Biodivers Conserv (2008) 17:393–405
DOI 10.1007/s10531-007-9257-4

ORIGINAL PAPER

The diversity and distribution of diatoms: from cosmopolitanism to narrow endemism

Pieter Vanormelingen · Elie Verleyen · Wim Vyverman

Received: 28 February 2007 / Accepted in revised form: 20 June 2007 / Published online: 12 October 2007

Abstract It has been claimed that microbial taxa will not exhibit endemism because their enormous populations remove dispersal as an effective constraint on geographical range. Here we review evidence that challenges this ubiquity hypothesis for the most speciose group of microbial eukaryotes, the diatoms. Detailed taxonomic inventories using fine-grained morphological characteristics, molecular markers, and crossing experiments have revealed that the geographic distribution of diatoms ranges from global to narrow endemic. Records of human-mediated introductions of exotic species further provide a strong indication that geographic dispersal was limiting in the past. Finally, recent studies have revealed that diatom community structure and diversity are influenced by geographical factors independent of environmental conditions. Diatom communities are thus regulated by the same processes that operate in macro-organisms, although possibly to a different degree, implying that dispersal limitation is significant and the endemism observed in isolated areas is real. These results underscore the pressing need to (1) continue research into diatom biology, ecology and the factors driving diatom species diversity and geographic distributions, and (2) protect relatively isolated areas against further introductions of exotic species.

Keywords Biogeography · Diatoms · Dispersal · Diversity · Endemism · Macroecology · Microorganisms · Ubiquity hypothesis

Introduction

The diversity and taxonomic composition of local communities result from a balance between processes operating on a regional scale, such as allopatric species formation and geographic dispersal, which both add species to communities, and processes capable of

Special Issue: Protist diversity and geographic distribution. Guest editor: W. Foissner.

P. Vanormelingen · E. Verleyen · W. Vyverman (✉)
Laboratory Protistology & Aquatic Ecology, Gent University, Krijgslaan 281 S8, 9000 Gent, Belgium
e-mail: Wim.Vyverman@UGent.be

promoting local extinction, including predation, competitive exclusion, and stochastic variation (Ricklefs 1987). While it is generally accepted that these processes shape the distribution and community diversity of macroscopic organisms (Leibold et al. 2004; Cox and Moore 2005), considerable controversy has arisen about their importance for microscopic organisms (<1 mm; Whitfield 2005; Green and Bohannan 2006; Martiny et al. 2006). According to advocates of the ubiquity hypothesis (Finlay 2002), the vast population sizes of micro-organisms drive ubiquitous dispersal (Baas-Becking 1934) and make local extinction virtually impossible (Fenchel and Finlay 2004). Geographic isolation is therefore absent and as a result, allopatric speciation should be rare or non-existent, which would explain the perceived low global morphospecies diversity of microbial eukaryotes (Finlay 2002). Evidence supporting the ubiquity hypothesis comes from high local to global morphospecies ratios for various groups of photosynthetic and heterotrophic protists (Finlay and Clarke 1999; Finlay and Fenchel 2004) and the maintenance of consistent patterns of local abundance or rarity on a global scale (Finlay and Clarke 1999; Finlay 2002). In contrast, various recent studies suggest that micro-organisms, like macro-organisms, do display restricted geographic ranges, as recently outlined in the moderate endemicity model (Chao et al. 2006; Foissner 2006). Evidence supporting this model includes observations on the allopatric divergence of cyanobacteria and archaea in hot springs (Papke et al. 2003; Whitaker et al. 2003), foraminifera occurring in the polar oceans (Darling et al. 2004, 2007), and fungi on a continental scale (Taylor et al. 2006). In addition, a positive correlation between habitat size and bacterial diversity (Bell et al. 2005; Reche et al. 2005), distinct soil ciliate faunas on different continents (Chao et al. 2006), and distance-decay relationships in microbial eukaryotes (Green et al. 2004) have been observed.

Diatoms are one of the most successful contemporary groups of photosynthetic eukaryotic micro-organisms. They inhabit almost any kind of aqueous environment, and can also occur as endosymbionts in dinoflagellates and foraminifers (Round et al. 1990). They have global significance in biogeochemical cycles, and provide 20–25% of globally fixed carbon and atmospheric oxygen (Mann 1999). Their hallmark is an intricately shaped and ornamented silica cell wall called the frustule, which provides a wealth of ultrastructural characters on which diatom classification is largely based (Round et al. 1990). As for most other groups of microscopic organisms however, remarkably little is as yet known about diatom biology, ecology, and the factors driving diatom species diversity and geographic distributions (Mann 1999; Chepurnov et al. 2004).

Below, we review diatom species diversity and biogeography. We start with a concise description of the current state of diatom species taxonomy, and how this influences our understanding of diatom species diversity and its spatial structuring. Next, we consider three lines of research which, taken together, draw a more subtle picture of diatom diversity and biogeography than that proposed by the ubiquity hypothesis. These are (1) assessments of the geographic distribution of diatom genera and species based on dedicated, fine-grained morphological investigations, sometimes in combination with molecular and crossing data; (2) well-documented accounts of human-mediated introductions, and (3) estimates of the relative influence of spatial and environmental factors in determining diatom community structure and diversity on multiple geographic scales. Finally, we highlight important areas for future research on diatom biogeography.

