

Conservation of protists: is it needed at all?

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Abstract Protists have scarcely been considered in traditional perspectives and strategies in environmental management and biodiversity conservation. This is a remarkable omission given that these tiny organisms are highly diverse, and have performed as key ecological players in evolutionary theatres for over a billion years of Earth history. Protists hold key roles in nearly all ecosystems, notably as participants in fluxes of energy and matter through foodwebs that centre on their predation on microbes. In spite of this, they have been largely ignored in conservation issues due to a widespread, naive belief that protists are ubiquitous and cosmopolitanly distributed. Nevertheless, recent research shows that many protists have markedly restricted distributions. These range from palaeoendemics (Gondwanan-Laurasian distribution) to local endemics. Our ignorance about the ultimate and proximate causes of such acute disparities in scale-dependent distributions of protists can be flagged as a singular reason to preserve these more cryptic participants in ecological and evolutionary dynamics. This argument is disturbing when one considers anthropogenic modifications of landscapes and the very poorly understood roles of protists in ecological processes in soils, not least in agroecolandscapes and hydrological systems. Major concerns include host specific symbiotic, symphoric and parasitic species which become

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extinct, unseen and largely unknown, alongside their metazoan hosts; change or loss of habitats; massive change or loss of type localities; and losses of unique genetic resources and evolutionary potential. These concerns are illustrated by examples to argue that conservation of protists should be integral to any strategy that traditionally targets vascular plants and animals. The ongoing decline in research capacity to inventory and classify protist diversity exemplifies a most acute symptom of the failures, at local, national and international levels, to support scientific responses to the biodiversity crisis. Responsible responses to these severe problems need to centre on the revival of natural history as the core discipline in biology.

Keywords Biodiversity · Genetic resources · Habitat loss · Idiographic and nomothetic science · Protist protection and conservation · Type locality · Taxonomic inventories

Protist conservation and conservation values in the climate of deficient knowledge

Contrasting conservation values

The conservation of protists has not been emphasized in their own right. This paper seeks to remedy this deficiency, within the constraints of space and insufficient knowledge. Coherent arguments to conserve protists invoke aesthetic, epistemic and utilitarian themes. We describe four value systems, biased to one of these three themes. We conclude by acknowledging that each system—*aesthetic, biophilic, ecosystem goods and services, evolutionary potential*—focuses a node interlinking an encompassing argument in support of protist conservation. The profile of a conservation strategy for protists awaits very overdue reception by human society. Several actions await attention which needs to be considered by conservation biologists and environmental managers, without further neglect.

Questions that centre on conservation of selected biota and/or landforms invoke arguments whose compatibility is not always recognized. One such distinct school of thought is underpinned by aesthetic values we hold about the natural world, and what is now called biodiversity. It is epitomized by what Aldo Leopold called the “wilderness ethic” (Meine and Knight 1999). Such aesthetic values extend to practical actions and activities in which environments and biodiversity are managed toward aesthetically based goals (Meffe et al. 1997). Aesthetically based conservation values also equate closely with biophilia (Wilson 1984).

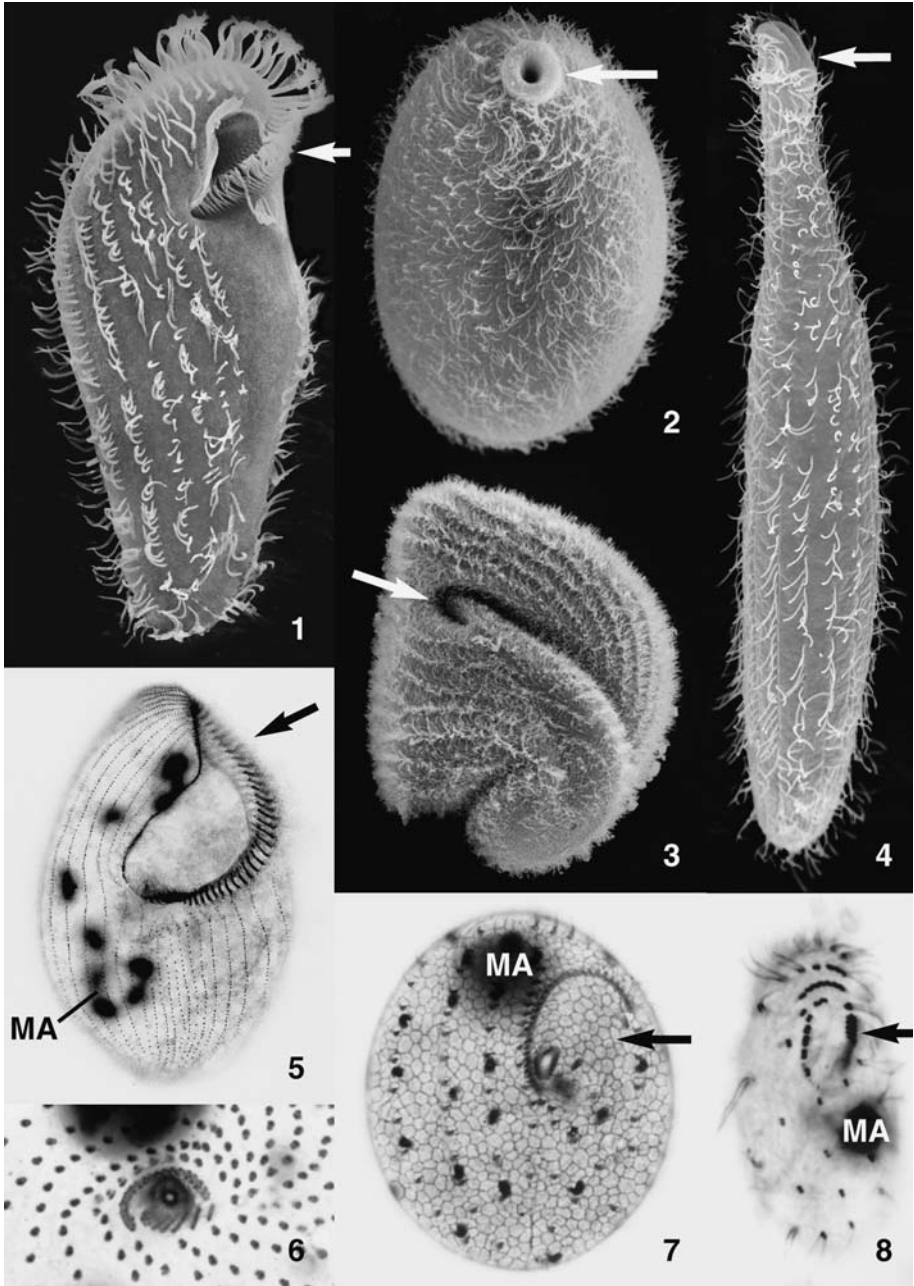
The second argument for conservation is considered more practicable, and is invariably seen to be at odds with any aesthetic-based school. This second school argues that conservation be moulded to maintain more utilitarian values of the environment that benefit humankind primarily (Western and Pearl 1989; Heywood and Watson 1995). It is epitomized by the concepts and arguments developed in ecological economics (Smith 1996) and centres on the values of ‘ecosystem goods and services’ (Westman 1977; Arrow et al. 1995; Baskin 1997; Costanza et al. 1997; Tilman et al. 1997). Its protagonists argue that demands by socio-economies on the ecological goods and services necessary to sustain humans and our activities (as interacting participants in the biosphere) overrule any argument to preserve a species, habitat or ecological landscape solely on any perceived aesthetic values. The ecosystem goods and services argument shares many similarities with the ‘use it or lose it’ arguments for sustainable utilization of biology, and especially biodiversity prospecting (Janzen 1993, 1998).

