

UC San Diego

UC San Diego Previously Published Works

Title

Introducing the Mangrove Microbiome Initiative: Identifying Microbial Research Priorities and Approaches To Better Understand, Protect, and Rehabilitate Mangrove Ecosystems.

Permalink

<https://escholarship.org/uc/item/2808j7hh>

Journal

mSystems, 5(5)

ISSN

2379-5077

Authors

Allard, Sarah M
Costa, Matthew T
Bulseco, Ashley N
et al.

Publication Date

2020-10-01

DOI

10.1128/msystems.00658-20

Peer reviewed



Introducing the Mangrove Microbiome Initiative: Identifying Microbial Research Priorities and Approaches To Better Understand, Protect, and Rehabilitate Mangrove Ecosystems

Sarah M. Allard,^a Matthew T. Costa,^b Ashley N. Bulseco,^c Véronique Helfer,^d Laetitia G. E. Wilkins,^e Christiane Hassenrück,^{f,g} Karsten Zengler,^{a,h,i} Martin Zimmer,^{d,j,k} Natalia Erazo,^b Jorge L. Mazza Rodrigues,^l Norman Duke,^{k,m} Vânia M. M. Melo,ⁿ Inka Vanwonterghem,^o Howard Junca,^p Huxley M. Makonde,^q Diego Javier Jiménez,^r Tallita C. L. Tavares,^s Marco Fusi,^{t,u} Daniele Daffonchio,^u Carlos M. Duarte,^u Raquel S. Peixoto,^{e,v} Alexandre S. Rosado,^{l,v} Jack A. Gilbert,^{a,b,i} Jeff Bowman^{b,i}

^aDepartment of Pediatrics, School of Medicine, University of California San Diego, La Jolla, California, USA

^bScripps Institution of Oceanography, University of California San Diego, La Jolla, California, USA

^cMarine Science Discipline, Eckerd College, St. Petersburg, Florida, USA

^dDepartment of Ecology, Leibniz Centre for Tropical Marine Research, Bremen, Germany

^eGenome and Biomedical Sciences Facility, University of California Davis, Davis, California, USA

^fTropical Marine Microbiology, Leibniz Centre for Tropical Marine Research, Bremen, Germany

^gMicropaleontology-Paleoceanography, Center for Marine Environmental Sciences, University of Bremen, Bremen, Germany

^hDepartment of Bioengineering, University of California San Diego, La Jolla, California, USA

ⁱCenter for Microbiome Innovation, University of California San Diego, La Jolla, California, USA

^jUniversity of Bremen, Faculty 02 Biology/Chemistry, Bremen, Germany

^kUICN SSC-Mangrove Specialist Group

^lDepartment of Land, Air, and Water Resources, University of California Davis, Davis, California, USA

^mCentre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Townsville, Australia

ⁿMicrobial Ecology and Biotechnology Laboratory, Federal University of Ceará, Fortaleza, Ceará, Brazil

^oAustralian Centre for Ecogenomics, The University of Queensland, Brisbane, Australia

^pRG Microbial Ecology: Metabolism, Genomics & Evolution, Microbiomas Foundation, Chia, Colombia

^qDepartment of Pure & Applied Sciences, Technical University of Mombasa, Mombasa, Kenya

^rMicrobiomes and Bioenergy Research Group, Department of Biological Sciences, Universidad de los Andes, Bogotá, Colombia

^sMarine Sciences Institute, Federal University of Ceará, Fortaleza, Ceará, Brazil

^tEdinburgh Napier University School of Applied Sciences, Edinburgh, United Kingdom

^uRed Sea Research Center, BESE, Biological and Environmental Sciences and Engineering Division, KAUST, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia

^vFederal University of Rio de Janeiro (UFRJ), Rio de Janeiro, Brazil

ABSTRACT Mangrove ecosystems provide important ecological benefits and ecosystem services, including carbon storage and coastline stabilization, but they also suffer great anthropogenic pressures. Microorganisms associated with mangrove sediments and the rhizosphere play key roles in this ecosystem and make essential contributions to its productivity and carbon budget. Understanding this nexus and moving from descriptive studies of microbial taxonomy to hypothesis-driven field and lab studies will facilitate a mechanistic understanding of mangrove ecosystem interaction webs and open opportunities for microorganism-mediated approaches to mangrove protection and rehabilitation. Such an effort calls for a multidisciplinary and collaborative approach, involving chemists, ecologists, evolutionary biologists, microbiologists, oceanographers, plant scientists, conservation biologists, and stakeholders, and it requires standardized methods to support reproducible experiments. Here, we outline the Mangrove Microbiome Initiative, which is focused around three urgent priorities and three approaches for advancing mangrove microbiome research.

Citation Allard SM, Costa MT, Bulseco AN, Helfer V, Wilkins LGE, Hassenrück C, Zengler K, Zimmer M, Erazo N, Mazza Rodrigues JL, Duke N, Melo VMM, Vanwonterghem I, Junca H, Makonde HM, Jiménez DJ, Tavares TCL, Fusi M, Daffonchio D, Duarte CM, Peixoto RS, Rosado AS, Gilbert JA, Bowman J. 2020. Introducing the Mangrove Microbiome Initiative: identifying microbial research priorities and approaches to better understand, protect, and rehabilitate mangrove ecosystems. *mSystems* 5:e00658-20. <https://doi.org/10.1128/mSystems.00658-20>.


Editor Jean-Baptiste Raina, University of Technology Sydney

Ad Hoc Peer Reviewers Janet Jansson, Pacific Northwest National Laboratory; Stacey Trevathan-Tackett, Deakin University.

The review history of this article can be read [here](#).

Copyright © 2020 Allard et al. This is an open-access article distributed under the terms of the [Creative Commons Attribution 4.0 International license](#).

Address correspondence to Sarah M. Allard, smallard@health.ucsd.edu, or Jeff Bowman, jsbowman@ucsd.edu.

 As the global footprint of mangroves and their associated ecosystem services diminish, this Perspective introduces the Mangrove Microbiome Initiative and outlines 3 research priorities and 3 approaches to advance the field of mangrove microbiome research.

