

Limiting factors and species diversity: a tale relating to the paradox of the plankton

Mark A. McPeck

Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire, USA

ABSTRACT

Question: How would a focus on limiting factors shape the development of conservation strategies that address biodiversity loss?

Background: Conservation challenges such as pollution via nutrient loading, loss of top predators associated with over-harvesting, and invasive species threaten biodiversity because they change the number and strengths of limiting factors in the community.

Theoretical basis: The limiting factors for a particular species are all the inorganic nutrients and species whose abundances shape the demographic rates of that species. The number of limiting factors that affect all the species at a given trophic level greatly influences the maximum number of species that can coexist, and the abundances of those limiting factors determine what ecological capabilities species must have to coexist.

Conservation implications: All conservation challenges cause biodiversity loss by changing the number and strengths of limiting factors, which are then propagated via indirect effects through the community. Thus, to restore biodiversity losses, conservation strategies should be rooted in an understanding of the limiting factors that regulate species abundances and how those strategies may affect the factors limiting species throughout the community.

Keywords: biodiversity loss, limiting factor, maximum species richness, paradox of the plankton.

INTRODUCTION

When I was a postdoc at the Archbold Biological Station in 1990, Dr H.J. Harvey of the National Trust of Great Britain came to give a seminar about conservation in the United Kingdom. He had been invited to Archbold to discuss the philosophy of conservation with our conservation biologists. He said that North American conservationists have a very different goal than their counterparts in the UK. He argued that we North Americans care too much about what is primeval and about trying to return ecosystems to their “natural state,” meaning to a state before significant human influence. He argued that in the UK, who could say what was primeval: ecosystems had been so altered by humans over the past 5,000 years that even if one could define an ecosystem’s “original states,” returning to those states would be impossible. He said (paraphrasing), “We

Correspondence: M.A. McPeck, Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA.
email: mark.a.mcpeek@dartmouth.edu

Consult the copyright statement on the inside front cover for non-commercial copying policies.

don't worry about what is primeval. *We simply try to conserve as many species as possible, regardless of which species they are or how we might have to do it.* That's why we do things like graze sheep in the fields above the White Cliffs of Dover" (e.g., Harper, 1969).

That seminar and the goal of "conserving as many species as possible" made a huge impression on me, particularly since it dovetailed quite nicely with the area of study I was pursuing—community ecology. A central focus of community ecology is to understand the processes that shape local species richness and diversity. Most ecosystems support hundreds to thousands of species, and the processes that foster this great diversity are a central focus of community ecology. Given that competition for limiting resources has been a central organizing principle of community ecology since Volterra (1926) propounded the first model of resource competition, explanations have centered primarily on resource competition. For example, over 60 years ago, Hutchinson (1961) described what he called the "paradox of the plankton." Most ponds and lakes harbor dozens to hundreds of phytoplankton species, even though during much of the year, they compete intensely for only a handful of resources. Hutchinson's primary hypothesis for how so many phytoplankton species might coexist on only a handful of limiting resources focused primarily on shifting competitive abilities of those phytoplankton species over the course of the year, and almost all subsequent explications of this problem have also focused on temporal variation in competitive abilities (e.g., Chesson and Warner, 1981; Huisman and Weissing, 1999, 2001, 2002; Litchman et al., 2004; Klausmeier, 2010; Li and Chesson, 2016).

While resource competition is surely an important process affecting most if not all species (everybody's got to eat), resource competition is not the sole ecological process affecting the abundance and persistence of species in a community. All species must also interact with "enemies" of various forms. Many herbivorous arthropods eat the phytoplankton in lakes. Terrestrial plants must deal with herbivores, seed predators, and nectar robbers. Almost all animals have predators that feed upon them. And each of these species may have dozens of pathogens (e.g., viruses, bacteria, fungi, metazoans) that limit their demographic capabilities. Many species also have mutualist partners that benefit their existence. Thus, understanding what maintains the great diversity in ecosystems must be approached with this broader conception of the interactions in which species engage.

With this perspective in mind, I would like to discuss in this essay what I believe to be one of the most underappreciated concepts in community ecology, namely the role and operation of limiting factors in shaping species richness in an ecosystem. Limiting factors are not simply limiting resources. All of this great diversity of species interactions can function as limiting factors. In a very fundamental way, the species richness in a community creates opportunities for additional species because the limiting factors shaping community structure potentially include every species embedded in that structure. Thus, the species richness in a community is a self-perpetuating feature, because each species can serve as a limiting factor for other species in the community: species richness and diversity begets species richness and diversity.

