

REVIEW

Divide and conquer: Spatial and temporal resource partitioning structures benthic cyanobacterial mats

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Abstract

Benthic cyanobacterial mats are increasing in abundance worldwide with the potential to degrade ecosystem structure and function. Understanding mat community dynamics is thus critical for predicting mat growth and proliferation and for mitigating any associated negative effects. Carbon, nitrogen, and sulfur cycling are the predominant forms of nutrient cycling discussed within the literature, while metabolic cooperation and viral interactions are understudied. Although many forms of nutrient cycling in mats have been assessed, the links between niche dynamics, microbial interactions, and nutrient cycling are not well described. Here, we present an updated review on how nutrient cycling and microbial community interactions in mats are structured by resource partitioning via spatial and temporal heterogeneity and succession. We assess community interactions and nutrient cycling at both intramat and metacommunity scales. Additionally, we present ideas and recommendations for research in this area, highlighting top-down control, boundary layers, and metabolic cooperation as important future directions.

KEYWORDS

benthic cyanobacterial mats, carbon cycling, microbial ecology, nitrogen cycling, nutrient cycling, resource partitioning, succession, sulfur cycling, trophic interactions

INTRODUCTION

Benthic cyanobacterial mats (BCMs) are complex, layered structures with high structural, spatial, and temporal heterogeneity (Figure 1). These BCMs consist of a consortium of bacteria, archaea, eukarya, viruses, and more, with the Cyanobacteria, Proteobacteria, and Bacteroidetes often dominating these communities (e.g., Cissell & McCoy, 2021; Stuij et al., 2023). Benthic cyanobacterial mats are vertically stratified in temperate marine (e.g., Carreira et al., 2015), hypersaline (e.g., Dillon et al., 2009), and freshwater systems (e.g., Borovec et al., 2010; Velázquez et al., 2017), while those in tropical marine systems have more distinct horizontal spatial differences (e.g., Cissell & McCoy, 2021). Mats have high metabolic and taxonomic diversity, and this metabolic diversity drives their functional structure (van

Gemerden, 1993). Benthic cyanobacterial mat formation is beneficial to the microbes involved, allowing for increased resistance against stressors such as chemical and oxidative stress (Burmølle et al., 2014).

Many complex synergistic interactions between microbial members shape mat ecology. However, these interactions have yet to be characterized and reviewed through the lens of niche theory in BCMs, exploring how temporal and spatial resource partitioning structures these complex communities. Indeed, coexistence of highly diverse microbial members within the same trophic level requires resource partitioning and species interactions to create a highly functioning community (Nemergut et al., 2013). Understanding BCMs within the context of niche theory would allow us to analyze the functional complexity of mats, the processes behind their persistence,

Abbreviations: BBD, black band disease; BCM, benthic cyanobacterial mat; DBL, diffusive boundary layer; DIN, dissolved inorganic nitrogen; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; SRB, sulfate reducing bacteria.



FIGURE 1 Benthic cyanobacterial mat (BCM) communities. (A) A BCM over sand in a temperate marine ecosystem in Shackleford Banks, North Carolina, USA (Credit: Madelina Marquez). (B) Cross-section view of the same BCM, showcasing vertical stratification of different organisms that create different layers due to nutrient cycling and partitioning within mats (Credit: Madelina Marquez). (C) A BCM in a tropical, marine, coral reef ecosystem, growing on to a small coral colony in Curaçao (Credit: Maya E. Powell).

and their interactions within the broader environment. Additionally, this lens would allow us to address our lack of understanding of how organisms interact both competitively and cooperatively within and externally to BCMs. Therefore, in this review, we assess how carbon, nitrogen, and sulfur cycling are structured by resource partitioning across spatial, temporal, and successional gradients across environments to determine general trends and to make recommendations for future studies to further elucidate how microbial and environmental interactions structure niche partitioning in BCMs.

Cyanobacterial mats exist in a wide variety of ecosystems, including some of the most extreme habitats (Prieto-Barajas et al., 2018). Here, we describe resource partitioning in both layered mats, such as those in temperate marine and freshwater ecosystems (Borovec et al., 2010; Carreira et al., 2015; Velázquez et al., 2017), and nonlayered mats, such as those in tropical marine ecosystems (Figure 1; Cissell & McCoy, 2021). Microbial mats create the distinct layered colors in the hot springs of Yellowstone National Park (e.g., Jørgensen & Nelson, 1988; Revsbech et al., 2016) and drive productivity at hydrothermal vents through chemolithoautotrophy (e.g., Grünke et al., 2011; Noffke et al., 2016; Treude et al., 2007). Oligotrophic arctic lake food webs are also supported by mat productivity (e.g., Andersson & Brunberg, 2006). Mats can persist for centuries

within lithified structures as stromatolites and microbialites (e.g., Breitbart et al., 2009; Casaburi et al., 2016; Paterson et al., 2008) or die off within weeks in marine ecosystems (e.g., Cissell & McCoy, 2023a). There, individual mat die-off happens relatively quickly, while the overall mat metacommunity at a reef scale remains stable over months to years (Cissell & McCoy, 2023a). The effects of scale are thus key to understanding overall mat persistence.

Early studies on BCMs utilized microscopy and microelectrodes to explore biogeochemical gradients and identify key groups of bacteria involved in important physiological processes such as photosynthesis (Figure 2a; Jørgensen et al., 1983; Stal, 1995). The ability of BCMs to fix nitrogen interested early researchers, who assessed this capacity alongside mats' responses to limiting nutrients such as phosphorus (e.g., Paeli et al., 1991, 1993). Microelectrode profiles of sulfur and morphological identification of putative sulfate reducing bacteria (SRB), chemolithoautotrophic bacteria, and anoxygenic phototrophs in layered mats elucidated the importance of sulfate and oxygen gradients in forming BCM communities (e.g., Jørgensen & Des Marais, 1986; Visscher et al., 1999). Much of the previous work on BCMs has focused on bottom-up processes, including nutrient input and light exposure, which are critical for BCM development, proliferation, and organization (e.g., Camacho et al., 2022; Ford et al., 2018; Paeli