Problems with diatom species taxonomy

As in many protist groups, diatom species taxonomy is notoriously messy (see Mann 1999 for a detailed review). This is mainly because taxon delineation has been (and still is) almost exclusively based on morphological features of the siliceous cell wall, without a full understanding of the underlying causes of morphological variation patterns. As a result, the description of new species has sometimes been based on morphological differences between allopatric populations which are purely phenotypic (Cox 1995). This can lead to the perception that species have restricted geographic distribution patterns. For example, the marine planktonic diatoms *Thalassiosira gravida* Cleve and *T. rotula* Meunier were originally considered to be two distinct species, the former being restricted to high latitudes and the latter to lower latitudes (Hasle 1976). Culture experiments showed however that valve morphology changes from typical *T. rotula* to typical *T. gravida* with decreasing temperature (Syvertsen 1977). Other examples of such taxonomic redundancy are given by Mann (1999). In addition, the gradual reduction in size associated with the diatom life cycle, can lead to pronounced changes in valve morphology (Round et al. 1990). During the 20th century, these findings led to a strong tendency to regard most morphological variability as purely phenotypic. The widely (i.e., globally) used European freshwater diatom floras of Hustedt (1927–1966) and Krammer and Lange-Bertalot (1986–1991) were strong advocates of this idea, and applied wide species boundaries. In addition, the use of these floras in non-European localities led to 'force-fitting' of diatom taxa to 'European' names (Tyler 1996). Lumping and force-fitting had severe consequences for our understanding of the ecology, diversity, and distribution of diatoms, as it not only stretched the morphological boundaries of many species, but also reinforced the idea that most diatom species have cosmopolitan distributions and are ecologic generalists (Kociolek and Spaulding 2000).

During the last decades however, it has become clear that subtle, discontinuous morphological variation patterns, which were hitherto assumed to be of no taxonomic significance, are instead generally correlated with variation in reproductive, molecular-genetic, physiological, and ecological characters (see review by Mann 1999 and references therein; Behnke et al. 2004; Beszteri et al. 2005; Créach et al. 2006; Lundholm et al. 2006; Amato et al. 2007). These studies suggest that many diatom species contain several subtly distinct, semi-cryptic entities that are worth taxonomic recognition at the species level, and that, as a consequence, diatom species diversity has been severely underestimated rather than overestimated. The actual global diversity of diatoms may therefore be an order of magnitude higher than the current number of described species, with up to 200,000 extant species (Mann and Droop 1996). Almost at the same time as these findings, the lumping trend among 'alpha taxonomists' has been halted and even reversed. In the Iconographia Diatomologica series (edited by Lange-Bertalot) alone, >1400 new diatom taxa have been described since 1995, many of which were previously regarded to be part of a morphological continuum within a single species. Importantly, it remains to be shown whether the application of a fine-grained taxonomy will result in range-splitting or ecological differentiation rather than merely increasing global species diversity.

The geographic distribution of diatoms: from cosmopolitan genotypes to endemic phenotypes

Under-sampling of suitable habitats and regions, and under-reporting of rare taxa are a real and severe problem for biogeographical studies of microscopic organisms and can lead to

underestimation of the geographic ranges of species (Lee and Patterson 2000; Finlay et al. 2002), even if diatom taxa have been well revised or when multimethod approaches are used. However, both phenomena will have a negligible effect if (1) biogeographic studies focus only on habitats that fulfill the environmental requirements of the taxa under investigation, (2) sample sizes are sufficiently large, and (3) the study taxa are locally abundant, making it less likely that they are overlooked elsewhere (assuming there is a close correlation between local and global abundance, Finlay et al. 2002). If these conditions are fulfilled and the species under consideration has consequently turned up in numerous samples, while its distribution is still found to be restricted to a small area, then its endemism is fairly certain (or at least its absence in the other investigated regions).

Phenotype-based approach: flagship taxa and fine-grained morphology

Morphology-based approaches to diatom biogeography can be used provided that published data are reviewed critically and intercalibrated. Given the fact that many descriptions and illustrations of 'difficult' species do not allow unambiguous evaluation of literature data, it is imperative that only conspicuous, easily recognizable taxa are dealt with, the so-called 'flag-ship' taxa (Tyler 1996; Foissner 2006). An alternative is to make a careful new morphological analysis of species in samples from different geographical regions in a single large-scale study, thereby by-passing the need for comparisons with previously published data (Chao et al. 2006). Below, we provide examples of morphologically well-studied, often conspicuous taxa for which there is strong evidence that they have restricted distributions.

While most of the >900 diatom genera are cosmopolitan (Fourtanier and Kociolek 2003), there are some notable exceptions. *Eunophora* (Eunotiophycidae; Fig. 1), a highly distinctive diatom genus comprising at least four species, was described by Vyverman et al. (1998) from Tasmania and New Zealand where it is a widespread and often abundant component of benthic diatom communities in oligo- to dystrophic lakes (Vyverman et al. 1995; Vanhoutte et al. 2006). There are no other reports of similar diatoms from the Northern Hemisphere, where a large number of studies on the benthic diatom flora of similar lakes have been conducted within the framework of coordinated international projects on the effects of acidification and eutrophication (PIRLA, Camburn et al. 1984–1986; SWAP, Stevenson et al. 1991; and EDDI, available on http://craticula.ncl.ac.uk/Eddi/jsp/, databases). Likewise, a query among over 700 diatomists via the diatom listserver (http://www.indiana.edu/~diatom/diatom.html) so far failed to reveal the presence of the genus outside Tasmania and New Zealand, implying that undersampling is of minor importance here. Another conspicuous diatom taxon which appears to display a restricted biogeographical range is the genus *Veigaludwigia* which was introduced by Rumrich et al. (2000) to accommodate two naviculoid species from southern Chile, viz. *Navicula urbana* and *N. willeri* (Krasske 1939), which are uniquely characterized by distinct internal small knobs on the valve face margin (Fig. 2). The genus has now been found in southern South America, Australia, and New Zealand (Vyverman et al. 1995 and unpublished; Villanueva and Maidana 1999; Flower 2005; Vanhoutte et al. 2006). Importantly, most of these studies were the first surveys for their regions, and inevitably involved only a limited number of samples, yet none failed to find *Veigaludwigia*, showing that undersampling and underreporting is not an issue. Notwithstanding the fact that northern temperate regions have been much more thoroughly investigated, *Veigaludwigia* has not yet been found there.

