

REVIEW ARTICLE

Fifteen important questions in the spatial ecology of diatoms

Janne Soininen  | Anette Teittinen 

Department of Geosciences and
Geography, University of Helsinki, Helsinki,
Finland

Correspondence

Janne Soininen, Department of Geosciences
and Geography, University of Helsinki,
Helsinki, Finland.
Email: janne.soininen@helsinki.fi

Abstract

1. Recently, studies about the spatial distribution of microbial species and communities have increased substantially. Freshwater diatoms are used as one of the most popular model taxa in such macroecological studies, but the most exciting patterns in the spatial ecology of diatoms have not been reviewed. Here, we identify 15 important questions about freshwater diatom ecology, review the major findings, and suggest novel research avenues.
2. We found that diatoms do not support classical latitudinal diversity gradient, species–area relationship or Rapoport's rule. We found some, albeit inconsistent support for an elevational diversity gradient, Bergmann's rule and niche conservatism. Diatoms do support a positive interspecific abundance–occupancy relationship like nearly all other taxa. With regards to metacommunity dynamics, diatom communities are typically structured by species sorting, but neutral dynamics or mass effects are also evident at large or small spatial scale, respectively.
3. Taken together, this review suggests that diatoms follow some classical biogeographical patterns similarly to larger taxa, but patterns are typically weaker than for macro-organisms. This may result because diatoms are typically relatively strongly controlled by local factors and often exhibit efficient stochastic dispersal processes both at small and large scales. More research is needed to build a more comprehensive view of diatom species–area relationships and latitudinal gradients in diversity, for example. In the future, well-replicated macroecological field experiments, diatom studies with intercontinental or global coverage, trait-based approaches, and DNA-based species identification would be fruitful avenues to shed more light into the spatial ecology of diatoms.

KEYWORDS

biodiversity, biogeography, lakes, macroecology, microalgae, streams

1 | INTRODUCTION

Spatial ecology studies how individuals, populations, and communities are related not only to their surrounding environment, but also to space. Typically, spatial ecology covers various scientific fields such as biogeography, macroecology, metacommunity ecology, and metapopulation ecology, where space has a distinct role in affecting how species interact with their environment. Traditionally, spatial ecology has focused on large, well-studied charismatic organismal

groups including mammals, birds, and larger plants. However, recently, spatial ecology of unicellular organisms such as bacteria, unicellular fungi, and algae, has been actively examined in terrestrial (Fierer & Jackson, 2006; Green et al., 2004; Horner-Devine, Lage, Hughes, & Bohannon, 2004), marine (Fuhrman et al., 2008) and freshwater ecosystems (Astorga et al., 2012; Vyverman et al., 2007). The recent literature also suggests that microorganisms exhibit large-scale spatial patterns, which are, however, often somewhat weaker than documented for larger taxa.

Diatoms are unicellular eukaryotic algae that have been in the focus of microbial macroecology recently (Passy, 2012; Soininen, Jamoneau, Rosebery, & Passy, 2016). Traditionally, diatoms have been used as bioindicators for various environmental factors such as acidity (Korhola, Weckström, & Nyman, 1999), nutrient loading (Winter & Duthie, 2000), and climatic factors (Pajunen, Luoto, & Soininen, 2017; Rühland, Paterson, & Smol, 2015; Weckström, Korhola, & Blom, 1997). A prerequisite for such bioindication is a proper understanding of underlying ecological and evolutionary processes affecting both the diatom regional distribution and local abundance. Due to historical reasons, difficulties in identifying some of the widely distributed species and the fact that diatom distributions are related to local environmental factors, the examination of major correlates of diatom community composition has long been centered on local environmental forcing instead of biogeographical factors. Traditionally, diatom distributions have been held mainly as cosmopolitan, following thus the idea of “everything is everywhere, but the environment selects” (Baas-Becking, 1934; Cermeño & Falkowski, 2009; Finlay, 2002). However, recently, the emerged view has been that also diatom communities show spatially structured patterns, largely similar to those observed for larger taxa (Keck, Franc, & Kahlert, 2018; Soininen, Paavola, & Muotka, 2004; Verleyen et al., 2009; Vyverman et al., 2007). Such spatial studies mostly use morphological species identification, but in the near future, DNA-based identification methods may give new insights into the spatial ecology of diatoms as such methods are not subject to somewhat subjective decisions in species identification.

The aim of this paper is to review the recent literature about diatom ecology by identifying 15 important questions in the spatial ecology of diatoms, which range from classical topics addressed in major biogeographical or macroecological text books (e.g. Gaston & Blackburn, 2000) to more recent issues of metacommunity ecology (Leibold et al., 2004). These questions thus range from a global focus

to ones more relevant for the smaller spatial scales. We review existing knowledge about these 15 themes and suggest additional research approaches that would help to provide a more comprehensive view of diatom ecology in the near future. In this review, we focus on freshwater diatoms. In lakes, spatial ecological studies of diatoms consider either pelagic or benthic habitats or both. In streams, studies mainly consider benthic habitats. In general, diatom communities in lakes should be more strongly dispersal limited than in streams, in which local sites are typically more connected with each other within a river system (Heino et al., 2015). Here, we exclude general freshwater or marine phytoplankton studies that comprise many algal groups. We hope our review will be interesting not only for diatomists, but also for researchers studying other microorganismal groups, such as bacteria or unicellular fungi, which have different functional roles in ecosystems compared with algae.

We first describe the number of papers published about spatial ecology of freshwater diatoms. Our Web of Science search (years 1990–2018) revealed that the spatial ecology of diatoms has attracted increased attention in recent years (Figure 1) allowing us to synthesise this field of science using relatively large number of articles. We used the following search strings (as topic): *Search 1*: “ecolog*” AND “diatom*” AND “stream*” NOT “plankt*”, *Search 2*: “ecolog*” AND “diatom*” AND “lake*” NOT “plankt*”, *Search 3*: “macroecolog*” AND “diatom*” NOT “marine” NOT “plankt*” and *Search 4*: “biogeogr*” AND “diatom*” NOT “marine” NOT “plankt*”. We thus excluded general plankton studies from the literature search. The results of our literature searches show that the number of diatom ecological studies in lakes and streams per year increased notably after 2002, with overall slightly higher number of lake studies than stream studies (Figure 1). Biogeographical studies of diatoms per year increased clearly after 2003 (c. 20–30 studies per year), whereas studies classified as macroecological have remained low. For stream studies, most articles have been published in the U.S.A.

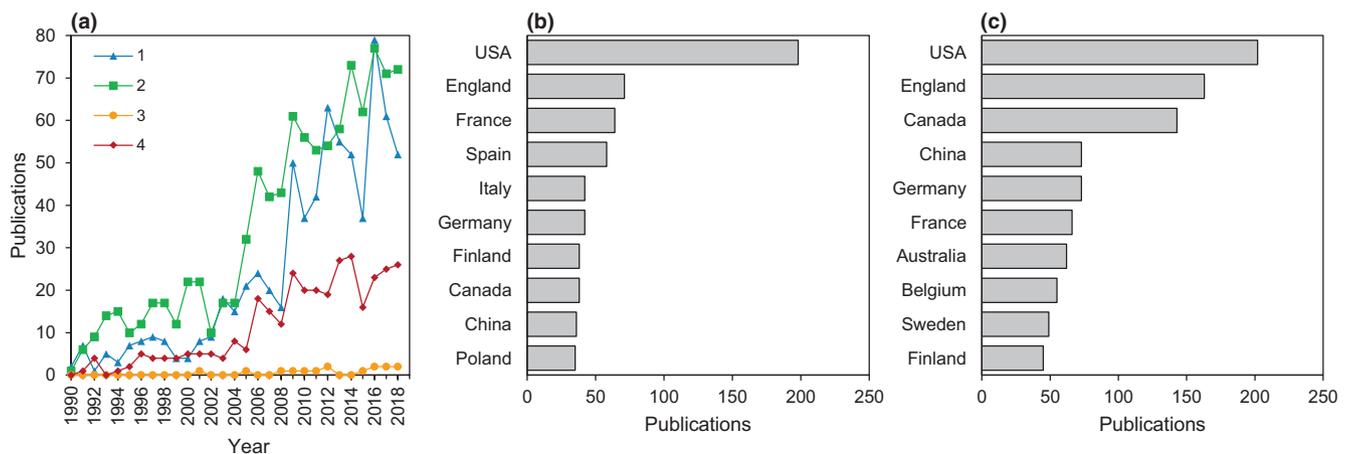


FIGURE 1 (a) The four literature searches from the Web of Science (years 1990–2018). Search 1 describes the number of studies about benthic diatom ecology in streams per year, Search 2 shows the number of benthic diatom ecology studies per year in lakes, Search 3 shows the number of biogeographical studies of freshwater benthic diatoms per year, and Search 4 shows the number of macroecological studies on freshwater benthic diatoms. (b) The number of publications during the years 1990–2018 in streams (Search 1) by different countries. (c) The number of publications during the years 1990–2018 in lakes (Search 2) by different countries

followed by U.K. and France. For lake studies, most articles originate from the U.S.A., U.K., and Canada.