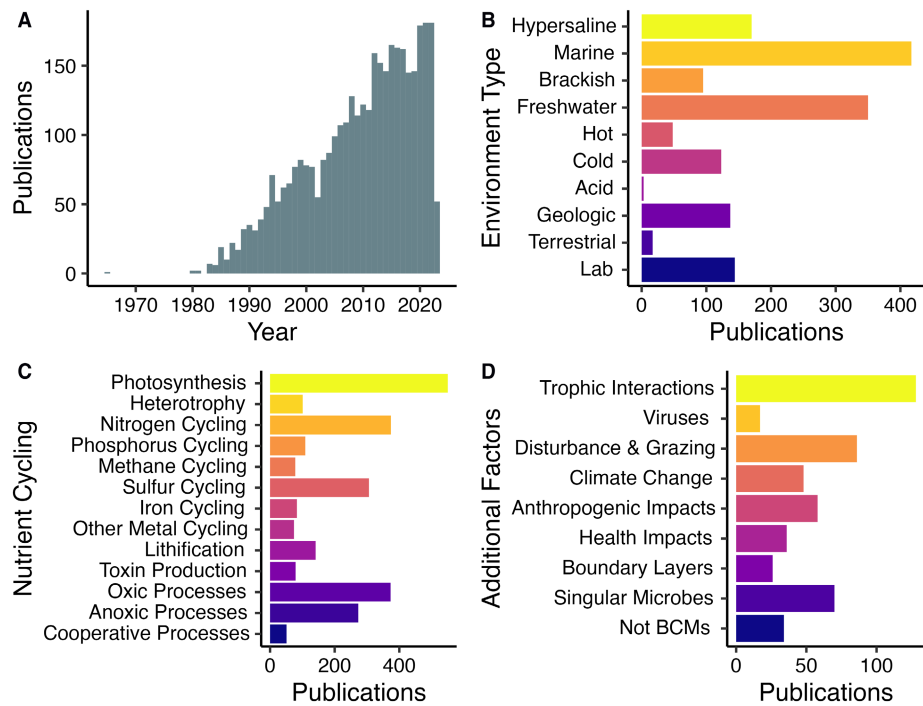


FIGURE 2 (A) All publications relating to benthic cyanobacterial mats (BCMs) from 1965 to 2023 based on our search terms. Publications on BCMS have steadily risen since the 1980s. (B) Environment types of all relevant publications. A majority of publications assessed BCMS in marine or freshwater settings. (C) Nutrient cycling processes of interest of all relevant publications. Photosynthesis and nitrogen cycling were the most studied forms of nutrient cycling, and most publications explored oxic processes. Metal cycling and cooperative interactions between BCM members appear to be not well studied. (D) Additional factors considered within all relevant publications. Of these additional factors, trophic interactions were in the most publications (although often not explicitly described), with viruses and boundary layers as two additional factors with very little data. Note that some relevant literature did not include BCMS (not BCMS). Each bar in B, C, and D represents a different factor.

et al., 1993). These processes have been and continue to be an integral part of BCM ecology, and we aim to review and expand upon current knowledge by focusing on how other trophic interactions and niche dynamics alter nutrient cycling within BCMS. Research priorities for understanding BCM communities have shifted greatly over time. In the past, the main focus of BCM studies was on descriptive studies that examined bacterial diversity within mats, and only more recently have mechanistic studies on the functional capabilities of BCM microbial members begun to be explored (Cissell & McCoy, 2021; Fan et al., 2015b; Grim et al., 2021; Lee et al., 2018; Mobberley et al., 2017; Woebken et al., 2015). As metagenomic and transcriptomic sequencing have become less costly, these techniques have also recently been utilized in BCMS, allowing for deeper understanding of fine-scale resource partitioning and spatial and temporal differences that influence and are influenced by the microbial composition (e.g., Cissell & McCoy, 2021; Nemergut et al., 2013; Varin et al., 2010; Viladomat et al., 2022). Here, we present an updated review on BCM communities and their biogeochemical cycling through a niche partitioning lens, linking spatial and temporal resource partitioning to functional nutrient cycling processes that affect mat proliferation across environments.

It is critical to understand the mechanisms behind mat growth and maintenance as BCMS continue to proliferate and potentially impact ecosystems around the globe by harboring toxic and pathogenic bacteria, smothering benthic organisms in tropical ecosystems, and more (de Bakker et al., 2017; Paerl & Paul, 2012; Quiblier et al., 2013). Climatic and anthropogenic changes, especially high nutrient input into aquatic systems, are driving these increases and causing shifts toward microbial-dominated ecosystems (Haas et al., 2016; Paul et al., 2005). Especially in coral reef ecosystems, dissolved organic carbon (DOC) and nitrogen inputs can create feedback loops that lead to further reef degradation, as they stimulate mat proliferation and overproduction of these nutrients (Brocke et al., 2018; Mueller et al., 2022). Benthic cyanobacterial mats can cause biofouling and biotoxicity, and they can negatively impact human and organismal health across ecosystems (Paerl & Paul, 2012; Quiblier et al., 2013; Ribeiro et al., 2022; Stuij et al., 2023; Wood et al., 2020). Although mats in temperate marine and freshwater ecosystems can provide benefits such as substrate stabilization, toxin production from these mats is expected to increase with climate change and can detrimentally affect mat consumers and water quality (Paerl & Paul, 2012). On

coral reefs, mat proliferation directly smothers benthic invertebrates and can block coral settlement, inhibiting coral recruitment (Kuffner et al., 2006; Paul et al., 2005; Ribeiro et al., 2022; Ritson-Williams et al., 2020). In addition, BCMs can act as reservoirs and potential vectors for pathogenic bacteria and are especially implicated in black band disease (BBD), a disease in which microbial members alter oxygen and sulfide dynamics of coral with destructive results (Carlton & Richardson, 1995; Cissell et al., 2022; Meyer et al., 2017; Myers et al., 2007; Sato et al., 2016, 2017; Wada et al., 2023). Additionally, removal of mat consumers due to anthropogenic pressures has increased BCM proliferation and community stability by removing natural top-down controls (Cissell & McCoy, 2022; Ford et al., 2018). Mat community structure is distinctly different between degraded and healthy habitats and correlates with higher anthropogenic nutrient inputs (Zubia et al., 2019). Nutrient reductions are a key component to BCM mitigation strategies, and future research into how decreasing specific nutrient inputs into ecosystems with BCMs is key for potentially decreasing their spread and has been proposed in many studies (Brocke et al., 2015; Paerl et al., 1993; Pinckney et al., 2011; Wood et al., 2020). However, management strategies to decrease BCMs focused on bottom-up forces have not always been as successful as anticipated (Florida Keys National Marine Sanctuary, personal communication to S. McCoy, July 31, 2020), potentially due to mat nutrient recycling that sustains redox gradients even without external nutrient inputs, and is still not well understood (Bolhuis et al., 2014; Cissell, 2022; Stal, 2012; Stal et al., 2019). Therefore, we advocate for increased research into potential top-down management alternatives and further understanding of how resource partitioning and nutrient recycling sustain BCM proliferation. As global and anthropogenic changes continue to cause BCM growth and ecosystem degradation, it is critical to understand how links between nutrient cycling, trophic structure, and top-down control may allow us to reduce mat proliferation, especially in coral reef ecosystems.

Mat communities are able to partition resources across small spatial and temporal scales, sharing limited resources such as space and nutrients (Menge & Sutherland, 1976). High levels of biodiversity within mats are maintained through this fine-scale partitioning, especially in layered mats, as are species interactions and tradeoffs (Hutchinson, 1961). Benthic cyanobacterial mats cycle a variety of nutrients depending on their composition and environmental conditions. These include the cycling of carbon, nitrogen, sulfur, phosphorus, calcium, iron, other trace metals, and toxins, which all affect mat resource partitioning (e.g., Bolhuis et al., 2014; Stal, 2012; Stal et al., 2019). This geochemical cycling within mats is inextricably

linked to mat community ecology. The cycling of carbon, nitrogen, and sulfur are especially relevant for our understanding of BCM dynamics. Gradients of these nutrients are created and sustained by the microbial members within mats, especially those layered mats in temperate ecosystems (Stal, 1995). Photosynthesis and carbon fixation drives mat function through energy production (e.g., Abed et al., 2010). Nitrogen fixation by mat members generates bioavailable nitrogen for biosynthesis (e.g., Brocke et al., 2018). Sulfur cycling generates favorable redox gradients for mat metabolism maintenance (e.g., Fike et al., 2008). Additionally, these metabolisms are important players in ecosystem-wide geochemical cycling and have effects far beyond a single mat.