Published 20 October 2020

KEYWORDS ecosystem rehabilitation, ecosystem services, mangrove, microbiome, rhizosphere

INTRODUCTION: GLOBAL ROLE OF MANGROVES AND THEIR ASSOCIATED MICROBIOMES

Mangroves, intertidal forests along tropical and subtropical coasts, are hot spots of productivity and biodiversity. These ecosystems yield valuable services for humanity, including cultural and religious value (1), habitat for fisheries species (2), plant products including timber, filtration of terrestrial runoff, and coastline stabilization against storm impacts (3, 4). Globally, mangroves are significant carbon sinks (4), mitigating climate change by removing atmospheric greenhouse gases through sequestration of organic matter in above- and below-ground biomass. Ultimately, the mangrove ecosystem buries autochthonous and allochthonous detritus in anoxic, saline sediments, where this “coastal blue carbon” can remain stable for millennia (5, 6). Many of the ecological functions that underpin these services are carried out or supported by the microorganisms that comprise the mangrove microbiome, including bacteria, archaea, fungi, and protists.

Despite their economic and ecological importance, mangroves are threatened globally (7), especially by coastal development and pollution (8), and potentially by projected sea level rise (9, 10). Research to uncover the microbe-mangrove interactions that maintain ecosystem services and resilience under changing conditions is urgently needed for successful conservation and rehabilitation (10), making the nascent study of mangrove microbiome functions a high priority (8). As we enter what the United Nations has designated the Decade of Ocean Science for Sustainable Development as well as the Decade on Ecosystem Restoration, building international collaboration working toward science-based management of coastal ecosystems is an extremely timely endeavor (11, 12).

This Perspective proposes microbiological research objectives and approaches to meet the mangrove management challenges of the 21st century. We have formed the Mangrove Microbiome Initiative (MMI), an international network of researchers advancing mangrove microbiome research through collaboration, discussion, and advocacy. The aim of this platform is to facilitate collaborative work and knowledge sharing among all researchers who wish to participate, strengthening our collective efforts toward understanding, protecting, and rehabilitating these important ecosystems. Research has so far only scratched the surface of understanding the diversity, function, and connectivity of mangrove microbiomes. Recent developments in -omics techniques and bioinformatic pipelines have changed the way we look at genes, species, and communities, opening new windows into mangrove ecology. A more complete understanding of mangrove-microbe interactions will support efforts to rehabilitate mangrove forests and sustain ecosystem services in the face of increasing anthropogenic stress. Here, we identify three priority research areas for mangrove microbiome research (priority 1 [P1], P2, and P3) and discuss three approaches to advancing the field (approach 1 [A1], A2, and A3) (Fig. 1).

PRIORITY RESEARCH AREAS

P1. Characterizing mangrove microbiomes across scales in a changing world.

Understanding and predicting the influence of global change on the mangrove microbiome is an important goal and a great challenge that offers opportunities to protect, manage, and mitigate impacts to threatened mangroves. At present, much of the work characterizing microbial communities in mangroves has been descriptive and limited in temporal and spatial range. While descriptive studies provide an important foundational understanding of the mangrove microbiome, there is a need to advance the field toward hypothesis-driven observational and experimental research to establish the mechanisms that underlie mangrove-microbe symbiosis in these variable and far-flung ecosystems. Achieving a mechanistic understanding requires detailed quantification of biotic (e.g., plant taxonomy, anatomy, and sediment fauna) and abiotic (e.g., temper-

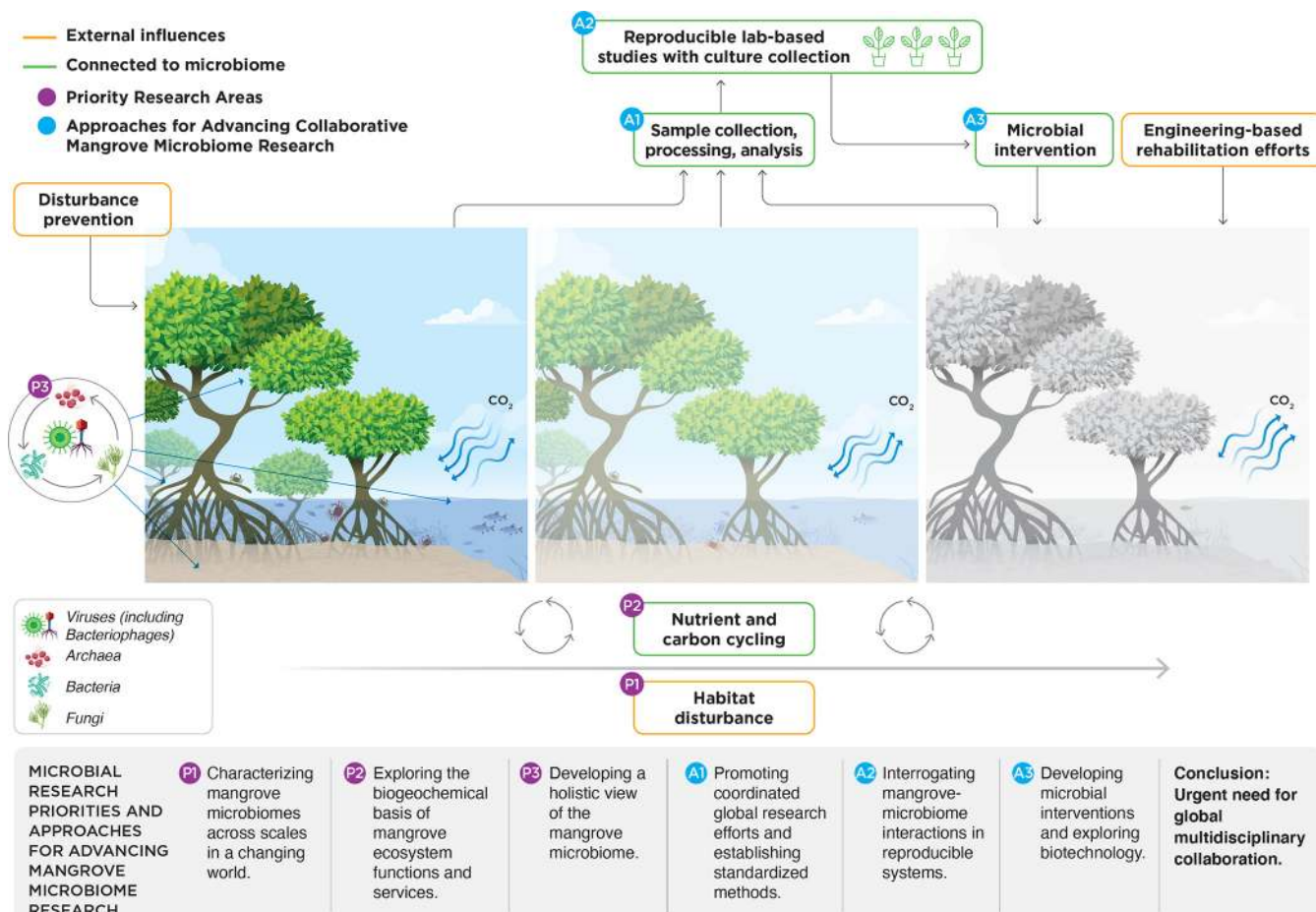


FIG 1 Microbial research priorities and approaches to better understand, protect, and rehabilitate mangrove ecosystems.