A third school of values motivating biodiversity conservation is also underpinned by an aesthetic argument. We term this the “biophilia” school. Its protagonists value particular groups of organisms, rather than biodiversity and environment per se. Although, this biophilia school is founded on aesthetic rationales, it extends to more academic interests in biodiversity and biology. At its more superficial, biophilia manifests in people’s identification with ‘flagship species’ (Figs. 1–8). Likewise, its aficionados spend millions on what is popularly called the petshop trade. It also manifests in the private and professional lifetimes of scientists who devote considerable resources to research and know their favourite organisms intimately. Biophilia expresses in the profound satisfaction, and values, founded in the detailed knowledge gained by lifetimes of studies of organisms and the natural world. These manifest as focused studies of selected taxa, a deeply professed fascination with, for example, ants (Holl Dobler and Wilson 1994) and protists (Kreutz and Foissner 2006). Such infatuations with the natural history of organisms, which we identify with this biophilic school, most certainly embrace conservation values placed on protists (Kreutz and Foissner 2006). This might indeed have been barely developed, considering the multifarious attractiveness of protists. The aesthetics resplendent in the astounding morphological variety of these minute organisms (especially in all their superb details revealed by modern technology) matches those of larger, more charismatic organisms.

For consider the aesthetic enjoyment aroused by paging through superb colour or scanning electron micrographs of protists, resplendent in the diversity of their translucent adaptations to microcosmic environments (Figs. 1–8). We venture to suggest that only a truly sad human being would not share in such biophilic experiences?! Biophilia is indeed characterized by marked individualism frequently based in passionate affinities for particular organisms, epitomized by the orchid cognoscenti (Hansen 2000). Nevertheless, it is a mistake to overlook the social, political and economic profundity represented in biophilia. It motivates lifetimes of research commitments, and is equally expressed when its aficionados are roused to conservation action.

Even so, economic and anthropocentric practicalities in conservation biology can sideline aesthetic and biophilic arguments, and confine any argument for protist conservation firmly in the ecosystem goods and services school. This introduces questions pertaining to ‘What do protists do in ecosystems?’ Such questions extend further to flesh out an evolutionary dimension to the ecosystem goods and services school. This deeper perspective on conservation values characterises the fourth school—termed ‘evolutionary potential’. This is structured by robust knowledge of the evolutionary history of biodiversity. In this context, questions and decisions in conservation biology employ knowledge which elucidates where and when species and clades evolved, and their relative abilities to persist in ecosystems altered by disturbances. The rationale of the evolutionary potential singles out clades and regions that exhibit phylogenetic uniqueness (Vane-Wright et al. 1991), and evolutionary vibrancy (Erwin 1991). A major argument for biodiversity conservation is founded on asymmetries of phylogenetic diversity (Faith 1994; Faith and Walker 1996; Faith and Trueman 2001). Equally important attention is demanded of what Erwin (1991) termed ‘evolutionarily vibrancy’. Taxa that form the rapidly evolving tips of phylogenetic trees, invariably represent the species rich, bushy clades that formed through recent radiations. It is these evolutionarily vibrant clades that can be expected to maintain the evolutionary potential to ride out environmental perturbations. These are better disposed to maintaining the performance of ecosystems than older, more phylogenetically distinctive, but less speciose clades (Erwin 1991).

Clades and species that score highly against both these criteria constitute prime candidates for conservation. More practicably, conservation actions should maintain the ecological



◀ **Figs. 1–8** Examples of soil ciliate flagship species with, likely, restricted geographic distributions. Both, scanning electron microscopy (1–4) and silver impregnation (5–8) were used for the identification of the ciliates. These methods reveal finest features and are thus indispensable in modern ciliate taxonomy. Arrows mark mouth area. MA – macronucleus **1:** So far, *Sauidithrix terricola*, an about 270 μm long, highly characteristic stichotrich ciliate, has been found only in field soil from Saudi Arabia and China (from Berger et al. 2006). **2:** *Enchelydium blattereri* was discovered in floodplain soil from Australia. This conspicuous species, which belongs to the haptorid gymnostomes, has a length of about 240 μm and a highly characteristic oral bulge (from Foissner et al. 2002). **3:** This is a not yet described colpodid flagship from a green river bed (an ephemeral part of the Chobe River which becomes a savannah during the dry season) in Botswana, Africa. It has a length of about 300 μm and is distinctly spiralized. **4:** A not yet described, about 200 μm long *Spathidium* (haptorid gymnostome) from soil of the Galapagos Islands. **5:** A not yet described, about 250 μm long heterotrich ciliate from soil of a mangrove forest in Venezuela. This species, which belongs to the genus *Condylotomides*, is a flagship because it is large and green due to countless cortical granules. **6:** *Fungiphrya strobli* is a functional flagship that belongs to the obligate mycophagous colpodids. So far, this species has been found only in soil from the Table Mountain in Cape Town, Republic of South Africa. The unique oral apparatus is recognizable in the centre of the micrograph. It comprises a semicircular undulating membrane on the upper margin of the oral area and seven short adoral ciliary rows on the lower margin of the oral area. Between undulating membrane and adoral ciliary rows, there is a black circle with a bright centre, which is the $\sim 2 \mu\text{m}$ long feeding tube, used to penetrate fungal hyphae and to transport their contents into the ciliate (from Foissner 1999a). **7:** *Apocolpodidium (Phagoon) macrostoma* is only 50 μm long, but conspicuous due to the huge oral apparatus with a semicircular undulating membrane. As yet, this species has been found only in soil from the Everglades of Florida, USA (from Foissner et al. 2002). **8:** *Pseudokreyella etoschensis* was discovered in the Etosha Pan, Namibia. Although it is only 20 μm long, it is a morphological flagship due to the complex somatic and oral ciliary pattern (from Foissner et al. 2002)

integrity of the biomes and habitats in which these organisms have evolved. Any measure of evolutionary potential requires a robust phylogeny of any biodiversity indicators that serves to identify landscapes with high phylogenetic uniqueness (Brooks and McLennan 2002). Thus, phylogenies of protists are critical to apply scientific criteria to distinguish clades and habitats that possess reservoirs of evolutionary potential most likely to accommodate environmental disturbances.

So far we have outlined four arguments to justify conservation of protists. These invoke reasons and values grounded in four schools: the aesthetic, ecosystem goods and services, biophilia, and evolutionary potential. We argue that the answers to conservation problems reside largely in the details of the biodiversity we seek to manage, and we conclude that an ecological, utilitarian imperative, based in maintaining ecosystem services, does not constitute the singular reason to justify conservation of protists. In fact, our argument for protist conservation is built on profound matters of aesthetics and knowledge. If any such argument purports to be scientifically informed, then its conservation actions and plans cannot escape strictures imposed by all four value systems. Before discussing conservation values of protists any further, we need to acknowledge our state of knowledge of biodiversity and protists.