It is important for future study of BCMs to prioritize research that takes into account the effects of environmental change and anthropogenic impacts. Literature on BCMs has evolved substantially in recent years and has just begun incorporating aspects such as top-down trophic interactions, including grazing and viral components (e.g., Cissell & McCoy, 2023a). Reviewing BCM structure and function through the lens of niche partitioning may allow us to assess the diverse mechanisms through which microbes cycle and recycle nutrients, sustaining mat growth. This is critical to understand, as it would allow us to discern key mechanisms that link mat structure and function and the ways we may be able to mitigate mat proliferation. To review all publications relating to BCMs and identify gaps within the literature, we conducted a literature search, extracted publications, and then categorized them based on environment, nutrient cycling, and other factors. We identified the need to utilize ecological theory of niche partitioning and trophic structure to assess how resource partitioning facilitates BCM maintenance and proliferation. Thus, we reviewed spatial and temporal resource partitioning and how it affects carbon, nitrogen, and sulfur cycling within BCMs. We then linked entire mat community nutrient cycling across longer time scales through succession (e.g., the “trophic dynamic viewpoint” of Lindeman, 1942, p. 399). We identify cooperation and metabolic handoffs, boundary layers, and top-down control as important areas of future and continuing research that will allow us to uncover the mechanisms behind BCM proliferation and stability and how we can halt their potential detrimental impacts on ecosystems.

LITERATURE SEARCH METHODS

In order to identify a framework and gaps in the literature, we conducted an initial literature search to examine all publications relating to BCMs. On May 15, 2023, we utilized two databases, Scopus and Google Scholar, to search article title, abstract, and full text

for the following search terms to filter publications: “benthic cyanobacterial mat” OR “benthic bacterial mat” OR “benthic microbial mat” OR “marine cyanobacterial mat” OR “marine bacterial mat” OR “marine microbial mat.” We included the terms “benthic microbial mat” and “marine microbial mat” to include mats without cyanobacteria, allowing us to capture all microbial mats. Although these mats are not the focus of this review, they provided context for how nutrient cycling occurs in very similar complex microbial systems. Publications on mats without cyanobacteria provide interesting information, most notably on microbial sulfur cycling as well as anoxic processes. These mats are denoted as “non-cyanobacterial mats” throughout this review and were included in our final selection of relevant publications.

In order to extract publications from these databases, we downloaded 2797 relevant publications directly from Scopus. To extract metadata from Google Scholar, we used the software Publish or Perish (Harzing, 2007) to extract publications in batches <1000 publications at a time. We completed three searches using the same search terms, restricting titles to specific years: 1900–2000 (511 publications), 2000–2013 (836 publications), and 2013–2024 (921 publications). We then combined all Google Scholar publications, omitting overlapping publications for 2000 and 2013, which resulted in 2142 publications. Then, we removed duplicates from these 4939 publications. Next, we put all 3738 final publications into a single spreadsheet and manually analyzed and categorized them based on environment type, nutrient cycling, additional factors, and article type (Figure 2).

We then analyzed and visualized our results. To do this, we used R (v4.3.0; R Core Team, 2023) in R Studio (v2023.06.0+421; Posit team, 2023) to complete all data analyses and ggplot2 (v3.4.3; Wickham, 2016), ggpvr (v0.6.0; Kassambara, 2023), and viridis (v0.6.4; Garnier et al., 2023) for all visualizations. All data and code associated with this manuscript are available on GitHub (https://github.com/mayapow/BCM_Review).

LITERATURE SEARCH RESULTS

Based on our search terms and the 3738 final publications, we determined that the publication relating to BCMS increased steadily from 1980 to the present (Figure 2a). Of these publications, 882 were primary research articles, 195 were review articles, 222 were inaccessible, 219 had no DOI and were not able to be used, and 2220 were not relevant. Since our search captured the full text of all articles, we ended up with quite a few publications that were not relevant, mainly due to the fact that they cited a sole paper on BCMS or included only brief information about BCMS in the discussion section. Only publications that included

information about BCMS in their methods or results section (primary research articles) or throughout the text (review articles) were deemed relevant and included in the final group.

We categorized all 1077 relevant and accessible publications by environment type, and there were 417 referring to marine environments including intertidal areas, 350 referring to freshwater environments including rivers, lakes, streams, and ponds, 170 referring to hypersaline areas including lakes and marine environments, 144 referring to laboratory environments including culture studies and mesocosm experiments, 137 referring to geologic environments including microbialites and stromatolites, 123 referring to extreme cold environments including mainly arctic and Antarctic lakes, 95 referring to brackish or estuarine environments, 48 referring to extreme hot environments including hydrothermal pools and vents, 17 referring to terrestrial environments mainly dry stream or lake beds, and 3 referring to acid pools (Figure 2b). Some publications analyzed multiple environments, and others were placed in the categories for two or more environments: For example, publications assessing stromatolites in marine ecosystems were categorized as both marine and geologic.

For nutrient cycling, we counted each time a publication assessed specific categories related to nutrient cycling. This resulted in 373 papers that studied nutrient cycling in oxic conditions, 273 studied nutrient cycling in anoxic conditions, 550 mentioned photosynthesis or other autotrophy, 101 assessed heterotrophy, 374 discussed nitrogen cycling, 306 analyzed sulfur cycling, 109 mentioned phosphorus cycling, 78 discussed methane cycling, 83 mentioned the use of iron in nutrient cycling, 74 mentioned the use of trace metals other than iron, 141 discussed lithification including silification or calcification, 79 assessed toxin production, and only 51 discussed metabolic cooperation or handoffs (Figure 2c). These categories often resulted in a lot of overlapping publications; for example, some publications mentioned sulfur cycling and anoxic conditions together.

Finally, we considered additional factors relevant to nutrient cycling in BCMS, including 128 publications that discussed trophic interactions including competition, 86 publications that analyzed mat disturbance including grazing, only 17 that discussed viruses, 48 that assessed climate change, 58 that mentioned anthropogenic impacts (most notably eutrophication), 36 that related to the health and disease of humans or other organisms, 26 that mentioned boundary layers (mainly diffusive boundary layers or DBLs), 70 that analyzed a single type of microbe within mats, and 34 that were still relevant to microbial nutrient cycling in systems such as biofilms but did not directly examine BCMS (Figure 2d, “Not BCMS”). Again, these factors also overlapped across all factors assessed.

These results allowed us to determine trends within the BCM literature since the 1980s. Overall, we determined that cycling of carbon, nitrogen, sulfur, and the interactions of these cycles within oxic and anoxic conditions have been critical for BCM growth and maintenance across ecosystems. We add to these concepts by linking resource partitioning to processes of succession in BCMs, which is not well described in these communities. Additionally, this search helped us identify gaps in the literature, including the need for a comprehensive review of trophic structure and niche partitioning, and areas for future research.