In fact, the cascading species losses throughout an ecosystem that occur when certain "key" species are greatly depressed or extirpated—e.g., sea otters from kelp forests (Estes and Palmisano, 1974; Estes et al., 1989), wolves from Yellowstone (Ripple et al., 2015), overfishing on coral reefs (Jackson et al., 2001; Shantz et al., 2020)—are exactly the features of the processes that reduce species richness and diversity because of the removal of limiting factors. Understanding the operation of limiting factors across a community can help us prevent species loss and promote the maintenance of diverse, functioning ecosystems.

BUILDING A DIVERSE FOOD WEB FROM SCRATCH

To illustrate the fundamental role of limiting factors to species richness and diversity, I want to utilize a thought experiment that applies the body of theory of mechanistic species interactions to build a multitrophic level food web with multiple species at each trophic level. I will forego all the math and simply point readers to the relevant papers if they care to see the gory details. This exercise also illustrates that the natural histories of the species of concern should be the foundation for defining robust conservation strategies: what I call mechanistic natural history (McPeck, 2022).

To begin, imagine an ecosystem that is completely devoid of life—for example, a freshwater lake that has no living creature in it. Furthermore, imagine that you have an extensive pool of species that you can introduce to this lake to create a fantastically diverse food web. However, the rule for assembling this food web is that you must add species sequentially and one species at a time. To be efficient, you must think carefully about each new species you add, so as to maximize the likelihood that the new species will be able to invade and maintain its population—that is, coexist in the strict ecological sense of that word—with all the other species already present.

The ecosystem of this imaginary lake that is initially devoid of life has some set of abiotic conditions (e.g., temperature range, pH, conductivity, light availability across its depth gradient) and abundances of inorganic and organic chemical compounds (e.g., various mineral compounds such as ammonia, nitrate, phosphate, silicate, and organics) that are present. The first introduced species will be successful if it can increase when rare and ultimately support a population under these abiotic conditions (MacArthur, 1972; Turelli, 1981; Chesson and Ellner, 1989; Law and Morton, 1993, 1996). Therefore, it must be either an autotroph (e.g., a phytoplankton species) or a heterotroph that can make its living foraging on the available inorganic and organic compounds (e.g., a bacterial or archaeal species). Choose a phytoplankton species such as the diatom *Asterionella formosa* and introduce an aliquot of cells to the lake. If it can successfully invade and coexist under these conditions, this population will initially have a cell division rate that is greater than its cell death rate. As the population of cells increases, the population will deplete light availability and the various inorganic and organic compounds it uses as resources, and in so doing it will decrease its cell division rate or increase its cell death rate (or both). The population of phytoplankton cells will increase until it reaches some high abundance at a steady state (e.g., a stable equilibrium or limit cycle).

This very simple example illustrates a number of key issues for the success of a species in a given ecosystem. First, when it is rare, its per capita birth rate must exceed its per capita death rate. This property ensures that the species can invade and also increase if it is perturbed to low abundance in the future: community ecologists call this “invasibility” (MacArthur, 1972; Turelli, 1981; Chesson and Ellner, 1989; Law and Morton, 1993, 1996). Whether a species can increase when rare is determined by how the ecological conditions it experiences when rare shape its per capita birth and death rates. Namely, are the concentrations of the limiting nutrients sufficiently abundant for this to be so. Second, once the species reaches its long-term steady-state abundance, its per capita birth and death rates will be approximately equal. This property implies that the ecological features of the ecosystem that make the species a successful invader may not be the same as those that regulate its abundance. Finally, the increase in this species’ abundance results in the depression of the abundances of various properties (e.g., light) and inorganic and organic compounds that are crucial to that increase. For example, the cell division rate of the diatom species may depend critically on the concentration of silica-containing compounds such as silicate (SiO_2) in the surrounding water (Titman, 1976; Tilman, 1977). The expansion of the diatom population depletes

silicate from the environment, and consequently the cell division rate of the diatom decreases (Titman, 1976; Tilman, 1977).

