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Rise of the rare biosphere: Thinking beyond climate envelopes for forecasting harmful algal blooms

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Ocean ecosystems are changing, and the climate envelope paradigm predicts a steady shift, approximately poleward, of species ranges. The Gulf of Maine presents a test case of this paradigm, as temperatures have warmed extremely rapidly. Some species have shifted northeastward, matching predictions. Others—namely harmful algal species like *Pseudo-nitzschia australis* and *Karenia mikimotoi*—do not appear to have followed climate trajectories, arriving as surprises in the Gulf of Maine. Rare-biosphere dynamics offer one possible ecological lens for understanding and predicting this type of surprise. Rare species in the plankton, possibly more so than southerly ones, may provide management challenges in the future. Improved monitoring and broader coordination of monitoring of the rare biosphere could help develop early warning systems for harmful and toxic algae. A better theoretical understanding of rare biosphere dynamics is also needed. A challenge for the next cohort of ecosystem projections is to predict the newly emerging harmful species of the type that catch us by surprise.

Keywords: Harmful algal bloom, Rare biosphere, Climate change, Forecasting, Gulf of Maine, *Karenia mikimotoi*, *Pseudo-nitzschia australis*

Introduction: The climate envelope paradigm

If one theme lies at the forefront of contemporary ecology, it is providing guidance about how our ecosystems will respond as climate changes. Plenty of fundamental ecology is embedded within this theme, but overshadowing so much ecological work is the very pressing issue of the changing planet. This global challenge without precedent calls for everyone, including ecologists, to view the world through new lenses.

As we prepare ourselves for a rapidly changing environment, key pieces of information are where and when species will occur. The need for this information holds for both common and rare species. One of the most standard methods of ecological analysis involves the climate envelope projection (Hijmans and Graham, 2006; Ibáñez et al., 2006). The idea is first to describe a species distribution using a species distribution model based on climatic covariates and then to project this distribution onto future conditions. Species distribution models describe the abundance, density, or occurrence of an organism as a function of the environment and the organism's ability to shape its range. Typically, this modeling approach uses a statistical model, though there are examples of mechanistic and process-based models (Pearson and Dawson, 2003; Hijmans and Graham, 2006), and temperature is usually the dominant explanatory variable. The approach has its roots in terrestrial ecology, where the land is divided into a fixed grid, over which conditions and species occurrence change and range maps shift following climate velocity vectors. Such projections attempt to answer the natural question: What will future ecosystems look like? In the ocean, there is evidence that these types of projections fall short of answering this question (Brun et al., 2015). In many cases, we will have to wait for future researchers and generations to confirm or refute our projections. However, recent instances of rapid warming can provide insights into whether the information provided by this approach is telling an accurate story and thus preparing us adequately.

One such example is the Gulf of Maine (United States and Canada), which over the past 15 years has been a case study in the effects of rapid climate change. Surface waters have warmed extremely rapidly, already reaching approximate projected year-2100 conditions (Pershing et al., 2015), and corresponding shifts in the ecosystem are already happening, from within the plankton to the endangered whales (Balch et al., 2012; Record et al., 2019). This rapid change has provided a valuable opportunity to discern whether the climate envelope paradigm for species distribution shifts plays out the way we expect. There are some cases where marine species have shifted predictably with changing isotherms. The northern shrimp (*Pandalus borealis*) supported a robust fishery in the Gulf of Maine at the