Recent revisions of selected diatom genera at the (morpho)species level corroborate these findings. A recent overview of the genus *Stauroneis* in the Antarctic and sub-Antarctic region (867 samples) and a careful comparison with earlier studies from the Arctic (500

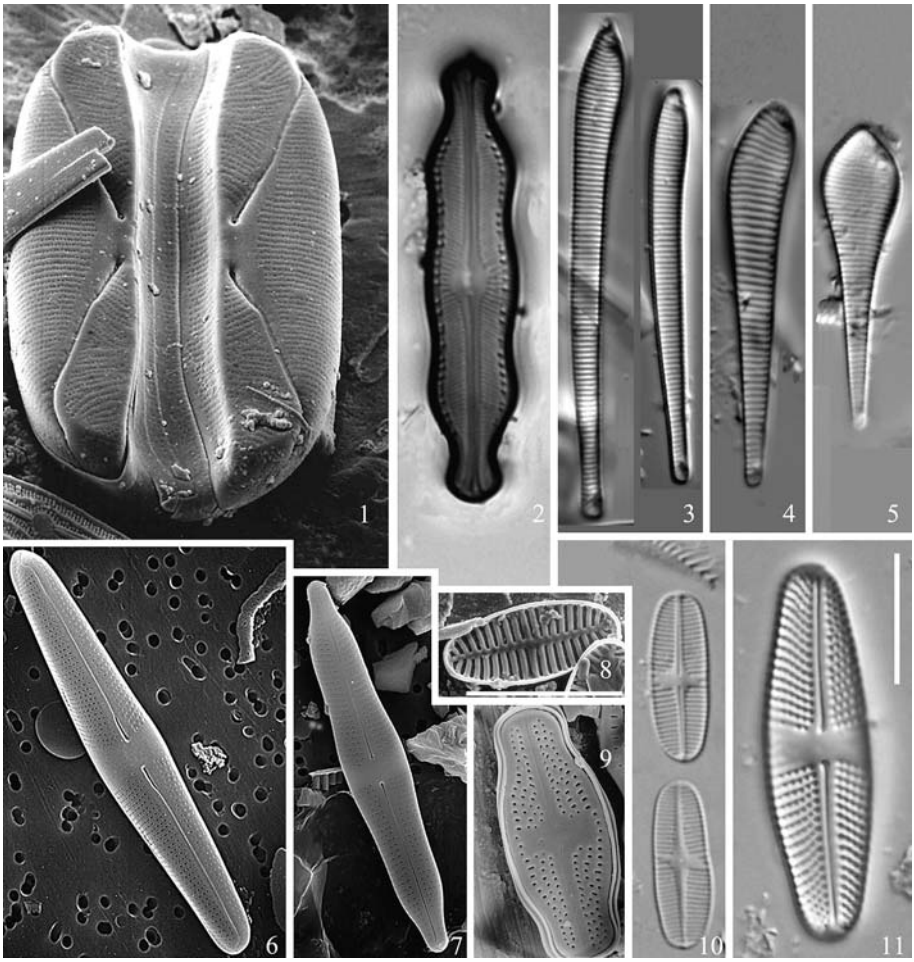

Fig. 1–11 Selected freshwater diatoms endemic to (parts of) the Southern hemisphere. (1) *Eunophora*, a diatom genus with a geographical distribution restricted to freshwater bodies in Tasmania and New Zealand. (2) *Veigaludwigia*, a diatom genus restricted in distribution to temperate regions of the Southern hemisphere. (3) *Actinella pulchella*, endemic to Australia (Tasmania) and New Zealand. (4) *Actinella aotearoaia*, endemic to Australia and New Zealand. (5) *Actinella comperei*, thus far only found in one lake in Tasmania. (6, 7) *Stauroneis* species endemic to the sub-Antarctic islands in the Indian Ocean, viz., *S. pseudomuriella* and *S. pseudosmithii*. (8–11) Diatom species characteristic of the Antarctic region, viz., *Planothidium quadripunctatum*, *Luticola muticopsis*, *Psammothidium abundans*, and *Achnanthes taylorensis*. Figures 3–4, 5, 6–7 and 8–11 were reprinted with permission from Sabbe et al. (2001), Sabbe et al. (2000), Van de Vijver et al. (2004), and Sabbe et al. (2003) respectively. All figures are on the same scale except Fig. 8. Scale bars, 10 μm

samples) revealed the presence of different *Stauroneis* floras in both regions (Van de Vijver et al. 2005; Figs. 6–7). In fact, out of a total of 59 species, only five were common to both regions. This agrees with other recent findings that the Arctic and Antarctic freshwater diatom floras have hardly any species in common (Spaulding and McKnight 1999). Not surprisingly, the five common *Stauroneis* species are recorded from all over the world. Moreover, the distribution of *Stauroneis* species is also restricted within the sub-Antarctic region: the *Stauroneis* flora from the Indian Ocean islands was quite different from that of