1. Is there a latitudinal richness gradient in diatoms?

Latitudinal diversity gradient (LDG) represents perhaps the mostly widely recognised macroecological pattern in nature. Even if the underlying causes of the LDG are still debated, its generality in nature has been documented for nearly all organismal groups and ecosystems (Hillebrand, 2004). However, LDG seems to be weaker for microbial taxa than for larger plants and animals (Fierer & Jackson, 2006; Soininen et al., 2016, but see Stomp, Huisman, Mittelbach, Litchman, & Klausmeier, 2011). Such a weak biogeographical pattern has been accounted for by the fact that microbes have small body size, but large cell densities and population sizes, and thus efficient dispersal across long distances. A second reason could be that microbes are typically severely under-sampled in the field resulting in large number of pseudo-absences in the datasets (Meyer et al., 2018). In essence, microbial data are typically presence-only data since true absences of species from sites can be rarely, if ever, verified in the field.

For freshwater diatoms, perhaps the earliest paper to address LDG comprehensively was a meta-analysis by Hillebrand and Azovski (2001). Using 148 local and 25 regional freshwater diatom data sets, compared with larger taxa such as trees, mammals, and other vertebrates, they showed that diatom LDG was significant but much weaker. Passy (2010) studied LDG (latitudinal range 25–50°N) in stream diatoms in the U.S.A. and found that richness and latitude had a distinct U-shaped relationship linked to nutrient supply. Moreover, Schiaffiano et al. (2016) reported a non-significant LDG (latitudinal range 45–63°S) for microeukaryotic lake taxa using molecular fingerprinting methods. In a global study, Soininen et al. (2016) documented an inverse LDG (latitudinal range 50°S–70°N) for stream diatoms with lower species richness near the equator and higher richness towards the poles. Such a counterintuitive pattern was possibly related to nutrient supply. In fact, inverse LDGs have also been reported for other biotic taxa such as molluscs and aphids (reviewed by Storch, Marquet, & Brown, 2007). Typically, underlying reasons for the inverse LDG are context-dependent but may be caused when a factor other than latitude drives richness. These factors can be resource (nutrients, light) availability or abundance of a keystone predator, for example. In the tropics, nutrient concentrations and light intensities may be lower than in temperate or boreal waters (Heino et al., 2018), and diatom communities, largely dependent on nutrient and light resources, may thus not be more diverse in the tropics than near the poles.

In summary, it is evident that freshwater diatoms do not show clear linear LDG observed for most of the studied taxa, but patterns have been context-dependent and perhaps related to nutrient supply. Studies of LDG need very extensive sampling requiring cooperation among research groups. In such joint research efforts, use of consistent methods in species identification, regardless of whether morphological or molecular DNA-based identification are used, is of

vital importance so that data can be merged reliably among different geographical regions.

2. Do diatoms exhibit elevational diversity patterns?

Elevational diversity gradients in larger organisms are among the most widely described patterns in spatial ecology, yet knowledge on elevational diversity of freshwater diatoms remains scarce. For species richness, the few studies addressing elevational gradients have revealed contrasting patterns. Studying a Nepalese river system (600–3,750 m above sea level [a.s.l.]), Ormerod et al. (1994) found that diatom richness decreased with increasing elevation. Similarly, Wang et al. (2011) reported that along an elevational gradient of 1,820–4,050 m a.s.l. in a Chinese stream, diatom richness showed a decreasing pattern associated with variation in nutrient supply. Recently, a study on South American lakes and streams (210–5,070 m a.s.l.) revealed more evidence for the negative effect of elevation on diatom richness (Benito et al., 2018a). In contrast, in a survey of Himalayan streams stretching from 350 to 4,700 m a.s.l., no apparent relationship between diatom richness and elevation was observed, possibly due to disturbance frequency in such systems (Jüttner, Chimonides, Ormerod, & Cox, 2010). Likewise, in a study on subarctic mountain streams (21–877 m a.s.l.), no richness–elevation patterns were found; instead, diatom richness was most strongly associated with water depth, presumably reflecting disturbance frequency and intensity prevailing at a site (Teittinen, Kallajoki, Meier, Stigzelius, & Soininen, 2016). Wang et al. (2017) examined six streams in mountainous regions of Norway, Spain, and China, and found decreasing (1) (same data as in Wang et al., 2011), unimodal (1), and non-significant (4) elevational patterns for diatom richness, with water pH as the most important local explanatory variable. Finally, Teittinen, Wang, Strömgård, and Soininen (2017) surveyed subarctic ponds covering elevations from 10 to 1,038 m a.s.l. and documented a unimodal richness–elevation trend, which was best explained by pH.

In addition to species richness, a few studies have examined elevational β -diversity of freshwater diatoms. To our knowledge, elevational β -diversity was first addressed by Wang et al. (2012), who examined such patterns along an elevational gradient of 1,820–4,050 m a.s.l. in a stream in China. While small-scale β -diversity of diatoms between adjacent sampling sites showed no significant elevational patterns, the community similarities decreased significantly with increasing elevational distance when examined across the entire elevational gradient (Wang et al., 2012). Declining diatom community similarities with elevational distance were also reported by Teittinen et al. (2016) for subarctic streams. In conclusion, while some studies have found clear elevational diversity patterns for freshwater diatoms, others have not. Such inconsistency suggests that the patterns are context-dependent and hinders drawing conclusions regarding their generality, especially for species richness. It seems that variation in diatom richness along mountainsides is not regulated by elevation and associated climatic gradients only but may instead be more directly associated with local factors, such as the frequency of disturbances (Jüttner et al., 2010; Teittinen et al., 2016) or pH (Teittinen et al., 2017; Wang et al., 2017). Future studies

should try to uncouple local factors from elevational (i.e. climatic) gradients using well-designed replicated field experiments where diatoms can freely colonise microcosms from the species pool.

3. Is there a species–area relationship in diatoms?

Even if species–area relationships (SARs) are relatively often studied for microbial taxa (e.g. Horner-Devine et al., 2004; Reche, Pulido-Villena, Morales-Baquero, & Casamayor, 2005 for bacteria and Stomp et al., 2011 for phytoplankton), SAR studies are extremely rare for freshwater benthic diatoms. One reason could be that the sampling for truly nested SARs in which larger area always contains the smaller area is notoriously difficult to conduct for microbes. Thus, the only feasible possibility is to study SARs across independent, but different sized sampling areas to reveal whether richness increases with area. The underlying reason for a possible SAR in benthic diatoms would be that larger samples comprise more habitat heterogeneity, that is, more microhabitats and stronger environmental heterogeneity (Cantonati, Füreder, Gerecke, Jüttner, & Cox, 2012). In a seminal paper by Patrick (1967), factors behind SARs in stream diatoms were studied, and findings suggested that species richness is influenced by the invasion rate, area, and the number of species in the species pool. In one of the few more recent studies about diatom SARs, Teittinen and Soininen (2015) did not find a significant SAR in spring diatoms, whereas Bolgovics, Ács, Várbíró, Görgényi, and Borics (2016) demonstrated that among lakes, ponds and pools, diatom richness increased with area. Thus, we think that much remains to be studied about SARs in benthic diatoms since even the generality of the pattern in different ecosystems is poorly resolved let alone the actual mechanism behind the SAR in diatoms.

4. Do diatoms comply with Rapoport's and Bergmann's rules?

Of the classical biogeographical rules, it appears that Rapoport's rule has been investigated for diatoms only along elevational gradient, not latitudinal. Rapoport's rule suggests that species that have more polar or higher elevational range also have larger ranges because climatic and other environmental variability increases along latitude or elevation. However, Wang et al. (2017) documented that diatoms do not follow elevational Rapoport's rule in several mountain datasets. Likewise, Teittinen et al. (2016) showed that even if community composition exhibited clear segregation along elevation, stream diatoms did not comply with elevational Rapoport's rule along mountainsides in the subarctic. These results may indicate either that other factors than climatic variability shape diatom range sizes or that determination of microbial range sizes is highly difficult in the field due to a relatively small sampling effort compared with the actual size of the local species pool.

Bergmann's rule suggests that the body size of an individual or species gets larger towards higher latitude, that is, in colder environments (Meiri & Dayan, 2003). Such a rule is important as body size is directly related to many biological rates and to how organisms perceive the surrounding environment they interact with. Organism size is also a useful predictor of diversity, abundance, species distribution

and range size, and the outcome of food web interactions (Hildrew, Raffaelli, & Edmonds-Brown, 2007). Bergmann's rule initially concerned only endothermic animals, but recently, some indication of such a pattern has emerged also in studies investigating ectotherms including algae. In one of the most comprehensive papers, Adams et al. (2013) found that in geothermally heated streams, diatoms were not smaller than in ambient temperature, neither at the species nor community level. Thus, the authors concluded that diatoms may represent an important exception to temperature–size rules. We note here, though, that temperature or latitude also affects aquatic biota in many other ways than simply through water temperature per se, such as affecting the length of growing season and ice-free periods. Some findings also exist that do support the Bergmann's rule in diatoms. Svensson, Norberg, and Snoeijis (2014) showed that average community cell volume of benthic diatoms in the Baltic Sea decreased with warmer temperatures under the influence of thermal effluents of a nuclear power plant. Likewise, Soininen and Kokocinski (2006) revealed that average maximum length of epilithic diatoms increased towards North in Finnish boreal streams (i.e. communities comprised larger species of diatoms in the North). In summary, it appears that there is some evidence for diatom cell sizes to become larger at colder temperatures, but the generality of such findings seems still uncertain. When studying Bergmann's rule, it is important to separate species-level body size (i.e. does size of individuals within a species get larger towards the poles) from community-level body size (i.e. do communities harbour larger-sized species towards the poles). In diatoms, spatial patterns of body sizes are exceptionally complex as diatom cell size decreases in cell divisions. Thus, cell sizes differ between different aged populations.

