

Neutral Theory and Plankton Biodiversity

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Keywords

neutral theory, competitive exclusion, trophic exclusion, phytoplankton biodiversity, community structuring, niches

Abstract

The biodiversity of the plankton has been interpreted largely through the monocle of competition. The spatial distancing of phytoplankton in nature is so large that cell boundary layers rarely overlap, undermining opportunities for resource-based competitive exclusion. Neutral theory accounts for biodiversity patterns based purely on random birth, death, immigration, and speciation events and has commonly served as a null hypothesis in terrestrial ecology but has received comparatively little attention in aquatic ecology. This review summarizes basic elements of neutral theory and explores its stand-alone utility for understanding phytoplankton diversity. A theoretical framework is described entailing a very nonneutral trophic exclusion principle melded with the concept of ecologically defined neutral niches. This perspective permits all phytoplankton size classes to coexist at any limiting resource level, predicts greater diversity than anticipated from readily identifiable environmental niches but less diversity than expected from pure neutral theory, and functions effectively in populations of distantly spaced individuals.

INTRODUCTION

For billions of years, life on Earth has been evolving, diversifying, and colonizing new habitats. Today, there are few spaces left on the surface of Earth that do not harbor some form of life, and the total number of extant species is bewildering. Indeed, so many species can be found in some habitats, even within a single trophic level, that the degree of coexistence is difficult to explain. This paradox of coexistence is the topic of an immense volume of theoretical and empirical scientific literature that spans from microbes to megafauna and from aquatic to terrestrial realms. It has attracted so much attention because biodiversity lies at the heart of biogeochemical function, resilience to environmental change, and energy transfer in complex food webs.

In his book *On the Origin of Species by Means of Natural Selection*, Darwin (1859) clearly indicated his philosophical position regarding the competitive exclusion-based niche partitioning of species by stating, “When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this!” (quoted in Alonso et al. 2006, p. 451). During the twentieth century, numerous laboratory experiments (often involving plankton) were conducted to test principles of resource-based competitive exclusion (e.g., Tilman 1977, 1981; Sommer 1985, 1986; Rothhaupt 1988, 1996), leading to a common default assumption of one niche, one species. How then do we account for the many examples where observed species diversity greatly exceeds the number of identifiable environmental niches, with the most famous example being phytoplankton diversity in the apparently unstructured surface mixing layers of the ocean and lakes (Hutchinson 1941, 1961)? Emergent explanations to this question have included undetected microniches (e.g., Brauer et al. 2015, Lynch & Neufeld 2015), chaotic fluctuations in species’ abundances resulting from multiresource competitions (e.g., Huisman & Weissing 1999, Huisman et al. 2001, Scheffer et al. 2003, Pearce et al. 2020), resource-based interspecies dependencies (i.e., metabolic networks) (e.g., Giovannoni et al. 2014, Mas et al. 2016), and dispersion-sustained disequilibria in community composition (i.e., immigration or physical dispersal causing transient co-occurrence of unequally fit species) (e.g., Follows & Dutkiewicz 2011; Masuda et al. 2017, 2020; Villa Martín et al. 2020), among others (Roy & Chattopadhyay 2007). In all of these cases, an attempt is made to account for species coexistence in a framework that conserves the fundamental tenets of niche-based competitive exclusion theory.

Population geneticists have also struggled with apparent unexplained diversity. Beginning in the 1920s, Fisher (1922, 1930) began investigating the role of random chance (i.e., neutral processes) on the survival and spread of genetic mutations, and Wright (1931, 1932) later evaluated neutral processes as a mechanism for adaptation. A variety of subsequent studies regarding neutral genetic drift ensued (see Leigh 2007) until Kimura (1968) ultimately proposed a general neutral theory for molecular evolution. Despite the prolonged development of neutral theory in population genetics, its extension to community ecology did not appear until late in the twentieth century with the pioneering work of Caswell (1976) and Hubbell (1979, 1997). This long delay in the extension of neutral theory to ecological systems is remarkable and likely reflects a deeply entrenched belief in niche-based competition. As voiced by Bell (2001, p. 2413), “Perhaps ecologists find it difficult to accept that the differences they so clearly recognize among their study species have no functional significance, whereas geneticists, dealing with spots on a gel, are more inclined to neutralism.”

By far the most impactful treatise on neutral theory in ecology is Hubbell’s (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Depending on the search engine employed, this publication has been cited between 5,000 and 10,000 times. Hubbell’s unified theory was intended as a framework relevant to all ecological systems, but his own research and many of the data sets

used to test his theory were focused on forests. It is therefore not surprising that a large fraction of the above-noted citations are from the terrestrial literature, yet even so, its relative absence from the aquatic literature is notable. Indeed, less than 2% of the publications citing Hubbell's treatise involve bacterioplankton, phytoplankton, and/or zooplankton, and even among these, many acknowledge neutral theory only in passing. If Bell (2001) was surprised by the reluctant transition of neutral theory from genetics to ecology in general, then this even greater barrier into aquatic sciences is astonishing. Notably, citations to neutral theory in the plankton ecology literature have risen from ~1 per year before 2005 to >15 per year presently.

Our interest in neutral theory stems from a series of publications developed during the first years of the COVID-19 pandemic (Behrenfeld et al. 2021a–c, 2022). Building on this foundation, the current review is intended to familiarize the reader with neutral theory and explore how this alternative interpretation may have relevance to plankton biodiversity. Our narrative begins with an overview of Hubbell's neutral theory, which is then expanded to accommodate nonneutral processes and contrasted with theories based on chaotic behavior and nondecisive interactions between individuals. We then focus specifically on the plankton and propose a neutral niche framework for aquatic biodiversity, highlighting key questions that remain unanswered and opportunities for future observations, modeling, and theoretical developments.

Earth is blessed with a rich diversity of species. Elucidating the underpinnings of sustained biodiversity can be challenging if the explanations are based solely on studies with long-lived organisms of relatively low abundance (e.g., trees, mammals, birds, or amphibians). The world of the plankton, with its astronomical numbers of individuals, rapid turnover rates, and physical dispersal characteristics, provides a unique playground for evaluating and refining interpretations of biodiversity. Neutral theory is relatively untested in the aquatic realm, but if it is melded with concepts on selection mechanisms, it may contribute to an advanced understanding of species coexistence, spatial distributions, and temporal evolution under a warming climate.

NEUTRAL IN A NUTSHELL

Probably no ecologist in the world with even a modicum of field experience would seriously question the existence of niche differences among competing species on the same trophic level. The real question, however, is...what niche differences, if any, matter to the assembly of ecological communities?...What continues to surprise me...is how far one can get with a neutral theory based on the strong assumption of functional equivalence. (Hubbell 2005, pp. 166, 171)

The above quotation clearly reveals Hubbell's recognition that niches can differentiate species distributions within a landscape, but also undeniable is that random processes impacting the birth and death of individuals can influence community composition and relative species abundances. This latter random element is often referred to as demographic stochasticity, but in Hubbell's unified neutral theory (UNT) (Hubbell 2001), it is called ecological drift. The UNT attempts to explain observed biodiversity patterns within a single trophic level based entirely on ecological drift and immigration (or speciation; see below), without resorting to more complicated and less constrained processes of niche-based competition. In particular, the UNT focuses on the relationship between species abundance (number individuals of a given species) and species rank (species ordered along the x axis from the most abundant to the least), and in many cases the theory yields remarkably accurate results (**Figure 1**).