In this example, silicate is one of the environmental factors that regulates the *Asterionella formosa* population. In a seminal paper, Levin (1970) identified environmental features such as silicate as a “limiting” or “regulating” factor for this species (limiting factor has become the more common moniker, and so I will use it here). A limiting factor is some feature of the environment that (1) influences the per capita birth or death rate of the species, and (2) changes in abundance with the abundance of the species it influences. Thus, any number of environmental features may be limiting factors to a given species. For *A. formosa*, light concentration, and the availabilities of ammonia, nitrate, phosphate, silicate, and many other inorganic compounds may all influence its per capita growth rate and be depleted as its abundance increases.

Now introduce a second phytoplankton species. For it to successfully invade and coexist, the combination of limiting resources for the new species must have not been depressed to levels by *A. formosa* at which this second species does not have a positive per capita population growth rate when it is introduced. Many potential invaders will not be successful because they do not have their per capita birth rate greater than their per capita death rate under the abundances of those limiting factors. However, if successful, its invasion and establishment will further reduce the abundances of these limiting factors because of the combined removal by both phytoplankton species, and *A. formosa*'s abundance will also decrease because the abundances of other limiting resources are reduced (MacArthur, 1969; Hsu et al., 1981; Tilman, 1982; Kleinhesselink and Adler, 2015; Letten et al., 2017; McPeck, 2019).

How many subsequent phytoplankton species can we introduce into this lake so that all have sustaining populations (i.e., coexist) with one another? Theory says that if the community comes to a stable point equilibrium (i.e., each species is regulated to the abundance where its per capita birth and death rates are equal), then the maximum number of phytoplankton species we can introduce and have coexist is equal to the number of limiting factors (Levin, 1970). For example, if only silicate were limiting, only one phytoplankton species would be present: the one that could depress silicate abundance lowest. With two limiting resources, two phytoplankton can coexist if each is more limited by a different resource (e.g., Tilman, 1982; Letten et al., 2017). With more than two limiting resources, the maximum number of coexisting phytoplankton species is equal to the number of limiting resources, but the constraint that each must be more limited by a different resource is relaxed (McPeck, 2019, 2022). Some may be more specialized in that they are limited primarily by only one or two, and others may be generalists that are more regulated by a large number of factors, but not significantly by any one (McPeck, 2019, 2022). Some forms of temporal variation in ecological conditions can permit more species than limiting factors to coexist, but the additional number of species is not large (Hsu et al., 1977; Armstrong and McGehee, 1980; Huisman and Weissing, 1999; Huisman et al., 2001). Thus, with or without temporal environmental variation, the number of limiting resources strongly influences the number of species competing for those that can coexist.

Because of this cap on species richness, Hutchinson (1961) described what he called the “paradox of the plankton,” namely that lakes typically have only a dozen or so limiting nutrients, but multiple dozens to hundreds of phytoplankton species can be found in moderate-sized lakes (for data on lakes across a huge size gradient, see Smith et al., 2005). His paradox was how so many phytoplankton species could coexist on so few limiting nutrients. The easiest solution to this paradox is that inorganic nutrients are not the only limiting factors impinging on the demographics of phytoplankton species. In addition to competing for light and inorganic nutrients, phytoplankton are fed upon by many grazing arthropod species. Such enemies also

limit each phytoplankton species' abundance on which they feed because the enemies elevate the per capita death rates of the phytoplankton, and so the abundance at which the phytoplankton species' birth and death rates are approximately equal is lowered.

Return to the situation where only *Asterionella formosa* had been introduced to the lake. Instead of introducing a second phytoplankton species, we could have chosen to introduce a crustacean, such as *Daphnia pulicaria*, that feeds on this diatom. *Daphnia pulicaria* could invade if *A. formosa* abundance is high enough to make *D. pulicaria*'s per capita birth rate higher than its per capita death rate when it is introduced (the same invasibility criterion applies to every species in the community). If so, *D. pulicaria* will increase in abundance until its demographic rates balance. In doing so, *A. formosa*'s abundance will decrease, and in turn the abundances of light and all the inorganic nutrients like silicate will increase. Note that we have now added a trophic level to our community to give a two-species food chain: a herbivorous crustacean feeding on an alga.