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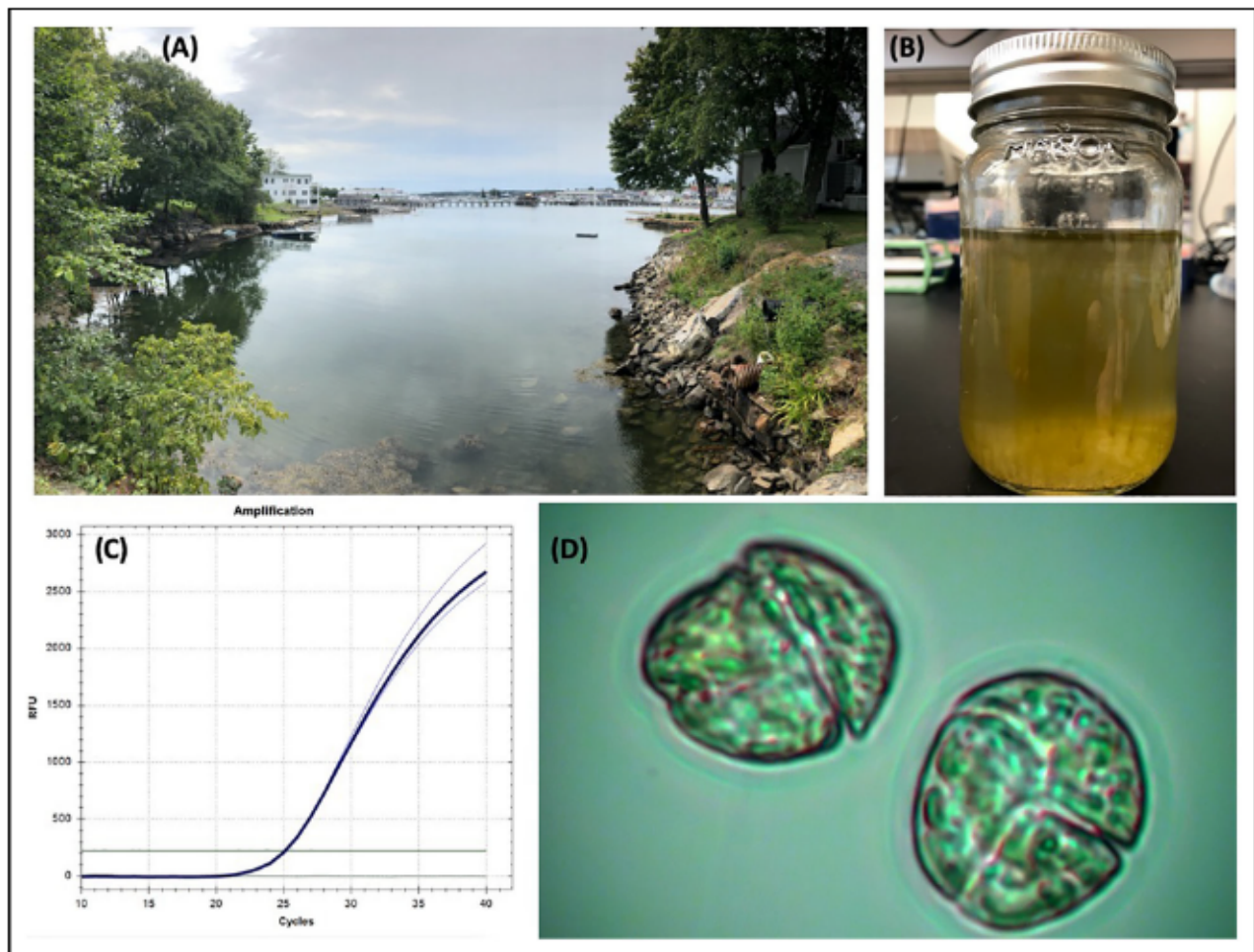Email: nrecord@bigelow.org

Figure 1. *Karenia mikimotoi* bloom in Boothbay Harbor, ME, USA. The harmful algal species *K. mikimotoi* is a relatively new component of the bloom-forming phytoplankton community in coastal Maine. A bloom of *K. mikimotoi* was detected at a site in Boothbay Harbor, ME (A) in September 2020. Water collected from the site at the time of the bloom showing the coloration and intense cell density (B); verification by quantitative polymerase chain reaction assay of the species identity as *K. mikimotoi*, adapting the approach employed by Wawrik et al. (2002) targeting the rbcL gene (C); and photomicrographs of the Boothbay Harbor *K. mikimotoi*—cells are approximately 20 μm in diameter (D). DOI: https://doi.org/10.1525/elementa.2020.00056.f1