5. Are freshwater diatoms cosmopolitan?

It has been suggested that especially marine diatoms living in the open ocean should often be cosmopolitan due to the lack of dispersal barriers (Cermeño & Falkowski, 2009). However, Casteleyn et al. (2010) argued using molecular evidence that even among marine planktonic diatoms, cosmopolitanism may not prevail. In their review, Vanormelingen, Verleyen, and Vyverman (2009) summarised knowledge about diatom distributions and concluded that diatoms do exhibit biogeographical patterns comparable with larger taxa and that there is a clear geographical distance effect in their distributions. Thus, there is some evidence supporting the idea that while there are some clearly cosmopolitan diatoms (e.g. *Gomphonema parvulum*, Abarca, Jahn, Zimmermann, & Enke, 2014 or *Pinnularia borealis*, Souffreau et al., 2013), many species are probably not. In relation to cosmopolitanism versus narrow endemism, the most exciting question is what are the traits favouring large or small range size in diatoms. For example, are cosmopolitan or sub-cosmopolitan species small or large and are these attached or non-attached species? And what are the traits most often associated with narrow distribution in diatoms? Do species with narrow distribution simply have very peculiar environmental demands rather than weak dispersal potential? A global analysis investigating diatom range sizes versus their traits would probably clarify this

important question. We need to acknowledge, however, that there are often cryptic species or species complexes in diatoms (Souffreau et al., 2013), which makes it extremely difficult to evaluate true diatom range sizes especially globally.

6. Is there niche conservation in diatoms?

Niche conservatism describes the scenario in which species retain similar characteristics or traits over time and space (Wiens et al., 2010). It has potentially important implications for understanding the biogeographic distributions of species. In modern times, the most feasible method to examine niche conservation is to identify whether the same species has similar ecological properties across geographically distant regions. In diatoms, the paper by Bennett, Cumming, Ginn, and Smol (2010) was probably the first to test whether niche conservation exists between continents; it compared the lake diatom pH optima in North America and Europe. They found that diatom pH optima were relative similar in the two continents, thus supporting niche conservation. However, more recently, Soininen et al. (2019) documented only weak niche conservation in stream diatoms with regards to chemistry variables (pH, conductivity, total P, and water temperature) and climate (annual precipitation, seasonality in precipitation, annual temperature, and annual temperature range) between the whole continental U.S.A. and the five test regions (Finland, France, New Zealand, Reunion Island, and Antilles). It appears that any definite conclusions over niche conservation in diatoms are premature at best and more global scale research is needed. This is complicated by the fact that it is difficult to separate local adaptation to environmental conditions from cryptic species in diatoms (Souffreau et al., 2013).

7. What is controlling local abundance or cell densities in diatoms?

The question of what is controlling population densities or abundances in ecology is related to both organism body size (Marquet, Navarrete, & Castilla, 1990) and to species distributions (Brown, 1984; Gaston, Blackburn, & Lawton, 1997). Typically, population density of species at the same trophic level scales with body size (M) as a $-3/4$ -power law, whereas densities tend to increase with species regional distribution due to various reasons such as niche breadth and position or metapopulation dynamics (Gaston et al., 1997). Passy (2008) investigated how diatom density was affected by cell size and regional distribution in benthic and planktonic stream habitats in the U.S. As hypothesised, she showed that density was a negative function of cell size and a positive function of distribution. She also highlighted that cell size was more strongly related to density in the benthic habitats than in plankton, which could occur because open space may be a critical resource for diatoms. Furthermore, more recently, Passy (2012) reported that species niche breadth is positively related to species densities in stream diatoms. The logic behind this could be that the species with large niche breadth can use various resources constantly in time even when living in highly variable ecosystems such as streams. With the help of such constant resource use, a species could maintain large population densities. Given that cell densities are critical for the degree of

primary production, examination of the drivers behind the cell density variation in diatoms is very important in the near future. For example, ongoing climate change may rapidly increase physical disturbances such as flooding or desiccation in streams and may thus have large impact on cell densities and benthic production.

8. What is controlling regional occupancy in diatoms?

Even if some diatoms tend to have continental or global distributions, within a region, diatoms may not be uniformly distributed across all localities as they typically show species-specific environmental preferences similar to those of multicellular organisms. Furthermore, it has been found that, despite differences in their broad-scale distribution, the regional distribution of diatoms may not be profoundly different from those of multicellular organisms (Heino & Soininen, 2005; Potapova & Charles, 2002; Soininen et al., 2004). Therefore, it could be expected that the degree of species regional occupancy (i.e. at how many sites a species occurs in a region) in diatoms would be similarly related to niche characteristics, dispersal ability, and body size, as have previously been found for multicellular organisms (Brown, 1984). Heino and Soininen (2006) studied the correlates of regional occupancy in stream diatoms and showed that occupancy was positively related with niche breadth and attachment ability, whereas occupancy decreased with niche marginality. These findings suggest firstly that the stream diatom species that have ability to stay attached even in higher current velocities maintain higher regional occupancy while loosely attached species diminish their populations when prone to shear stress by the currents. Secondly, findings indicate that niche properties are vital for the occupancy because species with large niche breadth are more capable of living in more variable physicochemical conditions. In contrast, species that prefer regionally marginal or atypical environmental conditions are less favoured and likely to have lower occupancy compared with species with typical environmental preferences. Recently, Rocha et al. (2018) explored how regional occupancy was related with niche characteristics and body size in stream organisms, including diatoms. Agreeing with Heino and Soininen (2006), they found that diatom occupancy was positively related to niche breadth, whereas it scaled negatively with niche position, suggesting that species with marginal niche position had lower occupancy. Moreover, they documented that smaller diatom species had higher occupancy than the larger species perhaps due to the fact that small-sized species are likely to have better dispersal ability (Finlay, 2002; Passy, 2007, 2012), which would facilitate their degree of regional occupancy.

9. Interspecific abundance–occupancy relationships in diatoms

The interspecific abundance–occupancy relationship (Brown, 1984) is one of the most classical topics in macroecology and widely documented for many larger taxa such as plants, birds, invertebrates, and fish from various types of ecosystems (Blackburn, Cassey, & Gaston, 2006). The causes of such positive relationship range from niche breadth or niche position (i.e. whether a species occurs at environmentally typical or at marginal sites) hypotheses to metapopulation dynamics and range

position hypothesis (reviewed by Gaston et al., 1997). Such a relationship has also been examined for freshwater diatoms and Soininen and Heino (2005) found a comparably strong relationship ($r = 0.60$) especially between maximum local abundance and regional occupancy. In a sister paper, they found that positive relationship in a smaller set of boreal streams was most likely to be related to niche position hypothesis (Heino & Soininen, 2006). More recently, Rocha et al. (2018) also documented a positive relationship between local mean abundance and occupancy of diatoms across 54 subarctic streams. They further found that the positive relationship was mainly explained by environmental niche position with a smaller effect by niche breadth. In summary, it appears that diatoms are no exception with regards to this macroecological rule. However, we think further studies should carefully consider how to describe the multiple dimensions of diatom niche breadths and positions in order to properly reflect the influence of all factors that are potentially important for diatoms.

10. Species-abundance distributions in diatoms

Species-abundance distribution (SAD) has fundamental significance in ecology and describes how the number of individuals is divided across species in a community (McGill et al., 2007). In biological communities, SADs range from a typical lognormal model with relatively even distribution of individuals to very uneven log linear or log series patterns (Magurran, 2004). For diatoms, Passy (2016) found that under higher nutrient supply in streams impacted by agriculture, SADs were more even than in nutrient-poor forested streams. Likewise, Passy et al. (2018) documented that SAD evenness increased with nutrient input in U.S. streams, but nutrients did not affect evenness in Finnish streams. However, they also emphasised that broad biogeographical patterns in SAD are not only controlled by water chemistry but also by climatic variables, especially temperature seasonality and temperature extremes. In summary, these few studies highlight the fact that macroecological patterns in SAD, as well as in richness, are jointly controlled by local environment and large-scale climatic factors. A general rule is that, for diatoms, local factors appear to be more important than for most macroscopic taxa for which distributions are typically well-explained by large-scale climatic variables (Kharouba, McCune, Thuiller, & Huntley, 2013).

