Deterministic and Stochastic Effects on Freshwater Diatom Biodiversity and Community Composition

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Abstract

Recent research on diatom metacommunities has focused on disentangling the assembly mechanisms driving species and functional composition and biodiversity across space and time, including deterministic (environmental filtering and biotic interactions) and stochastic processes (dispersal and ecological drift). In this chapter, we provide an overview of this research and outline future directions. Environmental filtering and dispersal have received the most attention, while biotic interactions and ecological drift have remained comparatively understudied and require more investigations. We discuss diatom species and functional responses

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to major environmental factors, operating at local scales, including inorganic and organic acidity, conductivity, and limiting nutrients, and at regional scales, namely land use and climate. Research has shown that both high rates of dispersal (mass effects) and low rates of dispersal (limited dispersal) are responsible for species and guild composition. We recommend further observational but also experimental investigations on the relative importance of assembly mechanisms across spatial and temporal scales and along latitudinal, longitudinal, and elevational gradients. Global change with respect to climate, land use, and dissolved organic matter has been recognized as an important driver of diatom compositional and biodiversity shifts. However, further modeling work and building harmonized global diatom databases that encompass spatial and temporal observations as well as morphological and molecular data may be necessary to forecast possible diatom community and functional responses in the decades ahead.

Keywords: Biotic interactions, dispersal limitation, ecological drift, environmental filtering, guilds, mass effects, niche, priority effects

4.1   Introduction

The overarching goal of this chapter is to provide a review of recent investigations on the assembly mechanisms driving freshwater diatom species and functional composition and biodiversity (see Table 4.1 for definitions and examples), identify knowledge gaps, and suggest future directions. These mechanisms include deterministic (environmental filtering and biotic interactions) and stochastic processes (dispersal and ecological drift) as well as priority effects (e.g., when dispersal coupled with biotic interactions over time lead to spatial variability in community composition) [4.1] [4.2]. Deterministic abiotic and biotic processes constrain species niches and generate predictable species distributions, consistent with the classical work of Hutchinson [4.3]. Species distributions are also subject to stochastic processes, related to random dispersal and random variability in birth and death rates (i.e., ecological drift), as suggested by the influential theories of island biogeography [4.4] and the unified neutral theory of biodiversity [4.5]. Dispersal can have opposing effects on species communities. High rates of dispersal (mass effects) can offset environmental filtering via source-sink effects, i.e., when propagules from source locations with favorable environmental conditions are dispersed to sink locations with unfavorable environmental conditions [4.6]. Low rates of dispersal, on the other hand, may prevent species from occurring in suitable habitats.

Table 4.1 A glossary of the main concepts discussed in this chapter with supporting evidence.

Concept	Definition	Supporting evidence
Metacommunity	A set of local communities that are connected by dispersal. Metacommunities are governed by assembly mechanisms, encompassing deterministic and stochastic processes (defined below).	Recent diatom metacommunity research shows that connectivity among sites is a key factor underlying biodiversity patterns. For example, in both lotic and lentic systems, limited dispersal due to isolation is a major force structuring diatom metacommunities even when deterministic processes are expected due to environmental variability [4.164].
Deterministic (niche) processes	Processes that generate predictable community responses, including environmental filtering and biotic interactions. They are also referred to as niche processes because the biotic response depends on species' ecological niches, i.e., the set of environmental conditions necessary for positive growth.	
Environmental filtering	Abiotic factors dictate the occurrence of species in a particular location.	The available empirical evidence suggests that lotic and lentic diatoms can be filtered out from the regional pool by physical (e.g., light, mixing), hydrological (e.g., discharge, water depth), and chemical factors (e.g., pH, nutrients, conductivity) [4.51] [4.165]

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Table 4.1 A glossary of the main concepts discussed in this chapter with supporting evidence. (*Continued*)

Concept	Definition	Supporting evidence
Biotic interactions	Positive (e.g., facilitation and commensalism) or negative interactions (e.g., competition and predation) constrain species assemblages.	Grazing pressure (e.g., by macroinvertebrates) may have comparatively little effect on diatom metacommunity patterns at larger scales [4.24]. Negative correlation between the abundances of two common stream diatoms, *Achnanthidium minutissimum* and *Cocconeis placentula*, was attributed to competitive exclusion at the local scale [4.108].
		Passy [4.106] developed a framework viewing guild density in benthic diatom metacommunities as a function of environmental gradients, space, and species interactions, both competitive and facilitative (measured as species richness of the competitor or facilitator guild, respectively). Testing of this framework revealed that guild density was controlled mostly by biotic interactions and/or the environment. However, at shorter environmental gradients in an experimental setting, biotic interactions did not appear to affect guild density [4.166]. Niche modeling approaches also concluded that biotic interactions did not structure species co-occurrences, which appeared to be "passive" [4.125].