southern end of its range but quickly declined beyond the point of supporting a fishery during the period of change (Eckert et al., 2017). Similarly, studies examining shifting ranges for lobster (*Homarus americanus*; Jaini et al., 2018; Goode et al., 2019), cod (*Gadus morhua*; Pershing et al., 2015), scallops (*Placopecten magellanicus*; Torre et al., 2019), and likely green crabs (*Carcinus maenas*; Neckles, 2015) support the climate envelope paradigm. Some species range shifts are more nuanced, showing some aspect of a climate envelope shift overlaid with other important drivers such as subsurface currents and dispersal dynamics, as seen in kelp communities (Witman and Lamb, 2018), the keystone copepod *Calanus finmarchicus* (Ji et al., 2017), and right whales (*Eubalaena glacialis*; Record et al., 2019). In general, although there is some local variability, climate velocity vectors point strongly from southern regions, such as the mid-Atlantic bight and southern New England, toward the Gulf of Maine (Kleisner et al., 2016), and further northeastward beyond. This poleward shift has been the primary lens, provided by the climate envelope paradigm,

through which we tend to view the future Gulf of Maine ecosystem (Nye et al., 2009).

There are, however, counterexamples to the prediction that species will follow climate velocity vectors. From a management point of view, some of the most challenging changes in the Gulf of Maine ecosystem have occurred within the planktonic community. Over the past few years, the appearance of blooms of new toxic and harmful phytoplankton species (**Figure 1**) along coastal Maine has led to shellfish recalls and temporary closures of shellfish harvesting. Within these communities is where the shifting climate envelope paradigm can fall short. For example, *Pseudo-nitzschia australis* blooms were recorded along the eastern coast of Maine in 2016 (Clark et al., 2019) and again in 2017, leading to closures and recalls for shellfish. This plankton species had not been recorded previously in coastal Maine, nor does it appear to be an invader from warmer southern waters: Previous observations of *P.-n. australis* come from northern Europe, southern South America, and the western coast of North America (**Figure 2**;
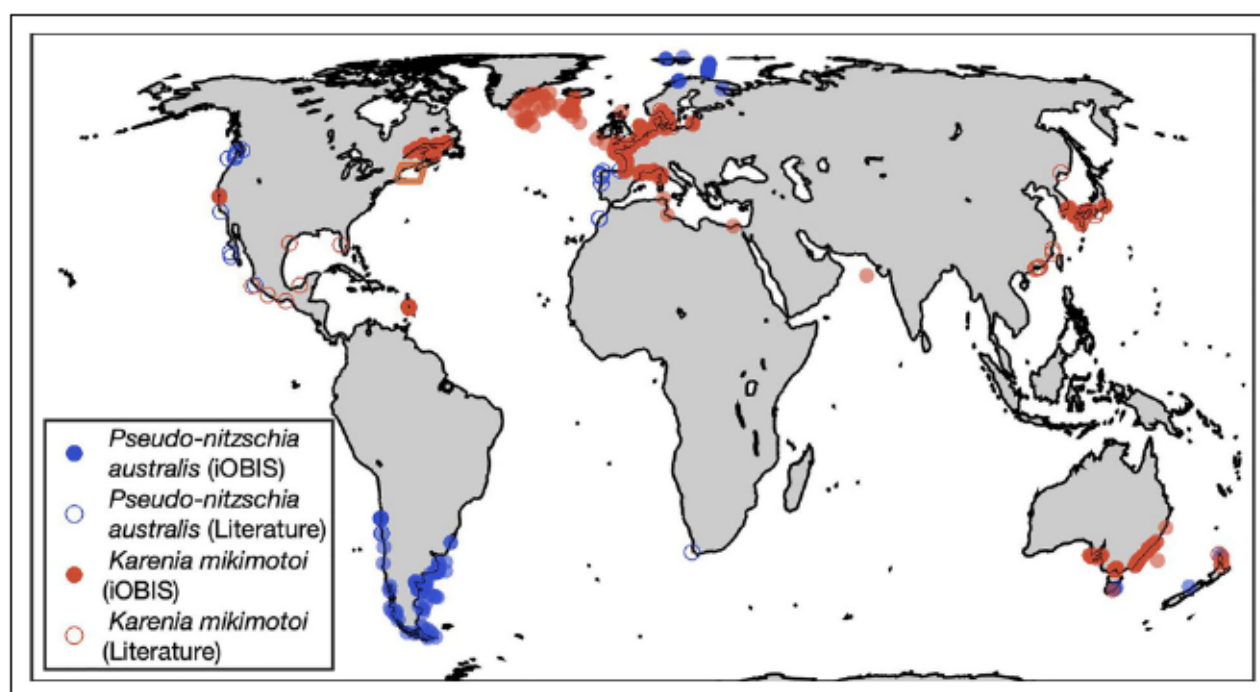
Figure 2. Historical observations of *Pseudo-nitzschia australis* and *Karenia mikimotoi* from literature and databases. Recorded detection locations for *P.-n. australis* and *K. mikimotoi* from the Ocean Biodiversity Information System database and from a literature review (**Table 1**) prior to the recent detections. Darker colors indicate a higher density of points. The orange box outlines the Gulf of Maine, where recent detections have occurred. DOI: https://doi.org/10.1525/elementa.2020.00056.f2