other sub-Antarctic islands. Although based on a more limited number of samples, similar restricted distribution patterns appear to be present in the genera *Actinella* (Sabbe et al. 2000, 2001) and *Muelleria* (Spaulding et al. 1999), and possibly also *Biremis* (Vyverman et al. 1997), *Fragilariforma* (Kilroy et al. 2003), *Gomphonema* (Kociolek et al. 2004), and *Kobayasiella* (Vanhoutte et al. 2004). In *Actinella*, most of the 43 species appear to be restricted to the Southern Hemisphere, viz. tropical South America (mainly Amazon basin, 18 spp.), sub-Saharan Africa (11 spp.), or the Australasian region (9 spp.), some of which are extremely abundant in acidic freshwater habitats (Sabbe et al. 2001; Figs. 3–5). Only three species occur in Europe, and only two *Actinella* species have as yet been recovered from different continents (namely *Actinella punctata* and *A. brasiliensis*). The genus *Muelleria* is restricted to the high latitudes of the Northern and Southern hemisphere and of the 15 species recorded, all but two are restricted to one of both hemispheres (Spaulding et al. 1999). A floristic and taxonomic survey of the diatom communities in 66 freshwater and saline lakes in three regions in continental eastern Antarctica revealed that at least 40% of the species recovered from one of the regions, the Larsemann Hills, were unknown outside Antarctica (Sabbe et al. 2003; Figs. 8–11). In meltwater streams in the McMurdo Dry Valleys, 60% of the diatoms encountered were taxa only known from Antarctica (Esposito et al. 2006). In a survey of 897 diatom samples across the United States, many gomphonemoid diatoms which were carefully morphologically examined are restricted to the eastern or western United States (Kociolek and Kingston 1999). Also, many examples can be given of species from other genera which are restricted to small geographic areas (Potapova and Charles 2002).

In marine environments, a careful morphological analysis of the Thalassonematiaceae (86 samples from all over the world) revealed that of the few species occurring in temperate to cold waters, one has a cosmopolitan distribution, one is restricted to the northern hemisphere and two others to the Southern Ocean (Hasle 2001). The remaining species are restricted to warmer waters where they may be widespread.

In conclusion, an increasing number of studies based on critical, fine-grained morphological analyses are in favor of the prevalence of restricted distribution patterns among diatom species. At a higher taxonomic level little evidence is found for endemism as, apart from a few convincing exceptions, diatom genera are cosmopolitan. At first glance, this contrasts sharply with macro-organisms where entire genera and even families are often endemic and might be viewed as proof for a higher chance of long-distance dispersal in diatoms. While this might very well be true, higher-order classifications are entirely subjective, and a careful comparison of the average age of genera of diatoms and macro-organism groups is needed before a general statement on the subject can be made.

The importance of species recognition: biological and phylogenetic species

The above-mentioned studies, based on morphology alone, show that different geographic areas can possess distinct diatom floras, even when one might expect that ecological conditions would be similar. On the other hand, many diatom morphospecies are said to be cosmopolitan (Krammer and Lange-Bertalot 1986–1991) and some of these do indeed seem to be very widely distributed. However, many are undoubtedly composed of several (semi)cryptic species. Therefore, it will often be necessary to assess species limits in diatoms based on reproductive compatibility or molecular data, as these are more objective criteria of genetic relatedness than morphological similarity (Mann 1999; Lundholm et al. 2006), and hence also the geographic range of these species. This might especially be true

in genera where only a few morphological characters are readily available (e.g., *Nitzschia*, Trobajo et al. 2006; *Eunotia*, Vanormelingen et al. 2007).

Many studies of (semi)cryptic variation patterns in diatoms have thus far focused on sympatric populations (Beszteri et al. 2005; Amato et al. 2007) and only a few studies have incorporated populations from remote locations. Clones assigned to the marine centric diatom *Skeletonema marinoi* (forming a clade with authenticated clones in analyses of LSU sequence data) were found in both the Pacific and Atlantic Oceans and in the Mediterranean Sea (Sarno et al. 2005; Godhe et al. 2006). However, the different populations could be differentiated on the basis of the ITS, D1–D3 regions of the LSU and RAPDs, indicative of restricted dispersal between the different locations (Godhe et al. 2006). In *Pseudonitzschia pungens*, three closely related but distinct ITS clades exist which have different distributions (Casteleyn et al. 2007). One clade is restricted to subtropical latitudes, the two other to temperate latitudes. Of the latter two, one appears to be restricted to the northeast Pacific, the second has a cosmopolitan distribution and was recovered from the northwest and northeast Atlantic, the northwest and northeast Pacific, and coastal waters of New Zealand. These results suggest that at least one ITS clade of this marine diatom is truly cosmopolitan. Importantly, strains from the two clades used for crossing experiments can cross and produce initial cells, independent of ITS differences, although viability and fertility of the F1 progeny was not further investigated. In northeast Atlantic *Pseudonitzschia pungens*, little population differentiation was found in the North Sea over a distance of 100 km and a period of 2 years, indicating high levels of dispersal on such small spatio-temporal scales (Evans et al. 2005). This contrasts strongly with *Ditylum brightwellii*, of which in a single fjord system, different straits, seasons, and years harbored highly differentiated populations, indicative of barriers to gene flow such as partial physical isolation and local adaptation to different environmental conditions (Rynearson and Armbrust 2004; Rynearson et al. 2006). However, there is also a possibility that it concerns closely related species, as there was also a clear divergence in morphology (valve diameter) and ITS rDNA (1.1%).

In freshwater habitats, which are typically more isolated, *Eunotia bilunaris* clones isolated from two locations in New Zealand and one in Tasmania, 450–2000 km apart, were reproductively compatible despite some differentiation in the ITS rDNA region (Vanormelingen et al. 2007). Clones of the *Sellaphora pupula* complex from sites thousands of kilometers apart were similarly capable of interbreeding (i.e., Scotland and Ukraine, Mann 1999; Scotland and the USA, Behnke et al. 2004) and, in one case, their common species identity was also confirmed by ITS sequence analysis (Behnke et al. 2004).

From the examples above it is clear that, thus far, it can only be concluded that at least a few marine diatom species are indeed cosmopolitan while the range of some freshwater species may span several thousands of kilometers (although population divergence apparently takes place over distances of 100s to 1000s of kilometres). Major efforts should therefore be directed towards assessing the distribution and evolutionary history of other morphospecies that have previously been presumed to be cosmopolitan generalists (e.g., *Navicula cryptocephala*) using crossing and molecular data. Until this is done, biogeographical analyses of these taxa are almost meaningless (Poulíčková and Mann 2006).