(*Continued*)

Table 4.1 A glossary of the main concepts discussed in this chapter with supporting evidence. (*Continued*)

Concept	Definition	Supporting evidence
Stochastic (neutral) processes	These processes have a random nature and include mass effects, dispersal limitation, and ecological drift.	
Mass effects	Species may be present in an unfavorable (sink) habitat due to dispersal from a favorable (source) habitat. Mass effects can thus offset the effects of niche processes.	Jamoneau *et al.* [4.16] reported mass effects shaping diatom metacommunities from mid- and downstream habitats. Vilmi *et al.* [4.167] reported mass effects structuring the diatom metacommunity of a large lake system where niche conditions (e.g., trophic status) varied among 81 studied sites.
Dispersal limitation	Species may be prevented from reaching suitable habitats due to distance or other dispersal barriers. Dispersal limitation can mask the effects of niche processes.	In headwater lotic systems, which are relatively isolated within the river network, dispersal limitation can override the effect of environmental conditions [4.127]. In lentic systems, the lack of connectivity among lakes may limit the ability of planktonic diatoms to reach suitable pelagic conditions [4.25].
Ecological drift	Random birth and death events determine species composition. Small habitats with few individuals are more prone to ecological drift.	We know of a single study testing for ecological drift and reporting that periphytic diatom community composition in shallow arctic lakes was not structured by drift [4.123].

(*Continued*)

Table 4.1 A glossary of the main concepts discussed in this chapter with supporting evidence. (*Continued*)

Concept	Definition	Supporting evidence
Priority effects	Early colonizers either inhibit or facilitate later recruits. Compositional differences among early colonizers due to random dispersal can result in different successional trajectories under similar environmental conditions.	The scant available evidence shows contrasting priority effects through new colonization and *in-situ* speciation driving later successional stages in Antarctica during the Plio-Pleistocene (last 2.58 Ma) [4.143]. In contrast, priority effects were unimportant in a short-term experimental study of stream benthic diatoms [4.168].
Guild system	Classification of diatoms into ecological guilds, based on resource utilization and disturbance resistance [4.23] [4.169].	Guild responses to deterministic and stochastic effects are generally context dependent.
Low-profile	Species growing close to the substate (e.g., prostrate, adnate, short erect cells, solitary cells, slow moving cells) with low nutrient demands and high resistance to physical disturbance.	In small subarctic streams, low-profile diatoms were mostly structured by local environmental factors [4.104]. Oligotrophy and high discharge led to dominance of the low-profile guild in high-mountain streams [4.111].
High-profile	Species with tall stature (e.g., filamentous, branched, tube forming, and colonial) adapted to high nutrient concentrations and with low resistance to physical disturbance.	In the absence of grazing, the high-profile guild had greater relative abundance than in the presence of grazing and increased with the number of added nutrients [4.62].

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Table 4.1 A glossary of the main concepts discussed in this chapter with supporting evidence. (*Continued*)

Concept	Definition	Supporting evidence
Motile	Fast-moving biraphid species with high nutrient demands and intermediate resistance to physical disturbance.	Motile diatoms had higher abundances in dammed rivers characterized by high total phosphorus concentrations and hydrological alterations (water flow, streambed lithology) [4.170].
Planktonic	Diatom species adapted to the water column but also occurring in the benthos due to sedimentation.	In Pyrenean lakes, planktonic diatoms were jointly affected by increased water pH in the hypolimnetic sediments and stochastic dispersal events during summer stratification [4.119].
Alpha diversity	A measure of species richness at a locality.	Environmental filtering prevailed over dispersal processes in controlling alpha diversity of stream algae; the environmental effect increased, while the dispersal effect decreased with latitude [4.150].
Beta diversity	A (dis)similarity measure of species composition (presence/absence or abundance) among samples (spatial and/or temporal).	Beta diversity of benthic diatoms from unimpacted streams in France and the US was driven by environmental filtering, while beta diversity in streams heavily enriched with nutrients was controlled by spatial processes across scales [4.129].

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Table 4.1 A glossary of the main concepts discussed in this chapter with supporting evidence. (*Continued*)

Concept	Definition	Supporting evidence
Niche breadth	The range of environmental conditions where a species can maintain positive growth. According to the resource use hypothesis, the niche breadth of a species determines its local abundance and regional distribution.	At a subcontinental scale, stream diatoms with wider niche breadths had greater local abundance and regional distribution [4.88]. At inter-continental scale, diatom niche breadth was not conserved among different regions of the world [4.171].
Niche position	Measures if a species occurs in common or marginal environmental conditions within the study area. According to the resource abundance hypothesis, the niche position of a species determines its local abundance and regional distribution.	Support for the niche position hypothesis, whereby rare species had preference for marginal environmental conditions, was generally found at smaller scales [4.171].

Much freshwater research over the past decades has pursued determination of the relative roles of deterministic and stochastic processes at spatial scales ranging from individual stream reaches to the globe and at ecological to evolutionary temporal scales [4.7] [4.8] [4.9] [4.10] [4.11] [4.12] [4.13] [4.14]. The classical microbiological idea that "everything is everywhere but the environment selects" [4.15] suggests that microorganisms are shaped exclusively by environmental filtering because their large populations preclude dispersal limitation. However, mounting evidence reveals that diatoms experience both mass effects and dispersal limitation [4.16] [4.17], manifesting in species and genera endemism in individual lakes (e.g., Lakes Titicaca and Baikal [4.18] [4.19]), regionally constrained floras

[4.20] [4.21], and distinct biogeographic regions [4.22]. Following the creation of the diatom guild system for benthic river diatoms [4.23], new efforts were directed towards elucidating the diatom functional responses to environmental and dispersal controls [4.24] [4.25] [4.26].