Biodiversity science, knowledge of protists and the taxonomic impediment

It cannot be overemphasized that many microbial assemblages have escaped discovery, let alone description (Margulis et al. 1986; Wall 1999). In all respects, our species' habitual overlooking of microorganismal biodiversity can be termed the "problem writ large" afflicting appreciation and cognisance of protists. It especially impacts on perceptions of their conservation importance. The plight of microorganisms, especially protists, is an apt example of taxonomic chauvinism and methodological challenges that bias the biodiversity sciences (Pawar 2003). These deficiencies magnify the importance of arguments that endorse investments in systematic biology founded on natural history (Cracraft 1996, 2002),

to rectify the Taxonomic Impediment (Hoagland 1996; Foissner 1999b; Cresswell and Bridgewater 2000; Cotterill 2002; Wheeler 2004). Any such discussion encounters acute uncertainties, with answers to such debate grounded (and indeed ubiquitously weakened) by deficiencies in our knowledge. What we continue to discover about protists highlights the conclusions of Donoghue and Alverson (2000) that biology is challenged by a new age of discovery.

Conservation decision-making pivots on understanding how the biota will respond to stresses and disturbances of ecosystems. In this respect, our knowledge of any biota (a species or an assemblage) ranges from the poor to non existent, no matter our scale of enquiry. Our ignorance of biodiversity dynamics reflects on glaring gaps in our knowledge, which extend from genes to ecosystems. In this respect, two aspects especially weaken conservation decisions. One, we have a very incomplete knowledge of where species occur in the biosphere. Two, the idiographic intricacies (unique facts) pertaining to species' natural history are known only for very few species, mostly angiosperms and vertebrates, and some parasites of humans and our domesticates. So we can only guess at how even the most common organisms influence ecological processes. As summarized by Wall (1999) for the ecology and biota of soil, what we think we might know about roles of protists in the biosphere exemplifies acute inadequacies of this knowledge, in all its multifariousness. Our ignorance is highlighted by recent discoveries of the phylogenetic and functional diversity of marine microbes (Moreira and López-García 2002; Gross 2007), and notably of protists along hydrothermal vents (Moreira and López-García 2003). These extreme magnitudes of undiscovered biodiversity constitute an especially pertinent example, given this essay's focus on conservation of the underappreciated microscopic realms of life! They raise many questions, not least pertaining to roles of marine protists in these hyperdiverse foodwebs. We repeat that considered in the context of how little we know about protists, these microscopic examples emphasize how biology is challenged by a new age of discovery (Donoghue and Alverson 2000).

Similarly to bacterial biodiversity, too few researchers have commented on conservation issues couched in anything approaching a protist-centric perspective! This contrasts against the mushrooms (macrofungi) for which a vast local and global literature exists (Hawksworth 1991). Thus, with few exceptions (Wells et al. 1983; Foissner 1994; Mann and Droop 1996; Staley 1997; Rondon et al. 1999), conservation of protists awaits attention in Red Data books, let alone focused scientific discussion. We suggest that a significant reason for this neglect is the widespread belief that most, or even all, protists exhibit a cosmopolitan distribution. Despite very poor biogeographic data, this belief has fostered sweeping statements that no protist can possibly be endangered (Finlay et al. 1996). Yet, evaluation of actual data (reviewed in Foissner 2006, 2007, and this issue) reveals that up to a third of protists have restricted distributions. These range from palaeoendemics (Laurasian and Pangaea endemics) to species exhibiting a highly local endemism. These spatially-nested patterns of endemism constitute a singular reason, in their own right, to place protists as a central concern in conservation biology, debate and policy.

Recently, the biotechnological potential of protists has been recognized. The genetic and metabolic diversity of protists represents a rich source of valuable compounds, such as omega-3 fatty acids, pigments, polymers and enzymes (Kiy 1997; Beck 2002; Hausmann et al. 2003). When considered against the framework of the hugely under explored diversity of protists (see below), we conclude that biodiversity prospecting of these microorganisms has barely been inaugurated.

According to Corliss (2000), a grand total of at least 213,000 protist species have been described, of which about 113,000 are fossil forms. However, Corliss (2000) included in

his estimation only few of the 130,000 described fungi (Hawksworth 2001). Corliss (2000) emphasized that his figures are likely gross underestimates: “On the basis of personal communication with many protistologists, I am obliged to draw the conclusion that, for numerous groups, vast numbers of unique protists do await description. Perhaps we have only scratched the surface regarding the biodiversity of these organisms”.

We agree! Furthermore, preliminary surveys of genetic diversity of protists point to significant levels of cryptic species that have been overlooked (Von der Heyden and Cavalier-Smith 2005; Scheckenbach et al. 2006). While there are likely 1.5 million fungal species, with ~130,000 (~9%) described (Hawksworth 2001) and up to 40,000 free-living ciliate species, of which only 4,500 (~11%) have been described (Foissner et al. this issue). The global magnitude of eukaryotic diversity likely encompasses 20 million arthropods alone; this is a conservative estimate, combining global estimates of insects (Stork 1997) with arachnids (Andre et al. 1994; Behan-Pelletier and Newton 1999).

Now, what do these statistics imply for the global diversity of protists? In contrast to the widespread belief that free-living protists are uninteresting and of little ecological significance, research through the past 20 years has shown that most eukaryotic biodiversity consists of protists (Hausmann et al. 2003). Protists are of great importance in all ecosystems, for instance, as producers of oxygen and, in microbial foodwebs, they are critical to fluxes of energy and matter through ecosystems (Fenchel 1987; Foissner 1987; Sorokin 1999). Furthermore, beyond important model organisms, most protists of epidemiological concern remain poorly known (Palmer et al. 1998; Beck 2002; Hausmann et al. 2003). It follows that the global diversity of protists approximates tens of millions of species, but this inference of global protist diversity needs further qualification. We argue that any such assessment of global protist diversity is challenged to incorporate two potentially significant determinants. Both reflect on the ecological opportunities open to adaptive radiations of protists since the Proterozoic (Cavalier-Smith 2006). One relates to the geomorphological extent and complexity of soil habitats available to protists. The second involves coevolutionary opportunities, and pertains to all the multicellular hosts potentially available to single celled eukaryotes. The significance of both determinants is enhanced by the fractal structuring of ecological resources available to protists at microscopic and mesoscopic spatial scales.

So firstly, we point out (as argued by Richter and Markewitz 1995) that the depths and complexities of soils and their biodiversity are still being bottomed (Andre et al. 1994). This especially applies to where ever deep regolith (Clarke 2003) supports microbes to depths of tens and hundreds of metres below the surface (as in tropical landscapes). These considerations obviously cannot exclude groundwater, especially in granitic and karstic landscapes. We ask what are the implications of such spatial complexity, inherent compartmentalized, in these subterranean landscapes, for protist diversity? How does such geomorphological complexity—at these fine-grained fractal dimensions—influence protist habitats, especially given the magnitudes of microbial biodiversity already discovered at these depths?

Secondly, we ask the same questions of the fine-grained habitats represented in the guts and tissues of multicellular organisms, which are even more compartmentalized than those in soil and regolith. Consider, furthermore, that these microbial and protist habitats, distributed within and amongst the Eucarya, are principally allopatric; because the diversity of these lineages has been parsed into tens of millions of extant species, each of which exhibits a unique evolutionary trajectory. Clearly, the extent and complexity of these subterranean and commensal resources, available to protists, present fertile research fields centred in protistology. Any such study of these significant regions of the biosphere is challenged

to elucidate the ecological and evolutionary dynamics entailed in fluxes of matter and turn-overs of organisms at these fine-grained micro- and meso-scales. Complementary questions and research challenges pertain to how ecological resources are divided up in underground landscapes and amongst multicellular organisms, respectively. We anticipate that this complexity of geomorphological and commensal niches has exercised profound controls on the evolution of protist diversity. It cannot be overemphasized the research challenges pertaining to these frontiers of ignorance are critical to understand and manage the biosphere, and especially geomorphological, edaphic and hydrological processes.