Human-mediated introductions

For micro-organisms such as diatoms, dispersal between localities is necessarily passive. Potential vectors for passive dispersal fall apart into four main categories; dispersal by water currents, by animals, by wind, and by humans (Kristiansen 1996). While water currents are an obvious dispersal mechanism between directly interconnected habitats, there are also studies indicating that wind and animals can carry smaller amounts of viable cells of at least the more resistant taxa over 10s to 100s of kilometers (Proctor 1959; Maynard 1968; Roy-Ocotla and Carrera 1993), although to our knowledge there is as yet little conclusive evidence for this. Human-mediated introductions of exotic species provide a strong indication that geographic dispersal by these natural vectors was limiting in the past, challenging the ubiquity hypothesis (Foissner 2006). The subsequent spread of these species provides opportunities to study the scale dependence of dispersal (Havel and Shurin 2004). In the absence of a documentary record showing the species' absence in a certain region, the paleoecological records in sediments provide a unique opportunity to assess the history of species occurrences (Willis and Birks 2006).

The best example of an introductory event for diatoms concerns the sudden appearance of *Asterionella formosa* in the sediment records of numerous lakes in New Zealand after 1880 (Harper 1994). *Asterionella formosa* is a widespread planktonic morphospecies and is frequently considered to be cosmopolitan; it is often seasonally dominant in eutrophic lakes (Krammer and Lange-Bertalot 1991). Detailed analysis of fossil material from 21 sediment cores (14 lakes) from New Zealand showed no trace of *A. formosa* in pre-European sediments, although it is now widespread, occurring in 45% of lakes for which phytoplankton records are available. The most likely vector for the introduction of *A. formosa* is the introduction of salmon ova into New Zealand lakes in the second half of the 19th century (Harper 1994). It is highly unlikely that the species was extremely (i.e., not detectably) rare before European settlement as it is a species that can occur across a wide range of environmental conditions, from oligo- to eutrophic (Harper 1994; Van Dam et al. 1994). Interestingly, *A. formosa* is also absent from other lake cores in Australasia, which might rule out environmental change due to the introduction of mammalian grazers as a cause for its sudden appearance. The recent spread in New Zealand of another exotic diatom, *Didymosphenia geminata* (Kilroy et al. 2007), is occurring long after the main human-induced environmental changes. Other convincing evidence for human mediated introduction of species (and hence previous dispersal limitation) among diatoms include the appearance of *Thalassiosira baltica* in the Laurentian Great Lakes (Edlund et al. 2000), and the North-American species *Gomphoneis minuta* and *Encyonema triangulum* in France (Coste and Ector 2000). Well-documented marine introductions include *Odontella sinensis* (Greville) Grunow (Ostenfeld 1908), and *Coscinodiscus wailesii* Gran & Angst (Edwards et al. 2001), which were introduced either via ship's ballast water or by aquacultural practices. *Coscinodiscus wailesii*, a large (175–500 µm diameter) species was previously only known from the Pacific Ocean, and was first recorded (on two independent occasions) in English coastal waters in 1977. It had never before been observed in the monthly plankton samples (Continuous Plankton Recorder, CPR) which were taken in the area since the early 1950s. It subsequently spread into European shelf areas and has now become a significant member of the phytoplankton community (Edwards et al. 2001). It is highly unlikely that *C. wailesii* was already present in very low numbers only to become one of the major phytoplankton species in the NE-Atlantic.

Partitioning the effect of history and environment

One major limitation associated with the above-mentioned studies on diatom biogeography showing that diatoms can have restricted distributions is that limited dispersal is not the only thing that could create a restricted geographic range. Spatial distance is often correlated with environmental distance. Moreover, next to human-mediated introductions, also environmental change through time may allow for shifts in species ranges. A big challenge is therefore to separate the effects of environmental heterogeneity—which everyone accepts will cause biological differences—from community divergences caused by dispersal limitation (Martiny et al. 2006). While it is often implicitly assumed that habitats in different geographic areas (or different points in time) are environmentally similar, e.g., in the Arctic and Antarctic, and that differences in species composition between regions are as a consequence due to restricted dispersal, this is not usually tested. However, there are statistical methods that control for the effects of environment while quantifying the spatial (or temporal) influence on community structure and diversity. These include partial mantel tests and variation partitioning (Borcard et al. 1992; Bonnet and Van de Peer 2002).

The influence of regional processes relative to local environmental factors on stream diatom community structure has been investigated by variation partitioning in two studies. In benthic stream diatom communities in the United States, while 9–26% of the total explained variation could be attributed to spatially correlated environmental parameters, 15–31% was explained by purely geographic variation (Potapova and Charles 2002). This was mainly due to species with restricted distributions not readily explainable by environmental factors. In a study of benthic diatom communities in boreal streams across Finland, a similar 24% of the total explained variation was accounted for by environmentally independent spatial variation, with 40% attributable to spatially structured environmental variables (Soininen et al. 2004).

In a global scale study of lacustrine diatom diversity it was shown that variation in both regional and local genus richness was best explained by geographical variables such as connectivity between lakes and the amount of isolation of lake districts (Vyverman et al. 2007). Local environmental variables were of minor importance, implying that dispersal limitation is important in determining diatom genus diversity. Similarly, Telford et al. (2006) found that local species richness optima in lake regions in Europe and North America are strongly dependent upon regional habitat availability. Lakes with the modal lake pH always had the highest local species richness, regardless of the value of the modal pH (which varied by more than 2.5 units). This suggests that, even at the high lake densities in that part of the northern hemisphere, local species richness can be constrained by dispersal, at least in the less prevalent habitats in a region. While these studies convincingly show a reduced local (and even regional) diversity due to dispersal limitation, they could be complemented by the experimental local introduction of species from the regional species pool in mesocosms installed in the field, as was done for zooplankton (Shurin 2000). This might provide definitive evidence for local diatom diversity to be reduced by extinction–colonization dynamics.