RESOURCE PARTITIONING STRUCTURES CARBON, NITROGEN, AND SULFUR CYCLING IN OXIC AND ANOXIC CONDITIONS ACROSS ECOSYSTEMS

Carbon cycling

Primary production in BCMs is fueled by light, which influences stratification of photosynthetic organisms that utilize different wavelengths of light, especially in layered mats (Figure 3; Jørgensen et al., 1983; Meier et al., 2021; Vigneron et al., 2018). Photosynthesis facilitates mat productivity and is fairly well studied in BCMs (Figure 2c). Cyanobacteria exist as aerobic primary producers, creating energy for mat communities in photic environments during the day (Stal et al., 2017). In addition to bacteria, eukaryotic taxa such as diatoms and Viridiplantae microalgae can

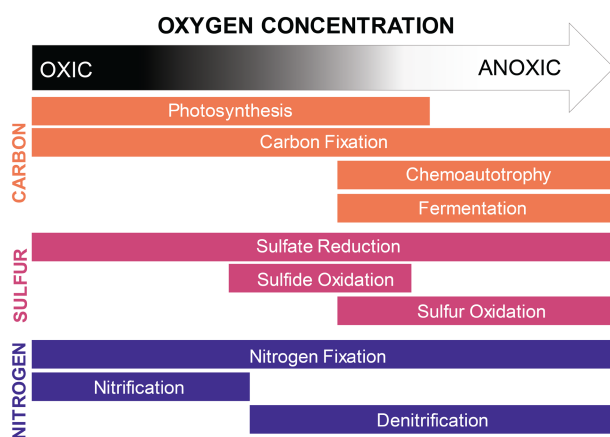


FIGURE 3 Overview of how processes within carbon, sulfur, and nitrogen cycling are partitioned across an oxygen gradient in benthic cyanobacterial mats (BCMs). Oxidic to anoxic conditions vary across space and time and are a major factor in how nutrient cycling is partitioned spatially and temporally in BCMs, especially in layered mats. Links between these cycles are created through redox coupling, direct metabolic cooperation, and inhibition by or dependence on geochemical gradients (e.g., photosynthesis may be inhibited by high sulfide concentration; Meier et al., 2021).

also dominate the surface of temperate, layered mats, contributing to photosynthesis (Hugh et al., 2013; Jørgensen et al., 1983; Khodadad & Foster, 2012). Metabolic capacity of BCMs has been determined to correlate with light and oxygen resource gradients (Dillon et al., 2020). Although cyanobacteria dominate where light penetrates in layered mats, many different species of bacteria can coexist here (Vigneron et al., 2018; Zhang et al., 2015). This coexistence may be promoted by spatial resource partitioning of various abiotic factors, especially in layered BCMs. Although discrete macroscopic vertical partitioning does not occur in some BCMs in tropical marine ecosystems, resource partitioning across small scales, horizontal differences, and competitive and cooperative interactions among microbial species create distinct differences in microbial composition and resource partitioning (Cissell & McCoy, 2021; Wong et al., 2018). Dynamics of competition and dispersal likely create microniches within aerobic space in mats, through spatial nonlinearity of competition, and mosaics of dispersal that affect local colonization and extinction (Chesson, 2000; Kerr et al., 2002; Levins & Culver, 1971). Additionally, fine-scale stratification of bacteria can occur within photic zone based on their UV-protection abilities and motility over diel cycles, along with light wavelengths and penetration depth into the mat (de los Ríos et al., 2015; Jørgensen & Nelson, 1988; Stal et al., 2017; Zhang et al., 2015). For example, the highest proportion of photosynthetic biomass was observed at a “deep [chlorophyll a] maximum” layer, below the short-wavelength radiation depth in freshwater layered mats in Antarctica (Vincent et al., 1993, p. 219). In addition to photosynthesis, organisms in BCMs have been observed to utilize many different strategies for sunlight capture and carbon fixation, such as anaplerotic CO₂ fixation and more (Figure 3; Stal et al., 2017; Vigneron et al., 2018).

Complex carbon cycling occurs within BCMs, including heterotrophic organic carbon degradation, methane cycling, and more (Figure 3; Abed et al., 2010; Canfield & Des Marais, 1993; Hubas et al., 2017; Stal et al., 2019; Vigneron et al., 2018). Trophic interactions that affect carbon cycling have not been well explored in this space but are potentially influenced by heterotrophy and nutrient recycling (Velázquez et al., 2017). Genes involved in carbon recycling within mats have displayed strong specialization, allowing various microbes to partition resources by utilizing different pathways such as the 3-hydroxypropionate cycle, carbon concentrating mechanisms, the Wood–Ljungdahl pathway, and others (Stal et al., 2019; Vigneron et al., 2018). These specific mechanisms represent the many potential ways in which carbon cycles into and within mats, and more work at finer scales is needed to be able to

fully trace the diversity of carbon fixation and carbon cycling throughout BCM communities.

In addition to spatial resource partitioning, mats exhibit strong diurnal patterns driven by photosynthetic bacteria. Carbon fixation is enhanced via CO₂ and follows diel patterns (Rothschild, 1994). At night, cyanobacteria and other oxygenic phototrophs switch to respiration to maintain energy production, favoring processes such as dissimilative nitrate and sulfate reduction (Cissell, 2022). This switch can cause mats to become anoxic within minutes (Villbrandt et al., 1990). Under anoxic conditions, a suite of obligate anaerobic processes can occur, such as fermentation, which utilizes many pathways with various redox reactions, resulting in products including CO₂, lactate, ethanol, and more (Figure 3; Stal & Moezelaar, 1997). Additionally, in noncyanobacterial mats in the complete absence of light, chemoautotrophic organisms can also take the role of driving mat productivity, fixing carbon from sources such as methane seeps to sustain redox gradients within mats (Figure 3; Grönke et al., 2011; Stromecki et al., 2022).

Complimentary to diel cycling, vertical migrations within BCMs have been extensively studied in areas like the Great Lakes sinkholes. Here, diel partitioning by light influences vertical migration of photosynthetic bacteria during the day and sulfur oxidizing bacteria at night, with the fastest motility of both occurring directly after dawn and dark (Figure 3; Biddanda et al., 2023). Thus, light and oxygen gradients often guide diel cycling in BCM communities. Some microbes, specifically cyanobacteria, are said to have genes encoding a circadian rhythm. The rhythmic transcription of genes in cyanobacteria has been observed to center around photosynthesis and nitrogen fixation (Hörnlein et al., 2020; Stal et al., 2019). The potential for circadian rhythms within other bacteria and how this process interacts with microbial communication is an important area for future research and represents a fascinating control on BCM nutrient cycling across diel cycles.

Overall, carbon and oxygen produced and fixed by photosynthesizing mat members create and sustain oxic gradients that affect the microbes around them. Once these gradients are set in place, they are often self-reinforcing: resource partitioning of photosynthetically fixed carbon and oxygen helps perpetuate necessary environmental gradients (Canfield & Des Marais, 1993; Hubas et al., 2017; Meier et al., 2021; Viladomat et al., 2022). Analyzing how biogeochemical cycling within mats affects not only the mats, but also the surrounding water column and ecosystem is critical, as carbon release from BCMs has been determined to be a significant contributor to tropical reef carbon cycling and microbialization (Brocke et al., 2015; Haas et al., 2016; Mueller et al., 2022). Linking evaluations of mats and their effects on nutrient cycling from individual organisms to ecosystems would allow for

prediction of how microbial resource partitioning can have ecosystem-wide effects.

Nitrogen cycling

Bioavailable nitrogen is a limiting nutrient in many environments. Most BCM communities can overcome this issue via nitrogen fixation by their diazotrophic members (Figure 3; Paerl et al., 1993). Diazotrophy has even been detected in deep sea sediments, where nitrogen fixation is driven by energy from chemoautotrophy (Dekas et al., 2018). Many different microbes within BCMs are capable of nitrogen fixation, and within this highly functionally redundant community, differences arise between species based on their interactions (Zehr et al., 1995). Functional and physiological heterogeneity varies widely between microbes, and in a temperate coastal microbial mat, bacteria even millimeters apart were observed to be enriched with differing levels of ¹⁵N (Woebken et al., 2012).