ature, salinity, tidal amplitude and frequency, and level of pollution) variables that can influence the composition and functions of the microbiome. Dynamic spatiotemporal factors such as fluctuating air exposure times, oxygen concentrations (13), and salinity levels (14), in addition to seasonal variations in rainfall (15), can affect the microbiome, thereby influencing mangrove productivity. At a fine spatial scale, vicinity to vegetation and crab burrows can also affect microbial metabolism (16, 17). To better understand these processes, sophisticated experimental designs, new technologies and analytical approaches, and directed intervention studies are required, as discussed below in Approaches.

P2. Exploring the biogeochemical basis of mangrove ecosystem functions and services. Mangroves support diverse communities of microorganisms in sediment layers, in the water column, and in and on their tissues (e.g., biofilms on mangrove roots) (18), and these communities play crucial roles in mangrove biogeochemistry and nutrient cycling (19, 20). Indeed, a large fraction of the carbon turnover in these ecosystems is carried out by sediment microbial heterotrophs (21). Bacterial oxygen consumption and sulfate reduction generate chemical conditions in mangrove sediments that slow organic matter turnover, favoring the establishment of a net carbon sink (22). In addition, microbial metabolism along sediment redox gradients drives the production and consumption of methane and nitrous oxide (19, 23), potentially resulting in net sources of these greenhouse gases (24). Microbes play a critical role in nitrogen cycling in mangrove sediments through a broad array of processes, including fixation, denitrification, and anammox (anaerobic ammonium oxidation) (19, 25). They contribute to remineralizing, and solubilizing otherwise unavailable phosphorus (26),

thereby mediating the availability and fluxes of nutrients that can potentially limit mangrove plant productivity (27, 28). This productivity fuels plant-product-based ecosystem services and provides the basis of the mangrove ecosystem food web (29–31), which feeds the valuable services of fisheries production and mangrove ecotourism (2, 32). In addition, microbes on root and leaf surfaces make micronutrients available, can provide defense against pathogens, and launch decay processes upon senescence (18, 33). While the relevance of these microbial processes to biogeochemical cycling and to the associated services of carbon sequestration and nutrient regulation have been demonstrated, mechanistic and predictive understanding is still in its infancy. The Approaches section below discusses how standardized, experimental, and process-based studies will move this field toward predictive understanding.

P3. Developing a holistic view of the mangrove microbiome. Although there are numerous studies on mangrove bacterial communities (e.g., 18, 34, 35), there are relatively few studies on fungi, protists, archaea, and viruses (including phage and eukaryotic viruses). This knowledge gap is further complicated by the complex structure of the mangrove root system. Many metazoan inhabitants of this system, including sponges, oysters, clams, and cockles, have their own distinct microbiomes that also contribute to ecosystem functioning. Future work must take into account the full extent of the taxonomic, functional, and structural diversity of the mangrove forest. It is essential, for example, to explore the evolution, ecology, and physiology of mangrove-associated microbial eukaryotes. Fungi and protists in particular are thought to play a significant role in the ecology of mangrove forests (36) and can be bioindicators of pollutants (37, 38). Unlike prokaryotes, their activity and function in natural ecosystems are not based on a large flexibility of their metabolic capacities but on the exploration of innovations in their structural complexity and behaviors (39). Fungi are capable of converting complex organic compounds into more easily accessible forms and provide infrastructure (i.e., fungal highways) along which bacteria migrate to areas with preferential nutrients, substrates, and redox conditions (40, 41). Among protists, thraustochytrids, known for their saprobic capabilities (42) and their ability to degrade highly recalcitrant organic matter, also play an essential role in organic matter turnover in mangrove ecosystems and can be an important food source for detritivores (43). Archaea represent another underexplored group in mangrove ecosystems. Ammonia-oxidizing archaea (and their bacterial counterparts) are common in mangrove sediments, as are methanogenic archaea. Beyond simple observations of community structure (44), however, very little is known about the function of mangrove-associated archaeal communities. Approaches to future mangrove microbiome research should be more inclusive of nonbacterial microorganisms to facilitate a more holistic understanding of the ecosystem.

APPROACHES FOR ADVANCING COLLABORATIVE MANGROVE MICROBIOME RESEARCH

A1. Promoting coordinated global research efforts and establishing standardized methods. Coordinated global efforts to ensure data quality and comparability are essential (45), as this enables integration for meta-analysis as well as more distributed analytical capability. The MMI will promote coordinated international mangrove monitoring networks and contribute to standardization of sampling, analytical procedures, and data archiving.

Robust experimental design (e.g., sufficient and appropriate replication) and sampling protocols are crucial to move beyond anecdotal observation and reduce the masking effect of confounding factors. Representative sampling requires consideration of the appropriate scale and target community (e.g., epibionts and endobionts) and how to address variation within sampling units (e.g., combining subsamples). Special attention should be paid to factors influencing microbial habitat, such as sediment depth (34, 46), light exposure (47), variety of root structures among and within mangrove tree species (48), and leaf senescence.

To embed our efforts in a larger scope beyond mangrove ecosystem boundaries, standards from existing initiatives (e.g., the Earth Microbiome Project) should be adapted for the generation of mangrove microbiome data (49). Our current toolbox to study the mangrove microbiome includes modern -omics techniques (metagenomics, metatranscriptomics, metaproteomics, and metabolomics), physiology and biochemistry (cultivation, colonization, and metabolic modeling), imaging (three-dimensional [3D] tomography, histology, electron microscopy, superresolution microscopy, and mass spectrometry), hypothesis-driven field studies, and the use of reproducible laboratory systems. The MMI platform will be used to circulate standard protocols adjusted to mangrove research for quality assurance and reproducibility. We envision a sustainable collaborative research approach where samples are collected and stored for a broad scope of future applications and where standardized metadata (including contextual information, analytical protocols, and bioinformatic pipelines) are accessible. Some existing international initiatives can be leveraged to meet this goal. For example, infrastructure to meet these aims can be supported by the establishment of mangrove monitoring programs in ILTER (International Long-Term Ecosystem Research) sites and the expansion of the ILTER network to cover sites from a broad range of mangrove environmental settings around the world (50). We recommend strict adherence to existing checklists for data archiving (51) and additional submission of nonmandatory parameters to improve compliance with the FAIR principle (Findable, Accessible, Interoperable, and Reusable [52]). The MMI will develop and promote the use of essential variables in coordination with GOOS (Global Ocean Observing System [53, 54]) to support concerted documentation and monitoring of the mangrove microbiome across spatial and temporal scales.