The UNT was constructed on the foundation of island biogeography theory (MacArthur & Wilson 1963, 1967), which posits that islands nearly always have fewer species than their adjacent mainland because extinction rates are higher (simply because the number of individuals is lower) and immigration of new species is slower. As extant diversity reflects the balance between species

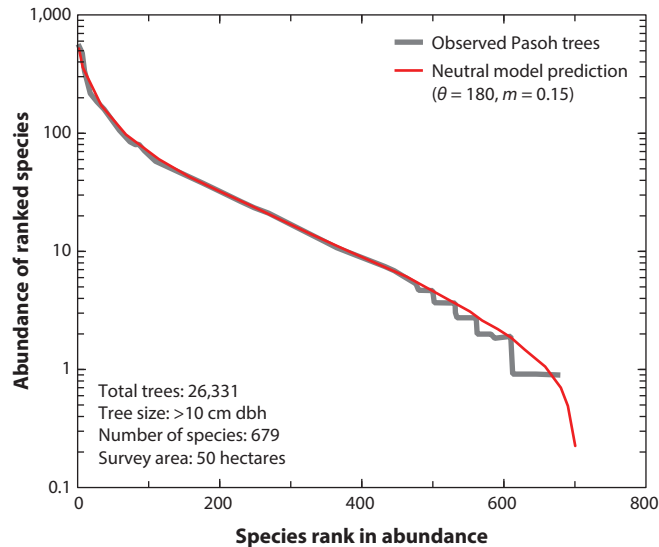


Figure 1

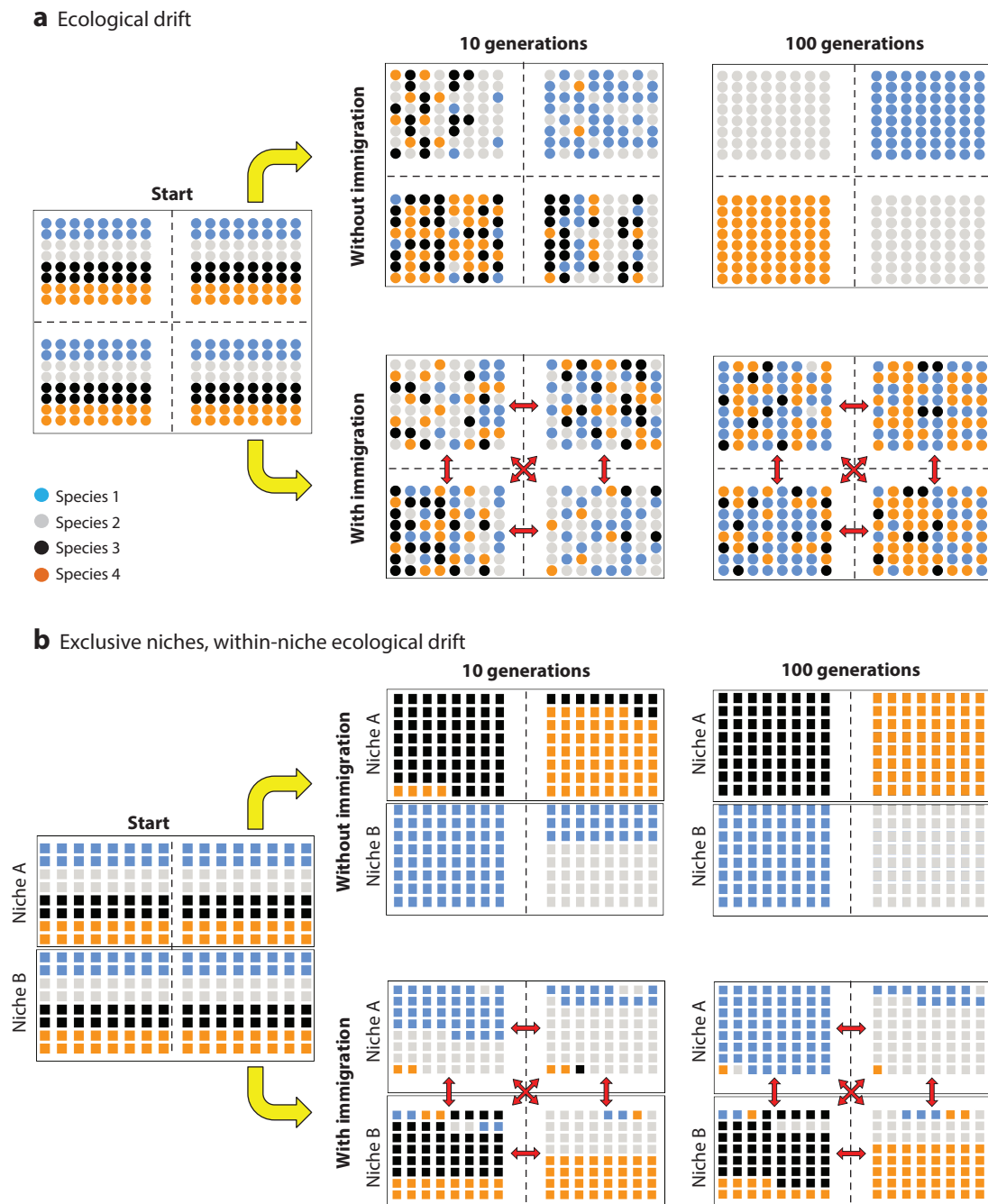
Example comparison between an observed species rank–abundance relationship and a prediction from Hubbell’s (2001) unified neutral theory. The gray line shows the measured abundance of tree species with diameters at breast height (dbh) of >10 cm in a 50-hectare plot in the Pasoh Forest Reserve, Malaysia. The red line shows the neutral theory prediction assuming a total community diversity (θ) of 180 and a dispersal limitation factor (m) of 0.15. Figure adapted from Hubbell (2001).

loss and gain, islands are expected to be less diverse. While this concept is rather intuitive, the radical aspect of island biogeography theory was that it portrayed ecological communities as being in a state of perpetual taxonomic disequilibrium and undergoing continual species replacements over time. This perspective clashed with the more widely held view of niches selecting for a subset of species that, thereafter, can potentially coexist indefinitely (at least so long as their environmental niche remains).

To arrive at his UNT, Hubbell made three fundamental assumptions. First, all organisms in a community within a given trophic level are identical in their per capita probabilities of giving birth, dying, and migrating (or speciating). It is important to note here that the term identical literally means exactly the same, as even small differences between species when played out over time would violate the assumption of neutrality, unless differences in one property (e.g., birth rate) are precisely countered by another property (e.g., death rate). Second, when an individual dies, it is randomly replaced by a new individual of any species within the immediate area with a probability proportional to the abundance of the different species in that area. For example, if a tree dies in the closed canopy of a rain forest, the newly opened real estate can be occupied by any species that managed to deposit seeds in that location, but the likelihood that seeds of a given species are present is dependent on the relative abundance of mature trees of that species within the distance limit of seed dispersal. This element of the UNT that considers the relative abundance of individuals is central to the theory because it allows predictions of a given species’ longevity in a community (i.e., species with more individuals are less susceptible to extinction), thereby distinguishing the UNT from island biogeography theory, in which ecological equivalence is considered at the species level rather than at the individual level. Finally, Hubbell assumed that landscapes are essentially saturated with individuals. Thus, any increase in one species must be accompanied by a

matching decrease in the collective number of all other species in the community. This stipulation is referred to as the zero-sum constraint.

To provide a more intuitive sense of neutral theory, the top subpanels of **Figure 2a** show a representation of four communities, each with 64 individuals, undergoing zero-sum ecological



(Caption appears on following page)

Figure 2 (Figure appears on preceding page)

Ecological community and metacommunity composition changes (*a*) under conditions of pure ecological drift and (*b*) with exclusive environmental niches. Each simulation starts with four ecological communities (separated by *dashed lines*) of 64 individuals representing four equally abundant species (*colored circles or squares*). With each generation of the communities, 50% of individuals are removed (death) and replaced (birth) with new individuals in proportion to the relative abundance of the remaining species. The middle and right columns of each panel show the abundance of each species in each community after 10 and 100 generations, respectively. The top row of each panel shows the model outcome in the absence of immigration between ecological communities. The bottom row of each panel shows the model outcome in the presence of immigration between ecological communities (indicated by *red arrows*), where immigration was modeled per generation by the ecological communities contributing four random members to each of the three other communities. In these lower subpanels, therefore, the metacommunity is the sum of all four ecological communities. In the pure ecological drift simulations (panel *a*), all species are assumed to have identical fitness. In the exclusive niche scenario (panel *b*), species 1 and 2 are assumed to be equally fit but better competitors than species 3 and 4 for environmental niche A, while species 3 and 4 are equally fit and better competitors in environmental niche B. After half the individuals were killed within each generation, the weaker competitors were repopulated in half their relative abundance, whereas the two better competitors within each community were repopulated in their relative proportion to fill the gaps. Note that in the bottom right subpanels of panels *a* and *b*, elevated species diversity is achieved through immigration under both pure drift and niche-based competitive exclusion. Thus, immigration as a mechanism for coexistence is not a unique element of neutral theory.