So far we have sketched out four significant arguments why protists cannot continue to be excluded, but need to become focal concerns in conservation plans and actions. In summary, these encompass: the biotechnology argument with respect to biodiversity prospecting (the importance of properties of protists in basic and applied science); their ecological roles in foodwebs; the restricted distributions—and thus overlooked endemism—of many species; and above all, the pervasive inadequacy of knowledge, especially considered in the light of inferred magnitudes of global biodiversity, and the microscopic complexity of protist habitats across the biosphere. This framework of our argument sets the stage to move on, and consider additional, major concerns bearing on the conservation of protists.

Major issues in protist conservation

At least one protist species becomes extinct with each metazoan lost to extinction

Our argument for greatly underestimated protist diversity highlights the significance of rates of speciation and extinction among multicellular organisms. Most higher animals (Metazoa) are associated with at least one host specific symbiotic, symphoric or parasitic protist species; often they host several or even many. Accordingly, the number of endangered or extinct species is at least twice as high as generally assumed; mycologists assume a rate of 1:6, that is, on average, six fungal species are found on each species of plant (Hawksworth 1991). For instance, more than 50 specific ciliate species were discovered on and in water beetles in the surroundings of the town of Erlangen, Germany (Matthes and Guhl 1975). In Austria, as elsewhere, such investigations are rare, but 60 out of the 127 species of water beetles known from Austria are endangered (Wewalka 1984), together with their specific ciliates. This situation parallels that in crustaceans and fish, which host a rich diversity of protists, many of which are still undescribed species. Specialized habitats in structurally complex landscapes are not only confined to soil and underlying regolith; for recently new species of ciliates were described in microhabitats supported within bromeliads. These specialized protists represent previously overlooked clades of protists endemic to Neotropical forest (Foissner 2002; Foissner et al. 2003). Wholesale losses of such specialized plant habitats would simultaneously extinguish the less obvious biodiversity they support.

Considered at a global scale, these examples point to an alarming trend, because most potential hosts never have been systematically investigated for protists; whilst those that were associated with already extinct host species are lost for ever. Unfortunately, this situation will persist in the near future because alpha-taxonomists are themselves threatened by extinction (Ziegler et al. 1997; Cotterill 2002). The losses of natural science collections and taxonomic expertise is caused by their neglect, and failures to appreciate the values of capacity building in these principal foundations of the biodiversity sciences. The continued

neglect of taxonomic resources equates to the losses of irreplaceable information in the Alexandrian libraries, but is perhaps more insidious (Cotterill 1997, 1999, 2002).

Change or loss of habitats

Disturbance and loss of habitats threaten not only plants and animals, but also protists which are sensitive indicators of environmental changes (Foissner 1987; Foissner et al. 1995; Lange-Bertalot 1997). Of special concern is the devastation and loss of rain forests, where many groups of protists are heavily under-researched, both in limnetic and terrestrial habitats. This deficiency becomes obvious when one looks at the earth's biodiversity hotspots, where 44% of all species of vascular plants and 35% of species in four vertebrate groups (birds, reptiles, amphibians, mammals) are found (Fig. 9): most hotspots are rain forests in the tropics and subtropics. This figure further highlights our drastic ignorance of protist diversity and biogeography. With the partial exception of the Mediterranean Basin, no or very sparse data are available on ciliates and many other protist groups from these hotspots.

Moreover, rain forests are not the only concern with respect to protist conservation; for consider important ecosystems in moderate climates, notably peatlands and bog ponds which contain highly specific and diverse protist assemblages. These have been investigated for ciliates only in Europe, but remain poorly known, pertinently across Asia. Kreutz and Foissner (2006) found about 800 protist species in a few *Sphagnum* ponds in the surroundings of the town of Constance, Germany. At least of these 100 species were undescribed, mainly amoebae and ciliates, and some of the undescribed species might be local endemics. Thus, Kreutz and Foissner (2006) concluded that this unique area be protected by law. A similar situation is known from European diatoms: most of the 417 oligo- or slightly mesotraphentic taxa are members of the "Red list" because oligotrophic and dystrophic habitats are especially prone to disturbance (Lange-Bertalot 1997).

Other poorly explored habitats are agroecolandscapes and groundwaters which are threatened by pollution and pesticide application (Foissner 1987; Novarino et al. 1994; DeLeo and Baveye 1997). We doubt whether anyone has extended the concept of biological

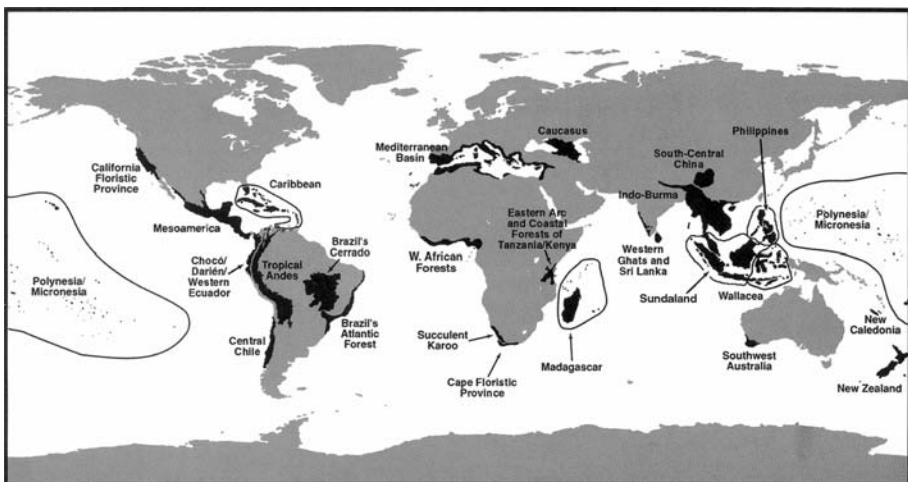


Fig. 9 The 25 biodiversity hotspots (after Myers et al. 2000)

magnification to consider possibilities of the accumulation of inorganic pollutants or residual pesticides in protists!

Loss of type localities

The type locality is the site where a previously unknown organism was first discovered and described for the first time; it is critical to taxonomy as the geographical place of capture or collection of the name-bearing type of a nominal species or subspecies. The extinction or massive habitat change of the type locality of a species by anthropogenic activities is always a great scientific loss for any described taxa it represents. Such losses of biodiversity are magnified in scale dependent manner in the case of protistology, because most protists are difficult to preserve, and precise resampling from the type locality is often required to solve taxonomic problems. For example, Nilsson (1986) was only able to recognize a new species of African *Stentor* after comparing it with a similar species resampled in Austria.

Moreover, protist type localities are not only threatened by such local destruction of habitats, but also by massive environmental changes. A pertinent example is the testate amoeba *Diffugia biwae*, a supposed local endemic of Lake Biwa in Japan. It was discovered in 1918 but disappeared in the 1980s, likely due to the heavy eutrophication of the lake (Ichise et al. 2004). Although, fortunately, it has been found recently in some lakes in China (Yang and Shen 2005), the genetic status of these geographically isolated populations awaits elucidation.