Schnetzer et al., 2013; McCabe et al., 2016). When or how the species first arrived is not clear, and unreported or unrecognized instances may have occurred in the past, but these impactful blooms are apparently a new phenomenon. Similarly, *Karenia mikimotoi* has recently been observed in the Gulf of Maine, presenting harmful blooms that are new to management (**Figure 1**), and prior observations around this region also do not suggest movement along climate velocity vectors (**Figure 2**; Li et al., 2019). As recently as 2015, these species were not considered potential threats to the Gulf of Maine. Now, they are foci of monitoring, research, and management challenges, which raises the question: In 5 years, what new toxic species will we be grappling with? In some cases, it could be southerly species. In many cases, however, the climate envelope paradigm does not appear to equip us to answer this question.

The rare biosphere surprise hypothesis
We can draw from other frontiers of ecological research to find alternative lenses for viewing this problem. One possibility is that the unexpected emergence of these species derives from rare biosphere dynamics. The rare biosphere is the long tail of diversity that persists at low, sometimes undetectable levels (Sogin et al., 2006). As local conditions change, new niches open, and rare species can shift to a dominant position within the abundance ranking (**Figure 3A–C**; Box 1; Countway et al., 2005; Caron and Countway, 2009; Logares et al., 2015). These species may have arrived at some point in the past via shipping and trade (e.g., ballast waters) or have been present naturally

but remained below detection limits due to environmental and community dynamics. With many decades of global shipping and transport of species through ballast water, it seems unlikely that the species never found their way to this region before, but the conditions supporting their intensive blooms are new. Even without secular changes in mean conditions, as is often the focus of climate projections, and without shifting climate envelopes, changes in variance around environmental conditions can rapidly change community composition (Pershing et al., 2019). Theoretical trait-based models of diversity (Record et al., 2014a, 2014b) support the prediction that as variance in conditions increases, the diversity of specialists increases, with many rare specialists becoming opportunistically abundant when conditions allow (**Figure 3D**). Multiple stressors, which increase the niche dimensionality, would amplify this effect (White et al., 2015). Collectively, this evidence points to a rare-biosphere hypothesis: *Rare species, more so than southerly ones, will become the emerging harmful species in the ocean microbiome as conditions change.*