A2. Interrogating mangrove-microbiome interactions in reproducible systems.

Mangrove ecosystems are threatened by a multitude of stressors, such as pollution, sea level rise, coastal development, and sediment salinization. There is an urgent need to better understand the impacts of these stressors on mangroves and their microbiomes. In contrast to observational studies, controlled lab-based experiments enable manipulation of specific disturbances and quantification of effects on microbial populations. Using new microbial ecology approaches and technologies, it is possible to predict and test response to perturbation and provide insight into the mechanisms behind these responses (55, 56). Controlled laboratory settings can yield reproducible results while eliminating environmental fluctuations and high costs often associated with field studies requiring large sample sizes (57). Model ecosystems with the potential to enable reproducible mangrove microbiome research range from highly controllable enclosed systems like EcoFABs (fabricated microbial ecosystems) (58, 59) to larger scale systems that introduce more variation and complexity (46, 60).

Generating robust synthetic microbial communities for use in these reproducible systems requires isolation of representative microorganisms, a historically challenging task. Successful approaches to reducing isolation bias include dilution to extinction (61, 62), encapsulation or separation (63, 64), and growth on chips (65, 66), all approaches that imitate the natural environment to a certain degree, e.g., by operating with low nutrient concentrations. Other top-down strategies, like dilution to stimulation (67) or targeting specific microbes based on gene content (68, 69), could be useful to develop specific mangrove-derived microbial consortia with desired functional roles (33), while automated cultivation procedures can lower cost and increase throughput. Expanding microbial culture collections from mangrove environments will be necessary to unravel beneficial plant-microbe interactions, including plant-health-promoting bacteria (33), and to provide necessary cultures for improving mangrove health in the future.

A3. Developing microbial interventions and exploring biotechnology. Specific threats to mangrove forests may be remediated or mitigated by manipulation of microorganisms. For example, *in situ* characterization of microbial biodegradation potential allows for the development of strategies for microbiome manipulation as a tool to prevent and/or mitigate oil impacts on mangroves (34, 37, 46, 70, 71), which are vulnerable to chronic oil spills (72). Of particular interest are oil-degrading, health-

promoting (ODHP) microbial consortia (33), which have dual functions: promoting oil degradation and improving ecosystem and plant health. Indeed, microbial consortia in mangrove sediments have been found to efficiently degrade oil, rendering them a potential resource of effective hydrocarbon-degrading bacteria that can be used as an inoculum for the purpose of bioremediation (73).

It is important to recognize that mangrove-health-promoting bacteria may have additional applications to agriculture and other systems. A recent study of the microbiome associated with propagules of the mangrove plant *Avicennia marina* in the Red Sea revealed plant-growth-promoting bacteria that enhance root development and mangrove establishment (42). In addition, bacterial strains isolated from mangroves have shown promise for salinity adaptation in agriculture (42) and for removal of cadmium and zinc from hazardous industrial residue (74), highlighting the biotechnological potential of mangrove-associated microbes to mitigate environmental impacts. By marshaling the full suite of modern -omics tools, there is great promise for the development of evidence-based ecosystem rehabilitation techniques for mangrove and agricultural ecosystem functioning.

CONCLUSION: URGENT NEED FOR GLOBAL MULTIDISCIPLINARY ACTION

To advance the field of mangrove microbiome research and to facilitate protection and rehabilitation of these crucial ecosystems, there is an urgent need for global multidisciplinary collaboration that leads to action. Here, we have identified three research priorities and three approaches to advance the field, and we have committed to building a broad, collaborative network of researchers across disciplines, including chemists, ecologists, evolutionary biologists, microbiologists, oceanographers, plant scientists, conservation biologists, and government representatives. Global collaboration to establish universal protocols with a constantly expanding and versatile toolbox will facilitate the collection of valuable data simultaneously and across the globe. Testing hypotheses to elucidate microbial metabolisms that support mangrove rehabilitation is critically dependent on field experiments extending over the multiyear time scale of intervention success or failure and on the consistent measurement of defined variables important for mangrove health assessment. While such an investment may seem unattractive in a fast-moving field, documentation of long-term results will be a rare and valuable contribution to global mangrove restoration and rehabilitation efforts and will be beneficial for successfully designing mangrove ecosystems for the provisioning of particular ecosystem services. Furthermore, these approaches will be valuable, not only for mangrove ecosystems, but will also have the potential for application to other coastal ecosystems and even terrestrial agricultural systems in the future.

With the establishment of the Mangrove Microbiome Initiative (<http://bmmo.microbe.net/mangrove-microbiome-initiative-mmi/>) as part of the Beneficial Microbes for Marine Organisms (BMMO) network, we seek to bridge the breadth of knowledge from researchers focusing on the ecology and physiology of mangrove systems and those with expertise in microbiology, high-throughput molecular methods, and bioinformatics. We welcome any interested researchers working on the mangrove microbiome to join our network through our website. This network provides a platform to establish common goals and foster collaboration among groups working around the globe and to share not only technical expertise but also crucial advice for overcoming logistical barriers and enabling long-term research and rehabilitation success. For increased awareness and longevity of research and interventions, engagement with local communities and buy-in from decision-makers is essential. Furthermore, with the high cost associated with accessing remote locations, the challenging logistics of obtaining permits for research sites, and the importance of prioritizing just practices for the extraction of samples and data from field sites, collaborative approaches from multiple research groups in multiple regions and countries would be most efficient.

As the global footprint of mangroves and their associated ecosystem services continue to diminish, advancement of the field of mangrove microbiome research is urgently needed. Microorganisms have seldom been included in ecosystem manage-

ment plans and policy, but as our understanding of their importance in maintaining ecosystem health and enhancing resilience in the face of global change grows (75), it is crucial to acknowledge their role and the opportunities that they provide.

ACKNOWLEDGMENTS

We thank Jonathan Eisen (ORCID <https://orcid.org/0000-0002-0159-2197>) and the microBENet platform for the full and kind support provided to the BMMO network and its initiatives.

M.F. acknowledges funding from the Natural Environment Research Council (NERC grant NE/S006990/1).