Loss of unique genetic resources

Protists are the ancestors of plants and animals (Cavalier-Smith 2006). It is unknown how well these tiny organisms fared in the global extinction crises that decimated biodiversity, notably the events that characterize the Permian-Triassic and Cretaceous-Tertiary boundaries, when up to 96% of biodiversity disappeared (Wilson 1989; Hallam and Wignall 1997). Persistence of many protist organization types and species through such long periods of geological time is likely the main reason for their great diversity. Thus, protists are not only important for understanding evolution of life, but also represent a unique reservoir of genetic peculiarities. Among others, three examples include: the dual genome of ciliates and some foraminiferans; the absolute strand polarity in kinetoplastid flagellates; and the unique nuclear apparatus of the Dinoflagellates (Puytorac et al. 1987; Hausmann et al. 2003; McGrath and Katz 2004).

The threats to any of the major suites of unique adaptations exhibited among protists (some mentioned above) appear insignificant, assuming it is unlikely that a whole clade will be driven to extinction by human activities. Nevertheless, local endemics may constitute exceptions to this generalization, and especially for monotypic and/or taxa that are very locally confined. This is exemplified by the plight of the curious soil fungus *Geosiphon pyriforme*. Although *G. pyriforme* is of almost macroscopic size (1–2 mm) and known since 1915, a region in the Spessart Mountains (Germany) remains its only known natural habitat (Schuessler and Kluge 2000). Usually, however, the genetic variation of individual species and, especially, of populations within species is threatened. Indeed, in micro-organisms (emphasizing the significance attached to losses of type localities) the destruction of a single small pool may cause the loss of unique genetic variation for ever, because such a pool might represent the entirety of the biodiversity represented by a specific protist genotype or morphotype (Mann and Droop 1996; Lange-Bertalot 1997; Shayler and Siver 2004).

The conservation relevance of protist biodiversity and evolutionary history

Deep and shallow evolutionary history of protists

Knowledge of the evolutionary relationships among protists is still hampered severely by lack of primary inventory data; for we can only guess at how many deeply unique species and clades of protists await formal discovery by taxonomists. Nevertheless, according to the evolutionary and ecology theory on which the biodiversity sciences are structured (Erwin 1991; Heywood and Watson 1995; Ormond et al. 1997; Reaka-Kudla et al. 1997; McKinney and Drake 1998), what we do know about the evolutionary history of protists reveals that they exhibit key credentials, which elevates their pertinence in considerations of evolutionary potential. Considered in light of the incidence of local endemics, protists appear to be comprised of at least some evolutionarily vibrant clades, with these speciose bushes rooted deep in geological time. Humanity would be wise to maintain all such evolutionary potential biodiversity in all its representativeness within protected area systems, and especially within landscapes managed according to the principles of ecosystem management. This especially applies to agroecolandscapes, drainage systems, and reservoirs of groundwater (Brooks and McLennan 2002).

Deep earth history, protists, and the evolution of predation

The deepest origins of protists extend beyond the Precambrian well into the Proterozoic (Cavalier-Smith 2006). Tantalizing questions arise as to when the first protists appeared on Earth's early continents, and began to prey on microbes. For this event constituted an evolutionary threshold in its own right, for it marked the origin of predation with all its associated complexities of coevolution (Bengtson 2002). This profound importance of protists in Earth history, and thus our study of it, gains a most intimate immediacy when we consider the origins of *Homo* in the context of parasitism and predation. Brain (1981) argued that exposure to predation was a significant agent that acted on the diversification of hominids in Neogene Africa. Moreover, our ancestors not only evolved in environments rich in vertebrate predators of primates, because *Homo* has interacted persistently with particular protozoa, namely *Plasmodium* and *Trypanosoma*. These two genera present as dominant parasites of *H. sapiens* today. Massive investments in research, toward their control, can only benefit from an evolutionary perspective (Lambrecht 1985). Yet, the literature too rarely reflects an appreciation of coevolutionary history we share with our parasites, nor the benefits of centering such study on a scaffolding of hominid evolution.

Nevertheless, a caveat must be emphasized here in how we conceptualize such evolutionary patterns. As with any taxa that we like to conceptualize as basal (Krell and Cranston 2004; Jenner 2006; Jenner and Wills 2007), and in absence of superbly preserved fossils, the attributes of ancestral protists will always remain subjects of intrigue. This situation is reinforced when we acknowledge the highly derived richness of adaptations exhibited amongst the morphologies and life histories of those relatively few protists known to science.

As inaugurated by Gause (1934), free-living protists and their prey present a rich resource to study coevolutionary dynamics. As importantly, it is postulated that ancestral protozoans invaded the plethora of habitats now exploited by parasites and mutualists, which include the organs and tissues of primates and all other vertebrates. This immense richness of ecological interactions and coevolutionary associations that are centred on free-living protists constitute the benchmarks against which to judge our idiographic discoveries,

and construct nomothetic generalisations. This cornucopia of biodiversity that has evolved in fine-grained patches across landscapes, at microscopic scales through deep geological time, presents 21st biologists with rich opportunities in comparative biology and parasitology. Biologists have barely begun to conceptualize these arenas of opportunity, yet alone explore them.

The origins of predation constitutes yet another sound argument for why we are behoven to keep rich assemblages of protists around for a little while longer in a biosphere that we humans increasingly exploit and change. We reiterate that protist-microbe assemblages constitute one of the deepest and richest legacies of coevolution; presumably they originated on the biosphere's oldest continents. It follows that vestiges of their ancient diversity persist across all continents descended from Laurasia and Gondwana, and indeed the latter's progenitors such as Rodinia. The scientific tools available to study these complexities of evolutionary history continue to improve rapidly. The rapid developments demonstrated in microbial genomics (Venter et al. 2003, 2004; Eisen 2007; Gross 2007) can greatly augment studies of protist taxonomy and ecology challenged to tease out autecologies, morphologies and life histories of the actual organisms.

We predict that surveys of the genomic and functional diversity of protists and their prey will especially benefit from shotgun-sequencing strategies (Venter et al. 2003, 2004; Eisen 2007). Nevertheless, any such genetic inventory methods are challenged to survey the complexity of eukaryote genome. Recent discoveries in protist taxonomy have highlighted organisms with respect to their unusual morphological adaptations, so these stand out as 'flagships' (Foissner 2006). It is fascinating to consider how much we stand to learn from more comprehensive and thorough inventories that collate knowledge of protist natural history in idiographic detail, and integrate these characterizations of their properties into generalizations detailing genomic and organismal trends in protist biology. It is important to emphasize that these discoveries and their formal description (cited above by Foissner) represent the efforts of a sole researcher challenged to inventory the immense diversity of soil ciliates, distributed across the fine-scaled patches that constitute the world's protist habitats. It cannot be overemphasized that these discoveries of the organismal diversity resplendent in protists have barely even begun, considering the richness of unexplored habitats. It is especially important to acknowledge how very little is known about any adaptations, ancient and derived, of protists in all their genomic, biochemical and physiological intricacies.