Nitrogen fixation activity is spatially and temporally partitioned in BCM communities. Severin et al. (2010) observed that transcripts associated with a large diversity of diazotrophs varied greatly over a diel cycle, which showcases the many different nitrogen fixation strategies temporally partitioned within BCMs. Nitrogenase activity is inhibited by oxygen, is only present when oxygen evolution is absent or low, and needs energy to occur (Bebout et al., 1993). One strategy diazotrophic bacteria employ to overcome this is utilizing heterocysts, which create spatially separated microanaerobic environments in which nitrogenase activity can occur (Figure 3; Beltrán et al., 2012). The presence of heterocysts and several other variations of spatial separation of oxygen from nitrogen fixation have been seen in BCM forming bacterial species across environments (Beltrán et al., 2012; Fernández-Valiente et al., 2001; Severin & Stal, 2008). Mats are, however, predominantly made up of nonheterocystous nitrogen-fixing bacteria, and nitrogen fixation must either be spatially (via anoxic microniches) or temporally separated from oxygen (Figure 3; Bergman et al., 1997; Bolhuis et al., 2010; Camacho et al., 2022; Severin & Stal, 2008; Villbrandt et al., 1990; Woebken et al., 2015). Nitrogen fixation can therefore occur at high rates overnight, and bacteria utilize energy from stored carbon to drive this process (Bebout et al., 1993; Omeregiet et al., 2004). Additionally, bacteria are still able to fix nitrogen during early sunrise, when light energy is harvested for nitrogen fixation and respiration without net oxygen production (Villbrandt et al., 1990). Indeed, nitrogen fixation in a hot spring microbial mat was observed to peak just after sunset and again in the early morning, when light began to stimulate photosynthesis, but did not yet surpass respiration as to generate inhibitory amounts of oxygen (Steunou et al., 2008). Metabolic coupling of carbon

and nitrogen fixation is highly energetically favorable for mats (Paerl et al., 1993). To this end, some bacteria are able to spatially partition nitrogen fixation and photosynthesis in other ways. For example, microbes in the genus *Lyngbya* are potentially able to laterally partition nitrogen fixation and photosynthesis across their filaments during periods of light (Kothari et al., 2013; Paerl et al., 1991). Overall, BCMs present strong examples of temporal resource partitioning, in which nitrogen-fixing bacteria are able to actively fix nitrogen across a diel cycle by utilizing a range of physiological and spatial partitioning strategies.

In BCMs, fixed nitrogen is transformed to ammonium or amino acids, which are either utilized by nitrogen fixing bacteria or released into the mat. These forms of fixed nitrogen can also be taken up directly from the environment and are crucial in systems without light, such as in the deep sea (Baker et al., 2013). Nitrification, in which microbes convert these metabolites to nitrate and nitrite, is either spatially or temporally separated in BCMs as an aerobic process (Figure 3; Stal, 2012). Many different bacteria engage in nitrification, and the differences in these nitrifiers are affected by geochemical gradients and temporal and spatial niches, with differences driven by salinity, ammonium, and temperature (Fan et al., 2015b). Diatoms are able to store nitrate and utilize it as an electron acceptor in dark environments and across diel cycles, potentially giving these eukaryotes a competitive advantage (Merz et al., 2021). Competition for ammonium can also affect differences in nitrifying bacterial abundance. Accordingly, nitrification is potentially higher in the summer due to increased competition over lower ammonium stocks (Christman et al., 2011; Fan et al., 2015b).

There is still a need for characterization of microenvironmental heterogeneity to understand how nitrifying bacteria are specialized across BCM niche spaces, following what has been done in terrestrial systems (Prosser & Nicol, 2012). Nitrate and nitrite are utilized by a wide variety of bacterial members. In anoxic niches within a BCM community, denitrifying bacteria utilize anammox to convert these bioavailable forms of ammonium, nitrate, and nitrite back to dinitrogen, releasing it from the mat community (Figure 3; Bonin & Michotey, 2006; Joye & Paerl, 1994; Stal, 2012). Denitrifying bacteria are highly diverse, and thus, community composition may heavily influence rates of denitrification (Fan et al., 2015a). Differences between bacteria that utilize the *nirS* and *nirK* genes for denitrification may also affect spatial and temporal partitioning, with *nirS* being more confined to permanent anoxic conditions and *nirK* more flexible across space and time (Figure 3; Desnues et al., 2007). Nitrate respiration was observed to drive diatom metabolism and competitively favored motile diatoms that utilize nitrate from the mat surface and migrate downward and dissimilate this nitrate to ammonium (Merz et al., 2021).

Although this is less common than denitrification, it represents yet another specialized metabolism that utilizes the unique spatial and temporal partitioning within BCM communities.

Nitrogen cycling in BCMs varies widely between ecosystems and across space and time. It is crucial to understand how this will impact ecosystem-level nitrogen cycling, especially in tropical ecosystems where mats are proliferating rapidly. For example, Bonin and Michotey (2006) traced nitrogen dynamics within a temperate BCM and discovered that their mat of interest was a nitrogen sink in winter yet a nitrogen source during the summer months. In addition to cycling fixed nitrogen, mat members can also take up dissolved organic or inorganic nitrogen (DON/DIN) from the environment, augmenting their growth. This has important implications where pollution and fertilizer cause a buildup of excess nitrogen in the water, which can artificially spur BCM growth. Work has been done to understand shifts in nutrient partitioning that alter metabolic equilibrium and organismal interactions based on external nutrient input. For example, Camacho et al. (2022) observed that nitrogen and phosphorus inputs caused changes in nitrogen metabolism, and shifted BCM community structure, causing higher phototrophic activity and increased exopolymeric substance (EPS) production. Benthic cyanobacterial mat proliferation is speculated to alter the nitrogen budget of coral reefs, as microbial mats are the largest contributors to nitrogen fixation in these ecosystems and release high levels of nitrogen back into the environment, potentially accelerating reef degradation (Brocke et al., 2018; Cardini et al., 2014; den Haan et al., 2014). Geochemical cycling within mats has the potential to create feedback loops between increased inputs of bioavailable nitrogen into aquatic environments and high releases from BCMs, which may continuously stimulate BCM growth and proliferation.

Sulfur cycling

Sulfur cycling in BCMs creates biogeochemical sulfide and sulfate gradients, which often increase in concentration with depth (Overmann & van Gemerden, 2000). Additionally, sulfide negatively correlates with oxygen concentrations (Visscher et al., 1992). These gradients are driven by spatially variable sulfate reduction, sulfide oxidation, as well as transport via differential diffusion (Figure 3; Fike et al., 2008). Overlap between biogeochemical zones, such as sulfide and oxygen, can create microniches, allowing for distinct microbial specialization (Meier et al., 2021). Sulfide oxidation can occur within overlapping areas of light and sulfide concentrations or well below the photic zone by an entirely different set of specialized bacteria (Figure 3; Grünke et al., 2011; Jørgensen & Des Marais, 1986). In addition to vertical stratification in layered mats, microscale

heterogeneity and microbial interactions therein create niche pockets within all layers that harbor small populations of microbes across mat types. Recent works have examined how resources within mats are partitioned by using the spatial distribution of functional genes. This has revealed new spatial resource partitioning where obligate anaerobic SRB were found in putative anoxic niches within oxic zones in BCMs (Figure 3; Wong et al., 2015, 2018).