11. The influence of climate versus local environment for the distribution of diatoms

Traditionally, diatom distributions have been studied with respect to local water chemistry variables. Paleolimnologists investigating lake diatoms were probably the first researchers widely interested in the relationship between climatic factors, such as water temperature (Pienitz, Smol, & Birks, 1995) and air temperature (Lotter, Birks, Hofmann, & Marchetto, 1997), and diatoms. They typically used surface sediment training data sets and sediment core data with transfer functions to infer long-term changes in temperatures and concluded that water temperature linked to ice cover and stratification was a strong factor shaping the diatom communities (Weckström et al., 1997). More

recently, temperature effects on diatoms have also been studied in streams. Potapova and Charles (2002) documented that at the U.S. national scale, diatom assemblages clearly responded to variation in temperature. Notably, mean aerial temperature explained more variation in diatom assemblages than water temperature. This may be due to the fact that snapshot measurements of water temperature are less reliable than long-term temperature data due to wide temporal variation. One has to keep in mind, though, that long-term aerial temperature data do not necessarily reflect accurately stream temperatures that are influenced by inputs from groundwater and snow melt waters for example, which are typically cold. Pajunen, Luoto, and Soininen (2016) examined the influence of climatic versus local water chemistry variables on boreal stream diatom distributions in Finland. They found that climatic variables, especially growing degree days, may be stronger drivers for diatom species distributions than local environmental variables even at regional scales (c. 1,000 km). It could be envisaged that the climatic influence is even stronger at subcontinental or intercontinental scales due to the much longer gradients in temperature. To conclude, it is evident that the role of climatic variables in shaping diatom distributions have been severely underestimated especially in streams (but for lakes, see e.g. Rühland et al., 2015) because water chemistry was expected to dominate. We emphasise the urgent need for a stronger research focus on the role of climate in driving diatom distributions.

12. Which environmental factors control diatom species richness?

The question of key environmental drivers of diatom community composition in lakes and streams has been widely addressed in diatom ecology literature in recent years. This topic was reviewed by Soininen (2007) and is therefore not discussed here in detail. Instead, we focus here on diatom richness gradients, which have also been studied extensively recently. In general, diatom richness patterns are not well-explained by any unique or joint effects of the independent variables in regression models, such as generalised linear models or machine learning approaches, and thus, residual variation in the models is high. For example, Heino et al. (2010) documented that environmental and spatial variables only explained 25.5% of the variation in species richness. In studies by Pajunen et al. (2017) and Teittinen et al. (2017), only 13 and 35% of richness variation was jointly explained by measured local, catchment, and climatic variables for lotic and lentic diatoms, respectively. Such high residual variation may be due to several factors: (1) diatoms as small-sized organisms are relatively easily disturbed by rapid physical or biotic disturbances, which may favour local coexistence because competitive exclusions are prevented, and may lead to unpredictable richness patterns; (2) benthic diatom samples in the field may comprise cells from various types of microhabitats, which may result in high small-scale richness variation among the local samples that cannot be accounted for by any standard field measurements; and (3) the distributions of unicellular organisms are overall relatively stochastic, for example, due to complex dispersal processes at multiple spatial scales and are difficult to link with any measured environmental drivers (Soininen, Korhonen, & Luoto, 2013). Future studies should look for new ways to characterise the environment and its fluctuations

at different scales. For example, continuous tracking of environmental variables in the field or sampling the communities in multiple time steps would possibly reveal new insights into richness–environment relationships in diatoms. Moreover, sampling of diatoms in different microhabitats, at different spatial scales (e.g. within a riffle in multiple locations and across riffles) in streams and in lakes located at different positions within the landscape would allow better understanding of diatom coexistence under field conditions.

Even if diatom richness patterns are difficult to explain, some evidence for general environmental drivers exists. Among the most typical key variables are conductivity (Benito et al., 2018a; Heino et al., 2010; Stenger-Kovács, Hajnal, Lengyel, Buzckó, & Padisák, 2016), pH (Benito et al., 2018a; Stenger-Kovács et al., 2016; Teittinen et al., 2017; Wang et al., 2017), total phosphorus (Pajunen et al., 2017; Wang et al., 2017), elevation (Benito et al., 2018a), silica (Teittinen et al., 2017), ice cover and thermal stratification in lakes (Rühland et al., 2015), and shading and water depth in streams (Wang et al., 2017). Often the relationships between explaining variables and richness are not linear but unimodal. This is well-documented for example by Wang et al. (2017) in the form of unimodal elevation–richness relationships. Such patterns may arise because richness may be lower at low elevations due to negative effects of human impacts and also low at the highest elevations due to harsh environmental conditions where only the strongest taxa survive.

Overall, it can be envisaged that diatom species richness cannot often be reliably linked with any environmental variables. As a biodiversity metric, it is not always a useful indicator of ecological status. For example, in eutrophic waters, species richness can be relatively high. In addition, species richness may not vary among sites (or through time) even if community composition differs broadly (Wetzel et al., 2012). Then, richness does not capture the actual changes in communities (Hillebrand et al., 2018)—even if composition may strongly affect how ecosystems function (Downing &

Leibold, 2002). Future studies should perhaps concentrate more on how richness varies across space per se. For example, is there clear spatial autocorrelation in species richness meaning that neighbouring sites have similar levels of species richness or do species-rich or species-poor communities merely represent randomly distributed small patches in the landscape? Few studies suggest that such autocorrelation in richness is typically relatively weak but may be significant at small spatial scales (Heino et al., 2010; Jyrkänkallio-Mikkola et al., 2017) suggesting some patchiness in diatom species richness.

13. Do diatoms comply with any available metacommunity theory?

Metacommunity refers to a set of local communities, which are linked by the dispersal of some species present in the communities (Leibold & Chase, 2018; Leibold et al., 2004). At the heart of metacommunity ecology are four archetypes (species sorting, mass effects, patch dynamics and neutral theory) that differ from each other by the degree to which species have similar or dissimilar responses to environment, whether the local patches vary in their environmental conditions and by the rate of dispersal of individuals among the patches (Figure 2). For example, dispersal rates vary among these archetypes so that, in neutral dynamics, dispersal is typically limited in space (i.e. localised); sorting dispersal in species is sufficient for successful population establishment whenever environmental conditions allow; and mass effects are produced by a dispersal surplus (Leibold & Chase, 2018). The extent to which biological communities comply with these four models has also been tested extensively for diatom communities.

In lotic diatoms, most studies suggest that communities are influenced by the combination of limited dispersal and species sorting by the environment (Dong et al., 2016; Heino et al., 2015; Wetzel et al., 2012). Alternatively, lotic diatoms could be driven by mass effects especially at smaller spatial scales at which species dispersal is efficient, assuming there are no obvious dispersal barriers in the study

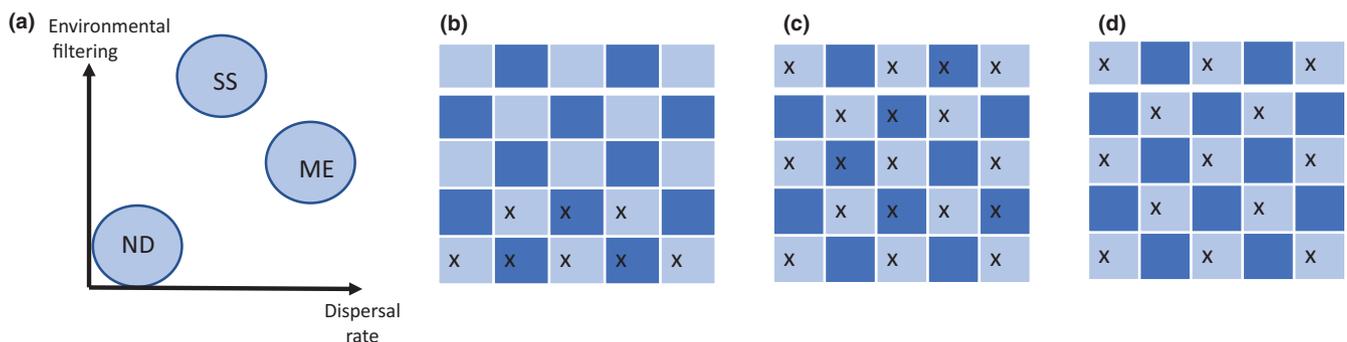


FIGURE 2 The main differences among the three metacommunity archetypes with regards to environmental filtering and dispersal rates. (a) The suggested location of neutral dynamics (ND), species sorting (SS), and mass effect (ME) along environmental filtering and dispersal rate axes. In ND, species occurrences are controlled by limited dispersal or ecological drift. In SS, species are filtered to sites by environment and dispersal rates are sufficient to ensure regional occurrence. In ME, species dispersal rates are so high that they can also occur at suboptimal sites. (b) The occurrence of a species in a landscape following ND. This species occurs both in suitable (light blue) and unsuitable (dark blue) sites and the occurrence is controlled by limited dispersal or ecological drift. (c) The occurrence of a species following mass effects. This species can be present not only in environmentally suitable sites, but may also inhabit unsuitable sites due to high dispersal rates. (d) The occurrence of a species following species sorting. This species only occurs at environmentally suitable sites. Dispersal is sufficient for the occurrence at any suitable site

area (Jamoneau, Passy, Soininen, Leboucher, & Tison-Rosebery, 2018). The mass effect suggests that species can be temporarily present at environmentally suboptimal sites if dispersal rates are high (e.g. typically in a downstream direction in lotic systems). Among lotic diatoms, there exists some evidence showing that the degree to which species follow neutral model, species sorting or mass effects may depend on species traits—motile species have been shown to comply with mass effects while low profile species may be more controlled by environmental filtering (Jamoneau et al., 2018).