Protists and the taxonomic impediment: natural history as the fundamental life science

It is most unfortunate that too few scientists distinguish between the idiographic and nomothetic properties of a science (Ghiselin 1997; Jenner and Wills 2007); and that all sciences are built on idiographic knowledge (unique particulars) which, when assembled to reveal sufficient patterns, allow us to derive nomothetic (law like) generalizations. For this dichotomy is mutualistic, and underpins the growth and integrity of knowledge, especially in the life sciences. Unfortunately a widespread failing among biologists is to ignore and denigrate these so called descriptive sciences that provide theorists and experimenters with primary knowledge in the form of idiographic details. Inadequate idiographic coverage in a discipline hamstring nomothetic synthesis. We reiterate that the acute lack of knowledge (constrained primarily by the Taxonomic Impediment) afflicts all aspects of protist biology. This constraint on generation of idiographic knowledge is an especially acute example of a pervasive hindrance to scientific progress. Stated bluntly, it is impossible to derive nomothetic generalizations when

one has too few idiographic facts. Clearly, major deficiencies need to be rectified in how science is taught and supported to rectify a most serious crisis in biology, and especially the biodiversity sciences.

These deficiencies in scientific policy and capacity especially hamstringing any policy and/or actions tasked to apply scientific knowledge of protists to their conservation. Our knowledge of the biology of protists will only advance from intensive inventories and field studies of these microorganisms across the world's habitats. Mandatory research actions in a global conservation strategy for protists need to place a premium on the development of these inventories. This can be optimally structured in a nested sampling design that targets representative habitats across continents. This research can borrow existing tactics and techniques from established initiatives and biodiversity research programmes, notably the All-Taxa-Biota Inventories (ATBIs), especially where they target commensals and parasites of multicellular organisms. In this respect, Wheeler (1995, 2004) advocated a combination of ATBIs and ABTIs (All-Biota-Taxonomic Inventories), which we suggest can be adapted to the challenges of protist inventories. Above all, the arguments of Herman (2002) and Schmidly (2005) especially apply to the plight of protist biology; for there is no better example than protistology for why biology has to return to teaching and support of natural history as the *sine qua none* of the biodiversity sciences. Until this situation is improved radically, it will remain very difficult, if not impossible, to study and monitor protist biodiversity.

Protist taxonomy and conservation: the future

Several interlinked threads of argument deserve reiteration. This essay has rallied evidence to scope out a conservation strategy that targets protists throughout the biosphere. It is grounded in an infallible utilitarian-based argument for protist conservation, where benefits of biodiversity centre “on potable water, clean air and fertile soils” (Gee 1992, p. 639). The persistence, resilience and resistance of biodiversity ultimately hinges on whether the integrity of ecosystems is maintained: across forests, savannahs, wetlands and agroecolandscapes, and especially the underlying regolith in which critical edaphic and hydrological processes occur. Only at their peril, can biology and society continue to ignore the diversity of protists in these landscapes, in all their intimate ecological dynamics as predators and mutualists. The integrity of soil ecosystems is founded on their processing of nutrients and matter across microscopic and mesoscopic scales. These and more encompassing ecological processes confer critical ecosystem services (Carson 1962; Daily 1997). These benefits of protist-microbial ecology and evolution are by no means confined only to terrestrial soils, but are equally important in hydrological processes. The very existence of this coevolutionary legacy remains very poorly appreciated, let alone researched, even though it has persisted in oceans and on continents since the Proterozoic. We can only guess at what we might learn about coevolution (with spin offs to understanding disease) from research that focuses on foodwebs involving protist predators and parasites in aquatic, marine and terrestrial habitats.

An immediate step toward remedying our global ignorance of protists, given their significance, is to embrace the research objectives of bold initiatives that emphasize the inventory and description of biodiversity as focal activities in 21st century biology. These were inaugurated in Systematics Agenda 2000 (1994) and subsequent initiatives (Wheeler 1995, 2004; Hoagland 1996; Foissner 1999b; Cresswell and Bridgewater 2000; Cotterill 2002). We single out contributions of the All-Species Foundation toward biotic inventory and taxonomy, which pivot on providing an on line compendium of biodiversity information.

Knowledge of each species is consolidated in a webpage to optimize the efforts of a very inadequate taxonomic workforce, and highlights its pivotal importance to all society (Wilson 2003; Kirkland-Berger 2005). An achievable goal is to collate all such information about the world's described protists: with salient aspects of the natural history of each species graphically depicted on web pages. Such an on line library of biodiversity will serve several integrated purposes. One is to highlight the diversity of protists in all their aesthetic attributes. As committed taxonomists, we are convinced that the success and persistence demanded of the scholarly study of biodiversity is best fostered at a young age; and we agree with Wilson (1984) that a deep-seated biophilia inaugurates the growth of such skills. What more apt subject for aspiring biologists than the study of protists? Such a synopsis of knowledge about protists and their biology (preserved in natural science collections, Cotterill 2002) serves as the foundation for 21st century researchers to investigate ecological and evolutionary questions, and solve conservation problems.

It is sad to consider that the infrastructure to research the natural history of protists is declining to extinction, largely driven by forces of ignorance. We can no longer allow such neglect and ignorance to isolate the appreciation and study of protists and their remarkable adaptations from exciting developments in 21st century science. Conservation of protists should obviously be integrated into environmentally sound systems of ecosystem management. Any such activity hinges on scientific monitoring of the biodiversity it seeks to conserve. It will continue to be impossible to monitor the integrity of protist diversity in any such habitat so long as institutions and nations continue to suffer from the near universal lack of expertise and commitments to survey and identify these organisms.

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References

- Andre HM, Noti M-I, LeBrun P (1994) The soil fauna: the last biotic frontier. *Biodivers Conserv* 3:45–56
- Arrow K, Bolin B, Costanza R et al (1995) Economic growth, carrying capacity, and the environment. *Science* 268:520–521
- Baskin Y (1997) *The work of nature: how the diversity of life sustains*. Island Press, Washington DC
- Beck E (eds) (2002) *Faszination Lebenswissenschaften*. Wiley-VCH, Weinheim
- Behan-Pelletier V, Newton G (1999) Linking soil biodiversity and ecosystem function – the taxonomic dilemma. *Bioscience* 49:149–153
- Bengtson S (2002) Origins and early evolution of predation. In: Kowalewski M, Kelley PH (eds) *The fossil record of predation*. The Paleontological Society Papers 8. The Paleontological Society, pp 289–317
- Berger H, Al-Rasheid KAS, Foissner W (2006) Morphology and cell division of *Saudithrix terricola* n. gen., n. sp., a large, stichotrich ciliate from Saudi Arabia. *J Eukaryot Microbiol* 53:260–268
- Brain CK (1981) *The hunters or the hunted? An introduction to African cave taphonomy*. Univ Chicago Press, Chicago
- Brooks DR, McLennan DA (2002) *The nature of diversity: an evolutionary voyage of discovery*. Univ Chicago Press, Chicago
- Carson R (1962) *Silent spring*. Houghton Mifflin Co., Boston
- Cavalier-Smith T (2006) Cell evolution and earth history: stasis and revolution. *Phil Trans R Soc B* 361:969–1006
- Clarke JDA (2003) The limits of regolith: a planetary scale perspective. In: Roach IC (eds) *Advances in regolith*. CRC, LEME, pp 74–77