Imagine that silicate is the only limiting nutrient for phytoplankton and that *A. formosa* is the best competitor for silicate, meaning that *A. formosa* can depress silicate abundance in the absence of any grazers on it to a level at which no other phytoplankton species in our available species pool can support a population. This means that in the absence of *D. pulicaria*, only one phytoplankton species—*A. formosa*—will be present in the lake. However, the introduction of *D. pulicaria* may increase silicate abundance (because *D. pulicaria* depresses *A. formosa*'s abundance) to a level at which another phytoplankton species can invade and coexist with *D. pulicaria* and *A. formosa*. However, if silicate is the only limiting nutrient, and *D. pulicaria* is the only grazer that feeds on the phytoplankton, at most one additional phytoplankton species can invade and coexist. This new phytoplankton species must have a positive per capita population growth when it invades, given the availability of silicate and the abundance of the grazer. Here, two limiting factors act on the phytoplankton guild, one limiting resource from below and one limiting predator from above, and so only two phytoplankton species can coexist at a stable equilibrium (Inouye, 1980; Leibold, 1989, 1996; Grover, 1994; Holt et al., 1994; McPeck, 1996, 2014).

Now that we have two phytoplankton species coexisting with silicate and *D. pulicaria* as limiting factors, we know that we cannot introduce any more phytoplankton because we are currently maxed out on their limiting factors. Is it now possible to introduce a second grazer species that feeds on phytoplankton? The two phytoplankton species are currently the limiting factors for the grazer trophic level, and so a second grazer can invade and coexist with *D. pulicaria* to feed on the two phytoplankton species: this is no different than two phytoplankton species coexisting on two limiting abiotic nutrients (Tilman, 1982). Any grazer that has a positive per capita population growth rate at the combined abundances of the two phytoplankton species with *D. pulicaria* already present can invade and coexist.

Once this second grazer species establishes, three limiting factors then impinge on the phytoplankton (i.e., silicate and the two grazer species), and so a third phytoplankton species can invade and coexist. The addition of the second grazer decreases the abundances of both phytoplankton species and so increases silicate abundance, which is what permits a third phytoplankton species to be able to invade and coexist. Any species that has a positive per capita growth rate at the combined silicate and grazer abundances can fill this food web position. And once three phytoplankton species coexist, a third grazer species above them can invade and coexist. And once three grazer species coexist, a fourth phytoplankton species can invade and coexist.

We can continue this exercise by adding additional trophic levels, and adding additional species to each trophic level, until we run out of possible new species in our hypothetical

species pool. So what are the general principles? One general principle is that species additions at one trophic level permit species additions at adjacent trophic levels. More phytoplankton species should be able to coexist in a lake if more abiotic limiting factors impinge on it from below, and more grazer species impinge on it from above. The second general principle is about adding trophic levels. Once the grazer trophic level is present, the ecological opportunity then arises for species that feed on the grazers. This will be true when grazer abundance can support a population of predators. After the first predator has established, the number of predator species will be limited by the number of grazer species present. Obviously, species to be added to the community must have demographic properties for those ecological conditions that give them a higher per capita birth rate than per capita death rate when they are rare.

What evidence supports such a theoretical conclusion? One of the best studied lake systems is Trout Lake in northern Wisconsin (e.g., Elser and Carpenter, 1988; Carpenter and Kitchell, 1993). In 2005–6, intensive monthly surveys recorded 84 phytoplankton species in Trout Lake (data downloaded from <https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-ntl&identifier=238> on August 22, 2019). In his paradox of the plankton paper, Hutchinson listed 19 possible limiting factors for phytoplankton, including light, CO₂, phosphorus, nitrogen, and sulfur compounds, plus 14 elements (Hutchinson, 1958). The Trout Lake surveys also found 68 species of herbivorous or omnivorous copepods, cladocerans, and rotifers that feed on those 84 phytoplankton species (data downloaded from <https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-ntl&identifier=37> on August 22, 2019). The 19 abiotic resources listed by Hutchinson plus the 68 phytoplankton grazers give a total of 87 limiting factors that impinge on the phytoplankton trophic level. While not dispositive, these observations are consistent with the prediction that the number of limiting factors at adjacent trophic levels strongly influences species richness at a given trophic level. In essence, diversity begets diversity.