Prospects

As reviewed above, different lines of research have recently challenged the ubiquity hypothesis for diatoms and show that diatom communities are controlled by the same processes affecting macro-organisms, although possibly not to the same degree. These studies

therefore underscore the need for conservation and the protection of isolated areas such as Tasmania, New Zealand, and Antarctica against further introductions of exotic species. However, it is also obvious that remarkably little is as yet known about the factors driving diatom species diversity and geographic distributions. Studies focusing on the mechanisms generating species diversity in this very diverse group of organisms are urgently needed. This includes molecular phylogenies to unravel the evolutionary history of species complexes or genera and their correlation with geography. This way, the occurrence and timing of such phenomena as allopatric divergence, long-distance dispersal, and adaptive radiations can be determined. Our efforts should also be further directed towards assessing the distribution of diatom species, using both crosses and molecular methods to confirm conspecificity in apparently cosmopolitan morphospecies. Within species, estimates of population divergence will be useful to assess dispersal distances and frequencies and to identify human-mediated introductions. It is also crucial to assess taxonomic turnover rates over different geographical scales (local to global) based upon taxonomically consistent datasets and to reveal what factors determine whether a diatom is endemic or widely distributed, such as habitat availability, abundance and stress resistance and survival during dispersal. Taken together, these data will allow to determine the relative importance of restricted dispersal in determining the diversity and geographic distribution of diatoms as compared to macro-organism groups, and thus an evaluation of, as not strictly true, how close to the truth the ubiquity hypothesis really was for diatoms.

Acknowledgments Part of the research presented in this review was financed by the Belgian Science Policy Office, the Fund for Scientific Research-Flanders and the Institute for the promotion of Innovation by Science and Technology in Flanders. Elie Verleyen is postdoctoral scientist with the Fund for Scientific Research. We thank Koen Sabbe for many valuable discussions, Wilhelm Foissner and an anonymous referee for their comments on an earlier version of the manuscript, and Bart Van de Vijver for kindly providing *Stauroneis* photographs.

References

Amato A, Kooistra WHCF, Levialdi Ghiron JH et al (2007) Reproductive isolation among sympatric cryptic species in marine diatoms. Protist 158:193–207

Baas-Becking LGM (1934) Geobiologie of inleiding tot de milieukunde. Van Stockum and Zoon, The Hague

Behnke A, Friedl T, Chepurnov VA et al (2004) Reproductive compatibility and rDNA sequence analyses in the *Sellaphora pupula* species complex (Bacillariophyta). J Phycol 40:193–208

Bell T, Ager D, Song J-I et al (2005) Larger islands house more bacterial taxa. Science 308:1884

Beszteri B, Ács É, Medlin LK (2005) Ribosomal DNA sequence variation among sympatric strains of the *Cyclotella meneghiniana* complex (Bacillariophyceae) reveals cryptic diversity. Protist 156:317–333

Bonnet E, Van de Peer Y (2002) zt: a software tool for simple and partial mantle tests. J Stat Softw 7(10):1–12. Available at http://www.jstatsoft.org

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73:1045–1055

Camburn KEJ, Kingston JC, Charles DE (1984–1986) PIRLA diatom iconograph. PIRLA Unpublished Report Series No 3. Department of Biology, Indiana University, Bloomington

Casteleyn G, Chepurnov VA, Leliaert F et al (2007) Pseudo-Nitzschia pungens (Bacillariophyceae): a cosmopolitan diatom species? Harmful Algae. doi:10.1016/j.hal.2007.08.004

Chao A, Li PC, Agatha S et al (2006) A statistical approach to estimate soil ciliate diversity and distribution based on data from five continents. Oikos 114:479–493

Chepurnov VA, Mann DG, Sabbe K et al (2004) Experimental studies on sexual reproduction in diatoms. Int Rev Cytol 237:91–154

Coste M, Ector L (2000) Diatomées invasives exotiques ou rares en France: principales observations effectuées au cours des dernières décennies. Syst Geogr Plants 70:373–400

Cox EJ (1995) Morphological variation in widely distributed diatom taxa: taxonomic and ecological implications. In: Donato M, Montresor M (eds) Proceedings of the 13th international diatom symposium. Biopress, Bristol, pp 335–345