This "rare biosphere surprise hypothesis" is in the early stages of examination, and many fundamental questions remain. For example, what are all of the rare species doing? Does the long tail of rare species in a rank-abundance curve confer resilience or stability or does it simply reflect random variation? Is it a reservoir for functional redundancy? Does our often-debated definition of "species" even adequately delineate the rare biosphere? We need a better theoretical understanding of the rare
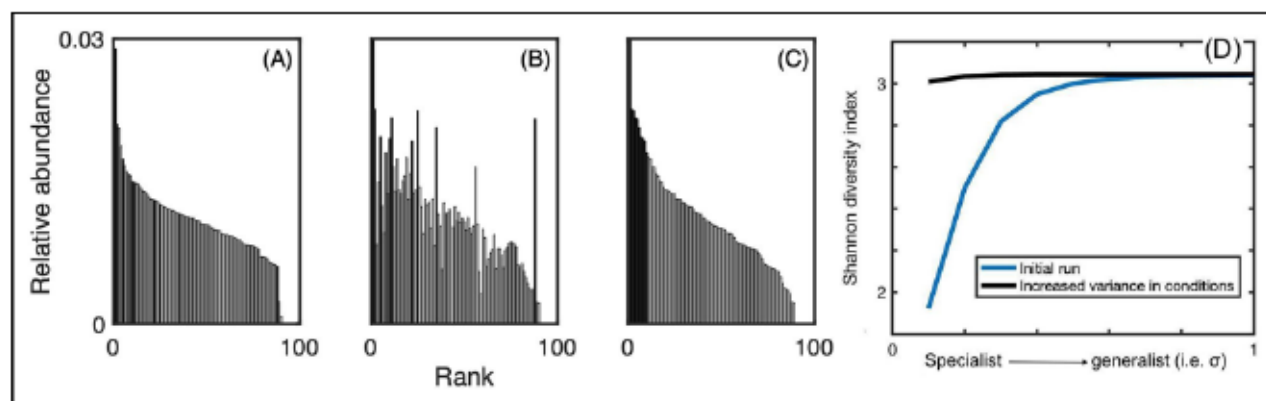
Figure 3. Illustrative example of rare biosphere dynamics using the φ-diversity model (Record et al., 2014a, 2014b; Box 1) as formulated as a trade-off between generalists and specialists (cf. Pershing et al., 2019). The φ model is built on a simplified population growth model with a community of interacting populations, derived from the theory that inspired the plankton paradox (Lotka, 1932; Hutchinson, 1961; Box 1). The model deals with a community of populations, which can represent species or other taxonomic delineations. (A–C) Rare species become dominant as conditions change (as hypothesized in Caron and Countway, 2009). (A) The initial rank-abundance curve. (B) Adjusted abundances after an environmental change, but with the initial ranking. (C) New ranking after the change. The dark bars highlight the 10 species that become most abundant after the change—the same 10 species in all three plots. (D) When variance in conditions changes, the diversity of specialists increases, as previously rare species temporarily exploit new conditions. DOI: https://doi.org/10.1525/elementa.2020.00056.f3

biosphere, particularly as it pertains to plankton, to answer these questions.

On the monitoring side, the proliferation of environmental DNA (eDNA) data sources (**Table 2**) could become a source of valuable information. Many of these programs are focused on the detection of key taxa—such as endangered/threatened species (Wood et al., 2019), species harmful to humans (Marquis et al., 2019), or commercially important species (Bayer et al., 2019; Marquis et al., 2020)—often using quantitative PCR and/or DNA metabarcoding to target those species (Coyne et al., 2005; Shaw et al., 2019). The use of eDNA is an emerging technique and more work is needed to establish eDNA as a consistent and reliable source of information, but it has potential applications for taxa beyond plankton. If such data sources are aggregated, an early warning system could cross-reference these data sources with global records of harmful species elsewhere. Particularly where the full planktonic community is measured, observations of changes in community composition in one region could be used to inform early warnings in other regions. This approach would require a global network of eDNA monitoring. Crowd science programs add to this potential, as eDNA technologies become more accessible, providing a means for early detection with coverage in time and space that is not feasible with conventional surveys. In the case of invasions, early warning can be crucial because of the time lag that sometimes exists between arrival and a major bloom. Yet a great deal of work remains to be done both to clarify what type of eDNA measurements are most biologically meaningful and will remain consistent as technology advances and to more fully account for microbial and planktonic

dynamics in assessing climate change impacts (Cavicchioli et al., 2019). A deeper understanding of the rare biosphere will require a critical evaluation of the techniques that capture the broader taxonomic diversity and functional potential in the gene pool. The question of taxonomic resolution, and species delineation, is at the frontier of biological research, and genomic technologies are a critical tool for resolving these issues (Pachiadaki et al., 2019). Even without eDNA technology, crowd science and community science programs have great promise for early warning systems (Record, 2017). A richer, spatio-temporally broad data set including rare taxa would lay the groundwork for developing a more comprehensive, mechanistic, and predictive theory of rare biosphere dynamics.