My focus here has been exclusively on explaining phytoplankton diversity. We can apply the same logic to the trophic level above them—that is, all those herbivorous and omnivorous copepods, cladocerans, and rotifers. These 68 species are limited by 84 phytoplankton species plus all the predatory crustaceans (e.g., predatory copepods and cladocerans), insects (e.g., *Chaoborus*), and fishes (e.g., *Lepomis macrochirus*, *Perca flavescens*) that feed on them. Thus, this trophic group has many fewer species than limiting factors. This is not surprising, since the number of limiting factors determines the *maximum* number of species that can coexist. Many additional planktivorous species could, in theory, be added to Trout Lake. However, only species that would have a greater per capita birth than per capita death rate when they were introduced, given the abundances of all the phytoplankton and predators, would be successful invaders. Perhaps those species do not exist in northern Wisconsin, and all the species in the regional assemblage that could invade have invaded. Or, perhaps, more will be successful when they finally invade in the future.

Limiting factors are not limited to species that interact with one another as consumers and resources (i.e., plants and herbivores, algae and grazers, predators and prey). Pathogens and mutualists can also be limiting factors that influence the number of coexisting species. Pathogens can limit the abundances of their hosts, just as consumers limit the abundances of their resources (e.g., Anderson and May, 1980, 1981; Holt and Pickering, 1985; Hall et al., 2005; Holt and Dobson, 2006; Keeling and Rohani, 2008; Bonsall and Holt, 2010), and so have very similar effect. Thus, every pathogen inflicting harm on their host may add to the species richness of a food web. Likewise, many species may compete for the rewards bestowed from interactions with mutualists (Bronstein, 2015). Mutualist partners can under limited circumstances promote coexistence of resource competitors (Johnson and Amarasekare, 2013; Johnson, 2021), but because mutualists tend to inflate the abundances of their partners, they can often exacerbate instead of ameliorate competitive interactions and so not promote coexistence

but rather shift competitive hierarchies (e.g., Revilla and Krivan, 2016, 2018; Jiang et al., 2017). Consequently, mutualists may not serve as limiting factors under all circumstances: their importance as a primary cause of coexistence among other species should receive much greater theoretical and empirical study.

CONSERVATION IMPLICATIONS

The importance of limiting factors is obvious in many of our worst examples of human-induced environmental degradations that cause major species loss. Such losses can occur because of the alteration of limiting factors below or above. The eutrophication of inland lakes because of phosphorus addition was one of the most detrimental human impacts to inland lakes that caused large-scale reductions in species richness (e.g., Dillon and Rigler, 1974; Schindler et al., 1978; Edmondson and Lehman, 1981; Zhang et al., 2019). Given that phosphorus is one of the major limiting resources for phytoplankton in many lakes (Schindler, 1977; Elser et al., 1990, 2007), the addition of large amounts of phosphorus to a lake removed it as a limiting factor on phytoplankton because it is now available in great excess and so relatively unresponsive to the abundance of organisms that consume it. Moreover, because it is in great excess, species that are more limited by phosphorus can now increase to great abundance, and consequently this will decrease the abundances of other limiting resources or inflate the abundances of their predators. These shifts in the abundances of alternative resources and predators are what drive species that are not as dependent on phosphorus for their success (see review and model results in McPeck, 2022). In this case, adding excess phosphorus has only removed one limiting factor, but most species are driven extinct by alterations in the abundances of the other limiting factors because of how a few species respond to the excess phosphorus. In effect, excess phosphorus indirectly causes the abundances of other limiting factors to move to values at which many species cannot support populations.

The reduction or extirpation of predators from over-harvesting also causes species losses through the same community effects as nutrient additions (Estes and Palmisano, 1974; Estes et al., 1989; Jackson et al., 2001). For example, the loss of biodiversity in kelp forests due to the extirpation of sea otters results from the removal of a strong limiting factor—namely, sea otter predation—on urchins and the consequent decrease in kelp on which urchins primarily feed (Estes and Palmisano, 1974). Conversely, the reintroduction of gray wolves to Yellowstone National Park has caused a substantial decrease in the elk population, which in turn has allowed alder and cottonwood trees to repopulate riparian areas of the park (Ripple and Beschta, 2012; Ripple et al., 2015; Beschta and Ripple, 2016).