drift following the assumptions defined above but without immigration. In this illustration, each community is initiated with four different species of equal abundance (16 individuals per community). With each cycle of mortality and birth, the four communities become dominated by some species while others become rare until, ultimately, each community is composed of a single species [i.e., the same outcome as classic niche-based competitive exclusion (Gause 1934, Hardin 1960)]. This monodominance happens quickly (50–100 generations) in our small communities (**Figure 2a**, top), but Hubbell (2001) showed that the same result is expected over sufficient time for realistic population sizes of, say, tropical tree communities. However, in contrast to niche-based competitive exclusion, a key property of neutral community dynamics is that the outcome of stochastic birth and death cycles plays out independently within each local community; thus, species that are becoming rare in one location may still have a firm foothold (and may even be dominant) in another location. Accordingly, if we now add immigration between communities, diversity is maintained in all communities and monodominance is avoided (**Figure 2a**, bottom). The steady-state diversity under neutral community dynamics (i.e., total number of species sustained in a community at equilibrium) is always a subset of the total possible number of species. The assumption of ecological equivalence between individuals is fundamental to these dynamics with immigration because it means that even a single individual of a given species migrating into a new community has a finite probability of becoming dominant over time and displacing other species, causing species composition to follow a random walk or ecological drift in time.

The steady-state diversity predicted by the UNT and its rank–abundance relationship for an ecological community of trophically similar, sympatric species (note that the UNT does not attempt to explain diversity between trophic levels) is dependent on the total number of individuals in the community and the rate of immigration. Large populations sustain higher diversity with a dominance–diversity distribution that is more lognormal-like (e.g., **Figure 1**). Small populations sustain fewer species, have a steep and geometric-like dominance–diversity distribution, and exhibit an increase in the variance of relative species abundance. The reason for these relationships is that the number of individuals of a given species within smaller communities, by default, is more likely to decrease to a point where random mortality and replacement results in extinction. Quantitatively, the UNT predicts that diversity (θ) in an ecological community is proportional to community size (J) and immigration rate (ν): $\theta = 2J\nu$ (Hubbell 2001). For the metacommunity (spatially distinct ecological communities linked through dispersal), the UNT predicts the same relationship of $\theta = 2J\nu$, but in this case ν is the speciation rate rather than the immigration rate.

Predictions of the UNT were originally made using numeric simulations (Hubbell 2001), but analytical solutions have since been described (e.g., Vallade & Houchmandzadeh 2003, Volkov et al. 2003, McKane et al. 2004). While these predictions can closely match observations (e.g., **Figure 1**), this success does not necessarily mean that neutral dynamics are responsible for community structuring (Chave 2004). The validity of the UNT interpretation rests solely on the assumption that all individuals are ecologically equivalent.

NEUTRAL NICHES

In Hubbell's (2001) UNT, all trophically similar individuals are assumed to participate in ecological drift as a single local community or single metacommunity. This is equivalent to saying that all individuals occupy a single niche. However, Purves & Pacala (2005) modeled metacommunities of two or more exclusive niches (i.e., species adapted to one niche cannot survive in other niches) with ecological drift operating independently in each niche. They showed that, when equilibrium species abundances for all niches are combined, the resultant rank–abundance prediction is identical to that for a single community with an equal total number of individuals undergoing ecological drift. More specifically, in metacommunities with a large number of individuals and a large number of species, the success of neutral theory in predicting the overall rank–abundance distribution is not evidence for an absence of strong and even diverse niche partitioning. Purves & Pacala (2005) also demonstrated that their results were robust to different forms of niche partitioning, such as spatially or temporally separated niches, and to smaller numbers of species within niches so long as niche separation was weak. In essence, their work promotes what we refer to herein as neutral niches within structured communities, wherein environmental and ecological niches play a deterministic role in selecting sets of specialized coexisting species, but within each of these niche sets the relative abundance of species is dominated by ecological drift.

Figure 2b provides a simple illustration that captures the essence of neutral niches in a structured environment. It begins with the same initial conditions as in **Figure 2a** but with the additional assumptions that the metacommunity is divided into two exclusive niches (A and B) and that species 1 and 2 are better adapted to niche A, while species 3 and 4 are better adapted to niche B. We then follow how the ecological communities and the metacommunity evolve over successive generations of mortality and birth. In the absence of immigration (**Figure 2b**, top row), the outcome of this model is deterministic at first, as one might expect, in that only species 1 and 2 occupy niche A and only species 3 and 4 occupy niche B (**Figure 2b**, top middle subpanel). From this point forward, species abundance in each community is nondeterministic, and ecological drift ultimately leads to only a single remaining species (**Figure 2b**, top right subpanel, just as in the top row of **Figure 2a**). Thus, the same diversity at the metacommunity level may be observed in the presence or absence of exclusive niches. If we now allow immigration between communities (including across niches), the outcome is not only sustained diversity in each community but also the presence of inferior competitors in each community (e.g., species 3 and 4 in niche A; **Figure 2b**, bottom row). Thus, enhancement of diversity through immigration is not a defining feature of neutral theory. The critical distinction here is that immigration between communities within a niche enhances stable coexistence because each migrating individual has a finite probability of surviving in the new community, whereas immigration between niches results in unstable coexistence because cross-niche invaders are doomed to exclusion due to poorer fitness in the invaded niche. The challenge in understanding biodiversity is identifying mechanisms enabling stable, not unstable, coexistence.

Stable coexistence within a neutral niche does not require equal fitness between species. Chesson (2000) developed a biodiversity theory in parallel with Hubbell, but one where sustained

diversity is the outcome of both equalizing and stabilizing mechanisms. Equalizing mechanisms function to minimize fitness inequalities between species in a niche, such as species A investing more into resource acquisition to enhance birth rates while species B invests in reduced predation such that the net effect (i.e., the difference between birth and death rates) is similar between the two species. Stabilizing mechanisms function by having a greater impact on intraspecific interactions than on interspecific interactions. Examples of stabilizing mechanisms include density-dependent predation [e.g., kill the winner (Thingstad & Lignell 1997)] and resource partitioning, whereby coexisting species are each primarily limited by different resources such that the proliferation of a given species has a greater negative effect on its own future growth potential than it does on that of other species. Stabilizing mechanisms act to counter fitness advantages that would otherwise cause one species to exclude all others. Hubbell's (2001) UNT is considered a special case of Chesson's (2000) theory (Adler et al. 2007) because the former's assumption that all individuals have equal birth and death rates implies identical fitness and, consequently, that no stabilizing mechanisms are at play. In Chesson's (2000) theory, stable coexistence does not imply that the relative density of different species is constant in time, but rather that any species whose abundance diminishes has the potential (due to stabilizing mechanisms) to recover its standing in the community. For example, if seasonal variations in growth conditions cause different species to proliferate at some times of the year and diminish during others, the stable coexistence of many species may still occur because these temporal niches allow rare species to recover prominence over the course of the annual cycle. This resistance to exclusion through periodic dominance is referred to as the storage effect (Chesson 1994).

Huisman & Weissing (1999, 2000) presented a mathematical framework enhancing species coexistence in the face of fitness differences that bears some resemblance to stabilizing mechanisms. In their theory, species are assumed to be intermediate competitors for resources; for instance, species 1 is the better competitor for resource 1 but becomes limited by resource 2, species 2 is the better competitor for resource 2 but becomes limited by resource 3, and species 3 is the better competitor for resource 3 but becomes limited by resource 1. With this construct, oscillations in dominance create chaotic fluctuations that allow the coexistence of many species (e.g., in one simulation, six species were sustained on only three limiting resources). Challenges with this theory, however, are that it is unclear how plausible the rules of intermediate competition are for natural ecosystems and that model outcomes are highly sensitive to slight changes in parameterization (Sarker et al. 2018).