Across diel cycles, sulfide-oxidizing bacteria, such as *Beggiatoa* spp., migrate vertically in layered mats based on where the oxygen–sulfide boundary occurs, remaining in anoxic conditions. At night, anoxic conditions penetrate throughout layered BCMs, and sulfide-oxidizing bacteria have been shown to migrate to the top of the mat in freshwater and marine systems (Biddanda et al., 2023; Jørgensen & Des Marais, 1986). Sulfate reduction can occur in both oxic and anoxic conditions, was observed to be most prevalent at the oxic–anoxic interface of these layered mats, and likely requires a similar specialized niche in less structured BCM communities (Figure 3; Visscher et al., 1992). Surprisingly, although they usually prefer anoxic conditions, SRB are also known to exist in high oxygen environments within BCMs (Figure 3; Jørgensen, 1994; Minz et al., 1999). Indeed, in some vertically stratified mats, SRB were highly abundant in oxic layers, while other taxa such as eukaryotes were more abundant in anoxic conditions (Minz et al., 1999).

Sulfur cycling is often coupled with other nutrient cycling to generate favorable redox reactions. For example, nighttime hydrogen cycling in hypersaline mats follows a diel pattern in which hydrogen is produced in anoxic conditions and consumed by SRB, which appears to result from fermentation of photosynthetic storage products by oxygenic phototrophs (Lee et al., 2014). Additionally, researchers have uncovered coupling of sulfate reduction with nitrogen fixation (Gier et al., 2016; Woebken et al., 2015) and SRB and cyanobacteria coupling with lithification (Wong et al., 2015). Fermentation in BCMs is often powered by sulfate reduction, which provides energy for metabolism during anoxic conditions across diel cycles or in dark environments (Lee et al., 2014; Stal & Moezelaar, 1997).

Redox coupling can result in detrimental impacts to other organisms, as interactions among sulfide oxidizing bacteria, sulfate reducing bacteria, and cyanobacteria are thought to be the causative agent of BBD in corals (Miller & Richardson, 2011; Sato et al., 2016, 2017). In BBD, small-scale vertical gradients of oxygen and sulfur are maintained within the band of bacteria, migrating across the coral surface. This sustains anoxic and sulfidic conditions and provides a niche for the consortium of BBD-causing bacteria (Carlton & Richardson, 1995). A BBD migration rate across a coral surface is directly affected by initial bacterial abundance, which can speed up the disease process

(Wada et al., 2023). For bacterial members involved in BBD, resistance to sulfide is key, and this allows them to survive within the BBD band niche space (Meyer et al., 2017). Similar patterns of spatial distribution of specific SRB and sulfide oxidizing bacteria within BCMs points to their potential to act as reservoirs and potential vectors of BBD (Cissell et al., 2022).

CONNECTING CYCLES: SUCCESSION AND THE EFFECTS OF DISTURBANCE ALTER BCM COMMUNITIES OVER LONGER TIME SCALES

BCM growth and formation have been theorized to follow successional patterns; however, these patterns have rarely been experimentally tested in mats. Here, we link carbon, nitrogen, and sulfur cycling to review potential mechanisms of succession in BCMs. Mats form to create functionally similar communities across environments and are thus thought to form via deterministic processes (Stegen et al., 2012). Succession of early mat microbial members facilitates further colonization by other members by stabilizing areas of sediment through EPS, which is especially key in temperate marine habitats but present across ecosystems (Boomer et al., 2009; Gerbersdorf & Wieprecht, 2015; Wada et al., 2023). Succession is thus limited by recruitment and dispersal, filtering which members are able to colonize the existing mat (Tilman, 1994). As new niche spaces are created, mats expand, making space for other phototrophs and heterotrophs and subsequently anaerobic sulfur and methane metabolizing bacteria in lower layers of stratified mats and in anoxic conditions across diel cycles (Gerbersdorf & Wieprecht, 2015). Depending on the ecosystem, diversity and composition of the mat, order of species colonization, and magnitude of disturbance, succession in BCMs can result in very divergent communities (Nemergut et al., 2013). Through models of facilitation, tolerance, or inhibition based on these factors, vastly different mat community compositions can arise, even within the same areas (Connell & Slatyer, 1977). We have yet to fully understand BCM community “lifecycles,” including whole-mat senescence and death that may also facilitate succession and regrowth (Cissell & McCoy, 2023a; Menge & Sutherland, 1976).

Where initial populations of microbes that form BCMs come from is a topic of great importance but with little concrete supporting evidence. Some authors have suggested potential “seed populations” of bacteria within sediments or the water column that could be feeding proliferation, given the right environmental conditions (Nemergut et al., 2013; Viladomat et al., 2022). Others describe fish feeding on BCMs (Cissell et al., 2019; Manning & McCoy, 2023), which may act as a vector for

mat proliferation and range expansion via their excretion, since cyanobacteria can survive passage through fish guts (Cissell & McCoy, 2023a; Lewin et al., 2003). Indeed, mats have only been observed to grow and proliferate on bare sediment over short time scales in experimental marine field conditions when seeded with BCM pieces (Brocke et al., 2015). This has ecosystem-wide consequences, as on a metacommunity scale, mats have been observed to rapidly colonize large areas of bare sediment, preventing other species from growing there (Brocke et al., 2018; Ford et al., 2018). Additionally, overgrowth of BCMs by macroalgae has been observed to inhibit mat growth, which points to a later successional state in some ecosystems (García-Robledo et al., 2012).

The effects of disturbance on succession are also understudied in BCM systems. Benthic cyanobacterial mats experience disturbance and stress through predation (grazing, viruses), hydrodynamic forces (hurricanes, tides, wind), and competition (shading, overgrowth by macroalgae). Tuchman and Stevenson (1991) discussed the importance of the effects of grazing on BCM succession in freshwater lake environments, highlighting how different species grazed selectively on mats, either inhibiting or enhancing succession. Recently, Cissell and McCoy (2023a) observed that macroscale disturbance did not negatively impact mat growth and even caused increased longevity, supporting the intermediate disturbance hypothesis (Connell, 1978). Furthermore, posthurricane BCM growth was observed to be rapid but did not follow distinct patterns of succession across mats (Lingappa et al., 2022). Thus, the specific effects of succession that support regrowth after disturbance have yet to be elucidated and are paramount to future research efforts on attempts to understand and potentially control BCM populations.

It is also important to consider the effects of unstable coexistence and functional redundancy in BCM communities. Benthic cyanobacterial mats have high diversity and often high functional redundancy (de Anda et al., 2018; Viladomat et al., 2022). Indeed, coexistence is continuously mediated by species turnover within a system and is often facilitated by disturbance (Chesson, 2000; Connell, 1978). Therefore, this functional redundancy can help facilitate mat coexistence and stability by buffering against biodiversity loss during disturbance (Lawton & Brown, 1994). Both functional redundancy and similar functional profiles among mats across ecosystems demonstrate that deterministic processes such as environmental filtering, including that via feedback from microbial mat metabolisms themselves (e.g., Kastman et al., 2016), may be important for the formation of mat microbial communities (Nemergut et al., 2013; Stegen et al., 2012).

In summary, environmental filtering and feedback loops create and sustain mat resource

partitioning across biogeochemical cycles (e.g., Kastman et al., 2016). Microscale habitat heterogeneity in vertical layered mats or horizontally across less structured BCMs creates spatial resource partitioning, allowing a vast diversity of microbes to exist within a single mat (e.g., Vigneron et al., 2018). Furthermore, diurnal patterns of light, temperature, and other abiotic factors affect microbial migration and activity over diel cycles, creating temporal resource partitioning (e.g., Biddanda et al., 2023). Mechanisms of succession affect mats over longer time scales and bring together the effects of temporal and spatial resource partitioning to build and sustain geochemical cycling within functional mat communities.

