food supply as factors modulating niche partitioning in two pelagic microtrophic ciliates. Limnol. Oceanogr., 53:446–455.
Montagnes, D. J. S. 1996. Growth responses of planktonic ciliates in the genera Strobilidium and Strombidium: Mar. Ecol. Prog. Ser., 130:241–254.
Montagnes, D. J. S. & Berges, J. A. 2004. Determining parameters of the numerical response. Microb. Ecol., 48:139–144.
Montagnes, D. J. S., Wilson, D., Brooks, S. J., Lowe, C. & Campey, M. 2002. Cyclical behaviour of the tide-pool ciliate Strombidium oculatum. Aquat. Microb. Ecol., 28:55–68.
Moser, M. & Weisse, T. 2011. The most acidified Austrian lake in comparison to a neutralized mining lake. Limnologica, 42:303–315.
Müller, H. 2000. Evidence of dormancy in planktonic oligotrich ciliates. Verh. Internat. Verein. Limnol., 27:3206–3209.
Müller, H., Schöne, A., Pinto-Coelho, R. M., Schweizer, A. & Weisse, T. 1991. Seasonal succession of ciliates in Lake Constance. Microb. Ecol., 21:119–138.
Munawar, M. & Lynn, D. H. 2002. Planktonic ciliates of the North American Great Lakes: Lakes Superior, Huron, Erie, and Ontario. Aquat. Ecosyst. Health, 5:345–354.
Neher, R. A. & Shraiman, B. I. 2011. Genetic draft and quasi-neutrality in large facultatively sexual populations. Genetics, 188:975–986.
Nemerzut, D. R., Schmidt, S. K., Fukami, T., O’Neill, S. P., Blinski, T. M., Stanish, L. F., Knemel, J. E., Darcy, J. L., Lynch, R. C., Wickey, P. & Ferrenberg, S. 2013. Patterns and processes of microbial community assembly. Microbiol. Mol. Biol. Rev., 77:342–356.
Nowak, M. A. 2006. Five rules for the evolution of cooperation. Science, 314:1560–1563.
Obolkinia, L. A. 2006. Planktonic ciliates of Lake Baikal. Hydrobiologia, 568:193–199.
Ogilvie, L. A. & Hirsch, P. R. 2012. Microbial Ecological Theory – Current Perspectives. Caister Academic Press, Norfolk.
Oliver, A., Lilley, A. K. & van der Gast, C. J. 2012. Species-time relationships for bacteria. In: Ogilvie, L. A. & Hirsch, P. R. (ed.), Microbial Ecological Theory – Current Perspectives. Caister Academic Press, Norfolk. p. 71–85.
Olsen, G. J., Lane, D. J., Giovannoni, S. J., Pace, N. R. & Stahl, D. A. 1986. Microbial ecology and evolution: a ribosomal RNA approach. Annu. Rev. Microbiol., 40:337–365.
Ongondo, G. O., Yasindi, A. W., Oduor, S. O., Jost, S., Schagerl, M., Sonntag, B. & Boenigk, J. 2013. Ecology and community structure of ciliated protists in two alkaline-saline Rift Valley lakes in Kenya with special emphasis on Frontonia. J. Plankton Res., 35:759–771.
Orsi, W., Edgcomb, V., Faria, J., Foissner, W., Fowle, W. H., Hohmann, T., Suarez, P., Taylor, C., Taylor, G. T., Vd’Ayn, P. & Epstein, S. S. 2012. Class Cariacotricha, a novel ciliate taxon from the anoxic Cariaco Basin, Venezuela. Int. J. Syst. Evol. Microbiol., 62:1425–1433.
Packruff, G. 2000. Protozooplankton in acidic mining lakes with special respect to ciliates. Hydrobiologia, 433:157–166.
Pedrós-Alió, C. 2006. Marine microbial diversity: can it be determined? Trends Microbiol., 14:257–263.
Pomeroy, L. R. 1974. The ocean’s food web: a changing paradigm. Bioscience, 24:499–504.
Preston, F. W. 1962. Time and space and the variation of species. Ecology, 41:612–627.
Preston, F. W. 1966. The canonical distribution of commonness and rarity: part I. Ecology, 43:185–215.
Prosper, J. I., Bohannan, B. J. M., Curtis, T. P., Ellis, R. J., Firestone, M. K., Freckleton, R. P., Green, J. L., Green, L. E., Killham, K., Lennon, J. J., Osborn, A. M., Solan, M., van der Gast, C. J. & Young, J. P. W. 2007. The role of ecological theory in microbial ecology. Nat. Rev. Microbiol., 5:384–392.
Reid, A. & Buckley, M. 2011. The Rare Biosphere. American Academy of Microbiology, Washington, DC. p. 1–29.
Ridley, M. 2004. Evolution. Blackwell Science Ltd, Malden, MA. p 681.
Rosenberg, E., Koren, O., Reshef, L., Efrony, R. & Zilber-Rosenberg, I. 2007. The role of microorganisms in coral health, disease and evolution. Nat. Rev. Microbiol., 5:355–362.
Sharon, P. L. 1993. Species richness, species composition and population dynamics of protists in experimental microcosms. J. Animal Ecol., 62:711–719.
Smetacek, V. 1981. The annual cycle of protozooplankton in Kiel Bight. Mar. Biol., 63:1–11.
Smetacek, V. 1985. The annual cycle of Kiel Bight plankton: a long-term analysis. Estuaries, 8:145–157.
Sogin, M. L., Morrison, H. G., Huber, J. A., Welch, D. M., Huse, S. M., Neal, P. R., Arrieta, M. & Herndl, G. J. 2006. Microbial diversity in the deep sea and the underexplored “rare biosphere”. Proc. Natl Acad. Sci. USA, 103:12115–12120.
Sommer, U. 1985. Seasonal succession of phytoplankton in Lake Constance. Bioscience, 35:351–357.
Sommer, U. 1989. The role of competition for resources in phytoplankton succession. In: Sommer, U. (ed.), Plankton Ecology. Springer Verlag, Berlin. p. 57–106.
Sommer, U., Glivicz, Z. M., Lampert, W. & Duncan, A. 1986. The PEG model of a seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol., 106:433–471.
Sommer, U., Adrian, R., De Senerpont Domis, L. N., Elser, J. J., Gaedke, U., Ibelings, B., Jeppesen, E., Lürling, M., Molinero, J. C., Mooij, W. M., van Donk, E. & Winder, M. 2012. Beyond the Plankton Ecology Group (PEG) Model: mechanisms driving planktonic succession. Annu. Rev. Ecol. Evol. Syst., 43:429–448.
Steele, J. A., Countway, P. D., Xia, L., Vigil, P. D., Berman, J. M., Kim, D. Y., Chow, C.-E. T., Sachdeva, R., Jones, A. C., Schwab, M., Rose, J. M., Hewsom, I., Patel, A., Sun, F., Caron, D. A. & Fuhrman, J. A. 2011. Marine bacterial, archaeal and protistan association networks reveal ecological linkages. ISME J., 5:1414–1425.
Stoeck, A., Edgcomb, V. P., Orsi, W., Filker, S., Breiner, H.-W., Yakimov, M. & Stoeck, T. 2013. Evidence for isolated evolution of deep-sea ciliate communities through geological separation and environmental selection. BMC Microbiol., 13:150.
Whittaker, R. H. 1972. Evolution and measurements of species diversity. *Taxon*, 21:213–251.