A more recent explanation for the paradox of coexistence focuses on phenotypic heterogeneity within a species and its consequences for time-averaged competitive interactions between individual cells. For example, Menden-Deuer et al. (2021) used noncooperative game theory to predict how individual-individual interactions give rise to population-level diversity, where the competitive ability of each individual reflects the sum of multiple fitness traits, such as resource acquisition, predator defense, and morphology. In their model, single competitive encounters between individuals are assumed to have nondecisive outcomes, such that an individual's fate is decided by the cumulative outcome of multiple competitions over a generation time. The outcome of this construct is that maximum intraspecific phenotypic heterogeneity allows unlimited coexistence of species because equal fitness can be achieved at the species level through unequal fitness at the individual level. A key assumption in this theory is that direct cell-to-cell competition occurs frequently in microbial communities.

In addition to the concepts highlighted above, many other [not necessarily mutually exclusive (Pigolotti & Cencini 2013)] explanations for stable coexistence within a trophic level have been proposed (e.g., Wilson 2011), including mathematical solutions without explicit links to ecological

processes (e.g., Record et al. 2014). The question at hand is, Do neutral processes contribute significantly to observed biodiversity in aquatic systems?

OCEAN NEUTRAL?

In the dense vegetation of a rain forest, it is easy to imagine how overlapping root systems (including associated mycorrhizae) and leaves of neighboring plants can easily result in direct competition for resources. Such is not the case for phytoplankton populations. The fact is that from highly oligotrophic ($<0.05 \mu\text{g chlorophyll L}^{-1}$) to highly eutrophic ($>50 \mu\text{g chlorophyll L}^{-1}$) conditions, phytoplankton cells are, on average, separated by >100 to nearly 400 body lengths and occupy only $\sim 0.000003\%$ to $\sim 0.002\%$ of the volume in which they are suspended (Behrenfeld et al. 2022). Under such conditions, zones of influence [i.e., boundary layers, ~ 9 times cell diameter (Karp-Boss et al. 1996)] from which cells can draw nutrients rarely overlap between individuals. In addition, although phytoplankton move in relation to each other and can even come in close enough proximity to collide and form aggregates, even small-scale Kolmogorov turbulence is insufficient to significantly increase the probability of overlapping boundary layers over the generation time of cells (Siegel 1998). We can therefore conclude that spatial distancing between phytoplankton in natural communities largely negates any potential for direct resource-based competitive exclusion (RBCE). It also implies that interpretations of stable coexistence among phytoplankton founded on the nondecisive outcomes of frequent and direct individual–individual interactions [e.g., as modeled by game theory (Huang et al. 2016, Menden-Deuer et al. 2021)] may not be mechanistically rooted. If phytoplankton rarely compete directly for resources, is niche partitioning within an ecological community even relevant to diversity? Indeed, could any system be better primed for domination by ecological drift than that of the distantly spaced phytoplankton?

Behrenfeld et al. (2021c) applied Hubbell's rules of zero-sum ecological drift to simulate phytoplankton populations ranging from 10,000 to 1,000,000 individuals, with each model run initiated with 10,000 ecologically equivalent species. Consistent with the UNT, the outcome of these simulations was that diversity eventually decreased to a single remaining species in the absence of immigration, and sustained diversity in the presence of immigration was directly proportional to immigration rate and population size (recall from above Hubbell's prediction that $\theta = 2J\nu$). This study also showed that the time (i.e., number of generations) required for the first stochastic loss of a species was directly proportional to population size (for our largest population, this was ~ 100 generations). The significance of this finding is that 1,000,000 individual phytoplankton can easily be found in only a few milliliters of natural seawater. If we extend our result to the number of phytoplankton encompassed in the volume of water physically homogenized within even a single day,¹ the necessary time for the first stochastic exclusion becomes comparable to the age of life on Earth (Behrenfeld et al. 2021c).

Given that the entire surface layer of the global ocean is homogenized on a timescale on the order of 1,000 years, this result leads to two strong conclusions: (a) Neutral theory provides no constraint on phytoplankton biodiversity, and (b) immigration is not necessary to sustain stable coexistence if only stochastic processes are at play. The latter conclusion is noteworthy because many of the publications in the aquatic ecology literature that aimed to test elements of neutral theory have focused on the relative importance of immigration (physical transport and mixing)

¹Typical horizontal eddy diffusion values for the upper ocean are $O(10^3 \text{ m}^2 \text{ s}^{-1})$, implying that the length scale for mixing in one day is $O(1,000 \text{ m})$. Typical number concentrations for phytoplankton in the ocean range from $<1 \text{ mL}^{-1}$ for large species to more than 10^5 mL^{-1} for the smallest species. Applying these concentrations to a homogenized water mass only 1 m deep by 1,000 m wide yields an onset time for significant stochastic exclusion of 10^5 – 10^{10} years.

versus environmental sorting (i.e., within-niche competition) (e.g., Chust et al. 2013, Chen et al. 2022, Pineda et al. 2022). The former conclusion is interesting because it raises the question, If phytoplankton generally do not experience direct cell-to-cell competition and neutral processes provide no constraint on diversity, why is phytoplankton diversity in the ocean so low compared with, for example, the diversity of terrestrial plants? This is the inverted paradox question posed by Behrenfeld et al. (2021c).

TOWARD A UNIFIED THEORY OF PLANKTON BIODIVERSITY

The framework we propose for interpreting the biodiversity and biogeography of the phytoplankton combines elements of niche partitioning and neutrality. At large geographic scales and between physically distinct layers of the water column, there is undeniable selection for planktic species based on environmental growth conditions (e.g., polar versus tropical, eutrophic versus oligotrophic, and surface versus deep communities). This environmental structuring implies niche-evolved fitness differences between species that cannot be compensated for by stabilizing mechanisms. However, the mechanism selecting for species within niches is not resource-based competition but rather an indirect form of competition involving trophic interactions (Holt 1977, Behrenfeld et al. 2021c). Specifically, the biomass and division rate of a phytoplankton community are perpetually in quasi-equilibrium with losses. For a given growth environment, species that share a common predator (or pool of predators) will be selected upon according to each species' division rate relative to the predatory loss rate (i.e., the division–loss balance). Thus, within these feeding size bins and assuming nonselective grazing, slower-dividing species will become rarer and faster-growing species more abundant with each turnover of the population, even in the absence of direct competition. With sufficient time, the only remaining species are those with fitness differences sufficiently small to be compensated for by stabilizing mechanisms, a process that Behrenfeld et al. (2021c) referred to as the trophic exclusion principle. Importantly, the timescale for trophic exclusion increases as division–loss balances converge, requiring thousands of generations for closely matched species (Behrenfeld et al. 2021c). Accordingly, stable coexistence is permitted for all species with equivalent division–loss differences integrated over the timescale for trophic exclusion, which can significantly exceed that of seasonal or even interannual environmental variability. Thus, the relative fitness of different species may change with the seasons, but it is the time-averaged balance of fitness and stabilizing processes that defines stable coexistence.