FUTURE DIRECTIONS

Research on BCMs continues to grow (Figure 2a). To form a more complete view of mats, it is imperative to incorporate a holistic ecosystem perspective into analyses of nutrient cycling and trophic interactions. Processes of microbial cooperation, competition, and top-down effects are crucial components to the understanding of microbial community composition, diversity, and function in other systems, but they have yet to be fully understood in BCMs. New technologies and techniques have recently created opportunities for understanding the functional mechanisms behind BCM intracommunity shifts. Here, we discuss new developments, then present three key areas of research that will expand our understanding of BCM community ecology: metabolic cooperation, DBLs, and top-down control.

New developments in molecular biology, cell biology, and biogeochemical techniques allow for mechanistic and predictive analyses of BCMs

Recent developments in “omics” techniques have made understanding the functional diversity of organisms all the more relevant. Studies within the last few years have used metagenomics and metatranscriptomics to capture the full diversity and functional potential of BCM communities (Cissell & McCoy, 2021; Grim et al., 2021; Lee et al., 2018; Wong et al., 2018). However, additional ventures into proteomics and metabolomics are still needed to dive deeper into the specific metabolites that microbial members are producing and potentially sharing between and across mat layers. Additionally, existing techniques from cell biology and geochemical analysis, including nanoscale secondary ion mass spectrometry (NanoSIMS) and fluorescent in situ hybridization (FISH), could continue to be leveraged toward these

goals. These techniques have been utilized in other systems, such as marine sediments, to assess cooperative interactions between anaerobic methane oxidizing archaea and SRB and will be extremely useful in BCMs (McGlynn et al., 2015). Spatiotemporal analysis of mats can be enhanced using artificial intelligence for image analysis to track mat community growth and senescence over time. Additionally, using this in tandem with modeling to assess mat community succession, migration, and proliferation could provide a novel way to make predictions about how BCMs will affect biogeochemical cycling based on ecosystem level mat cover. These techniques would allow us to move from solely descriptive work to experimental and mechanistic studies of the functional capabilities of BCM communities and their dynamics.

Metabolic cooperation among BCM community members creates community stability

Mat communities are deeply connected and potentially function as symbiotic metaorganisms, maintaining community stability. However, the extent to which cooperation versus competition structures microbial communities is still contentious and may differ between temperate layered mats and less structured tropical mats. Many studies have highlighted how competitive interactions are key (e.g., Ghoul & Mitri, 2016; Palmer & Foster, 2022). Competitive interactions among bacteria can also be intransitive instead of in strict competitive hierarchies, creating varying mosaics of bacteria that can even allow for coexistence under certain conditions (Kerr et al., 2002). Alternatively, metabolic cooperation allows organisms living in close proximity to share resources, sustain redox gradients, and promote nutrient recycling (Hug & Co, 2018; Varin et al., 2010; Zelezniak et al., 2015). One way that mats are believed to stay connected is through direct metabolic cooperation via microbe–microbe interactions and nutrient sharing (Des Marais, 2003). These interactions have been mentioned in the BCM literature; however, only 50 publications (and around half of them review articles) have discussed the potential for direct metabolic cooperation. Metabolite sharing, microbial quorum sensing, and metabolic coupling that results in genome streamlining are several of the potential mechanisms for metabolic cooperation in BCMs.

The sharing of inorganic nutrients has been explored tangentially in mats via measurements of redox gradients and metabolite utilization. However, only a few potential forms of direct cooperation and specific sharing of metabolites (metabolic handoffs) have been discussed. For example, in methane metabolism, acetate from the Wood–Ljungdahl pathway

may be directly utilized by hydrogenotrophic methanogens (Wong et al., 2018). Hydrogen produced by cyanobacteria can provide an electron donor for several anaerobic processes within BCMs, including fueling sulfate reduction and anoxygenic photosynthesis (Guerrero & Berlanga, 2016). Additionally, SRB and colorless sulfur bacteria isolated from BCMs have been observed to grow syntrophically during oxygen limitation in culture (van den Ende et al., 1997). Indeed, it is likely that metabolic cooperation is an extremely common and critical process for maintenance of mat stability and structure.

Cissell and McCoy (2021) revealed many potential areas for metabolic coupling in tropical BCMs through metatranscriptomics. They found that several microbial metabolic pathways, most notably nitrogen and sulfur cycling, were carried out by many different bacteria when bacterial genomes only encoded a single step in a metabolic pathway, revealing genome reduction and potentially obligate cooperation between members (Cissell, 2022). The less structured nature of tropical marine BCMs may potentially facilitate more cross-cycle metabolic handoffs. This follows the Black Queen Hypothesis, in which as microbes utilize shared or “leaked” nutrients from neighboring microbes, and over evolutionary time, they are able to increase their fitness via adaptive gene loss, only maintaining necessary functions (Morris et al., 2012). Tracking these metabolic handoffs and the ways in which microbes directly interact within the mat community is the next step in uncovering just how connected BCM communities are. We advocate for increased research on linkages between community ecology and metabolomics to understand pairwise species interactions, whether through direct measurement of metabolic handoffs or calculated network link associations to visualize more complete interaction webs from the perspectives of these cooperative interactions (Dai et al., 2022). Additionally, it is critical to assess metabolic handoffs in both layered and less structured mats to assess how structural differences may facilitate or inhibit nutrient sharing in these systems.

Much of the recent BCM research on direct microbial interactions and cooperation focuses on microbial communication. Quorum sensing is a concentration-dependent mechanism of sending signals among and within microbial species that is potentially mediated through EPS in BCMs (Decho et al., 2011; Gerbersdorf & Wieprecht, 2015; Montgomery et al., 2013; Stal et al., 2019). Acyl-homoserine lactone (AHL) autoinducers have been identified within layered BCMs and exhibit diel patterns potentially driven by photosynthesis (Decho et al., 2009). However, autoinducers are not produced by and cannot affect all species (Decho et al., 2011). Therefore, continued research on microbial quorum sensing and which specific

microbial members are interacting, and at what cell densities, is imperative to the understanding of mat-wide communication. This may also provide insights into how niches and communication will change with community turnover and across diel cycles, as some species are able to interact more collaboratively than others.