REFERENCES

- Walters BB, Rönnebäck P, Kovacs JM, Crona B, Hussain SA, Badola R, Primavera JH, Barbier E, Dahdouh-Guebas F. 2008. Ethnobiology, socio-economics and management of mangrove forests: a review. *Aquat Bot* 89:220–236. <https://doi.org/10.1016/j.aquabot.2008.02.009>.
- Aburto-Oropeza O, Ezcurra E, Danemann G, Valdez V, Murray J, Sala E. 2008. Mangroves in the Gulf of California increase fishery yields. *Proc Natl Acad Sci U S A* 105:10456–10459. <https://doi.org/10.1073/pnas.0804601105>.
- Kathiresan K, Rajendran N. 2005. Coastal mangrove forests mitigated tsunami. *Estuar Coast Shelf Sci* 65:601–606. <https://doi.org/10.1016/j.ecss.2005.06.022>.
- Twilley RR, Chen RH, Hargis T. 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water Air Soil Pollut* 64:265–288. <https://doi.org/10.1007/BF00477106>.
- Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC. 2003. Global carbon sequestration in tidal, saline wetland soils. *Glob Biogeochem Cycles* 17:1111. <https://doi.org/10.1029/2002GB001917>.
- Nellemann C, Corcoran E, Duarte CM, Valdrés L, Young CD, Fonseca L, Grimsditch G. 2009. Blue carbon — the role of healthy oceans in binding carbon. A rapid response assessment. UN Environment, GRID-Arendal.
- Feller IC, Friess DA, Krauss KW, Lewis RR. 2017. The state of the world's mangroves in the 21st century under climate change. *Hydrobiologia* 803:1–12. <https://doi.org/10.1007/s10750-017-3331-z>.
- Trevathan-Tackett SM, Sherman CDH, Huggett MJ, Campbell AH, Laverock B, Hurtado-McCormick V, Seymour JR, Firl A, Messer LF, Ainsworth TD, Negandhi KL, Daffonchio D, Egan S, Engelen AH, Fusi M, Thomas T, Vann L, Hernandez-Agreda A, Gan HM, Marzinelli EM, Steinberg PD, Hardtke L, Macreadie PI. 2019. A horizon scan of priorities for coastal marine microbiome research. *Nat Ecol Evol* 3:1509–1520. <https://doi.org/10.1038/s41559-019-0999-7>.
- Saintilan N, Khan NS, Ashe E, Kelleway JJ, Rogers K, Woodroffe CD, Horton BP. 2020. Thresholds of mangrove survival under rapid sea level rise. *Science* 368:1118–1121. <https://doi.org/10.1126/science.aba2656>.
- Friess DA, Yando ES, Abuchahla GMO, Adams JB, Cannicci S, Canty SWJ, Cavanaugh KC, Connolly RM, Cormier N, Dahdouh-Guebas F, Diele K, Feller IC, Fratini S, Jennerjahn TC, Lee SY, Ogurcak DE, Ouyang X, Rogers K, Rowntree JK, Sharma S, Sloey TM, Wee AKS. 2020. Mangroves give cause for conservation optimism, for now. *Curr Biol* 30:R153–R154. <https://doi.org/10.1016/j.cub.2019.12.054>.
- Waltham NJ, Elliott M, Lee SY, Lovelock C, Duarte CM, Buelow C, Simenstad C, Nagelkerken I, Claassens L, Wen CK-C, Barletta M, Connolly RM, Gillies C, Mitsch WJ, Ogburn MB, Purandare J, Possingham H, Sheaves M. 2020. UN Decade on Ecosystem Restoration 2021–2030—what chance for success in restoring coastal ecosystems? *Front Mar Sci* 7:71. <https://doi.org/10.3389/fmars.2020.00071>.
- Ryabinin V, Barbière J, Haugan P, Kullenberg G, Smith N, McLean C, Troisi A, Fischer A, Aricò S, Aarup T, Pissierssens P, Visbeck M, Enevoldsen HO, Rigaud J. 2019. The UN Decade of Ocean Science for Sustainable Development. *Front Mar Sci* 6:470. <https://doi.org/10.3389/fmars.2019.00470>.
- Giomli F, Barausse A, Duarte CM, Booth J, Agusti S, Saderne V, Anton A, Daffonchio D, Fusi M. 2019. Oxygen supersaturation protects coastal marine fauna from ocean warming. *Sci Adv* 5:eaax1814. <https://doi.org/10.1126/sciadv.aax1814>.
- Chambers LG, Guevara R, Boyer JN, Troxler TG, Davis SE. 2016. Effects of salinity and inundation on microbial community structure and function in a mangrove peat soil. *Wetlands* 36:361–371. <https://doi.org/10.1007/s13157-016-0745-8>.
- Lee RY, Porubsky WP, Feller IC, McKee KL, Joye SB. 2008. Porewater biogeochemistry and soil metabolism in dwarf red mangrove habitats (Twin Cays, Belize). *Biogeochemistry* 87:181–198. <https://doi.org/10.1007/s10533-008-9176-9>.
- Booth JM, Fusi M, Marasco R, Mboobo T, Daffonchio D. 2019. Fiddler crab bioturbation determines consistent changes in bacterial communities across contrasting environmental conditions. *Sci Rep* 9:3749. <https://doi.org/10.1038/s41598-019-40315-0>.
- Gillis LG, Snavely E, Lovelock C, Zimmer M. 2019. Effects of crab burrows on sediment characteristics in a *Cerriops australis*-dominated mangrove forest. *Estuar Coast Shelf Sci* 218:334–339. <https://doi.org/10.1016/j.ecss.2019.01.008>.
- Holguin G, Vazquez P, Bashan Y. 2001. The role of sediment microorganisms in the productivity, conservation, and rehabilitation of mangrove ecosystems: an overview. *Biol Fertil Soils* 33:265–278. <https://doi.org/10.1007/s003740000319>.
- Reis CRG, Nardoto GB, Oliveira RS. 2017. Global overview on nitrogen dynamics in mangroves and consequences of increasing nitrogen availability for these systems. *Plant Soil* 410:1–19. <https://doi.org/10.1007/s11104-016-3123-7>.
- Shiau Y-J, Chiu C-Y. 2020. Biogeochemical processes of C and N in the soil of mangrove forest ecosystems. *Forests* 11:492. <https://doi.org/10.3390/f11050492>.
- Alongi DM. 1988. Bacterial productivity and microbial biomass in tropical mangrove sediments. *Microb Ecol* 15:59–79. <https://doi.org/10.1007/BF02012952>.
- Kristensen E, Bouillon S, Dittmar T, Marchand C. 2008. Organic carbon dynamics in mangrove ecosystems: a review. *Aquat Bot* 89:201–219. <https://doi.org/10.1016/j.aquabot.2007.12.005>.
- Giani L, Bashan Y, Holguin G, Strangmann A. 1996. Characteristics and methanogenesis of the Balandra lagoon mangrove soils, Baja California Sur, Mexico. *Geoderma* 72:149–160. [https://doi.org/10.1016/0016-7061\(96\)00023-7](https://doi.org/10.1016/0016-7061(96)00023-7).
- Rosentreter JA, Maher DT, Erler DV, Murray RH, Eyre BD. 2018. Methane emissions partially offset “blue carbon” burial in mangroves. *Sci Adv* 4:eaa04985. <https://doi.org/10.1126/sciadv.aao4985>.
- Fernandes SO, Michotey VD, Guasco S, Bonin PC, Loka Bharathi PA. 2012. Denitrification prevails over anammox in tropical mangrove sediments (Goa, India). *Mar Environ Res* 74:9–19. <https://doi.org/10.1016/j.marenvres.2011.11.008>.
- Vazquez P, Holguin G, Puente ME, Lopez-Cortes A, Bashan Y. 2000. Phosphate-solubilizing microorganisms associated with the rhizosphere of mangroves in a semiarid coastal lagoon. *Biol Fertil Soils* 30:460–468. <https://doi.org/10.1007/s003740050024>.
- Feller IC, McKee KL, Whigham DF, O'Neill JP. 2003. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* 62:145–175. <https://doi.org/10.1023/A:1021166010892>.
- McKee KL, Feller IC, Popp M, Wanek W. 2002. Mangrove isotopic ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) fractionation across a nitrogen vs. phosphorus limitation gradient. *Ecology* 83:1065–1075. <https://doi.org/10.2307/3071914>.
- Odum WE, Heald EJ. 1975. The detritus-based food web of an estuarine mangrove community, p 265–286. In *Estuarine research*, vol 1. Chemistry, biology, and the estuarine system. Academic Press, New York, NY.
- Abrantes KG, Johnston R, Connolly RM, Sheaves M. 2015. Importance of mangrove carbon for aquatic food webs in wet–dry tropical estuaries. *Estuaries Coasts* 38:383–399. <https://doi.org/10.1007/s12237-014-9817-2>.
- Demopoulos AWJ, Fry B, Smith CR. 2007. Food web structure in exotic