Diatoms are excellent model organisms for investigating metacommunity assembly processes. First, diatoms are species-rich, representing the most speciose eukaryotic algal group in marine and freshwater environments with more than 200,000 estimated extant species [4.27]. Second, diatoms are easy to sample and are sensitive to environmental stimuli (e.g., water chemistry, climate), which makes them invaluable bioindicators [4.28] [4.29]. Third, diatoms have different modes of dispersal, including instream, aerial (e.g., by wind), and overland (e.g., zoochory), which contribute to broad distributions and enable reaching of suitable/preferred habitats [4.30]. Fourth, the preservation of diatom frustules in the sediment allows the assessment of historical processes of metacommunity assembly [4.31] and may provide new insights into patterns over time. Fifth, the high rates of speciation of ecologically important diatom taxa (e.g., *Nitzschia*) provide opportunities to study evolutionary processes, such as symbiotic relationships among algal groups [4.32]. The availability of new resources and tools, including species inventories of understudied regions (e.g., tropics) and ecosystems (e.g., islands) [4.33] [4.34], and ecological modeling [4.35] will broaden the research on the importance of different assembly mechanisms.

However, the presence of cryptic species or species complexes [4.36], represents a taxonomical challenge for measuring biodiversity and assessing the effects of assembly mechanisms in freshwater diatoms. At the same time, the continued development and refinement of genetic metabarcoding approaches hold great potential for advancing our understanding in this context [4.37] [4.38]. Recent studies have found conspecific variability in environmental preferences, which can further hamper the detection of an environmental signal in community composition. For instance, Pérez-Burillo *et al.* [4.39] demonstrated that genetic variants within some key freshwater diatom species (e.g., *Achanthidium minutissimum* and *Fistulifera saprophila*) differ in their ecological preferences. New spatially explicit databases of occurrence of molecularly distinct taxonomic units need to be built [4.40], which would allow distinguishing finer patterns in community response to environmental conditions [4.41]. Combining both established knowledge on morphotaxa and new knowledge derived from genetic data will be a way forward to resolving community assembly mechanisms within freshwater diatom species complexes [4.42].

There are also data and statistical challenges in assessing the roles of assembly mechanisms. First, the increasing amount of collected information by spatial ecology studies in diatoms (reviewed in Soininen and Teittinen [4.43]) often outpaces the capacity of researchers to progress towards metacommunity generalizations. Second, dispersal *per se* is difficult to measure because diatoms can disperse through water flow, air, human activities, and animal vectors, including introduced species [4.44] [4.45], and thus spatial proxies or classical statistical methods to account for dispersal effects (e.g., variance partitioning) may not be accurate. Third, context dependencies may cause assembly mechanisms to depend on geographic location. All these issues require synthesis if we are to use the available diatom information efficiently. This chapter is organized around five themes, which review deterministic and stochastic factors, their relative effects, interactions, and variability through time and space. Finally, a set of research questions and ways forward are suggested to guide future diatom metacommunity research.

4.2   Deterministic Effects on Diatom Metacommunities

Diatoms respond to environmental factors that operate at local and regional scales. Among the most influential local factors in streams and lakes are conductivity, pH, nutrient concentrations, and depth [4.46]. Conductivity has major effects on diatom distribution in both freshwater and brackish waters via ion composition and secondary salinization effects [4.47]. Both high and low pH can constrain diatom diversity. Acidification by inorganic acid deposition has adversely impacted diatom biodiversity in streams and lakes located in the northeastern United States and northern Europe [4.48] [4.49]. Conversely, Teittinen *et al.* [4.50] discovered a reduction in diatom richness with increasing pH between 4.4 and 8.5 in over 140 subarctic ponds, aligning with a growing body of evidence for diatoms adapted to acidic water conditions [4.51] [4.52]. Notably, diatoms are sensitive not only to the amount of acidity but also to the type of acidity. Thus, streams naturally acidified by dissolved organic carbon (DOC) possess greater diatom richness than inorganically acidified streams due to reduced aluminum toxicity [4.53] [4.54]. Dissolved organic carbon is on the rise in eastern North America and northern and central Europe, causing brownification of streams and lakes [4.55] [4.56]. As dissolved organic carbon can mitigate aluminum toxicity in acid streams and increase bioavailability of

macro- and micronutrients, brownification may have a positive effect on diatom biodiversity [4.53]. However, brownification may also negatively impact algal biodiversity by promoting mixotrophic algae, competitively displacing diatoms and other phototrophic algae [4.57]. Research on the impacts of brownification on diatoms remains limited, necessitating further investigations in this area to achieve a comprehensive understanding of the contingencies in the diatom responses.