Williams, P. J. L. 1981. Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kieler Meeresforsch. Sonderschr.*, 1:1–28.

Wilmes, P. 2012. Genome-based and functional differentiation: hallmarks of microbial adaptation, divergence and speciation? In: Ogilvie, L. A. & Hirsch, P. R. (ed.), Microbial Ecological Theory – Current Perspectives. Caister Academic Press, Norfolk. p. 1–23.

Woelfl, S. 2007. The distribution of large mixotrophic ciliates (Stentor) in deep North Patagonian lakes (Chile): first results. *Limnologica*, 37:28–36.

Wölf, S., Zippel, B. & Packroff, H. 1998. Planktongesellschaften der mitteldeutschen Tagebauresteuern. Deutsche Gesellschaft für Limnologie, Frankfurt, Germany. p. 376–380.

Wright, S. 1931. Evolution in Mendelian populations. *Genetics*, 16:97–159.

Wright, S. 1932. The roles of mutation, inbreeding, crossing and selection in evolution. *Int. Congr. Genetics*, 6:356–366.

Wright, S. 1938. Size of population and breeding structure in relation to evolution. *Science*, 87:430–431.

Xu, Y., Shao, C., Miao, M. & Song, W. 2013. Redescription of *Parasosporum vestita* (Kahl, 1928) comb. nov. (Ciliophora, Plagio- pylida), with notes on its phylogeny based on SSU rRNA gene. *Eu. J. Protistol.*, 49:106–113.

Yasindi, A. W. & Taylor, W. D. 2003. Abundance, biomass and estimated production of planktonic ciliates in Lakes Victoria and Malawi. *Aquat. Ecosyst. Health*, 6:289–297.

Zarraonaindia, I., Smith, D. & Gilbert, J. 2013. Beyond the genome: community-level analysis of the microbial world. *Biol. Philos.*, 28:261–282.

Zeng, Y.-X., Zhang, F., He, J.-F., Lee, S., Qiao, Z.-Y., Yu, Y. & Li, H.-R. 2013. Bacterioplankton community structure in the Arctic waters as revealed by pyrosequencing of 16S rRNA genes. *A. van Leeuwenhoek J. Microb.*, 103:1309–1319.

Zilber-Rosenberg, I. & Rosenberg, E. 2008. Role of microorganisms in the evolution of animals and plants: the hologene theory of evolution. *FEMS Microbiol. Rev.*, 32:723–735.

**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Regulation of population dynamics in idealized common vs. rare species. In common species the individual cell size and the population size are, on average, large; note that the latter can vary considerably (not shown), depending on the dynamic interplay between resource supply and growth rates (both increasing the population size) and predation and parasitism (both decreasing the population size). The competitive ability of common species is usually high. In rare species individual cell size and population size are both small and vary little, because the loss processes (predation and parasitism) are also permanently low. The competitive ability of rare species is generally low.