Another element in our framework is that trophic exclusion has the important attribute of independently regulating diversity in different size classes. Specifically, while some grazers feed wholesale across the phytoplankton size domain [e.g., gelatinous tunicates feeding with mucous webs (Sutherland et al. 2010, Dadon-Pilosof et al. 2019)], the absolute size range grazed upon by herbivores is generally proportional to their average prey size (Hansen et al. 1994, Sommer & Sommer 2006, Fuchs & Franks 2010, Kiørboe 2011, Wirtz 2012, Hébert et al. 2017, Behrenfeld et al. 2021a). This phenomenon plays a decisive role in controlling phytoplankton size distributions (Kerr 1974; Kiefer & Berwald 1992; Behrenfeld et al. 2021a, 2022) and implies that trophic exclusion functions within, not between, feeding size ranges (Behrenfeld et al. 2021c, 2022). For example, consider a surface mixed layer in an oligotrophic ocean region. The maximum potential division rate of different phytoplankton species will be determined by size-dependent diffusion rates and far-field nutrient concentrations. The total number of individual phytoplankton in each size class will be determined by the predator–prey balance between loss rate and division rate [higher division rates sustain higher equilibrium biomass, but often in a less than 1:1 manner (Behrenfeld et al. 2021a, 2022)]. In an oligotrophic system with particularly low nutrients, the division rate of the smallest phytoplankton will be significantly higher than that of the larger

phytoplankton, and predator–prey balances will thus yield an abundance of smaller species that sequester a lion’s share of the limiting resource. However, because each phytoplankton size class is in balance with its own set of predators (whose abundance changes in parallel with that of its prey), the advantage of being small in a low-nutrient environment can only cause a steepening of the size distribution slope and not the exclusion of larger species. As nutrients increase, the smallest species quickly reach their maximum potential division rate (and thus an equilibrium standing stock), while the division rates and biomass of larger species progressively increase, causing the size distribution of the phytoplankton community to become less steep (Behrenfeld et al. 2021a, 2022).

In the above scenario, trophic relations between phytoplankton and predators create a diversity of size-structured ecological niches within the broader environmental (physical or chemical) niches. The neutrality in our framework lies in the fact that, in each size-dependent ecological niche, stable coexistence of many species can occur so long as fitness differences (e.g., enhanced resource acquisition and division rate) are countered by stabilizing mechanisms (*sensu* Chesson 2000). For phytoplankton, these stabilizing elements may include selective grazing, density-dependent susceptibility to viral infection and lysis, morphological grazing deterrents, allelopathy, metabolic networking, storage effects, mixotrophy, and others.

Is the trophic exclusion principle significantly different from classic RBCE? Yes. In its simplest form, RBCE predicts that the number of coexisting species will be equal to the number of limiting resources (Tilman 1977, 1981; Sommer 1985, 1986; Rothhaupt 1988). By contrast, under trophic exclusion mechanisms, the number of limiting resources is irrelevant to sustained diversity because coexistence is determined by relative fitness differences (irrespective of which resource determines a given species’ fitness) and compensating effects of stabilizing mechanisms. In the absence of size-structured ecological niches, RBCE also predicts that all individuals within a trophic level compete, such that the species that can draw a limiting resource to the lowest level while maintaining its balance with loss rates will exclude all others [i.e., the R^* rule (Tilman 1980, 1982)]. By contrast, the trophic exclusion framework predicts that all phytoplankton size classes will coexist despite tremendous differences in resource acquisition capabilities, consistent with field observations (Venrick 1990, Reynolds & Stramski 2021). Behrenfeld et al. (2022) presented a simple ecosystem model demonstrating this stable coexistence across size classes (albeit at profoundly different concentrations) for the full range of nutrient concentrations found in the open ocean. Finally, the trophic exclusion framework is not compromised by the large spatial distancing of cells in natural communities that undermines RBCE. What is not different between the trophic exclusion principle and classic RBCE is a neutral element. Specifically, the simplest form of RBCE defined above can be expanded to instead state that, for each limiting resource, all species with the same net balance of fitness and stabilization over the timescale of selection can coexist and that the total number of species in a community is the sum of unique coexisting species across all limiting resources.

Summarizing this section, we propose that broad environmental niches select for sets of compatible phytoplankton species. Within each of these environmental niches, size-structured ecological niches exist where selection acts within, not between, size classes. In each size class, stable coexistence is achieved through equalizing and stabilizing mechanisms, where the equalizing mechanism results in sufficiently small fitness differences that annual to interannual timescales are required for further selection. Accordingly, coexisting species can exhibit strong differences in relative fitness on short timescales but nearly equal fitness when integrated over longer periods that, with the addition of stabilizing processes, gives rise to long-term stability. When stable coexistence is reached, we predict that the relative abundance of different species in each size-structured ecological niche will follow neutral dynamics [i.e., yielding lognormal rank–abundance distributions (e.g., Spatharis et al. 2009)]. Because proportional feeding size ranges of grazers and size-dependent division rates create steeply sloped phytoplankton size distributions (Behrenfeld

et al. 2021a, 2022), rank–abundance distributions for each ecological niche will have different shapes [reflecting differences in species number and population abundances within each niche (Hubbell 2001)]. Consequently, a long-tailed rank–abundance distribution is expected when evaluated over the entire phytoplankton size domain, which is consistent with observations (Barberán et al. 2014). One unknown in this interpretation of phytoplankton biodiversity (which thus points to areas for future research) is the relative importance of equalizing and stabilizing mechanisms. The necessity for stabilizing mechanisms depends on the strength of the equalizing forces, which then raises the question, How similarly fit are the species in a neutral niche?

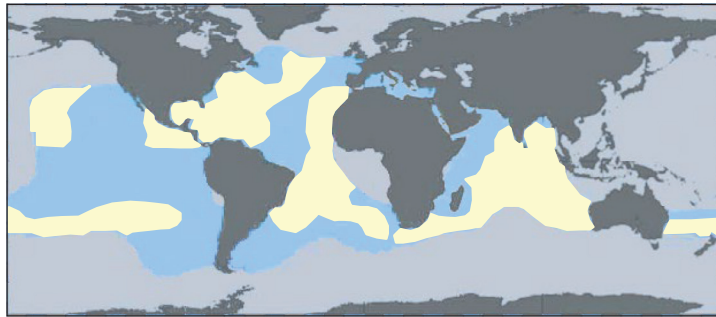
A RAZOR'S EDGE

Under the trophic exclusion framework, fitness equalization is only relevant within, not between, size-structured ecological niches. We are unaware of any field experiments directly measuring fitness in these niches, but some insights have been provided indirectly. For example, Ustick et al. (2021) conducted an open-ocean survey of *Prochlorococcus* genes associated with nutrient utilization. They found that as nitrogen stress increases, *Prochlorococcus* genotypes express an increasing capacity to take up and utilize more oxidized forms of nitrogen, beginning with ammonia and urea and then moving on to nitrite and nitrate (**Figure 3a**). Similarly, when inorganic phosphate is limiting, genotypes are found that can broadly assimilate dissolved organic phosphorus (**Figure 3b**). While Ustick et al. (2021) provided a unique global view of ocean nutrient limitation, what we found most interesting was not the increasing toolbox for nutrient use with increasing stress (yellow areas in **Figure 3a,b**), but rather the absence of these genes when ammonia and inorganic phosphate are in sufficient supply (blue areas in **Figure 3a,b**). This finding suggests that the selective pressure of trophic exclusion is so great that the minuscule cost of carrying a few extra genes that broaden a cell's repertoire of nutrient sources is enough for its elimination from a community. Clearly, selection by trophic exclusion can act as a razor's edge, even at the genotype level. However, a caveat here is that *Prochlorococcus* genotypes are likely so similar in all other aspects that little room remains for alternative morphological, physiological, or other evolved strategies enabling broader coexistence.

A second attribute of *Prochlorococcus* related to trophic exclusion is its geographic restriction to warm ocean waters ($\sim 10^{\circ}\text{C}$ and above) (Partensky et al. 1999). Intriguingly, Goericke (2011) proposed that this apparent temperature threshold reflects a tendency for cooler waters to have elevated organic substrate concentrations that support large bacteria sharing a common predator with *Prochlorococcus*. Given sufficient substrate, large bacteria have the potential for higher growth rates than *Prochlorococcus* because of their lower costs for cell replication. This fitness difference would, through trophic exclusion, lead to the demise of *Prochlorococcus* and is a reasonable interpretation of why low-temperature genotypes are not found (i.e., low-temperature gene products would still not overcome the heterotrophic advantage) (Moore et al. 1995). Goericke's (2011) insight also explains why *Prochlorococcus* can be absent in warm upwelling regions and why its temperature cutoff at higher latitudes varies between regions (i.e., temperature is only a proxy for the competition with heterotrophic bacteria), as illustrated in the model by Follett et al. (2022). Conversely, the success of *Prochlorococcus* in warm oligotrophic waters of severely diminished labile organic substrates likely reflects the photoautotrophic lifestyle permitting higher division rates than are achievable by comparably sized bacteria, allowing trophic exclusion to tip the balance in favor of the photoautotroph.