Cox CB, Moore PD (2005) Biogeography—an ecological and evolutionary approach. 7th edn. Blackwell, Oxford
Créach V, Ernst A, Sabbe K et al (2006) Using quantitative PCR to determine the distribution of a semicryptic benthic diatom, *Navicula phyllepta* (Bacillariophyta). J Phycol 42:1142–1154
Darling KF, Kucera M, Pudsey CJ et al (2004) Molecular evidence links cryptic diversification in polar planktonic protists to Quaternary climate dynamics. PNAS 101:7657–7662
Darling KF, Kucera M, Wade CM (2007) Global molecular phylogeography reveals persistent Arctic circumpolar isolation in a marine planktonic protist. PNAS 104:5002–5007
Edlund MB, Taylor CM, Schelske CL et al (2000) *Thalassiosira baltica* (Grunow) Ostenfeld (Bacillariophyta), a new exotic species in the Great Lakes. Can J Fish Aquat Sci 57:610–615
Edwards M, John AWG, Johns DG et al (2001) Case history and persistence of the non-indigenous diatom *Coscinodiscus wailesii* in the north-east Atlantic. J Mar Biol Ass UK 81:207–211
Esposito RMM, Horn SL, McKnight DM et al (2006) Antarctic climate cooling and response of diatoms in glacial meltwater streams. Geophys Res Lett 33, Art. No. LO7406
Evans KM, Kuhn SF, Hayes PK (2005) High levels of genetic diversity and low levels of genetic differentiation in North Sea *Pseudo-Nitzschia pungens* (Bacillariophyceae) populations. J Phycol 41:506–514
Fenchel T, Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. Bioscience 54:777–784
Finlay BJ (2002) Global dispersal of free-living microbial eukaryote species. Science 296:1061–1063
Finlay BJ, Clarke KJ (1999) Ubiquitous dispersal of microbial species. Nature 400:828
Finlay BJ, Fenchel T (2004) Cosmopolitan metapopulations of free-living microbial eukaryotes. Protist 155:237–244
Finlay BJ, Monaghan EB, Maberly SC (2002) Hypothesis: the rate and scale of dispersal of freshwater diatom species is a function of their global abundance. Protist 153:261–273
Flower RJ (2005) A taxonomic and ecological study of diatoms from freshwater habitats in the Falkland Islands, South Atlantic. Diatom Res 20:23–96
Foissner W (2006) Biogeography and dispersal of micro-organisms: a review emphasizing protists. Acta Protozool 45:111–136
Fourtanier E, Kociolek JP (2003) Catalogue of the diatom genera (vol 14, pg 190, 1999). Diatom Res 18:245–258
Godhe A, McQuoid MR, Karunasagar I et al (2006) Comparison of three common molecular tools for distinguishing among geographically separated clones of the diatom *Skeletonema marinoi* Sarno et Zingone (Bacillariophyceae). J Phycol 42:280–291
Green J, Bohannan JM (2006) Spatial scaling of microbial diversity. TREE 21:501–507
Green JL, Holmes AJ, Westoby M et al (2004) Spatial scaling of microbial eukaryote diversity. Nature 432:747–750
Harper MA (1994) Did Europeans introduce *Asterionella formosa* Hassall to New Zealand? In: Kociolek JP (ed) Proceedings of the 11th International Diatom Symposium 1990. California Academy of Sciences, San Francisco, pp 479–484
Hasle GR (1976) The biogeography of some marine planktonic diatoms. Deep-Sea Res 23:319–338
Hasle GR (2001) The marine, planktonic diatom family Thalassionemataceae: morphology, taxonomy and distribution. Diatom Res 16:1–82
Havel JE, Shurin JB (2004) Mechanisms, effects, and scales of dispersal in freshwater zooplankton. Limnol Oceanogr 49:1229–1238
Hustedt F (1927–1966) Die Kieselalgen Deutschlands, Österreichs und der Schweiz. In: Rabenhorst L (ed) Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, Bd. 7(2). Akad Verlagsges, Leipzig
Kilroy C, Sabbe K, Bergey EA et al (2003) New species of *Fragilariforma* (Bacillariophyceae) from New Zealand and Australia. New Zeal J Bot 41:535–554
Kilroy C, Biggs BJ, Vieglais CC (2007) *Didymosphenia geminata* in New Zealand: a science response to help manage an unwanted, invasive freshwater diatom. In: Abstract book, ASLO Aquatic Sciences meeting. Santa Fe (New Mexico), 4–9/02/2007
Kociolek JP, Kingston JC (1999) Taxonomy, ultrastructure, and distribution of some gomphonemoid diatoms (Bacillariophyceae: Gomphonemataceae) from rivers in the United States. Can J Bot 77:686–705
Kociolek JP, Spaulding SA (2000) Freshwater diatom biogeography. Nova Hedwigia 71:223–241
Kociolek JP, Spaulding SA, Sabbe K et al (2004) New *Gomphonema* (Bacillariophyta) species from Tasmania. Phycologia 43:427–444
Krammer K, Lange-Bertalot H (1986–1991) Bacillariophyceae. In: Ettl H, Gerloff, J, Heynig H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa, vol. 2(1), 876 pp (1986), vol. 2(2), 596 pp (1988), vol. 2(3), 576 pp (1991), vol. 2(4), 437 pp (1991). Fischer, Stuttgart/Jena
Krasske G (1939) Zur Kieselalgenflora Südchiles. Arch Hydrobiol 35:349–468
Kristiansen J (1996) Dispersal of freshwater algae—a review. Hydrobiologia 336:151–157