- Corliss JO (2000) Biodiversity, classification, and numbers of species of protists. In: Raven PH, Williams T (eds) Nature and human society. The quest for a sustainable world. National Academy Press, Washington, pp 130–155
- Costanza R, d'Arge R, de Groot R et al (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260
- Cotterill FPD (1997) The Second Alexandrian Tragedy, and the fundamental relationship between biological collections and scientific knowledge. In: Nudds JR, Pettitt CW (eds) The value and valuation of natural science collections. Geological Society, London, pp 227–241
- Cotterill FPD (1999) Toward exorcism of the ghost of W.T. Thistleton-Dyer: a comment on “overduplication” and the scientific properties, uses and values of natural science specimens. *Taxon* 48:35–39
- Cotterill FPD (2002) The future of natural science collections into the 21st century. Conferencia de clausura. In: Actas del I Simposio sobre el Patrimonio Natural en las Colecciones Públicas en España (Vitoria, 25–27 Septiembre 2001). Departamento de Cultura, Diputación Foral de Alava, Vitoria, pp 237–282
- Cracraft J (1996) Systematics, biodiversity science, and the conservation of the Earth's biota. *Verh Dt Zool Ges* 89:41–47
- Cracraft J (2002) The seven great questions of systematic biology: an essential foundation for conservation and sustainable use of biodiversity. *Ann Miss Bot Gard* 89:127–144
- Cresswell ID, Bridgewater P (2000) The global taxonomic initiative – quo vadis? *Biol Int* 38:12–16
- Daily GC (1997) Nature's services: societal dependence on natural ecosystems. Island Press, Washington DC
- DeLeo PC, Baveye P (1997) Factors affecting protozoan predation of bacteria clogging laboratory aquifer microcosms. *Geomicrobiol J* 14:127–149
- Donoghue MJ, Alverson WS (2000) A new age of discovery. *Ann Miss Bot Gard* 87:110–126
- Eisen JA (2007) Environmental genome shotgun sequencing: its potential and challenges for studying the hidden world of microbes. *PLoS Biol* 82:384–388
- Erwin TL (1991) An evolutionary basis for conservation strategies. *Science* 253:750–752
- Faith DP (1994) Genetic diversity and taxonomic priorities for conservation. *Biol Conserv* 68:69–74
- Faith DP, Trueman JWH (2001) Towards an inclusive philosophy for phylogenetic inference. *Syst Biol* 50:331–350
- Faith DP, Walker PA (1996) How do indicator groups provide information about the relative biodiversity of different sets of areas? On hotspots, complementarity and pattern-based approaches. *Biodivers Lett* 3:18–25
- Fenchel T (1987) Ecology of protozoa. Springer, Berlin and Tokyo
- Finlay BJ, Corliss JO, Esteban G et al (1996) Biodiversity at the microbial level: the number of free-living ciliates in the biosphere. *Q Rev Biol* 71:221–237
- Foissner W (1987) Soil protozoa: fundamental problems, ecological significance, adaptations in ciliates and testaceans, bioindicators, and guide to the literature. *Prog Protistol* 2:69–212
- Foissner W (1994) Kommentar zur Gefährdungssituation der Einzeller (Protozoa). In: Gepp J (ed) Rote Listen gefährdeter Tiere Österreichs, Band 2. Moser, Graz, pp 317–319
- Foissner W (1999a) Description of two new, mycophagous soil ciliates (Ciliophora, Colpodea): *Fungiphrya strobli* n. g., n. sp. and *Grossglockneria ovata* n. sp. *J Eukaryot Microbiol* 46:34–42
- Foissner W (1999b) Protist diversity: estimates of the near-imponderable. *Protist* 150:363–368
- Foissner W (2002) Morphology and ontogenesis of *Bromeliophrya brasiliensis* gen. n., sp. n, a new ciliate (Protozoa: Ciliophora) from Brazilian tank bromeliads (Bromeliaceae). *Acta Protozool* 42:55–70
- Foissner W (2006) Biogeography and dispersal of micro-organisms: a review emphasizing protists. *Acta Protozool* 45:111–136
- Foissner W (2007) Dispersal and biogeography of protists: recent advances. *Jpn J Protozool* 40:1–16
- Foissner W, Xu K (2007) Monograph of the Spathidiida (Ciliophora, Haptoria). Volume II: Spathidiidae and Pharyngospathidiidae. Monographiae biol (in preparation)
- Foissner W, Berger H, Blatterer H et al (1995) Taxonomische und ökologische Revision der Ciliaten des Saprobien-systems - Band IV: Gymnostomatea, *Loxodes*, Suctorina. Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft 1/95:1–540
- 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, Strueder-Kypke M, van der Stay GWM et al (2003) Endemic ciliates (Protozoa, Ciliophora) from tank bromeliads (Bromeliaceae): a combined morphological, molecular and ecological study. *Eur J Protistol* 39:365–372
- Gause GF (1934) The struggle for existence. Williams and Wilkins, Baltimore
- Gee H (1992) The objective case for conservation. *Nature* 357:639
- Ghiselin MT (1997) Metaphysics and the origin of species. State Univ New York, New York