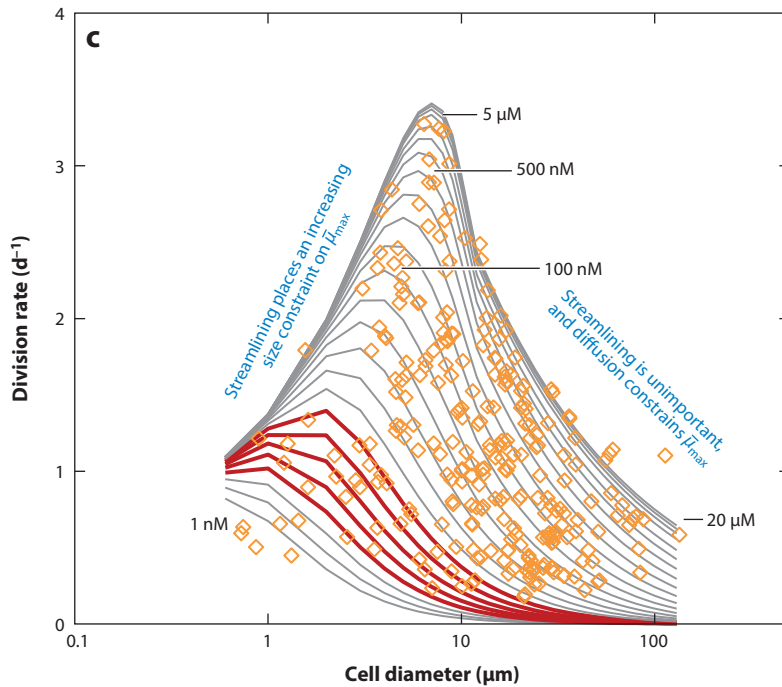
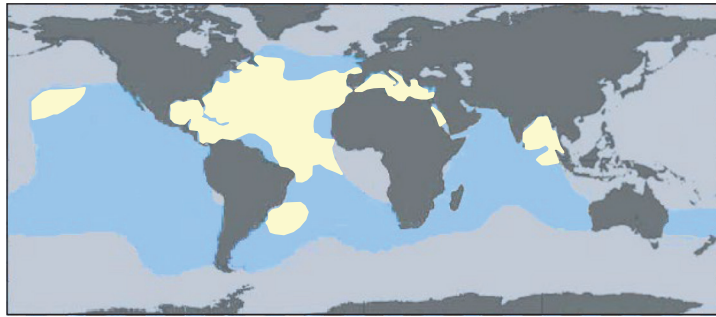
Diffusion-based constraints on maximum phytoplankton division rates ($\bar{\mu}_{\text{max}}$) suggest that *Prochlorococcus* ($\sim 0.6\ \mu\text{m}$) is likely growing at near $\bar{\mu}_{\text{max}}$ even at the nanomolar-scale nutrient concentrations (S_{∞}) of oligotrophic ocean gyres (red lines in **Figure 3c**), which explains why genotypes with expanded nutrient toolboxes gain little advantage in many regions and are selected

a Nitrogen stress



- Low-stress genes only
- Medium- or high-stress genes
- No data
- Land

b Phosphorus stress



(Caption appears on following page)

Figure 3 (Figure appears on preceding page)

Physiological factors influencing the outcome of trophic exclusion. (a,b) Dominance of *Prochlorococcus* genotypes in the global ocean defined by the presence of genes for utilizing reduced versus oxidized forms of nitrogen (panel a) and inorganic versus organic forms of phosphate (panel b). When nutrient availability is sufficient (blue areas), only reduced nitrogen sources (ammonia and urea) and inorganic phosphate are used. When nutrient availability is lower (yellow areas), more oxidized nitrogen forms (nitrite and nitrate) and organic phosphate are used. Panels adapted from Ustick et al. (2021) with permission from the American Association for the Advancement of Science. (c) Physical limits and observed limits in phytoplankton division rates as a function of cell diameter. Gray lines indicate the maximum cellular division rates ($\bar{\mu}_{\max}$) permitted by physical diffusion across cell boundary layers for far-field nitrogen concentrations ranging from 1 nM to 20 μ M, and red lines correspond to typical nutrient concentrations measured in oligotrophic ocean gyres (data are from Behrenfeld et al. 2022). Orange diamonds indicate the maximum cellular division rates measured in laboratory cultures for a wide range of phytoplankton species (data are from Behrenfeld et al. 2021b).

against (blue areas in **Figure 3a**). Between 0.6 and 8 μ m, division rates decrease with cell size at low S_{∞} , but $\bar{\mu}_{\max}$ at high S_{∞} increases with size (**Figure 3c**). This latter observation likely reflects volume-based physical restrictions on the cellular machinery (membrane area, protein content, etc.) that can be accommodated for faster growth (Raven 1994, Behrenfeld et al. 2021b). At cell diameters above $\sim 8 \mu$ m, diffusion potential strongly limits division rates across the full range of S_{∞} . If we now compare these diffusion-based values for $\bar{\mu}_{\max}$ with size-dependent maximum division rates ($\mu_{\max}$) measured in the laboratory (orange diamonds in **Figure 3c**), we find that most species fall notably short of their potential. Similar underperformance is observed among species for nutrient uptake rates at limiting concentrations (i.e., the initial slope of nutrient–division rate relationships) (e.g., Aksnes & Egge 1991, Flynn et al. 2018, Behrenfeld et al. 2022). The key question here is how we rationalize the persistence of species in nature that appear grossly unfit in terms of nutrient assimilation. Is this a hallmark of alternative life strategies where reduced performance in resource acquisition is traded for better predator defense, or is it associated with a particular stabilizing factor? Understanding the evolutionary significance of such differences between species (and genotypes) is fundamental to unlocking mysteries of the neutral niche.

Behrenfeld et al. (2021b) attempted to link specific morphological (e.g., frustule or large vacuole), physiological (e.g., high $\mu_{\max}$), and behavioral (e.g., triggered mass sinking events) attributes of diatoms to their successful and stable occupation of ecological niches over a broad size range. This study proposed that, for some diatom species, these attributes have been evolutionarily tuned for a blooming lifestyle based on temporarily outrunning predation. Behrenfeld et al. (2021a) expanded this idea into a broader conceptual mandala of community structuring. In the mandala (**Figure 4**), all environmental niches have a persistent, size-structured series of ecological neutral niches occupied by a diversity of species selected through trophic exclusion for similar fitness. In unstable environmental niches, this baseline diversity is augmented by a successional sequence of species with unique physiological–morphological characteristics targeting finely separated temporal niches, where persistence in the community relies on storage effects.

Our quantitative understanding of the multidimensional tradespace that defines success in neutral niches is far from complete. Continued empirical and theoretical work is needed to mechanistically interpret fitness equalization among coexisting species and capture time-integrated neutral dynamics in ecosystem models. What we can say is that there are no Darwinian demons (i.e., organisms that can do everything well) (Leimar 2002) in nature because any advantage in one arena comes at a cost in others (Holt 1977, Jessup & Forde 2008).

STREAMLINING OR FULL MONTY?