- and native mangroves: a Hawaii-Puerto Rico comparison. *Oecologia* 153:675–686. <https://doi.org/10.1007/s00442-007-0751-x>.
32. Tanner MK, Moity N, Costa MT, Marin Jarrin JR, Aburto-Oropeza O, Salinas-de-León P. 2019. Mangroves in the Galapagos: ecosystem services and their valuation. *Ecol Econ* 160:12–24. <https://doi.org/10.1016/j.ecolecon.2019.01.024>.
 33. do Carmo FL, dos Santos HF, Martins EF, van Elsas JD, Rosado AS, Peixoto RS. 2011. Bacterial structure and characterization of plant growth promoting and oil degrading bacteria from the rhizospheres of mangrove plants. *J Microbiol* 49:535–543. <https://doi.org/10.1007/s12275-011-0528-0>.
 34. Andrade LL, Leite DC, Ferreira EM, Ferreira LQ, Paula GR, Maguire MJ, Hubert CR, Peixoto RS, Domingues RM, Rosado AS. 2012. Microbial diversity and anaerobic hydrocarbon degradation potential in an oil-contaminated mangrove sediment. *BMC Microbiol* 12:186. <https://doi.org/10.1186/1471-2180-12-186>.
 35. Jiang X-T, Peng X, Deng G-H, Sheng H-F, Wang Y, Zhou H-W, Tam NF-Y. 2013. Illumina sequencing of 16S rRNA tag revealed spatial variations of bacterial communities in a mangrove wetland. *Microb Ecol* 66:96–104. <https://doi.org/10.1007/s00248-013-0238-8>.
 36. Cheung MK, Wong CK, Chu KH, Kwan HS. 2018. Community structure, dynamics and interactions of bacteria, archaea and fungi in subtropical coastal wetland sediments. *Sci Rep* 8:14397. <https://doi.org/10.1038/s41598-018-32529-5>.
 37. Santos HF, Cury JC, Carmo FL, Rosado AS, Peixoto RS. 2010. 18S rDNA sequences from microeukaryotes reveal oil indicators in mangrove sediment. *PLoS One* 5:e12437. <https://doi.org/10.1371/journal.pone.0012437>.
 38. Ghizelini AM, Martins KG, Giebelmann UC, Santoro E, Pasqualetta L, Mendonça-Hagler LCS, Rosado AS, Macrae A. 2019. Fungal communities in oil contaminated mangrove sediments – who is in the mud? *Mar Pollut Bull* 139:181–188. <https://doi.org/10.1016/j.marpolbul.2018.12.040>.
 39. Grossart H-P, Massana R, McMahon KD, Walsh DA. 2020. Linking metagenomics to aquatic microbial ecology and biogeochemical cycles. *Limnol Oceanogr* 65:S2–S20. <https://doi.org/10.1002/lno.11382>.
 40. Kohlmeier S, Smits THM, Ford RM, Keel C, Harms H, Wick LY. 2005. Taking the fungal highway: mobilization of pollutant-degrading bacteria by fungi. *Environ Sci Technol* 39:4640–4646. <https://doi.org/10.1021/es047979z>.
 41. Warmink JA, Nazir R, Corten B, van Elsas JD. 2011. Hitchhikers on the fungal highway: the helper effect for bacterial migration via fungal hyphae. *Soil Biol Biochem* 43:760–765. <https://doi.org/10.1016/j.soilbio.2010.12.009>.
 42. Soldan R, Mapelli F, Crotti E, Schnell S, Daffonchio D, Marasco R, Fusi M, Borin S, Cardinale M. 2019. Bacterial endophytes of mangrove propagules elicit early establishment of the natural host and promote growth of cereal crops under salt stress. *Microbiol Res* 223–225:33–43. <https://doi.org/10.1016/j.micres.2019.03.008>.
 43. Wong MKM, Vrijmoed LLP, Au DWT. 2005. Abundance of thraustochytrids on fallen decaying leaves of *Kandelia candel* and mangrove sediments in Futian National Nature Reserve, China. *Bot Mar* 48:374–378.
 44. Sahoo NK, Gupta SK, Rawat I, Ansari FA, Singh P, Naik SN, Bux F. 2017. Sustainable dewatering and drying of self-flocculating microalgae and study of cake properties. *J Clean Prod* 159:248–256. <https://doi.org/10.1016/j.jclepro.2017.05.015>.
 45. Dubilier N, McFall-Ngai M, Zhao L. 2015. Microbiology: create a global microbiome effort. *Nat News* 526:631–634. <https://doi.org/10.1038/526631a>.
 46. Machado LF, de Assis Leite DC, da Costa Rachid CTC, Paes JE, Martins EF, Peixoto RS, Rosado AS. 2019. Tracking mangrove oil bioremediation approaches and bacterial diversity at different depths in an *in situ* mesocosms system. *Front Microbiol* 10:2107. <https://doi.org/10.3389/fmicb.2019.02107>.
 47. Capdeville C, Pommier T, Gervais J, Fromard F, Rols J-L, Leflaive J. 2019. Mangrove facies drives resistance and resilience of sediment microbes exposed to anthropic disturbance. *Front Microbiol* 9:3337. <https://doi.org/10.3389/fmicb.2018.03337>.
 48. Srikanth S, Lum SKY, Chen Z. 2016. Mangrove root: adaptations and ecological importance. *Trees* 30:451–465. <https://doi.org/10.1007/s00468-015-1233-0>.
 49. Thompson LR, Sanders JG, McDonald D, Amir A, Ladau J, Locey KJ, Prill RJ, Tripathi A, Gibbons SM, Ackermann G, Navas-Molina JA, Janssen S, Kopylova E, Vázquez-Baeza Y, González A, Morton JT, Mirarab S, Xu ZZ, Jiang L, Haroon MF, Kanbar J, Zhu Q, Song SJ, Kosciolk T, Bokulich NA, Lefler J, Brislaw CJ, Humphrey G, Owens SM, Hampton-Marcell J, Berg-Lyons D, McKenzie V, Fierer N, Fuhrman JA, Clauset A, Stevens RL, Shade A, Pollard KS, Goodwin KD, Jansson JK, Gilbert JA, Knight R, Earth Microbiome Project Consortium. 2017. A communal catalogue reveals Earth’s multiscale microbial diversity. *Nature* 551:457–463. <https://doi.org/10.1038/nature24621>.