While many investigations have examined the responses of diatom community and trait richness and composition to macronutrient enrichment (reviewed in Poulíčková and Manoylov [4.58]), there is a notable paucity of research on the effects of the number of nutrients at high supply, including both macronutrients and micronutrients. In terrestrial systems, global studies have demonstrated that biodiversity declines as more nutrients become non-limiting because of fewer opportunities for tradeoff [4.59] [4.60]. In contrast, there are only a few aquatic investigations showing the opposite response, whereby benthic diatom and algal richness increased when macro- and micronutrients were available at high concentrations [4.61] [4.62] [4.63]. One of the potential reasons for this disparity is that in the spatially complex algal benthos, nutrient enrichment promotes the establishment of overstory species with high nutrient demand without negatively affecting the understory species tolerant of nutrient limitation. These results indicated that coexistence in terrestrial and benthic systems is driven by different processes, namely competition for nutrients and light in the former but complementarity and resource partitioning in the latter [4.64]. Yet, additional experimental research on this topic is needed to ascertain the generality of this conclusion.

Diatom species richness and composition are also controlled by regional environmental characteristics either directly or indirectly through their influence on local conditions [4.65] [4.66]. For instance, the proportion of wetlands in river catchments has a positive effect on diatom richness. This is because wetlands export DOC, which as discussed, reduces aluminum toxicity in streams acidified by inorganic acid deposition [4.53] and increases bioavailability of essential micronutrients such as iron [4.67] [4.68]. Land use is another factor with important, yet complex effects on diatom communities. On the one hand, it may promote diatom species richness by increasing nutrient availability due to agriculture [4.69] [4.70] and light due to deforestation [4.71]. On the other hand, higher urbanization intensity may result in a lower diatom richness driven by an increase of pollution-tolerant taxa [4.72].

Climate and its anthropogenically driven changes play a pivotal role as regional constraints on diatom communities. For instance, global warming has resulted in increased water temperature, reduced ice-cover, and enhanced stratification and wind strength in lakes [4.73]. A common response is the compositional shift in planktonic diatoms toward smaller-celled taxa, including many Cyclotelloid species in the last decades [4.74] [4.75] [4.76]. Changes in turbidity of the water column, often associated with alterations in stratification, can lead to changes in light penetration to the benthos, impacting photosynthetic processes [4.77]. Rühland *et al.* [4.78] reviewed evidence for increased diatom biomass following recent atmospheric temperature increase and anthropogenic nitrogen deposition in remote lakes. Indeed, diatom communities in these ecosystems have undergone direct climate-driven changes, primarily through the extension of ice-free seasons [4.79], though contrasting evidence has been found in tropical aquatic ecosystems [4.80].

Investigating the co-variation of environmental variables is critical for a comprehensive understanding of the deterministic processes shaping diatom biodiversity. For instance, nutrients co-vary with conductivity in many freshwater and brackish ecosystems, making it difficult to explain diatom biodiversity responses to individual factors [4.81] [4.82]. Experimental studies controlling for different environmental impacts (e.g., salinity and productivity) can be very informative in this respect [4.83]. Notably, climate and land use-driven eutrophication have strong interactive effects on aquatic communities [4.84]. Consequently, broad biogeographical gradients of diatom richness and abundance distribution cannot be explained with climate variability alone but require information on both climate and nutrients [4.85], and future studies should pursue this research direction.

Diatom response to environmental filtering depends on niche breadth and position. With respect to niche breadth, species are classified as specialists with narrow niches vs. generalists with broad niches. According to the resource use hypothesis [4.86], generalists are locally abundant and regionally prevalent because they can tolerate a broad range of conditions. In contrast, the resource abundance hypothesis suggests that species with high local abundance and regional prevalence are adapted to resources that are regionally common [4.87]. In this case, the species' niche position, i.e., the set of preferred environmental conditions, determines its abundance and distribution. Diatom research has been important in this debate by providing support for both hypotheses, although the resource use hypothesis tends to be more frequently corroborated at larger scales. Thus, at a subcontinental scale, stream diatoms with wider niche breadths had greater local abundance and regional distribution, consistent with the

resource use hypothesis, while adaptation to common vs. rare conditions was inconsequential [4.88]. At comparable spatial scales, evidence also suggests that the broader the niche the wider the distribution of stream and lake diatoms [4.89] [4.90]. In contrast, studies at smaller scales have shown support for the resource availability hypothesis by demonstrating that species with more marginal niche position are rarer [4.91] [4.92] [4.93].

Species' environmental preferences determine the magnitude and direction of environmental filtering, and it is informative to explore the responses of individual ecological groups in conjunction with the total community. For example, acid stress severity and heterogeneity impacted diatom turnover (beta diversity) in Adirondack streams, but this response was driven mostly by acid-sensitive as opposed to acid-tolerant diatoms [4.48]. The distributional changes forced by global warming were projected to be greater in warm-water diatoms (positive) than in cold-water diatoms (negative), leading to higher overall local species richness (alpha diversity) but lower beta diversity [4.94], the latter phenomenon known as biotic homogenization [4.95]. Anthropogenic warming can also be the main driver of homogenization in the Arctic continent due to the loss of circumpolar diatom species [4.96]. In tropical reservoirs, diatom biotic homogenization was driven by eutrophication, whereby tolerant species inhabiting oligo-mesotrophic systems were able to expand to eutrophic systems [4.97]. As global change impacts intensify, diatoms can be used as an early warning system to understand impending environmental deterioration. For example, acidification can cause subtractive heterogenization when beta diversity increases due to the elimination of acid-sensitive species from the most impacted sites and this compositional shift can serve as an early warning of environmental degradation [4.48]. Diatom ecologists should take advantage of the available climatic (e.g., HydroATLAS [4.98], WorldClim [4.99], Global Forest Change [4.100]), land use, and human density projections [4.101] for the upcoming decades and investigate how richness and composition of diatom communities and ecological groups may respond to continued anthropogenic impacts and whether these responses vary geographically.