Lakes are inherently more isolated for passively dispersing diatoms than stream networks especially if they lack interconnecting streams. Lake diatoms have been relatively rarely studied using the metacommunity concept. In one of these exceptions, Benito, Fritz, Steinitz-Kannan, Vélez, and McGlue (2018b) studied diatoms in number of lake clusters in the Andes and neighbouring lowlands and found that according to variance partitioning, dispersal mechanisms indicating neutral dynamics were a major contributor to diatom metacommunity structure, but in a highly context-dependent fashion across lake clusters. For example, in the Andean Altiplano and adjacent lowlands of Bolivia, diatom metacommunities were niche assembled but constrained either by dispersal limitation or mass effects. The outcomes of the specific metacommunity are dependent on size of the area, environmental heterogeneity, and ecological guild under consideration. Moreover, Vilmi, Tolonen, Karjalainen, and Heino (2017) studied littoral diatom metacommunities within a large oligotrophic lake in Finland. An interesting finding was that the compliance with mass effects varied among diatom morphological guilds (e.g. between low-profile and high-profile diatoms), indicating that there are certain differences in dispersal propensity between the guilds. In such a system without an evident water chemistry gradient, species sorting dynamics were weak. Szabo, Lengyel, Padisák, and Stenger-Kovács (2018) studied metacommunity patterns in soda pans in the Carpathian Basin and documented that metacommunity dissimilarities were mainly related to species turnover, not nestedness (Baselga, 2010). Furthermore, their analysis revealed that species sorting was the strongest factor related to community variation. To conclude, freshwater diatom metacommunities are typically structured by species sorting by the environment, but especially at larger scales, communities also comply with neutral dynamics. At smaller spatial scales, pure spatial component in the data is most likely to be due to mass effects. More generally, metacommunity studies are often plagued with spurious correlations between environment and space. We think that novel variation partition approaches that try to separate spatially structured environmental variation from spurious correlations between space and environment (e.g. Clappe, Dray, & Peres-Neto, 2018) would be essential for a better separation of environmental and spatial components in diatom studies.

14. Co-occurrence analysis and nestedness in diatoms

Ecological assembly rules refer to certain ecological *rules*, which investigate the circumstances under which species can co-occur at sites and were originally introduced by Diamond (1975). Assembly rules are

actually formed after searching for meaningful patterns in nature and how local communities are assembled from species pool, and include e.g. co-occurrence analyses (i.e. are there species combinations or pairs of species that tend to co-occur less frequently than by chance leading to *forbidden combinations* or checkerboard distribution) and patterns of nestedness. Nestedness refers to a situation where communities at species-poor sites are subsets of the communities at more species-rich sites. Heino and Soininen (2005) were among the first ones to investigate assembly rules in diatoms. They found that boreal stream diatoms exhibited significant nestedness and also found some species pairs that did occur much less frequently than by chance alone. However, at the same time, they acknowledged that nestedness patterns were perhaps weaker than for larger taxa and that checkerboard distributions could result from different environmental preferences, not from interspecific competition. In diatoms, such interactions may take place at very small spatial scales not detectable from routine diatom sampling. Moreover, at least in streams, competitive exclusions may be uncommon because of frequent physical disturbances that hinders such species exclusions.

More recently, nestedness in diatoms has been examined e.g. by Soininen (2008) and Tornés and Ruhí (2013). Overall, these studies suggest that diatoms do exhibit nestedness but it is typically weaker than among larger taxa. The reason could be that, as one of the main underlying factors for nestedness is ordered colonisation–extinction dynamics, and that for diatoms extinctions are not typical due to high dispersal rates, nestedness also is often relatively weak. Moreover, diatom distributions are often idiosyncratic due to random dispersal events, which tends to weaken nestedness pattern (Soininen, 2008). Bottin, Soininen, Alard, and Rosebery (2016) developed an approach that could account for species environmental preferences when investigating co-occurrences. They found that among stream diatoms, biotic interactions, especially competitive exclusions are not typical, but rather that communities are structured by colonisation patterns such as priority effects and mass effects. Such environmentally constrained null models add realism to systems where species are strongly structured by abiotic factors such as in diatoms.

15. Trait-based approaches in diatoms

Trait-based approaches (McGill, Enquist, Weiher, & Westoby, 2006) are currently used widely in ecological and environmental studies. Their key idea is that environment selects species based on their traits, not species identity, and thus trait variation may reflect better the environmental features than taxonomic composition. Trait-based approaches have been developed rather extensively for phytoplankton communities (Kruk et al., 2010; Reynolds, Huszar, Kruk, Naselli-Flores, & Melo, 2002). In lake diatoms, researchers have long been using planktonic to benthic species ratios to reflect major environmental changes such as water level fluctuations. Perhaps the earliest study on diatom traits exclusively in benthic habitats is the study by Passy (2007). She divided river benthic diatoms into low profile, high profile and motile guilds with an idea that these groups would respond differently to resources (nutrient, light) and disturbances (flow conditions, grazers). The low-profile diatoms are likely to be resource-limited but

TABLE 1 A summary table of the 10 selected important research questions or topics for the spatial ecology of diatoms

Question	Main findings	Key references
1. Drivers of diatom species richness	Key local factors: conductivity, pH, phosphorus, thermal stratification	Heino et al. (2010), Röhland et al. (2015), Wang et al. (2017)
2. Latitudinal richness gradient	No consistent linear latitudinal gradient	Passy (2010), Schiaffiano et al. (2016)
3. Species–area relationship	No consistent support (very few studies only)	Patrick (1967), Teittinen and Soininen (2015)
4. Abundance–/occupancy relationship	Positive relationship	Heino and Soininen (2005), Rocha et al. (2018)
5. Rapoport's rule	No support (studied only along elevation)	Wang et al. (2017)
6. Bergmann's rule	Some studies support, some do not	Adams et al. (2013), Svensson et al. (2014)
7. Niche conservatism	Some studies support, some do not	Bennett et al. (2010)
8. Patterns in elevational diversity	Species richness shows variable patterns along elevation	Wang et al. (2011), Teittinen et al. (2017), Wang et al. (2017)
9. Main metacommunity theory for diatoms	Species sorting seems to dominate but communities are also affected by neutrality and mass effects. Mass effects are typical at smaller spatial scales	Heino et al. (2015)
10. Nestedness	Diatom communities are typically nested, but nestedness is weaker than for larger taxa	Heino and Soininen (2005), Tornés and Ruhí (2013)

will be resistant to physical disturbance. The high-profile diatoms are not resource-limited as they have access to nutrients and light but disturbance-stressed because they would be prone to flow disturbance and grazers. The motile diatoms can select the most suitable habitat and are comparatively free of both resource limitation and disturbance stress. She found highly predictable variation in these guilds along nutrient and disturbance gradients in test regions in the U.S. and Bulgaria. Such trait division has since then been used successfully in a number of papers and related with stream environmental features (e.g. Dong et al., 2016) and also in lakes (Benito et al., 2018b).

Tapolczai, Bouchez, Stenger-Kovács, Padisák, and Rimet (2016) recently suggested two trait-based methods: (1) using

ordination techniques to form groups of species with similar traits based on literature or experiments; and (2) identifying groups of species adapted to certain environmental conditions in the same way as functional groups are defined in phytoplankton (Reynolds et al., 2002). One of the recent trait-based approaches for all stream algae was introduced by Lange, Townsend, and Matthaei (2016), where traits are grouped in trait categories and coupled e.g. with resource acquisition, resistance to disturbance and predator avoidance. Recently, Soininen et al. (2016) showed that, at the global scale, a trait-based approach for stream diatoms better reflected environmental gradients across regions while taxonomical composition was more related to spatial location of the

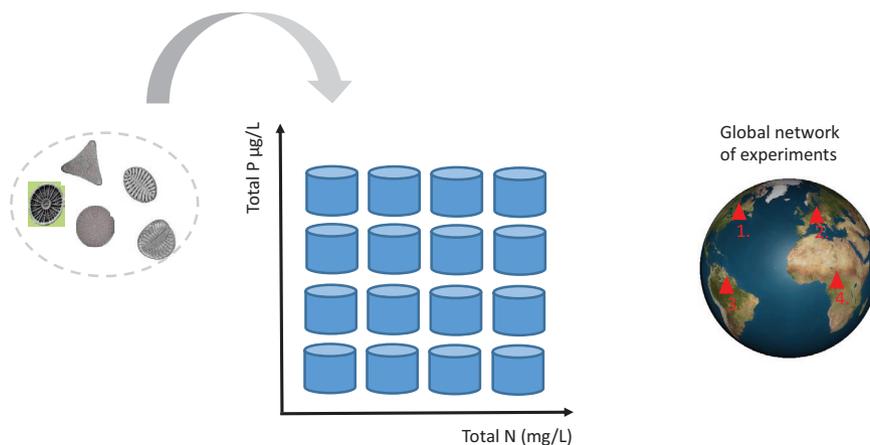


FIGURE 3 An example of macroecological experiment in the field using diatoms (or any other microbes colonised passively). Local environmental conditions can be manipulated e.g. using two-way factorial (N + P) experiment while letting diatoms freely colonise the local microcosms from the air. Diatom colonisation dynamics can be followed using a number of artificial tiles, which are sampled one-by-one through time until the end of the experiment. Such an experimental setting can be replicated in space to build a network and conducted e.g. at different continents, latitudes, or elevation or at islands with varying distance from the continent

sampling sites. Thus, it appears that the trait-based approach may be useful especially for diatom studies aiming to reveal environmental changes. Collectively, some freshwater diatom studies have moved on from taxonomical approaches and started to use trait-based methods in order to better reflect and predict rapid the environmental changes we currently face. We suggest that researchers examine diatom trait structure further especially at large intercontinental or global scales. This is because at such large scales, diatom bioindicators may have surprisingly low reliability due to the differences in regional species pools (i.e. same indicator species may not be present in all regions) and in species' ecological preferences (i.e. species may have different environmental preferences in different regions due to local adaptation; Soininen et al., 2019; Telford, Vandvik, & Birks, 2006). Such studies may be thus useful when developing new ways to monitor surface water quality with diatoms.