The rare biosphere surprise hypothesis is still a hypothesis, and whether it provides a useful lens for viewing, understanding, and coping with rapid climate changes and their associated ecological effects remains to be seen. Still, the environment continues to deliver surprises that often catch us unprepared, particularly when it comes to human health hazards. The climate envelope paradigm is certainly useful in many contexts, especially for smooth, gradual changes that closely track temperature. On the other hand, the approach might not tell us which new species will be management concerns within 5 or 10 years. In the Gulf of Maine, a wide range of new environmental niches are expected to open by 2050, including changes to currents and acidification, in addition to warming (Pershing et al., n.d.; Siedlecki et al., 2021). Merely translating ecological communities poleward is clearly insufficient when preparing for the potentially problematic species we will be managing. A

Table 1. Published observations of *Pseudo-nitzschia australis* and *Karenia mikimotoi*, including peer-reviewed sources and professional reports where latitude–longitude locations can be determined to the nearest 10th degree, excluding the recent appearances in the Gulf of Maine. DOI: https://doi.org/10.1525/elementa.2020.00056.t1

Latitude	Longitude	Reference
Pseudo-nitzschia australis		
−43.0	−64.0	Almandoz et al. (2017)
−27.1	−70.9	Alvarez et al. (2009)
−30.3	−71.5	Alvarez et al. (2009)
34.2	−119.9	Andersen et al. (2006)
44.7	−1.2	Ayache et al. (2019)
40.7	−8.8	Churro et al. (2009)
32.9	−8.9	Ennaffah et al. (2012)
32.8	−9.0	Ennaffah et al. (2012)
48.5	−123.0	Hasle and Lundholm (2005)
42.4	−8.8	Hasle and Lundholm (2005)
−34.2	18.2	Hasle and Lundholm (2005)
24.8	−112.7	Hernández-Becerril (1998)
25.7	−113.3	Hernández-Becerril (1998)
47.7	−124.4	Holtermann et al. (2010)
46.6	−126.1	Holtermann et al. (2010)
46.8	−124.1	Holtermann et al. (2010)
47.2	−124.2	Holtermann et al. (2010)
48.3	−124.7	Holtermann et al. (2010)
43.6	−3.1	Orive et al. (2013)
19.1	−104.4	Rivera-Vilarelle et al. (2013)
30.7	−116.6	Santiago-Morales and García-Mendoza (2011)
43.4	−8.3	Zapata et al. (2011)
42.4	−8.8	Zapata et al. (2011)
42.2	−8.8	Zapata et al. (2011)
42.8	−9.0	Zapata et al. (2011)
Karenia mikimotoi		
−38.2	144.8	Andersen (2011)
19.0	−91.8	Escobar-Morales and Hernández-Becerril (2015)
18.9	−105.0	Escobar-Morales and Hernández-Becerril (2015)
17.1	−100.3	Escobar-Morales and Hernández-Becerril (2015)
15.9	−95.1	Escobar-Morales and Hernández-Becerril (2015)
34.3	136.7	Faust and Gulledge (2002)
50.4	−4.1	Garces et al. (2006)
56.9	11.5	Hällfors (2004)
54.9	14.1	Hällfors (2004)