Environmental filtering triggers functional changes in diatom communities, which have been primarily evaluated using Passy's [4.23] guild classification [4.102] [4.103] [4.104]. An intercontinental study found that compared to diatom taxonomic composition, guild composition responded more strongly to environmental filtering, which suggests that guilds are particularly suitable for assessing global change effects [4.12]. Specifically, total phosphorus and species richness were positively correlated in motile taxa but negatively in high-profile and low-profile taxa. In addition to their

distinct resource preference, ecological guilds also differ in niche breadth and thermal preferences. For instance, Lindholm *et al.* [4.105] found that planktonic diatoms are more specialized than the high-profile guild in boreal streams. A subcontinental stream study reported that low-profile and high-profile diatoms had preference for cold water, while motile diatoms occurred mostly in warmer waters, which has important implications for diatom distribution and biomass production under climate change [4.94].

The influence of biotic interactions on diatom composition has been poorly investigated (Table 4.1). However, a recent study suggested that stream diatom guilds and functional groups conform to three interaction modes: shared preference, distinct preference, and facilitative [4.106]. The shared preference mode encompasses species that have either broad tolerance to environmental conditions or competitive advantages in benign conditions, where they become dominant. Exemplifying this mode, the abundance of the tolerant low-profile guild was suppressed by higher richness of the dominant motile guild. In the distinct preference mode, species have different optima but can engage in negative interactions in areas where their environmental preferences overlap. Examples of this interaction mode are acidophilus and acidobiontic species, whose abundance was lower at high richness of the competitor. Finally, the facilitative mode includes species providing (donors) or receiving benefits (recipients) under stressful conditions. In favorable conditions, the recipients may competitively suppress the donors. Nitrogen fixing diatoms are donors of bioavailable nitrogen, and consistent with facilitation, higher richness of these diatoms was associated with increased abundance of the recipient motile guild, which has high nutrient demands. In contrast, greater richness of the motile guild decreased donor's abundance, consistent with competition. Other research examined the biotic effects of grazer abundance on diatom composition and documented only small effects compared to local environment and space [4.24] [4.107]. Álvarez-Cobelas *et al.* [4.108] found evidence of competitive exclusion within benthic diatom populations of the same genus and recommended consideration of biotic interactions at local scales before scaling up metacommunity processes to the catchment scale.

4.3   Stochastic Effects on Diatom Metacommunities

High dispersal rates can dampen the effect of local environmental conditions due to mass effects [4.1]. Mass effects maintain a flux of poorly

adapted species and are challenging to measure in passive dispersers. Leboucher *et al.* [4.109] developed a new method for identification of diatoms influenced by mass effects. They suggested that benthic diatoms most prone to mass effects exhibit the following characteristics and patterns: strong spatial responses, narrower niche breadths (i.e., specialists), and weak negative co-occurrence. The sensitivity of species to mass effects was proposed as a new ecological trait that should be considered in both fundamental research, such as investigating the interplay between environmental factors and dispersal-in controlling species distribution, and applied research, such as water quality assessment [4.17] [4.109].

The lack of connectivity among sites or presence of spatial barriers may limit the ability of species to reach suitable habitats, leading to dispersal limitation. Although dispersal is a random process, in lotic systems, it is strongly influenced by flow directionality [4.110] [4.111]. Additionally, different dispersal processes may dominate along the watercourse with dispersal limitation being more prevalent upstream and mass effects, at mid- to downstream stretches [4.16].

Diatoms can exhibit variations in dispersal owing to differences in body size, attachment to the substrate, and their guild affiliation. Very few studies have assessed the importance of diatom body size for dispersal. In an investigation of diatom occurrences in over 200 locations along three 100-m reaches of a New York stream, Passy [4.113] demonstrated that the number of occurrences declined with body size, suggesting that smaller species, with a higher number of occurrences, were better dispersers. Attached diatoms appear to have lower dispersal ability than phytoplankton species [4.114]. Differences were also observed among diatom guilds. Thus, in US streams, low-profile taxa occurred in significantly more localities than high-profile and motile taxa, which was indicative of better dispersal of the low-profile guild [4.115]. In contrast, stronger spatial influence on the low-profile and high-profile guilds compared to the motile guild was attributed to stronger dispersal limitation [4.24]. Furthermore, motile diatoms have been shown to be strongly affected by mass effect in some systems [4.16], but less so in others [4.111]. In steep mountain streams, low-profile diatoms were influenced by mass effect, while limited dispersal was shown for high-profile diatoms [4.25]. Other studies have found non-significant differences in species distribution when comparing patterns across guilds in upstream refugia [4.116]. These conflicting findings imply that the guild responses to dispersal appear to be context dependent. It is also possible that different authors use different guild designations for the same species, e.g., by considering only the three original guilds (low-profile, high-profile, and motile) vs. distinguishing a fourth one (planktonic), by lumping species