- Gross L (2007) Untapped bounty: sampling the seas to survey microbial biodiversity. *PLoS Biol* 85:371–376
- Hallam A, Wignall P (1997) Mass extinctions and their aftermath. Oxford Univ Press, Oxford
- Hansen E (2000) Orchid fever: a horticultural tale of love, lust and lunacy. Pantheon Books, New York
- Hausmann K, Hülsmann N, Radek R (2003) Protistology. Schweizerbart, Berlin Stuttgart
- Hawksworth DL (2001) The magnitude of fungal diversity: the 1.5 million species estimate revisited. *Mycol Res* 105:1422–1432
- Herman SG (2002) Wildlife biology and natural history: time for a reunion. *J Wildl Manage* 66:933–946
- Heywood VH, Watson RT (1995) Global biodiversity assessment. Cambridge Univ Press, Cambridge
- Hoagland KE (1996) The taxonomic impediment and the convention on biodiversity. *ASC News* 24:61–62, 66–67
- Holldobler B, Wilson EO (1994) Journey to the ants: a story of scientific exploration. Harvard Univ Press, Cambridge, MA
- Ichise S, Morita T, Wakabayashi T et al (2004) Disappearance and its past distribution of the endemic protista *Diffflugia biwae* Kawamura, 1918 in lake Biwa, Central Japan. *Rep Shiga Pref Inst Pub Health & Environ Sci* 39:57–63 (in Japanese)
- Janzen DH (1993) Taxonomy: universal and essential infrastructure for development and management of tropical wildland biodiversity. In: Sandlund OT, Schei PJ (eds) Norway/UNEP expert conference on biodiversity. NINA, Trondheim, pp 100–113
- Janzen DH (1998) Gardenification of wildland nature and the human footprint. *Science* 279:1312–1313
- Jenner RA (2006) Unburdening evo-devo: ancestral attractions, model organisms, and basal baloney. *Dev Genes Evol* 216:385–394
- Jenner RA, Wills MA (2007) The choice of model organisms in evo-devo. *Nat Rev Genet* 8:311–319
- Kirkland-Berger J (2005) Mission possible: All-Species Foundation and the call for discovery. *Proc Calif Acad Sci Suppl* 56:114–118
- Kiy T (1997) Biotechnology of Protozoa. In: Abstracts of the 10th international congress of protozoology, Sydney
- Krell F-T, Cranston PS (2004) Which side of the tree is more basal? *Syst Entomol* 29:279–281
- Kreutz M, Foissner W (2006) The *Sphagnum* ponds of Simmelried in Germany: a biodiversity hot-spot for microscopic organisms. *Protozool Monogr* 3:1–267
- Lambrecht FL (1985) Trypanosomes and hominid evolution. *Bioscience* 35:640–646
- Lange-Bertalot H (1997) A first ecological evaluation of the diatom flora in Central Europe. Species diversity, selective human interactions and the need of habitat protection. *Lauterbornia* 31:117–123
- Mann DG, Droop SJM (1996) Biodiversity, biogeography and conservation of diatoms. *Hydrobiologia* 336:19–32
- Margulis L, Chase D, Guerrero R (1986) Microbial communities: invisible to the scrutiny of naturalists, most microbial communities have escaped description. *Bioscience* 36:160–170
- Matthes D, Guhl W (1975) Systematik, Anpassungen und Raumparasitismus auf Hydrophiliden lebender operculariformer Epistyliden. *Arch Protistenk* 117:110–186
- McGrath CL, Katz LA (2004) Genome diversity in microbial eukaryotes. *Trends Ecol Evol* 19:32–38
- McKinney ML, Drake JA (eds) (1998) Biodiversity dynamics: turnover of populations, taxa and communities. Columbia Univ Press, New York
- Meffe G, Contributors (1997) Principles of conservation biology, 2nd edn. Sinauer Press, Sunderland
- Meine C, Knight RL (1999) The essential Aldo Leopold: quotations and commentaries. Univ Wisconsin Press, Wisconsin
- Moreira D, López-García P (2002) The molecular ecology of microbial eukaryotes unveils a hidden world. *Trends Microbiol* 10:31–38
- Moreira D, López-García P (2003) Are hydrothermal vents oases for parasitic protists? *Trends Parasitol* 19:556–558
- Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Nilsson JR (1986) The African heterotrich ciliate, *Stentor andreseni* sp. nov., and *S. amethystinus* Leidy. *Biol Skr Dan Vid Selsk* 27:1–43
- Novarino G, Warren A, Kinner NE et al (1994) Protists from a sewage-contaminated aquifer on Cape Cod, Massachusetts. *Geomicrobiol J* 12:23–36
- Ormond RFG, Gage JD, Angel MV (1997) Marine biodiversity: patterns and processes. Cambridge Univ Press, Cambridge
- Palmer SR, Soulsby L, Simpson DIH (1998) Zoonoses: biology, clinical practice, and public health control. Oxford Univ Press, Oxford
- Pawar S (2003) Taxonomic chauvinism and the methodologically challenged. *Bioscience* 53:861–864
- Puytorac P de, Grain J, Mignot J-P (1987) Précis de protistologie. Boubée et Fondation Singer Polignac, Paris

- Reaka-Kudla ML, Wilson DE, Wilson EO (1997) Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington DC
- Richter DD, Markewitz D (1995) How deep is soil? *Bioscience* 45:600–609
- Rondon MR, Goodman RM, Handelsman J (1999) The Earth's bounty: assessing and accessing soil microbial diversity. *Trends Biotechnol* 17:403–409
- Scheckenbach F, Wylezich C, Mylnikov AP et al (2006) Molecular comparisons of freshwater and marine isolates of the same morphospecies of heterotrophic flagellates. *Appl Environ Microbiol* 72:6638–6643
- Schmidly DJ (2005) What it means to be a naturalist and the future of natural history at American universities. *J Mammal* 86:449–456
- Schuessler A, Kluge M (2000) *Geosiphon pyriforme*, an endocytobiosis between fungus and cyanobacteria, and its meaning as a model system for arbuscular mycorrhizal research. In: Hock B (ed) *The Mycota*, vol 9. Springer, Berlin, pp 151–161
- Shayler HA, Siver PA (2004) Description of a new species of the diatom genus *Brachysira* (Bacillariophyta), *Brachysira gravida* sp nov from the Ocala National Forest, Florida, USA. *Nova Hedwigia* 78:399–409
- Smith F (1996) Biological diversity, ecosystem stability and economic development. *Ecol Econ* 16:191–203
- Sorokin YI (1999) Aquatic microbial ecology. Backhuys Pub, Leiden
- Staley JT (1997) Biodiversity: are microbial species threatened? *Comment. Curr Opin Biotechnol* 8:340–345
- Stork N (1997) Measuring global biodiversity and its decline. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) *Biodiversity II: understanding and protecting our biological resources*. Joseph Henry Press, Washington DC, pp 41–68
- Systematics Agenda 2000 (1994) *Systematics Agenda 2000. Charting the biosphere*. Technical report. Amer Mus Nat Hist, New York
- Tilman D, Naeem S, Knops J et al (1997) Biodiversity and ecosystem properties. *Science* 278:1866–1867
- Vane-Wright RI, Humphries CJ, Williams PH (1991) What to protect?—Systematics and the agony of choice. *Biol Conserv* 55:235–254
- Venter JC, Levy S, Remington K et al (2003) Massive parallelism, randomness and genomic advances. *Nat Genet* 33:219–227
- Venter JC, Remington K, Heidelberg JF et al (2004) Environmental genome shotgun sequencing of the Sargasso Sea. *Science* 304:66–74
- Von der Heyden S, Cavalier-Smith T (2005) Culturing and environmental DNA sequencing uncover hidden kinetoplastid biodiversity and a major marine clade within ancestrally freshwater *Neobodo designis*. *Int J Syst Evol Microbiol* 55:2605–2621
- Wall DH (1999) Soil biodiversity – life in soil. In: Cracraft J, Grifo F (eds) *The living planet in crisis: biodiversity science and policy*. Columbia Univ Press, New York, pp 124–128
- Wells SM, Pyle RM, Collins NM (1983) *The IUCN invertebrate red data book*. Gresham Press, Old Woking, Surrey, UK
- Western D, Pearl M (1989) *Conservation for the twenty-first century*. Oxford Univ Press, Oxford
- Westman WE (1977) How much are nature's services worth? *Science* 197:960–964
- Wewalka G (1984) Rote Liste der gefährdeten Schwimmkäfer Österreichs (Dytiscidae, Coleoptera). In: Gepp J (ed) *Rote Listen gefährdeter Tiere Österreichs*, 2nd edn. BM Gesundheit und Umweltschutz, Wien, pp 123–126
- Wheeler QD (1995) Systematics, the scientific basis for inventories of biodiversity. *Biodivers Conserv* 4:476–489
- Wheeler QD (2004) Taxonomic triage and the poverty of phylogeny. *Phil Trans Roy Soc Lond* 359:571–583
- Wilson EO (1984) *Biophilia: the human bond with other species*. Harvard Univ Press, Cambridge MA
- Wilson EO (1989) Bedrohung des Artenreichtums. *Spektrum der Wissenschaft* 11:88–95
- Wilson EO (2003) Encyclopedia of life. *Trends Ecol Evol* 18:77–80
- Yang J, Shen Y (2005) Morphology, biometry and distribution of *Diffugia biwae* Kawamura 1918 (Protozoa: Rhizopoda). *Acta Protozool* 44:103–111
- Ziegler W, Bode H-J, Mollenhauer D et al (1997) *Biodiversitätsforschung. Ihre Bedeutung für Wissenschaft, Anwendung und Ausbildung. Fakten, Argumente und Perspektiven*. Kleine Senckenberg-Reihe 26:1–68