TABLE 1. *(continued)*

Latitude	Longitude	Reference
33.4	135.8	Haywood et al. (2004)
−37.0	175.3	Haywood et al. (2004)
50.4	−4.1	Haywood et al. (2004)
−37.9	144.9	Haywood et al. (2004)
59.5	10.5	Haywood et al. (2004)
34.0	131.8	Haywood et al. (2004)
27.6	−97.1	Henrichs et al. (2013)
47.0	−2.2	Hernández Fariñas et al. (2017)
34.5	128.0	Jeong et al. (2017)
54.2	7.9	Kraberg et al. (2019)
26.3	119.9	Luo et al. (2018)
25.6	119.7	Luo et al. (2018)
27.3	−82.6	Mikulski et al. (2005)
33.6	131.3	Mikulski et al. (2005)
22.5	114.4	Qi et al. (2004)
22.3	113.6	Qi et al. (2004)
22.6	114.5	Qi et al. (2004)
22.6	115.0	Qi et al. (2004)
−34.7	172.9	Rhodes and Smith (2018)
43.0	131.9	Shevchenko et al. (2019)
33.0	131.9	Yuasa et al. (2018)

Table 2. Environmental DNA open-data portals and data aggregators in development for aquatic systems, as of the publication of this article. DOI: https://doi.org/10.1525/elementa.2020.00056.t2

Data Portal	Data Type	Hosting Institution	Link
Aquatic eDNAtlas	Targeted species detection	Rocky Mountain Research Station	https://www.fs.fed.us/rm/boise/AWAE/projects/the-aquatic-eDNAtlas-project.html
Australian Microbiome Initiative	Multiple	Consortium	https://data.bioplatforms.com/
Earth microbiome project	Taxonomic counts	Consortium	https://earthmicrobiome.org/
eDNA detections in Great Bay Habitats	Taxonomic detections	University of New Hampshire	https://gbhabitat.herokuapp.com/
ME-eDNA	Taxonomic counts	Bigelow Laboratory for Ocean Sciences, University of Maine	https://edna.bigelow.org/
MGnify	Multiple	European Bioinformatics Institute	https://www.ebi.ac.uk/metagenomics/
TARA Oceans Data Portal	Taxonomic counts	Tara Oceans	http://www.taraoceans-dataportal.org/

challenge for the next cohort of ecosystem projections is to predict the newly emerging species of the type that catch us by surprise. Framed as a forecasting challenge, it can drive new monitoring efforts and improved theoretical understanding of the dynamics of rare taxa. We will need new ways of viewing ecosystems and their dynamics if we are to be proactive in adapting to climate-driven changes.

Box 1. The φ model for diverse community.

The φ model is built on a simplified population growth model with a community of interacting populations. The abundance of the ith population is N_i, and the dynamics are described by:

$$dN_i/dt = \mu_i N_i - \delta_i \mathbf{N}^{1-\varphi} N_i^{1+\varphi},$$

where μ_i and δ_i are, respectively, the growth rate and mortality rate for the ith population, $\mathbf{N}$ is the sum of abundance over the full community, and φ is an interaction parameter that structures coexistence within the community (Record et al., 2014a, 2014b). Each population has an environmental niche described by two parameters: an optimal environmental condition for growth, τ_i, and a spread around that optimal condition, σ_i. Thus, μ_i is a function of the environmental variable (T) shaped by the two parameters τ_i and σ_i:

$$\mu_i(T) = \exp(-(T - \tau_i)^2/(2\sigma_i^2))/\sqrt{(2\pi\sigma_i^2)}.$$

This function could represent different taxa or different strategies within a taxon. In either case, it formulates the trade-off between higher growth rate at optimal conditions (specialist) and lower growth rate but wider range of suitable conditions (generalist) across a range of environmental conditions. The equilibrium community, described by $N_i* = (\mu_i/\delta_i)^{1/\varphi} \left(\sum_i (\mu_i/\delta_i)^{1/\varphi} \right)^{\varphi-1}$, allows us to explore the community structure (i.e., rank abundance or comparative diversity of specialists vs. generalists) as we change the variance around the environmental condition T. The community properties illustrated (**Figure 3**) each represent the mean of an ensemble of 10 randomized runs.

Competing interests
The authors are aware of no competing interests.

Author contributions

· Substantial contributions to conception and design: NRR, PDC.
· Acquisition of data: NRR.
· Analysis and interpretation of data: NRR.
· Drafting this article or revising it critically for important intellectual content: NRR, PDC, KK, JAFR.
· Final approval of the version to be published: NRR, PDC, KK, JAFR.

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