belonging to the same genus into a single guild, or due to subjectivity, given the lack of an international database on diatom guild affiliations. Although the use of diatom guilds for understanding community composition in relation to spatial factors has been criticized as too coarse [4.30], a growing number of studies have detected spatial differences among diatom guilds, suggesting untapped potential in evaluating guilds to identify spatial patterns. Future research should focus on unraveling why guild responses to dispersal vary idiosyncratically or depending on the specific context, as this understanding can lead to more accurate interpretations of spatial dynamics within diatom communities.

As dispersal effects are measured after accounting for environmental influences, omission of environmental variables with an impact on diatom distribution may lead to biased dispersal assessment. In rivers, for example, solar radiation, discharge, riparian shade, and groundwater inputs that can change over short distances [4.117] are rarely investigated. Likewise, in lakes, water level is often used as a surrogate for unquantified but ecologically important variables with potentially independent effects on diatoms, e.g., light penetration, vegetation type, and oxygen levels [4.118]. Microhabitat heterogeneity and characteristics are also difficult to evaluate [4.120] and can be strong determinants of species assemblages, e.g., within reach variability in flow velocity [4.14]. Within lakes, diatoms can also disperse through the movement of water, hence forming metacommunities inhabiting the open water vs. the littoral zone [4.119].

Ecological drift, stemming from random birth and death rates, has been among the most overlooked drivers of diatom community structure [4.43], despite its early recognition as an important community assembly process for diatoms [4.121]. In a set of 48 alpine lakes, Keck *et al.* [4.122] analyzed sedimentary micro-eukaryotic taxa, including diatoms, and reported a joint effect of long-term ecological drift and anthropogenic nutrient increase on the temporal change of species composition. Conversely, Remmer *et al.* [4.123] did not find evidence of ecological drift in the periphyton of Arctic lakes.

4.4   Relative Importance of Deterministic and Stochastic Effects on Diatom Metacommunities

An ongoing research effort is determining the relative contributions of environmental filtering and dispersal on diatom metacommunities. Some studies have found local factors to be more influential [4.24] [4.124], others

have discovered dispersal to prevail [4.125], yet others have reported that the combination of these factors is important [4.16] [4.30] [4.116]. Lindholm *et al.* [4.104] examined benthic diatom communities from 55 small subarctic streams and found that the most important explanatory factors varied among diatom guilds and between specialists vs. generalists. For the low-profile and motile guilds, local environment was the most important driver, while the high-profile guild was equally structured by local environmental and spatial variables. Spatial variables dominated the assembly of the planktonic guild and specialists, while generalists were more strongly driven by coarser, catchment-level environmental conditions. The contributions of metacommunity processes at larger spatial and temporal scales have been less studied in diatoms than in macroorganisms [4.126]. However, substantial advances have been made over the past years, revealing that at subcontinental to intercontinental scales, diatom and guild richness and composition and diatom abundance distribution were driven by environmental filtering and dispersal constraints [4.12] [4.85].

The dominance of a particular metacommunity process depends on environmental settings such as isolation, trophic status, and scale. For instance, headwater streams are relatively isolated in the river network and dispersal limitation can either override the effect of environmental filtering [4.127] or operate in concert with it [4.24]. Dispersal limitation can also be a major driver of benthic diatom communities in isolated lakes [4.106] [4.128]. Using an innovative landscape approach and an intercontinental dataset (France and the US), Leboucher *et al.* [4.129] showed that across scales, beta diversity was driven by environmental filtering in unimpacted streams, but by spatial processes in heavily nutrient-enriched streams. This was attributed to a shift in species composition along the gradient of nutrient impact from specialists, with close association with the environment, to generalists, more strongly driven by dispersal. In 22 Mediterranean shallow ponds, Nistal-García *et al.* [4.130] found that epiphytic diatom communities generally varied in response to local environmental conditions and attributed this finding to the comparatively smaller scale. However, at larger spatial scales, diatom species composition may vary more closely with geographic distances among the study water bodies than with local environment, as shown in disparate aquatic habitats such as Antarctic lakes [4.22] and Atlantic salt marshes [4.131]. Future research should aim to identify environmental settings and scales where environmental filtering and dispersal have comparable vs. different importance and thus unravel how communities are shaped by the interplay of the environment and space.