2 | CONCLUSIONS AND OUTLOOK

To conclude, based on evidence assembled so far, diatoms do not seem to lend consistent support for classical biogeographical patterns such as LDG, SAR, or Rapoport's rule (Table 1). However, there seems to be somewhat stronger support for elevational diversity gradients, Bergmann's rule and niche conservatism. Diatoms do support positive interspecific abundance-occupancy relationship, a finding which seems consistent across virtually all taxa. With regards to metacommunity dynamics, diatom communities are typically structured by species sorting, but neutral dynamics may be evident at larger spatial scales, whereas mass effects could be acting at small spatial scales within which species dispersal among sites is effective. In the future, we hope that researchers will consider (1) investing more resources in spatially replicated macroecological field experiments (Bell, 2010; Wang, Pan, Soininen, Heino, & Shen, 2016) in which local environmental conditions can be manipulated while letting diatoms (and any other microbes) colonise microcosms freely from air (Figure 3). Applied at large spatial scales, this approach would give more insights into diatom biogeographical patterns and the influence of species pools on local communities since the water chemistry could be controlled for across experimental sites. Such an approach would thus help us to reveal better whether the view "everything is everywhere, but the environment selects" applies for diatoms. We also suggest that (2) more diatom studies with intercontinental or global coverage and with consistent sampling effort and methodology across different geographical regions. With relevant climatic, land use and water chemistry data, such intercontinental or global diatom database would be valuable for evaluating the roles of different environmental drivers and biogeographical factors on diatoms. We also encourage researchers to (3) combine morphological species identification with DNA-based approaches (Kerमारrec et al., 2013) and trait-based methods (Passy, 2007) in order to elaborate the spatial ecology of diatoms. New identification tools would be useful not only for basic research, but also for diatom-based biomonitoring

approaches, which build on proper understanding of observed species distributions and their underlying drivers. Likewise, trait-based approaches may provide new instruments to understand and predict rapid environmental changes ecosystems currently face. Finally (4), we see great potential in the fossil evidence, such as in ancient DNA, to better understand modern diatom distributions (Nanjappa, Audic, Romac, Kooistra, & Zingone, 2014).

ACKNOWLEDGMENTS

We thank John P. Smol and one anonymous referee for the constructive comments on our manuscript.

CONFLICT OF INTEREST

Authors declare no conflict of interest.

ORCID

Janne Soininen  <https://orcid.org/0000-0002-8583-3137>

Anette Teittinen  <https://orcid.org/0000-0002-0531-4530>

REFERENCES

- Abarca, N., Jahn, R., Zimmermann, J., & Enke, N. (2014). Does the cosmopolitan diatom *Gomphonema parvulum* (Kutzing) have a biogeography? *PLoS ONE*, *9*, e86885. <https://doi.org/10.1371/journal.pone.0086885>
- Adams, G. L., Pichler, D. E., Cox, E. J., O'Gorman, E. J., Seeney, A., Woodward, G., & Reuman, D. C. (2013). Diatoms can be an important exception to temperature-size rules at species and community levels of organization. *Global Change Biology*, *19*, 3540–3552.
- Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R., & Muotka, T. (2012). Distance decay of similarity in freshwater communities: Do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography*, *21*, 365–375. <https://doi.org/10.1111/j.1466-8238.2011.00681.x>
- Baas-Becking, L. G. M. (1934). *Geobiologie of inleiding tot de milieukunde*. The Hague, The Netherlands: W.P. Van Stockum & Soon.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Bell, T. (2010). Experimental tests of the bacterial distance–decay relationship. *ISME Journal*, *4*, 1357–1365. <https://doi.org/10.1038/ismej.2010.77>
- Benito, X., Fritz, S., Steinitz-Kannan, M., Tapia, P. M., Kelly, M. A., & Lowell, T. V. (2018a). Geo-climatic factors drive diatom community distribution in tropical South American freshwaters. *Journal of Ecology*, *106*, 1660–1672. <https://doi.org/10.1111/1365-2745.12934>
- Benito, X., Fritz, S., Steinitz-Kannan, M., Vélez, M. I., & McGlue, M. M. (2018b). Lake regionalization and diatom metacommunity structuring in tropical South America. *Ecology and Evolution*, *8*, 7865–7878. <https://doi.org/10.1002/ece3.4305>
- Bennett, J. R., Cumming, B. F., Ginn, B. K., & Smol, J. P. (2010). Broad-scale environmental response and niche conservatism in lacustrine diatom communities. *Global Ecology and Biogeography*, *19*, 724–732.
- Blackburn, T. B., Cassey, P., & Gaston, K. J. (2006). Variations on a theme: Sources of heterogeneity in the form of the interspecific relationship

- between abundance and distribution. *Journal of Animal Ecology*, 75, 1426–1439. <https://doi.org/10.1111/j.1365-2656.2006.01167.x>
- Bolgovics, Á., Ács, É., Várbiro, G., Görgényi, J., & Borics, G. (2016). Species area relationship (SAR) for benthic diatoms: A study on aquatic islands. *Hydrobiologia*, 764, 91–102. <https://doi.org/10.1007/s10750-015-2278-1>
- Bottin, M., Soininen, J., Alard, D., & Rosebery, J. (2016). Diatom co-occurrence shows less segregation than predicted from niche modeling. *PLoS ONE*, 11, e0154581. <https://doi.org/10.1371/journal.pone.0154581>
- Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, 124, 255–279. <https://doi.org/10.1086/284267>
- Cantonati, M., Füreder, L., Gerecke, R., Jüttner, I., & Cox, E. J. (2012). Crenic habitats, hotspots for freshwater biodiversity conservation: Toward an understanding of their ecology. *Freshwater Science*, 31, 463–480. <https://doi.org/10.1899/11-111.1>
- Casteleyn, G., Leliaert, F., Backeljau, T., Debeer, A.-E., Kotaki, Y., Rhodes, L., ... Vyverman, W. (2010). Limits to gene flow in a cosmopolitan marine planktonic diatom. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 12952–12957. <https://doi.org/10.1073/pnas.1001380107>
- Cermeño, P., & Falkowski, P. G. (2009). Controls on diatom biogeography in the ocean. *Science*, 325, 1539–1541. <https://doi.org/10.1126/science.1174159>
- Clappe, S., Dray, S., & Peres-Neto, P. R. (2018). Beyond neutrality: Disentangling the effects of species sorting and spurious correlations in community analysis. *Ecology*, 99, 1737–1747. <https://doi.org/10.1002/ecy.2376>
- Diamond, J. M. (1975). *Assembly of species communities*. In M. L. Cody, & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–444). Cambridge, MA: Harvard University Press.
- Dong, X., Li, B., He, F., Gu, Y., Sun, M., Zhang, H., ... Cai, Q. (2016). Flow directionality, mountain barriers, and functional traits determine diatom metacommunity structuring of high mountain streams. *Scientific Reports*, 6, 24711. <https://doi.org/10.1038/srep24711>
- Downing, A. L., & Leibold, M. A. (2002). Ecosystem consequences of species richness and composition in pond food webs. *Nature*, 416, 837–841. <https://doi.org/10.1038/416837a>
- Fierer, N., & Jackson, R. B. (2006). The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 626–631. <https://doi.org/10.1073/pnas.0507535103>
- Finlay, B. J. (2002). Global dispersal of free-living microbial eukaryote species. *Science*, 296, 1061–1063. <https://doi.org/10.1126/science.1070710>
- Fuhrman, J. A., Steele, J. A., Hewson, I., Schwalbach, M. S., Brown, M. V., Green, J. L., & Brown, J. H. (2008). A latitudinal diversity gradient in planktonic marine bacteria. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 7774–7778. <https://doi.org/10.1073/pnas.0803070105>
- Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and process in macroecology*. Oxford, UK: Blackwell. <https://doi.org/10.1002/9780470999592>
- Gaston, K. J., Blackburn, T. M., & Lawton, J. H. (1997). Interspecific abundance-range size relationships: An appraisal of mechanisms. *Journal of Animal Ecology*, 66, 579–601. <https://doi.org/10.2307/5951>
- Green, J. L., Holmes, A. J., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., ... Beattie, A. J. (2004). Spatial scaling of microbial eukaryote diversity. *Nature*, 432, 747–749. <https://doi.org/10.1038/nature03034>
- Heino, J., Bini, L. M., Karjalainen, S. M., Mykrä, H., Soininen, J., Vieira, L. C. G., & Diniz-Filho, J. A. F. (2010). Geographical patterns of micro-organismal community structure: Are diatoms ubiquitously distributed across boreal streams? *Oikos*, 119, 129–137. <https://doi.org/10.1111/j.1600-0706.2009.17778.x>
- Heino, J., Melo, A. S., Jyrkänkallio-Mikkola, J., Petsch, D. K., Saito, V. S., Tolonen, K. T., ... Siqueira, T. (2018). Subtropical streams harbour higher genus richness and lower abundance of insects compared to boreal streams, but scale matters. *Journal of Biogeography*, 45, 1983–1993. <https://doi.org/10.1111/jbi.13400>
- Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshwater Biology*, 60, 845–869. <https://doi.org/10.1111/fwb.12533>
- Heino, J., & Soininen, J. (2005). Assembly rules and community models for unicellular organisms: Patterns in diatoms of boreal streams. *Freshwater Biology*, 50, 567–577. <https://doi.org/10.1111/j.1365-2427.2005.01346.x>
- Heino, J., & Soininen, J. (2006). Regional occupancy in unicellular eukaryotes: A reflection of niche breadth, habitat availability, or size-related dispersal capacity? *Freshwater Biology*, 51, 672–685. <https://doi.org/10.1111/j.1365-2427.2006.01520.x>
- Hildrew, A., Raffaelli, D., & Edmonds-Brown, R. (2007). *Body size: The structure and function of aquatic ecosystems*. Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/cbo9780511611232>
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163, 192–211. <https://doi.org/10.1086/381004>
- Hillebrand, H., & Azovski, A. I. (2001). Body size determines the strength of the latitudinal diversity gradient. *Ecography*, 24, 251–256. <https://doi.org/10.1034/j.1600-0587.2001.240302.x>
- Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., ... Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, 55, 169–184. <https://doi.org/10.1111/1365-2664.12959>
- Horner-Devine, M. C., Lage, M., Hughes, J. B., & Bohannon, B. J. M. (2004). A taxa-area relationship for bacteria. *Nature*, 432, 750–753. <https://doi.org/10.1038/nature03073>
- Jamoneau, J., Passy, S. I., Soininen, J., Lebourcier, T., & Tison-Rosebery, J. (2018). Beta diversity of diatom species and ecological guilds: Response to environmental and spatial mechanisms along the stream watercourse. *Freshwater Biology*, 63, 62–73. <https://doi.org/10.1111/fwb.12980>
- Jüttner, I., Chimonides, P. D. J., Ormerod, S. J., & Cox, E. J. (2010). Ecology and biogeography of Himalayan diatoms: Distribution along gradients of altitude, stream habitat and water chemistry. *Fundamental and Applied Limnology*, 177, 293–311. <https://doi.org/10.1127/1863-9135/2010/0177-0293>
- Jyrkänkallio-Mikkola, J., Meier, S., Heino, J., Laamanen, T., Pajunen, V., Tolonen, K. T., ... Soininen, J. (2017). Disentangling multi-scale environmental effects on stream microbial communities. *Journal of Biogeography*, 44, 1512–1523. <https://doi.org/10.1111/jbi.13002>
- Keck, F., Franc, A., & Kahlert, M. (2018). Disentangling the processes driving the biogeography of freshwater diatoms: A multiscale approach. *Journal of Biogeography*, 45, 1582–1592. <https://doi.org/10.1111/jbi.13239>
- Kermarrec, L., Franc, A., Rimet, F., Chaumeil, P., Humbert, F., & Bouchez, A. (2013). Next-generation sequencing to inventory taxonomic diversity in eukaryotic communities: A test for freshwater diatoms. *Molecular Ecology Resources*, 13, 607–619. <https://doi.org/10.1111/1755-0998.12105>
- Kharouba, H. M., McCune, J. L., Thuiller, W., & Huntley, B. (2013). Do ecological differences between taxonomic groups influence the relationship between species' distributions and climate? A global meta-analysis using species distribution models. *Ecography*, 36, 657–664. <https://doi.org/10.1111/j.1600-0587.2012.07683.x>