Genome streamlining refers to selection that reduces the metabolic capabilities of a cell yet conveys a competitive advantage by decreasing costs for cell replication through minimization of cell size and complexity. Streamlining can provide a sufficient fitness advantage to drive

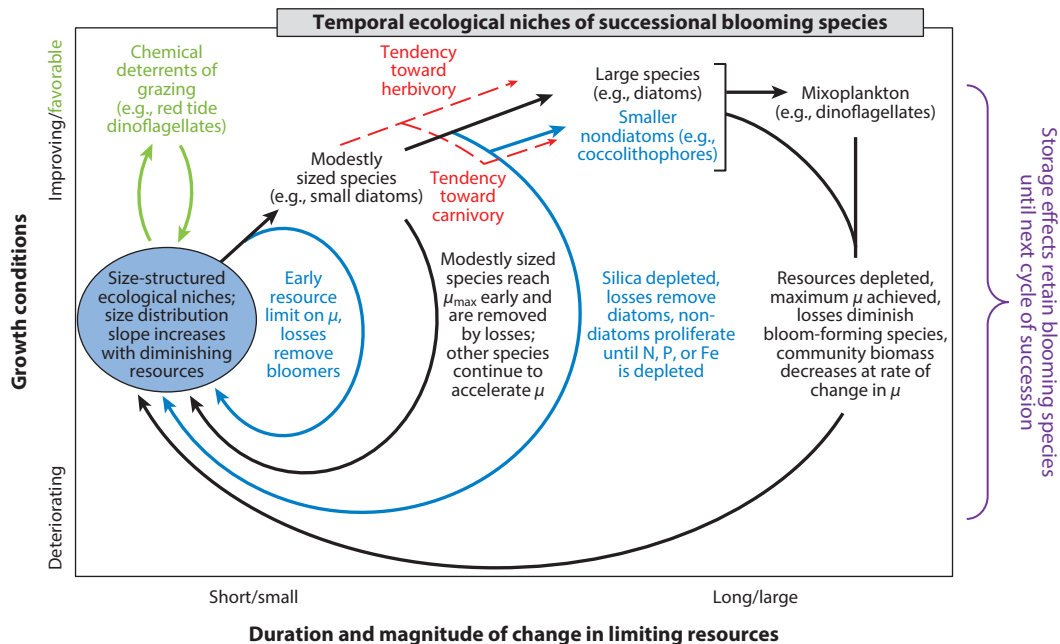


Figure 4

Conceptual mandala depicting aspects of phytoplankton community structuring. The determinant axes of the mandala are the duration and magnitude of change in limiting resources and the trajectory of growth conditions. In temporally stable environmental niches (*blue circle*), size-dependent predator feeding size ranges create noncompeting ecological niches within which trophic exclusion defines species diversity through fitness differences and stabilizing mechanisms. All phytoplankton size classes can coexist across the full range of resource concentrations observed in natural waters, but total phytoplankton biomass decreases with decreasing nutrient supply and the size distribution slope steepens. In unstable environmental niches, temporal ecological niches are created by successions of species with evolved bloom-forming physiologies (represented by *blue and black arrows*). Blooming in these species is achieved through accelerations in division rates (μ) that decouple division and loss rates. Rightward-pointing black arrows indicate successions of bloom-forming species where large cells ultimately dominate bloom biomass if the amplitude of change in growth conditions is sufficiently large, which may then be followed by a rise in mixotrophic species. Leftward-pointing blue and black arrows indicate variations on the return pathway from the successional events, which are associated with different nutrient stoichiometries and cell sizes, while rates of return are dictated by the resource-limited rate of decrease in μ . The rightmost blue path is associated with silicon limitation of diatoms and a shift in the feeding tendencies of omnivore predators (*red dashed arrows*). Green arrows indicate an alternative succession scenario where blooming in a favorable high-nutrient but stable environment selects for species that chemically suppress grazing (e.g., toxic algal blooms of red tide dinoflagellates). Bloom-forming species rely on storage effects to retain their presence in the community. Figure based on Behrenfeld et al. (2021a).

trophic exclusion, as noted above regarding *Prochlorococcus* genotypes. Streamlined genomes in microorganisms are characterized by small size, highly conserved core genes and few pseudogenes, low ratios of intergenic spacer to coding DNA, and low numbers of paralogs (Giovannoni et al. 2014). Streamlining can occur when a particular cellular requirement is provided from the external environment in sufficient quantity that some of a cell's biosynthetic operons can be turned off permanently. The unexpressed biosynthetic genes are therefore no longer under selective pressure for function and will decay to pseudogenes by mutation and eventually be lost (Giovannoni et al. 2014).

Streamlining appears to be a pervasive phenomenon in bacterioplankton (e.g., Button & Robertson 2001, Giovannoni et al. 2005) and can increase community diversity by creating metabolic networks where different species become increasingly dependent on reliable external subsidies from the community [social cheaters, as in the black queen hypothesis (Morris

et al. 2012)]. Diversity enhancement through metabolic networking is anticipated to be greatest in stable, low-resource environments (e.g., lower-latitude ocean gyres). The minute and abundant Pelagibacterales (SAR11) are an extreme example of streamlining (Giovannoni et al. 1990, Morris et al. 2002, Schattenhofer et al. 2009). The genome of *Pelagibacter* is so spare that it even lacks core functions that are nearly universally distributed among other bacterioplankton (Giovannoni et al. 2014). A key to *Pelagibacter* success is its focus on simple oxidation reactions of low-molecular-weight metabolites, including one-carbon metabolism (Sun et al. 2011). Thus, as genome streamlining proceeds, it progressively limits options on suitable resources (even chemical bonds) to those that are sufficiently ubiquitous in the environment that they can meet demands for growth.

Streamlining should convey less competitive advantage in resource-rich and temporally variable environments. With respect to phytoplankton, we might refine this statement to suggest that streamlining is likely most advantageous at the transition between limiting and replete resources. For *Prochlorococcus*, streamlining the nutrient toolbox is an effective strategy because large ocean regions are sufficiently nutrient replete that a diverse toolbox is unnecessary. However, division rates become increasingly susceptible to diffusion limitation as cell size increases (**Figure 3c**). Even at the size of marine *Synechococcus* ($\sim 1\text{--}2\ \mu\text{m}$), streamlining may be disadvantageous under oligotrophic conditions as selection will favor larger genomes (the full monty) that enhance fitness by broadening the range of utilizable resources. Another important aspect of streamlining is that, at cell sizes less than $\sim 8\ \mu\text{m}$, associated cell size reductions appear to place physical constraints on $\bar{\mu}_{\text{max}}$ that can convey a fitness advantage for larger species in this size range when resources are elevated (above the red lines in **Figure 3c**), even if temporarily, because of storage effects (Chesson 2000, Pearce et al. 2020). For phytoplankton larger than $\sim 8\ \mu\text{m}$, it can be envisioned that full-monty strategies may be the rule more than the exception, at least in terms of nutrient acquisition.

In bacteria and archaea, genome size is directly proportional to the number of coding genes (Shuter et al. 1983) (**Figure 5a**), suggesting minimized intergenic spacers and pseudogenes across the size domain (Giovannoni et al. 2005). In phytoplankton, similar streamlining may exist in the smallest size classes, but for most eukaryotes the number of coding genes is not correlated with genome size (Gregory 2001). Instead, the more than five orders of magnitude range in genome size of eukaryotes largely results from random insertions and deletions of noncoding DNA (ncDNA) (Oliver et al. 2007). During replication, coding genes are copied before ncDNA, and it has been proposed that increases in ncDNA reduce mutation rates by allowing more time during replication to correct mistakes in functional genes (Herrick 2011). Irrespective of this interpretation, one clear significance of ncDNA content is that it correlates with cell size (**Figure 5a**) and thus influences the predator pool to which a given phytoplankton species is susceptible (Behrenfeld et al. 2021c). Recognizing that ncDNA content evolves in a manner proportional to genome size (Oliver et al. 2007) and is, to first order, independent of functional gene evolution, one might predict that species richness within the eukaryotic phytoplankton domain will likewise be inversely related to cell size. Genome data from the circumglobal *Tara* Oceans program strongly support this prediction (Behrenfeld et al. 2021c) (**Figure 5b**). This finding adds another dimension to our trophic exclusion framework: Smaller phytoplankton size classes must accommodate greater diversification, albeit perhaps with limited scope for fitness differences among species.