Disturbance regimes can also exert substantial influence upon diatom community structure and determine the relative importance of deterministic and stochastic assembly processes. Hutchinson [4.3] proposed that the temporally and spatially variable nature of aquatic environments facilitate the coexistence of multiple taxa by limiting the intensity and duration of competitive interactions. Bramburger *et al.* [4.64] used a novel method of quantifying ecological specialization in groups of taxa (assemblages or genera) in analogous tropical and temperate systems. They demonstrated that tropical assemblages were characterized by higher species richness, greater ecological specialization, and resource partitioning associated with spatially diverse, temporally stable habitats. These findings agree with the time-stability hypothesis [4.132] [4.133]. This mechanism has been implicated in the development of species flocks among diatoms [4.134] and other groups. Further experimental perturbations of tropical benthic diatom communities induced responses that were inconsistent with competition but rather with ongoing niche partitioning [4.135].

Given the significance of diatoms as bioindicators, it is imperative to investigate how stochasticity may shape diatom metacommunities and interfere with biological and environmental influences. Traditionally, the relative importance of dispersal and niche processes in community assembly has been determined by variance partitioning, but Vilmi *et al.* [4.112] developed a new approach, which calculates the strength of these processes along a continuum, i.e., Dispersal-Niche Continuum Index (DNCI). Comparing stream diatom, macroinvertebrate, and fish communities from US Mid-Atlantic hydrological subregions, they found that smaller organisms were more strongly controlled by dispersal. This highlights the need to better account for spatial processes in biological monitoring, particularly in situations where dispersal is facilitated, e.g., dam removal [4.136], or non-point diffuse pollution from land use changes [4.137].

4.5   Assembly Processes Over Time

Historical contingencies, such as priority effects, defined as the competitive or facilitative effects of early colonizers on later recruits, have been rarely studied in a diatom metacommunity context. In an experimental study, Härnström *et al.* [4.138] resurrected *Skeletonema marinoi* resting cells and found intraspecific priority effects in the geographic distribution of open water and fjord populations. Priority effects through cell resurrection are still not well understood in freshwater diatoms. However, *Aulacoseira*

granulata has been identified as a candidate species for experimental studies on priority effect because it may prevent establishment of other locally adapted species [4.139]. Using recent (ca. 150 years ago) paleolimnological observations, Benito *et al.* [4.140] did not find historical influences of past assemblage composition on current diatom assembly processes in a set of 14 lakes from the tropical Andes with varied levels of connectivity. Clearly, more research is necessary to determine the role of priority effects relative to other assembly processes as well as which species are responsible for the observed patterns within the metacommunity.

Unlike microorganisms such as bacteria, which mostly lack fossil records, diatoms provide a rich data source for studying historical events, including tectonic or paleoclimatic changes. Diatoms' short generation times enable tracing past events of environmental filtering and dispersal at shorter time scales, ranging from hundreds to thousands of years. This offers valuable insights into the historical dynamics of diatom communities and their responses to environmental changes over extended periods [4.141]. At centennial time scales, Winegardner *et al.* [4.142] observed an increase in diatom richness in modern sediments compared to pre-industrial times, likely associated with the arrival of new species via dispersal. At longer, geological scales, Pinseel *et al.* [4.143] reported that environmental filtering as a result of Miocene cooling and Plio-Pleistocene glaciations, drove multiple extinction events in Antarctic diatom flora. Community assembly of the diatom plankton in the 1.9-million-year-old Lake Ohrid was governed by environmental filtering, and to a lesser extent and in more recent times, by competition [4.13]. Diatom paleolimnological observations can also help elucidate whether past environmental filtering processes are consistent with the timing of diversification among and within lineages, which are typically inferred using genomic analyses of extant communities [4.144].

When spatially replicated diatom time series are available, which is comparatively rare, it is possible to determine the dominant community assembly processes over space and time. Bramburger *et al.* [4.145] demonstrated that dispersal was important in assembling local benthic diatom communities at annual time scales in individual Indonesian lakes (6-500 km^2), but as colonization progressed, niche-based processes began to dominate over dispersal through biotic interactions. At paleolimnological scales, Benito *et al.* [4.128] examined species richness in four high-elevation lakes in the tropical Andes and discovered consistent patterns of regional long-term dry/warm climatic variability significantly influencing local diatom diversity. These results suggest a lack of dispersal barriers over the last

2000 years and that regional "seed" sources are maintained over periods of millennia, enabling local recovery of diatoms in response to fluctuation between less favorable and favorable conditions. Similarly, 1-million-year-old cores from Lake Towuti (Sulawesi, Indonesia) showed repeated shifts between benthic and planktonic, mostly endemic assemblages persisting over tens of thousands of years [4.146]. These shifts were associated with long-term oscillations in mixing regimes and nutrient availability driven by global glacial/interglacial cycles [4.147]. The recurrent appearance of highly similar assemblages over such long periods further emphasizes the role of seed banks in providing long-term community resilience. It also underscores the powerful influence of deterministic mechanisms as drivers of community structure over geologic time scales.

Distinguishing the impacts of past dispersal events, both within and across geographically distant systems, from the influence of current stochastic and deterministic processes is a major challenge. This differentiation is essential to gain a comprehensive understanding of the underlying mechanisms shaping community dynamics across different temporal scales. Although not yet implemented for diatom metacommunity time series, recent studies applied null models to measure the relative strength of stochastic and deterministic processes by randomization of beta-diversity dissimilarity matrices [4.148] [4.149]. To our knowledge, however, no studies have adopted a null modeling approach to separate the effects of past from present dispersal effects, and thus, more research is needed.