- Korhola, A., Weckström, J., & Nyman, M. (1999). Predicting the long-term acidification trends in small subarctic lakes using diatoms. *Journal of Applied Ecology*, *36*, 1021–1034. <https://doi.org/10.1046/j.1365-2664.1999.00461.x>
- Kruk, C., Huszar, V. L. M., Peeters, E. T. H. M., Bonilla, S., Costa, L., Lurling, M., ... Scheffer, M. (2010). A morphological classification capturing functional variation in phytoplankton. *Freshwater Biology*, *55*, 614–627. <https://doi.org/10.1111/j.1365-2427.2009.02298.x>
- Lange, K., Townsend, C. R., & Matthaei, C. D. (2016). A trait-based framework for stream algal communities. *Ecology and Evolution*, *6*, 23–36. <https://doi.org/10.1002/ece3.1822>
- Leibold, M. A., & Chase, J. M. (2018). *Metacommunity ecology. Monographs in population biology* 59. Princeton, NJ: Princeton University Press. <https://doi.org/10.1515/9781400889068>
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., ... Gonzales, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*, 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Lotter, A. F., Birks, H. J. B., Hofmann, W., & Marchetto, A. (1997). Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology*, *18*, 395–420. <https://doi.org/10.1023/a:1007982008956>
- Magurran, A. E. (2004). *Measuring biological diversity*. Oxford, UK: Blackwell Publishing.
- Marquet, P. A., Navarrete, S. A., & Castilla, J. C. (1990). Scaling population-density to body size in rocky intertidal communities. *Science*, *250*, 1125–1127. <https://doi.org/10.1126/science.250.4984.1125>
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., ... White, E. P. (2007). Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, *10*, 995–1015. <https://doi.org/10.1111/j.1461-0248.2007.01094.x>
- Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, *30*, 331–351. <https://doi.org/10.1046/j.1365-2699.2003.00837.x>
- Meyer, K. M., Memiaghe, H., Korte, L., Kenfack, D., Alonso, A., & Bohannan, B. J. M. (2018). Why do microbes exhibit weak biogeographic patterns. *The ISME Journal*, *12*, 1404–1413. <https://doi.org/10.1038/s41396-018-0103-3>
- Nanjappa, D., Audic, S., Romac, S., Kooistra, W. H. C. F., & Zingone, A. (2014). Assessment of species diversity and distribution of an ancient diatom lineage using a DNA metabarcoding approach. *PLoS ONE*, *9*, e103810. <https://doi.org/10.1371/journal.pone.0103810>
- Ormerod, S. J., Rundle, S. D., Wilkinson, S. M., Daly, G. P., Dale, K. M., & Jüttner, I. (1994). Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. *Freshwater Biology*, *32*, 309–322. <https://doi.org/10.1111/j.1365-2427.1994.tb01128.x>
- Pajunen, V., Luoto, M., & Soininen, J. (2016). Climate is an important driver for stream diatom distributions. *Global Ecology and Biogeography*, *25*, 198–206. <https://doi.org/10.1111/geb.12399>
- Pajunen, V., Luoto, M., & Soininen, J. (2017). Unravelling direct and indirect effects of hierarchical factors driving microbial stream communities. *Journal of Biogeography*, *44*, 2376–2385. <https://doi.org/10.1111/jbi.13046>
- Passy, S. I. (2007). Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. *Aquatic Botany*, *86*, 171–178. <https://doi.org/10.1016/j.aquabot.2006.09.018>
- Passy, S. I. (2008). Species size and distribution jointly and differentially determine diatom densities in U.S. streams. *Ecology*, *89*, 475–484. <https://doi.org/10.1890/07-0405.1>
- Passy, S. I. (2010). A distinct latitudinal gradient of diatom diversity is linked to resource supply. *Ecology*, *91*, 36–41. <https://doi.org/10.1890/09-0545.1>
- Passy, S. I. (2012). A hierarchical theory of macroecology. *Ecology Letters*, *15*, 923–934. <https://doi.org/10.1111/j.1461-0248.2012.01809.x>
- Passy, S. I. (2016). Abundance inequality in freshwater communities has an ecological origin. *The American Naturalist*, *187*, 502–516. <https://doi.org/10.1086/685424>
- Passy, S. I., Larson, C. A., Jamoneau, A., Budnick, W., Heino, J., Lebourcier, T., ... Soininen, J. (2018). The biogeographical patterns of species richness and abundance distribution in stream diatoms are driven by climate and water chemistry. *The American Naturalist*, *192*, 605–617. <https://doi.org/10.1086/699830>
- Patrick, R. (1967). The effect of invasion rate, species pool, and size of area on the structure of the diatom community. *Proceedings of the National Academy of Sciences of the United States of America*, *58*, 1335–1967.
- Pienitz, R., Smol, J. P., & Birks, H. J. B. (1995). Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology*, *13*, 21–49. <https://doi.org/10.1007/bf00678109>
- Potapova, M. G., & Charles, D. F. (2002). Benthic diatoms in USA rivers: Distributions along spatial and environmental gradients. *Journal of Biogeography*, *29*, 167–187. <https://doi.org/10.1046/j.1365-2699.2002.00668.x>
- Reche, I., Pulido-Villena, E., Morales-Baquero, R., & Casamayor, E. O. (2005). Does ecosystem size determine aquatic bacterial richness? *Ecology*, *86*, 1715–1722. <https://doi.org/10.1890/04-1587>
- Reynolds, C. S., Huszar, V., Kruk, C., Naselli-Flores, L., & Melo, S. (2002). Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, *24*, 417–428. <https://doi.org/10.1093/plankt/24.5.417>
- Rocha, M. P., Bini, L. M., Siqueira, T., Hjort, J., Grönroos, M., Lindholm, M., ... Heino, J. (2018). Predicting occupancy and abundance by niche position, niche breadth and body size in stream organisms. *Oecologia*, *186*, 205–216. <https://doi.org/10.1007/s00442-017-3988-z>
- Rühland, K. M., Paterson, A. M., & Smol, J. P. (2015). Lake diatom responses to warming—reviewing the evidence. *Journal of Paleolimnology*, *54*, 1–35. <https://doi.org/10.1007/s10933-015-9837-3>
- Schiaffano, M. R., Lara, E., Fernandez, L. D., Balague, V., Singer, D., Seppey, C. C. W., ... Izaguirre, I. (2016). Microbial eukaryote communities exhibit robust biogeographical patterns along a gradient of Patagonian and Antarctic lakes. *Environmental Microbiology*, *18*, 5249–5264. <https://doi.org/10.1111/1462-2920.13566>
- Soininen, J. (2007). Environmental and spatial control of freshwater diatoms—a review. *Diatom Research*, *22*, 473–490. <https://doi.org/10.1080/0269249x.2007.9705724>
- Soininen, J. (2008). The ecological characteristics of idiosyncratic and nested diatoms. *Protist*, *159*, 65–72.
- Soininen, J., & Heino, J. (2005). Relationships between local population persistence, local abundance and regional occupancy of species: Distribution patterns of diatoms in boreal streams. *Journal of Biogeography*, *32*, 1971–1978. <https://doi.org/10.1111/j.1365-2699.2005.01342.x>
- Soininen, J., Jamoneau, A., Rosebery, J., Lebourcier, T., Wang, J., Kokocinski, M., & Passy, S. I. (2019). Stream diatoms exhibit weak niche conservation along global environmental and climatic gradients. *Ecography*, *42*, 346–353. <https://doi.org/10.1111/ecog.03828>
- Soininen, J., Jamoneau, A., Rosebery, J., & Passy, S. I. (2016). Global patterns and drivers of species and trait composition in diatoms. *Global Ecology and Biogeography*, *25*, 940–950. <https://doi.org/10.1111/geb.12452>