 50. Muelbert JH, Nidzieko NJ, Acosta ATR, Beaulieu SE, Bernardino AF, Boikova E, Bornman TG, Cataletto B, Deneudt K, Eliason E, Kraberg A, Nakaoka M, Pugnetti A, Ragueneau O, Scharfe M, Soltwedel T, Sosik HM, Stanisci A, Stefanova K, Stéphan P, Stier A, Wikner J, Zingone A. 2019.ILTER – The International Long-Term Ecological Research Network as a platform for global coastal and ocean observation. *Front Mar Sci* 6:527. <https://doi.org/10.3389/fmars.2019.00527>.
 51. Yilmaz P, Kottmann R, Field D, Knight R, Cole JR, Amaral-Zettler L, Gilbert JA, Karsch-Mizrachi I, Johnston A, Cochrane G, Vaughan R, Hunter C, Park J, Morrison N, Rocca-Serra P, Sterk P, Arumugam M, Bailey M, Baumgartner L, Birren BW, Blaser MJ, Bonazzi V, Booth T, Bork P, Bushman FD, Buttigieg PL, Chain PSG, Charlson E, Costello EK, Huot-Creasy H, Dawyndt P, DeSantis T, Fierer N, Fuhrman JA, Gally RE, Gevers D, Gibbs RA, Gil IS, Gonzalez A, Gordon JJ, Guralnick R, Hankeln W, Highlander S, Hugenholtz P, Jansson J, Kau AL, Kelley ST, Kennedy J, Knights D, Koren O, Kuczynski J, et al. 2011. Minimum information about a marker gene sequence (MIMARKS) and minimum information about any (x) sequence (MIxS) specifications. *Nat Biotechnol* 29:415–420. <https://doi.org/10.1038/nbt.1823>.
 52. Wilkinson MD, Dumontier M, Aalbersberg IJJ, Appleton G, Axton M, Baak A, Blomberg N, Boiten J-W, da Silva Santos LB, Bourne PE, Bouwman J, Brookes AJ, Clark T, Crosas M, Dillo I, Dumon O, Edmunds S, Evelo CT, Finkers J, Gonzalez-Beltran A, Gray AJG, Groth P, Goble C, Grethe JS, Heringa J, ‘t Hoen PAC, Hooft R, Kuhn T, Kok R, Kok J, Lusher SJ, Martone ME, Mons A, Packer AL, Persson B, Rocca-Serra P, Roos M, van Schaik R, Sansone S-A, Schultes E, Sengstag T, Slater T, Strawn G, Swertz MA, Thompson M, van der Lei J, van Mulligen E, Velterop J, Waagmeester A, Wittenburg P, Wolstencroft K, et al. 2016. The FAIR Guiding Principles for scientific data management and stewardship. *Sci Data* 3:160018. <https://doi.org/10.1038/sdata.2016.18>.
 53. Lehmann A, Nativi S, Mazzetti P, Maso J, Serral I, Spengler D, Niamir A, McCallum I, Lacroix P, Patias P, Rodila D, Ray N, Giuliani G. 2020. GEOessential – mainstreaming workflows from data sources to environment policy indicators with essential variables. *Int J Digit Earth* 13:322–338. <https://doi.org/10.1080/17538947.2019.1585977>.
 54. Bax NJ, Miloslavich P, Muller-Karger FE, Allain V, Appeltans W, Batten SD, Benedetti-Cecchi L, Buttigieg PL, Chiba S, Costa DP, Duffy JE, Dunn DC, Johnson CR, Kudela RM, Obura D, Rebelo L-M, Shin Y-J, Simmons SE, Tyack PL. 2019. A response to scientific and societal needs for marine biological observations. *Front Mar Sci* 6:395. <https://doi.org/10.3389/fmars.2019.00395>.
 55. Mendes R, Kruijt M, de Bruijn I, Dekkers E, van der Voort M, Schneider JHM, Piceno YM, DeSantis TZ, Andersen GL, Bakker PAHM, Raaijmakers JM. 2011. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science* 332:1097–1100. <https://doi.org/10.1126/science.1203980>.
 56. Zuñiga C, Zaramela L, Zengler K. 2017. Elucidation of complexity and prediction of interactions in microbial communities. *Microb Biotechnol* 10:1500–1522. <https://doi.org/10.1111/1751-7915.12855>.
 57. Santos HF, Carmo FL, Paes JES, Rosado AS, Peixoto RS. 2011. Bioremediation of mangroves impacted by petroleum. *Water Air Soil Pollut* 216:329–350. <https://doi.org/10.1007/s11270-010-0536-4>.
 58. Zengler K, Hofmockel K, Baliga NS, Behie SW, Bernstein HC, Brown JB, Dinneny JR, Flöge SA, Forry SP, Hess M, Jackson SA, Jansson C, Lindemann SR, Pett-Ridge J, Maranas C, Venturelli OS, Wallenstein MD, Shank EA, Northen TR. 2019. EcoFABs: advancing microbiome science through standardized fabricated ecosystems. *Nat Methods* 16:567–571. <https://doi.org/10.1038/s41592-019-0465-0>.
 59. Zhalnina K, Zengler K, Newman D, Northen TR. 2018. Need for laboratory ecosystems to unravel the structures and functions of soil microbial communities mediated by chemistry. *mBio* 9:e01175-18. <https://doi.org/10.1128/mBio.01175-18>.
 60. Finn M, Kangas P, Adey W. 1999. Mangrove ecosystem development in Biosphere 2. *Ecol Eng* 13:173–178. [https://doi.org/10.1016/S0925-8574\(98\)00097-4](https://doi.org/10.1016/S0925-8574(98)00097-4).
 61. Button DK, Schut F, Quang P, Martin R, Robertson BR. 1993. Viability and