4.6   Assembly Processes Over Space

An intriguing but not well researched question is how diatom metacommunity processes vary at broad spatial scales, e.g., across latitudes. It is generally predicted that the importance of environmental filtering would increase with latitude as climatic conditions become harsher, while the role of dispersal would be higher at low latitudes, where species are more specialized and with smaller ranges. An algal study (diatoms and soft algae) tested these predictions by examining the relative impacts of environmental filtering vs. spatial variables on richness and beta diversity along a latitudinal gradient [4.150]. Although niche processes dominated across latitudes, as predicted they became stronger at higher latitudes, while dispersal processes became stronger at lower latitudes but only for species richness, not beta diversity. However, this study encompassed only 19 latitudinal degrees and did not include tropical regions. An investigation of

lake diatoms from lower latitudes (8°N–30°S), focusing on species compo-sition at a guild level, found that consistent with expectations, at lower lati-tudes spatial effects explained more variability in the low- and high-profile guilds than the environment. Yet, motile and planktonic guilds were not structured by spatial factors near the equator [4.25]. Therefore, further research is needed at broader latitudinal ranges to determine how deter-ministic and stochastic processes control diatom composition at species and guild levels.

Elevational gradients also modulate the assembly processes driving dia-tom composition, but as with latitudinal gradients, research is limited. In Chinese rivers, He *et al.* [4.151] reported that dispersal effects were more prominent than the effects of the local environment across elevation. Conversely, Kurthen *et al.* [4.152] compared two groups of streams in a high mountain region and demonstrated that the group with lower net-work connectivity experienced stronger environmental filtering. An inves-tigation of stream diatom composition at three spatial scales, within riffle, within basin, and across basins, revealed that environmental filtering was the strongest at the smallest scale, while the importance of dispersal pro-cesses increased with scale [4.149]. Given the results from these recent stream and lake studies, showing latitudinal, elevational, and scale depen-dence of diatom and algal community assembly, we advocate for further research on community assembly processes along broader latitudinal and scale gradients as well as along longitudinal and elevational gradients and in a wider range of aquatic ecosystems.

4.7   Concluding Remarks and Future Directions

In order to test hypotheses on deterministic and stochastic large-scale dia-tom community assembly process, it is necessary to build extensive and taxonomically and functionally harmonized databases. Freshwater diatom databases have been compiled in recent years at large spatial extents [4.33] [4.153], including those generated by national monitoring programs, such as the US National Water-Quality Assessment Program and the National Rivers and Streams Assessment, and the Canadian Circumpolar Diatom Database [4.154]. In Europe, some countries and regions have generated dia-tom databases to fulfill the European Water Framework Directive [4.155]. While some European databases are easily accessible through websites (e.g., https://environment.data.gov.uk/ecology/explorer/, https://datos-superficiales.chebro.es/WCASF/ or https://www.freshwaterecology.info)

or supplementary materials in published papers [4.156] [4.157], others have proven difficult to obtain (e.g., [4.158]). Diatom paleolimnological datasets from Pleistocene and Holocene have been complied into the Neotoma paleoecological database but are biased geographically toward northern latitudes [4.153]. Overall, most of the aforementioned databases were generated with a standardized sampling protocol but may require taxonomic harmonization. A key challenge is to generate platforms that would allow diatom researchers to add new data, harmonize them, and obtain existing data at scales from populations to biogeography [4.159]. The use of genetic metabarcoding approaches provides emerging opportunities to improve database harmonization through exploring taxonomic-free approaches [4.160]. However, community assembly research based on molecular-based datasets (e.g., Diat.barcode [4.161]) is still in its infancy [4.162]. A further challenge for metacommunity research is the lack of ecological information on diatom species particularly those identified by molecular approaches, as well as the absence of harmonization of functional attributes, such as guild affiliation. Combining both established knowledge on morphotaxa and new knowledge derived from genetic data might be one way forward [4.163].

In this review, we outlined current knowledge of the assembly mechanisms structuring diatom species and guild composition and biodiversity along spatial and temporal gradients. We showed that both deterministic and stochastic processes control diatom metacommunities, but their relative roles may vary spatially and temporally. Most of the research to date has focused on environmental filtering and dispersal. Further observational and experimental investigations are thus needed to determine how biotic interactions and ecological drift contribute to diatom assembly. We also recommend syntheses of the already substantial data on assembly mechanisms to elucidate their spatial (latitudinal, longitudinal, and elevational) and scale dependence across aquatic ecosystems. The advancement of diatom functional biogeography will be useful in discerning whether assembly mechanisms vary across levels of biological organization. Expansion of existing diatom databases by combining morphological, ecological, and molecular information as well the implementation of in silico experiments testing the roles of deterministic and stochastic processes, will further improve our understanding of the drivers of diatom metacommunities across ecosystems for the purposes of fundamental and applied science. Assessing whether the relative roles of assembly processes may shift with global change and if such shift is spatially dependent are important avenues of future research.

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