- Soininen, J., & Kokocinski, M. (2006). Regional diatom body size distributions in streams—does size vary along environmental, spatial and diversity gradients? *Ecoscience*, 13, 271–274. <https://doi.org/10.2980/11195-6860-13-2-271.1>
- Soininen, J., Korhonen, J. J., & Luoto, M. (2013). Stochastic species distributions are driven by organism size. *Ecology*, 94, 660–670. <https://doi.org/10.1890/12-0777.1>
- 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. <https://doi.org/10.1111/j.0906-7590.2004.03749.x>
- Souffreau, C., Vanormelingen, P., Van de Vijver, B., Isheva, T., Verleyen, E., Sabbe, K., & Vyverman, W. (2013). Molecular evidence for distinct Antarctic lineages in the cosmopolitan terrestrial diatoms *Pinnularia borealis* and *Hantzschia amphioxys*. *Protist*, 164, 101–115. <https://doi.org/10.1016/j.protis.2012.04.001>
- Stenger-Kovács, C., Hajnal, É., Lengyel, E., Buzsák, K., & Padišák, J. (2016). A test of traditional diversity measures and taxonomic distinctness indices on benthic diatoms of soda pans in the Carpathian basin. *Ecological Indicators*, 64, 1–8. <https://doi.org/10.1016/j.ecolind.2015.12.018>
- Stomp, M., Huisman, J., Mittelbach, G. G., Litchman, E., & Klausmeier, C. A. (2011). Large-scale biodiversity patterns in freshwater phytoplankton. *Ecology*, 92, 2096–2107. <https://doi.org/10.1890/10-1023.1>
- Storch, D., Marquet, P. A., & Brown, J. H. (Eds.). (2007). *Scaling biodiversity*. Cambridge, UK: Cambridge University Press.
- Svensson, F., Norberg, J., & Snoeijs, P. (2014). Diatom cell size, coloniality, and motility: Trade-offs between temperature, salinity and nutrient supply with climate change. *PLoS ONE*, 9, e109993. <https://doi.org/10.1371/journal.pone.0109993>
- Szabo, B., Lengyel, E., Padišák, J., & Stenger-Kovács, C. (2018). Benthic diatom metacommunity across small freshwater lakes: Driving mechanisms, diversity and ecological uniqueness. *Hydrobiologia*, 828, 183–198.
- Tapolczai, K., Bouchez, A., Stenger-Kovács, C., Padišák, J., & Rimet, F. (2016). Trait-based ecological classifications for benthic algae: Review and perspectives. *Hydrobiologia*, 776, 1–17. <https://doi.org/10.1007/s10750-016-2736-4>
- Teittinen, A., Kallajoki, L., Meier, S., Stigzelius, T., & Soininen, J. (2016). The roles of elevation and local environmental factors as drivers of diatom diversity in subarctic streams. *Freshwater Biology*, 61, 1509–1521. <https://doi.org/10.1111/fwb.12791>
- Teittinen, A., & Soininen, J. (2015). Testing the theory of island biogeography for microorganisms—patterns for spring diatoms. *Aquatic Microbial Ecology*, 75, 239–250. <https://doi.org/10.3354/ame01759>
- Teittinen, A., Wang, J., Strömgård, S., & Soininen, J. (2017). Local and geographical factors jointly drive elevational patterns in three microbial groups across subarctic ponds. *Global Ecology and Biogeography*, 26, 973–982. <https://doi.org/10.1111/geb.12607>
- Telford, R. J., Vandvik, V., & Birks, H. J. B. (2006). Dispersal limitations matter for microbial morphospecies. *Science*, 312, 1015. <https://doi.org/10.1126/science.1125669>
- Tornés, E., & Ruhí, A. (2013). Flow intermittency decreases nestedness and specialization of diatom communities in Mediterranean rivers. *Freshwater Biology*, 58, 2555–2566. <https://doi.org/10.1111/fwb.12232>
- Vanormelingen, P., Verleyen, E., & Vyverman, W. (2009). The diversity and distribution of diatoms: From cosmopolitanism to narrow endemism. *Biodiversity and Conservation*, 17, 159–171.
- Verleyen, E., Vyverman, W., Sterken, M., Hodgson, D. A., De Wever, A., Juggins, S., ... Sabbe, K. (2009). The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. *Oikos*, 118, 1239–1249. <https://doi.org/10.1111/j.1600-0706.2009.17575.x>
- Vilmi, A., Tolonen, K. T., Karjalainen, S. M., & Heino, J. (2017). Metacommunity structuring in a highly-connected aquatic system: Effects of dispersal, abiotic environment and grazing pressure on microalgal guilds. *Hydrobiologia*, 790, 125–140. <https://doi.org/10.1007/s10750-016-3024-z>
- Vyverman, W., Verleyen, E., Sabbe, K., Vanhoutte, K., Sterken, M., Hodgson, D. A., ... De Wever, A. (2007). Historical processes constrain patterns in global diatom diversity. *Ecology*, 88, 1924–1931. <https://doi.org/10.1890/06-1564.1>
- Wang, J., Meier, S., Soininen, J., Casamayor, E., Pan, F., Tang, X., ... Shen, J. (2017). Regional and global elevational patterns of microbial species richness and evenness. *Ecography*, 40, 393–402. <https://doi.org/10.1111/ecog.02216>
- Wang, J., Pan, F., Soininen, J., Heino, J., & Shen, J. (2016). Nutrient enrichment modifies temperature-biodiversity relationships in large-scale field experiments. *Nature Communications*, 7, 13960. <https://doi.org/10.1038/ncomms13960>
- Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X., & Shen, J. (2011). Contrasting patterns in elevational diversity between microorganisms and macroorganisms. *Journal of Biogeography*, 38, 595–603. <https://doi.org/10.1111/j.1365-2699.2010.02423.x>
- Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X., & Shen, J. (2012). Patterns of elevational beta diversity in micro- and macroorganisms. *Global Ecology and Biogeography*, 21, 743–750. <https://doi.org/10.1111/j.1466-8238.2011.00718.x>
- Weckström, J., Korhola, A., & Blom, T. (1997). The relationship between diatoms and water temperature in thirty subarctic Fennoscandian lakes. *Arctic and Alpine Research*, 29, 75–92. <https://doi.org/10.2307/1551838>
- Wetzel, C. E., Bicudo, D. C., Ector, L., Lobo, E. A., Soininen, J., & Bini, L. M. (2012). Distance decay of similarity in Neotropical diatom communities. *PLoS ONE*, 7, e45071. <https://doi.org/10.1371/journal.pone.0045071>
- Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., ... Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, 13, 1310–1324. <https://doi.org/10.1111/j.1461-0248.2010.01515.x>
- Winter, J. G., & Duthie, H. C. (2000). Epilithic diatoms as indicators of stream total N and total P concentration. *Journal of the North American Benthological Society*, 19, 32–49. <https://doi.org/10.2307/1468280>

How to cite this article: Soininen J, Teittinen A. Fifteen important questions in the spatial ecology of diatoms.

Freshwater Biol. 2019;00:1–13. <https://doi.org/10.1111/fwb.13384>