When genome streamlining results in reduced cell size, a concomitant effect is an increase in cell surface-to-volume ratio. While increases in this ratio convey a significant fitness advantage when boundary layers for diffusion overlap between cells (Button 1991, 1998; Giovannoni et al. 2014), differences in this ratio between species should be of far less consequence to biodiversity when trophic exclusion dominates community structuring because competition is restricted to

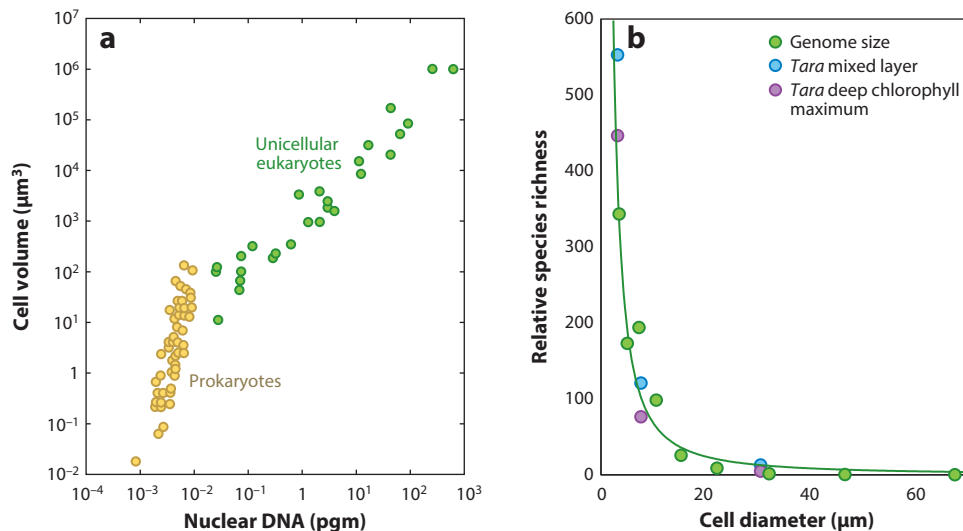


Figure 5

Linkages among genome size, cell size, and species richness. (a) Relationships between DNA content and cell volume for unicellular eukaryotes (green circles) and prokaryotes (yellow circles). Panel adapted from Shuter et al. (1983) with permission from *The American Naturalist*. (b) Relative phytoplankton species richness predicted from genome size evolution (green circles) and as measured from the surface mixed layer (blue circles) and deep chlorophyll maximum (purple circles) during the *Tara* Oceans expedition. Panel adapted from Behrenfeld et al. (2021c) (CC BY 4.0).

like-sized organisms within the feeding range of shared predators. In other words, under trophic exclusion constraints, cell size is not a master variable governing competitive outcomes, as it is often portrayed in the ecological literature.

NEUTRAL NICHES IN A COMPETITIVE WORLD

Our conception of the governing processes defining community structure and diversity influences how we interpret observations of natural ecosystems and construct models to capture their dynamics and make future predictions. Hubbell's (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* represents a major scientific contribution to this end because it challenged ecologists to question the pervasive neo-Darwinian interpretation of community assemblies simply through the monocle of niche-based competitive exclusion. However, Hubbell's UNT does not, in fact, provide an explanation for biodiversity and biogeography. This is because it begins with an assumption that all individuals within a trophic level are ecologically equivalent and fails to explain how this equivalence comes to be. The answer to this latter question is that ecological equivalence is the outcome of nonneutral processes (i.e., selection based on species differences). Agreement between neutral theory predictions and observations (e.g., **Figure 1**) is, nevertheless, a very noteworthy finding because it may imply that stable diversity in extant ecosystems reflects a limit where fitness similarity and stabilizing mechanisms prohibit any further down-selection of species, and the dynamics of the resultant neutral niche are dominated by stochastic processes.

Here, we have outlined a framework for understanding biodiversity and community structuring that melds neutral aspects with strong selection through trophic exclusion. This latter element is of fundamental importance in the case of the phytoplankton because it imposes strong selective pressure despite the large spatial distancing between cells in natural populations that undermines

the foundation of classic RBCE. The trophic exclusion principle also permits all phytoplankton size classes to coexist across the full natural range of resource concentrations and predicts size–abundance relationships consistent with observations (Behrenfeld et al. 2021a, 2022). Finally, it addresses the aforementioned shortfall of neutral theory by providing an explanation for why (near) fitness equivalence emerges within ecological–environmental niches.

Understanding limits on diversity in size-dependent ecological niches created through trophic exclusion is an aspect of our theory where future work is most needed. Current ecosystem models are of limited value in this respect because they are constructed in an explicitly nonneutral manner. Specifically, phytoplankton types in models are assigned physiological attributes that emphasize fitness differences rather than minimizing them. Even for the model presented by Behrenfeld et al. (2022), where all phytoplankton size classes are retained at all nutrient levels, monodominance of either the diatom or nondiatom type was pervasive in most size classes because fitness trade-offs and stabilization mechanisms were not included (the only factors determining selection were the extent of cell vacuolation and diffusional consequences of swimming versus sinking). One element of biodiversity where contemporary models can be particularly valuable is in dissecting the likely contribution of stable versus unstable coexistence in observational data. More precisely, field measurements of plankton diversity chronicle both species that are neutral competitors and those that are found at a location only because they have been physically transported from a more suitable habitat within a time window shorter than that required for their inevitable exclusion. This latter, unstable coexistence is what current ecosystem models can explore (e.g., Barton et al. 2010; Follows & Dutkiewicz 2011; Hellweger et al. 2014; Masuda et al. 2017, 2020).

Looking forward, we might conceive of the NEUTral Ocean (NEUTON) model where equalizing and stabilizing mechanisms are represented with greater fidelity. For characterization of fitness differences, this model must encapsulate cost–benefit trades for adaptation, including investment strategies for resource acquisition to enhance cell division (Flynn & Skibinski 2020), investments that influence loss rates, physiological adaptations that allow blooming under specific environmental conditions (Behrenfeld et al. 2021b), and within-species phenotypic variations (Beckmann et al. 2019, Menden-Deuer et al. 2021, Ward & Collins 2022). Also required is a more thorough consideration of processes that counter fitness differences, such as selective grazing within a trophic level (Armstrong 2003, Wirtz 2013), herbivory–carnivory switching in predators, mixotrophic behavior (Ward et al. 2011), density-dependent susceptibility to viral infection (Thingstad 2000, Weitz et al. 2015), within-trophic-level species interactions (Scheffer et al. 2003, Fox et al. 2010), growth conditions that trigger viruses to switch from a predominantly temperate lifestyle to a lytic stage (Knowles et al. 2020), and signaled population suicide to enhance the success of progeny following sexual reproduction (Behrenfeld et al. 2021b). A major obstacle in creating the NEUTON model is that we simply do not have quantitative empirical data for parameterizing diverse equalizing and stabilizing processes, and the data we do have are limited largely to culturable strains that may not be representative of the uncultured majority (Giovannoni et al. 2014). In lieu of this, perhaps one near-term approach would be through reverse engineering, essentially asking what costs would have to be associated with different investment strategies to yield stable coexistence of diverse and physiologically distinct species. Would such an evaluation yield a continuum of potential solutions or a set of discrete solutions?

The failure of neutral theory alone in constraining the potential biodiversity of the plankton is due to the spatial independence of ecological drift and the sheer number of cells in homogenized water masses. Under trophic exclusion, selection occurs in parallel across the full spatial domain of a given environmental niche, yielding coherent selection that ensures excluded species cannot be recovered simply through immigration between ecological communities. A question remains, however, of whether neutral dynamics within each size-dependent ecological niche still allow for

unlimited diversity. This question is yet to be answered, but we can offer two potential pieces to the puzzle suggesting that the answer may be no. First, with each genetic invention that conveys a fitness advantage to a species (e.g., a slight improvement in resource use efficiency) or set of species (e.g., a modified network), diversity in an ecological niche will decrease (potentially dramatically) because previously equal competitors will now be removed over time through trophic exclusion. Thus, extant diversity is constrained by the relative cadence of advantageous invention and neutral diversification (Behrenfeld et al. 2021c). A second factor may be time's arrow. Retaining a foothold in an ecological niche requires continued adaptive refinements to keep pace with other evolving species. However, options for refinement are not unlimited but instead must build upon the framework of past generations (essentially, adding new patches to outdated solutions). These time-evolved constraints on adaptation, or “ghosts of competition past” (Picoche & Barraquand 2020, p. 2239), must also place a limit on the diversity of neutral niches.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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