Flow speed and DBLs affect mat structure and niche partitioning

Diffusive boundary layers are defined as the area of flow between zero flow at the surface of a stationary solid and the free stream of fluid, within which particles only move via diffusion (Vogel, 1994). Benthic cyanobacterial mats exist within the DBL, directly above and even within the sediment surface. Diffusion across DBLs directly impacts the rate of mass flux between the BCM surface and water flow, especially in low flow speed environments (Jørgensen & Revsbech, 1985). Thus, DBLs are extremely important to our understanding of mat function and nutrient cycling, as build-ups of excess nutrients (or lack thereof) within the DBL can create strong geochemical gradients, influencing mat community structure and biogeochemical cycling. We determined that only 27 publications had addressed the effects of DBLs on BCMs (Figure 2d). Thus, few researchers have considered how DBLs may completely alter biogeochemical cycling within BCMs. Additionally, the effects of DBLs on, within, and outside of mat community structure have yet to be deduced. Bouma-Gregson et al. (2019) observed that higher flow speeds decreased the availability of anoxic niche space, making mats within high flow environments more metabolically simple than mats from other studies. Direct comparison of mats in multiple different flow environments is necessary for our understanding of how diversity, complexity, and niche structure changes in response to flow speed. Although we know from Mueller et al. (2022) that BCMs can release excess dissolved organic matter and create hypoxic conditions at their surface, we still lack an understanding of DBL thickness, longevity, and the effects an anoxic DBL will have on other mat community members, competitors, and consumers. Most publications have examined the effects of oxygen concentrations within DBLs (e.g., Dillon et al., 2009; van Erk et al., 2023). We propose that understanding the effects of DBLs on the flux of other nutrients, such as bioavailable nitrogen and sulfur, is critical to our understanding of how nutrients are transferred between microbial members across diel cycles. Deep understanding of these nutrient diffusion gradients, in and out of BCMs, will allow for greater prediction of nutrient recycling within mats and handoffs among microbes mediated by migration.

Top-down interactions structure BCMs through selective pressures

Top-down controls on mat populations are understudied and key to our understanding of mat nutrient cycling and community dynamics. Selective predation or viral lysis of key mat members may destabilize metabolic cycling and redox reactions within the mat (sensu Paine, 1980). The importance of predation also depends on the community complexity and diversity, including functional redundancy that influences palatability (Menge & Sutherland, 1976).

Top-down interactions structure ecosystems through selective predation of various members. The differences in the strengths of these interactions allow us to discern how communities and energy flow will change under predation pressure (Paine, 1980). Grazing of cyanobacteria and BCMs has been seen in coral reef environments by predators including fish, sea cucumbers, and other invertebrates (Cissell et al., 2019; Cruz-Rivera & Paul, 2000; Ford et al., 2021; Manning & McCoy, 2023; Ribeiro et al., 2022; Thacker et al., 2001). In addition to top-down control in tropical ecosystems, mats in temperate marine and freshwater ecosystems also experience grazing pressure from fish, ciliates, gastropods, and more (Ackermann et al., 2011; Aguilera et al., 2013; Armitage & Fong, 2004; Clements et al., 2017; Gerbersdorf & Wieprecht, 2015; Tuchman & Stevenson, 1991). Grazing can also impact the ability of mats to attach to substrates and reduce biostabilization, affecting these temperate ecosystems (Gerbersdorf & Wieprecht, 2015). Eukaryotic mat members including protists are also known to consume bacteria and structure BCM communities through selective grazing (Khodadad & Foster, 2012). Indeed, selective grazing of mats and various mat members is often species specific. Many fish species have been observed to consume coral reef BCMs; however, French angelfish (*Pomacanthus paru*) and four common parrotfish species have been observed to preferentially graze on BCMs over other materials and take many consecutive bites (Cissell et al., 2019; Manning & McCoy, 2023). In contrast, in another reef system, macroalgal consumption was greatly preferred over BCMs, and no BCMs were consumed by fish, even in treatments with mixed macroalgal and mat communities, likely due to high mat toxicity in this environment (Ribeiro et al., 2022). Indeed, toxicity and chemical defenses are important drivers of BCM success and diet preferences across ecosystems (Capper et al., 2016; Cruz-Rivera & Paul, 2000). Elucidating the effects of predation and top-down control on BCMs is an important area for future research. As BCMs continue to grow, it is essential to consider the effects of grazers on mats and, potentially, utilize top-down control to ameliorate detrimental proliferation of mats in tropical systems and monitor how top-down control may reduce mat overgrowth but affect biostabilization in temperate ecosystems (Ford et al., 2018; Gerbersdorf & Wieprecht, 2015).

Viruses are an important underrepresented area within the BCM literature and are an essential part of mat nutrient cycling. In areas with very low BCM predation by fish and other macropredators, viruses can represent the main top-down control on mats. Viruses help structure mats via horizontal gene transfer, affecting microbial metabolisms (Stal et al., 2019). Viral dynamics within mats have only recently begun to be studied, and their spatial distribution has been observed to be most abundant in top layers and positively correlated with prokaryote abundance, but surprisingly not with oxygenic phototrophs (Carreira et al., 2015). Defense genes specifically targeting viruses and coevolution between viruses and specific bacteria have been observed in BCMs, showing potential key interactions between microbes in mats (Guajardo-Leiva et al., 2018; Wong et al., 2018). Viruses can influence mats via lysis, but these effects are density dependent wherein dynamics may favor lysogeny at high densities (Cissell & McCoy, 2023b, 2023c). Furthermore, selective lysing of microbial members may disrupt metabolically connected populations, affecting mat nutrient cycling and competitive and cooperative interactions, completely restructuring BCM communities.

In addition to predation and viral lysis, disturbance due to organismal movement or hydrodynamics can alter BCM community structure. Maintenance of functional diversity is upheld by functional redundancy, which is a common theme in mats across environments (Nemergut et al., 2013). Viladomat et al. (2022) used metagenomic datasets to show how functional redundancy was common in BCMs, and mats maintained the same physiological cycles despite the specific species involved. This functional redundancy makes mats resilient to perturbations and allows for maintenance of BCM community stability across desiccation and subsequent rewetting in stream beds, which has been observed to result in higher cooperation under wet conditions (de Anda et al., 2018). Disturbance also often affects layered mats differently with higher stress in surface layers from ultraviolet light, predation, oxidation, and osmotic and xenobiotic stressors (Berlanga et al., 2022). The effects of disturbance, predation, and viral lysis on mat community stability are still not clear and require further research to understand how the potentially unequal top-down effects on different BCM community members will affect mat nutrient cycling and homeostasis.

CONCLUSIONS

Mats are structured by resource partitioning across space, time, and successional state. It is paramount to understand BCM structure and function to be able to assess how community dynamics are created and

sustained through biogeochemical gradients. Benthic cyanobacterial mat communities create feedback loops that facilitate mat proliferation, even releasing copious amounts of carbon and nitrogen back into the environment (Brocke et al., 2015, 2018; Mueller et al., 2022). Mechanisms of how these feedback loops are connected to broader biogeochemical cycles and for the uptake and release of other elements such as sulfur still remain unknown. This represents an important and critically overlooked input into many biogeochemical cycles, especially in coastal areas, an input that will likely continue to increase under future climate conditions.

It is key to understand how anthropogenic changes, specifically warming and increased nutrient inputs, will affect BCM maintenance and proliferation. If we continue along the current trajectory, BCMs will likely continue to flourish, effecting change on ecosystem structure and function through mechanisms such as overgrowth, toxicity, and the local alterations of biogeochemical cycles. Therefore, evaluating BCM community dynamics is critical to our overall understanding of mat structure and function. Although some components of nutrient cycling and resource partitioning in mats are well understood, studies have often evaluated mats in steady-state conditions. In order to elucidate how BCM dynamics exist in the field, we must focus research efforts on analyzing how community members interact directly through handoffs, how redox reactions within BCMs are affected by overlying boundary layers, and how community assembly is structured by top-down effects. We advocate for future research that leverages the principles of microbial community ecology and cutting edge molecular and biogeochemical technology to examine mat community dynamics holistically in our changing world.

AUTHOR CONTRIBUTIONS

Maya E. Powell: Conceptualization (equal); writing – original draft (lead); writing – review and editing (equal).

Sophie J. McCoy: Conceptualization (equal); writing – review and editing (equal).

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