- isolation of marine bacteria by dilution culture: theory, procedures, and initial results. *Appl Environ Microbiol* 59:881–891. <https://doi.org/10.1128/AEM.59.3.881-891.1993>.
62. Rappé MS, Connon SA, Vergin KL, Giovannoni SJ. 2002. Cultivation of the ubiquitous SAR11 marine bacterioplankton clade. *Nature* 418:630–633. <https://doi.org/10.1038/nature00917>.
63. Zengler K, Toledo G, Rappé M, Elkins J, Mathur EJ, Short JM, Keller M. 2002. Cultivating the uncultured. *Proc Natl Acad Sci U S A* 99:15681–15686. <https://doi.org/10.1073/pnas.252630999>.
64. Ma F, Xie Y, Huang C, Feng Y, Yang G. 2014. An improved single cell ultrahigh throughput screening method based on in vitro compartmentalization. *PLoS One* 9:e89785. <https://doi.org/10.1371/journal.pone.0089785>.
65. Bollmann A, Lewis K, Epstein SS. 2007. Incubation of environmental samples in a diffusion chamber increases the diversity of recovered isolates. *Appl Environ Microbiol* 73:6386–6390. <https://doi.org/10.1128/AEM.01309-07>.
66. Jalili-Firoozinezhad S, Gazzaniga FS, Calamari EL, Camacho DM, Fadel CW, Bein A, Swenor B, Nestor B, Cronce MJ, Tovaglieri A, Levy O, Gregory KE, Breault DT, Cabral JMS, Kasper DL, Novak R, Ingber DE. 2019. A complex human gut microbiome cultured in an anaerobic intestine-on-a-chip. *Nat Biomed Eng* 3:520–531. <https://doi.org/10.1038/s41551-019-0397-0>.
67. Jiménez DJ, Korenblum E, van Elsas JD. 2014. Novel multispecies microbial consortia involved in lignocellulose and 5-hydroxymethylfurfural bioconversion. *Appl Microbiol Biotechnol* 98:2789–2803. <https://doi.org/10.1007/s00253-013-5253-7>.
68. Cross KL, Campbell JH, Balachandran M, Campbell AG, Cooper SJ, Griffen A, Heaton M, Joshi S, Klingeman D, Leys E, Yang Z, Parks JM, Podar M. 2019. Targeted isolation and cultivation of uncultivated bacteria by reverse genomics. *Nat Biotechnol* 37:1314–1321. <https://doi.org/10.1038/s41587-019-0260-6>.
69. Tyson GW, Banfield JF. 2005. Cultivating the uncultivated: a community genomics perspective. *Trends Microbiol* 13:411–415. <https://doi.org/10.1016/j.tim.2005.07.003>.
70. dos Santos HF, Cury JC, do Carmo FL, dos Santos AL, Tiedje J, van Elsas JD, Rosado AS, Peixoto RS. 2011. Mangrove bacterial diversity and the impact of oil contamination revealed by pyrosequencing: bacterial proxies for oil pollution. *PLoS One* 6:e16943. <https://doi.org/10.1371/journal.pone.0016943>.
71. Lamendella R, Strutt S, Borglin S, Chakraborty R, Tas N, Mason OU, Hultman J, Prestat E, Hazen TC, Jansson JK. 2014. Assessment of the Deepwater Horizon oil spill impact on Gulf coast microbial communities. *Front Microbiol* 5:130. <https://doi.org/10.3389/fmicb.2014.00130>.
72. Duke NC. 2016. Oil spill impacts on mangroves: recommendations for operational planning and action based on a global review. *Mar Pollut Bull* 109:700–715. <https://doi.org/10.1016/j.marpolbul.2016.06.082>.
73. Tiralerdpanich P, Sonthiphand P, Luepromchai E, Pinyakong O, Pokethitiyook P. 2018. Potential microbial consortium involved in the biodegradation of diesel, hexadecane and phenanthrene in mangrove sediment explored by metagenomics analysis. *Mar Pollut Bull* 133:595–605. <https://doi.org/10.1016/j.marpolbul.2018.06.015>.
74. Aniszewski E, Peixoto RS, Mota FF, Leite SGF, Rosado AS. 2010. Bioemulsifier production by *Microbacterium* sp. strains isolated from mangrove and their application to remove cadmium and zinc from hazardous industrial residue. *Braz J Microbiol* 41:235–245. <https://doi.org/10.1590/S1517-83822010000100033>.
75. Cavicchioli R, Ripple WJ, Timmis KN, Azam F, Bakken LR, Baylis M, Behrenfeld MJ, Boetius A, Boyd PW, Classen AT, Crowther TW, Danovaro R, Foreman CM, Huisman J, Hutchins DA, Jansson JK, Karl DM, Koskella B, Welch DBM, Martiny JHB, Moran MA, Orphan VJ, Reay DS, Remais JV, Rich VI, Singh BK, Stein LY, Stewart FJ, Sullivan MB, van Oppen MJH, Weaver SC, Webb EA, Webster NS. 2019. Scientists' warning to humanity: microorganisms and climate change. *Nat Rev Microbiol* 17:569–586. <https://doi.org/10.1038/s41579-019-0222-5>.