Lee WJ, Patterson DJ (2000) Heterotrophic flagellates (Protista) from marine sediments of Botany Bay, Australia. J Nat Hist 34:483–562
Leibold MA, Holyoak M, Mouquet N et al (2004) The metacommunity concept: a framework for multiple-scale community ecology. Ecol Lett 7:601–613
Lundholm N, Moestrup Ø, Kotaki Y et al (2006) Inter- and intraspecific variation of the *Pseudo-Nitzschia delicatissima* complex (Bacillariophyceae), illustrated by rRNA probes, morphological data and phylogenetic analysis. J Phycol 42:464–481
Mann DG (1999) The species concept in diatoms. Phycologia 38:437–495
Mann DG, Droop SJM (1996) Biodiversity, biogeography and conservation of diatoms. Hydrobiologia 336:19–32
Martiny JBH, Bohannan BJM, Brown JH et al (2006) Microbial biogeography: putting microorganisms on the map. Nat Rev Biogeogr 4:102–112
Maynard NG (1968) Significance of air-borne algae. Z allg Microbiol 8:225–226
Ostenfeld CH (1908) On the immigration of *Biddulphia sinensis* Grev. and its occurrence in the North Sea during 1903–1907. Meddelelser fra Kommissionen for Havundersogelser, Plankton 1(6):1–25
Papke RT, Ramsing NB, Bateson MM et al (2003) Geographical isolation in hot spring cyanobacteria. Environ Microbiol 5:650–659
Potapova MG, Charles DFC (2002) Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. J Biogeogr 29:167–187
Poulíčková A, Mann DG (2006) Sexual reproduction in *Navicula cryptocephala* (Bacillariophyceae). J Phycol 42:872–886
Proctor VW (1959) Dispersal of freshwater algae by migratory waterbirds. Science 130:623–624
Reche I, Pulido-Villena E, Morales-Baquero R et al (2005) Does ecosystem size determine aquatic bacterial richness? Ecology 86:1715–1722
Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. Science 235:167–171
Round FE, Crawford RM, Mann DG (1990) Diatoms: biology and morphology of the genera. Cambridge Univ. Press, Cambridge
Roy-Ocotla G, Carrera J (1993) Aeroalgae: responses to some aerobiological questions. Grana 32:48–56
Rumrich U, Lange-Bertalot H, Rumrich M (2000) Diatoms of the Andes, from Venezuela to Patagonia/Tierra del Fuego, and two additional contributions. ARG Gartner Verlag KG, Königstein
Rynearson TA, Armbrust EV (2004) Genetic differentiation among populations of the planktonic marine diatom *Ditylum brightwellii*. J Phycol 40:34–43
Rynearson TA, Newton JA, Armbrust EV (2006) Spring bloom development, genetic variation, and population succession in the planktonic diatom *Ditylum birghtwellii*. Limnol Oceanogr 51:1249–1261
Sabbe K, Vanhoutte K, Vyverman W (2000) *Actinella comperei* sp. nov. (Eunotiaceae, Bacillariophyta): a new endemic freshwater diatom from Tasmania (Australia). Syst Geogr Plants 70:237–243
Sabbe K, Vanhoutte K, Lowe RL et al (2001) Six new *Actinella* (Bacillariophyta) species from Papua New Guinea, Australia and New Zealand: further evidence for widespread diatom endemism in the Australasian region. Eur J Phycol 36:321–340
Sabbe K, Verleyen E, Hodgson DA et al (2003) Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. Antarct Sci 15:227–248
Sarno D, Kooistra WHCF, Medlin LK et al (2005) Diversity in the genus *Skeletonema* (Bacillariophyceae). II. An assessment of the taxonomy of *S. costatum*-like species with the description of four new species. J Phycol 41:151–176
Shurin JB (2000) Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology 81:3074–3086
Soininen J, Paavola R, Muotka T (2004) Benthic diatom communities in boreal streams: community structure in relation to environmental and spatial gradients. Ecography 27:330–342
Spaulding SA, McKnight DM (1999) Diatoms as indicators of environmental change in Antarctic freshwaters. In: Stoermer EF, Smol JP (eds) The diatoms: applications for the environmental and earth sciences. Cambridge Univ. Press, Cambridge, pp 245–263
Spaulding SA, Kociolek JP, Wong D (1999) A taxonomic and systematic revision of the genus *Muelleria*. Phycologia 38:314–341
Stevenson AC, Juggins S, Birks HJB et al (1991) The surface waters acidification project paleolimnology programme: modern diatom/lake-water chemistry data set. Ensis pub., London
Syvertsen EE (1977) *Thalassiosira rotula* and *T. gravida*: ecology and morphology. Nova Hedwigia, Beih 54:99–112
Taylor JW, Turner E, Townsend JP et al (2006) Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. Philos T R Soc B 361:1947–1963

Telford RJ, Vandvik V, Birks HJB (2006) Dispersal limitation matters for microbial morphospecies. Science 312:1015

Trobajo R, Mann DG, Chepurnov VA et al (2006) Taxonomy, life cycle and auxosporulation *of Nitzschia fonticola* (Bacillariophyta). J Phycol 42:1353–1372

Tyler PA (1996) Endemism in freshwater algae, with special reference to the Australian region. Hydrobiologia 336:127–135

Van Dam H, Mertens A, Sinkeldam J (1994) A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. Neth J Aquat Ecol 28:117–133

Van de Vijver B, Beyens L, Lange-Bertalot H (2004) The genus *Stauroneis* in the Arctic and (Sub-)Antarctic regions. Biblthca diatomol 51:1–317

Van de Vijver B, Gremmen NJM, Beyens L (2005) The genus *Stauroneis* (Bacillariophyceae) in the Antarctic region. J Biogeogr 32:1791–1798

Vanhoutte K, Verleyen E, Vyverman W et al (2004) The freshwater diatom genus *Kobayasiella* (Bacillariophyta) in Tasmania, Australia. Aust Syst Bot 17:483–496

Vanhoutte K, Verleyen E, Sabbe K et al (2006) Congruence and disparity in benthic diatom community structure of small lakes in New Zealand and Tasmania. Mar Freshw Res 57:789–801

Vanormelingen P, Chepurnov VA, Mann DG et al (2007) Congruence of morphological, reproductive and ITS rDNA sequence data in some Australasian *Eunotia bilunaris*. Eur J Phycol 42:61–79

Villanueva VD, Maidana NI (1999) Diatoms (Bacillariophyta) from Pulmari lake (Nuequen, Argentina). Biologia 54:1–10

Vyverman W, Vyverman R, Hodgson D et al (1995) Diatoms from Tasmanian mountain lakes: a reference data-set (TASDIAT) for environmental reconstruction and a systematic and autecological study. Bibl diatomol 33:1–193

Vyverman W, Sabbe K, Vyverman R (1997) Five new freshwater species of *Biremis* (Bacillariophyta) from Tasmania. Phycologia 36:91–102

Vyverman W, Sabbe K, Mann DG et al (1998) *Eunophora* gen. nov. (Bacillariophyta) from Tasmania and New Zealand: description and comparison with *Eunotia* and amphoroid diatoms. J Phycol 33:95–111

Vyverman W, Verleyen E, Sabbe K et al (2007) Historical processes constrain patterns in global diatom diversity. Ecology 88:1924–1931

Whitaker RJ, Grogan DW, Taylor JW (2003) Geographic barriers isolate endemic populations of hyperthermophilic Archaea. Science 301:976–978

Whitfield J (2005) Biogeography: is everything everywhere? Science 310:960–961

Willis KJ, Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity conservation. Science 314:1261–1265