Given everything discussed so far, it may seem counterintuitive that adding a species may drive native species to very low abundances or extinction (Didham et al., 2005; Clavero et al., 2009; Doherty et al., 2016; Linders et al., 2019). However, it is also crucial to take into account the limiting factors of a system when considering the environmental problems caused by invasive species. Both the number and magnitudes of limiting factors determine whether particular species are able to coexist. For any particular species, coexistence requires that resources and mutualists are sufficiently abundant and enemies are not too abundant for the species to be able to invade when rare (Chesson, 2000; McPeck, 2022). The invasive species may directly harm native species, such as invasive mammalian predators greatly inflating the mortality rates of evolutionarily novel prey (Doherty et al., 2016). In these cases, the invasive predator does represent an additional limiting factor that has been added to the community, but the mortality that it inflicts is greater than what many of the native species can sustain. Pathogens can have the same direct effects, such as the devastation caused by the introduction of avian malaria to the Hawaiian Islands (Warner, 1968; van Riper et al., 1986; Lapointe et al., 2012).

Other types of invasive species that drive natives extinct may do so via indirect effects, much like excess phosphorus loading does. The establishment of such an invasive species alters the abundances of the factors limiting other species to levels at which other species cannot support a population, via decreasing resource abundances or inflating predator abundances, or both. For example, the invasive tree *Prosopis juliflora* has a wide range of effects on the East African drylands through indirect effects on changing both the species composition and abundances of many native species (Linders et al., 2019).

What does addressing biodiversity loss in various contexts in the framework of limiting factors actually entail? For over-harvesting of herbivores or predators, the primary original information that is necessary is which species were most limited because of direct interactions with the over-harvested species. These “released” species that have had a major limiting factor removed may be exactly the species that become problematic because they may now be able to increase to high abundance. Consequently, identifying them originally may be difficult, because the over-harvested species may have kept them at very low abundances (e.g., macroalgae on coral reefs are a primary example (Zaneveld et al., 2016)). Their identities may best be identified in diet preference studies and not diet content analyses (i.e., what do the over-harvested species prefer to eat instead of what they actually eat, since a highly preferred prey may be driven to very low abundance or may shift to safer habitats to reduce exposure to the predator, and so appear only very rarely in the predator diet). The follow-on issue is, then, what species are these “released” species going to affect the most because of their abundance increases and why will these consequences ensue.

Designing strategies to combat the consequences of invasive species also hinges on identifying the limiting factors that are perturbed by the presence of the invasive, and then determining how other species are impacted by these changes. For invasive plants, the first critical information needed is what abiotic resources (e.g., light, water, phosphorus and nitrogen compounds) might they deplete below levels at which many native plants can support populations and what consumers (e.g., herbivores, seed predators, parasitic gallers) and pathogens might they inflate to abundances that become problematic for other species. If the invasive is a predator, the primary information may be easier to gather since it would involve which species this invasive kills and consumes most.

It should be clear from these thought experiments and examples that focusing on a single species cannot address the issues needed to develop sound conservation strategies, and this is true whether the goal is to mitigate the effects of an invasive species or save a charismatic species from extinction. The critical issues all involve identifying the circuits of indirect species interactions that propagate through the community. This circuitry is always apparent in conservation responses. For example, the reintroduction of wolves to Yellowstone had great positive benefits on riparian vegetation, which resulted from an unexpected but important indirect effect mediated by the reduction of the elk population (Beschta and Ripple, 2016). In fact, wolf reintroduction may also have benefited frugivorous birds through the increase of berry-producing trees and shrubs that also resulted from elk reduction (Beschta and Ripple, 2012). Each and every species is embedded in a community and ecosystem, and altering any one species’ abundance either up (e.g., restoration) or down (e.g., eradication) will ripple through the entire ecosystem.

Thus, to accomplish the goal of our seminar speaker, Dr Harvey, to “conserve as many species as possible,” a fundamental understanding of the factors that limit species across the community of interest is critical. The mindset of limiting factors forces one to consider the full set of processes that shape species’ demographics and the workings of how direct and indirect species interactions shape those demographic rates. One of the major traps in this is to only

consider certain types of species interactions (e.g., resource competition) as the only driver of the effects one is considering: the paradox of the plankton is no paradox at all if one remembers that all those phytoplankton species also have herbivores and omnivores that feed on them, mutualists that benefit them, and pathogens that infect them. Individuals of all species must garner resources for themselves while trying to not become a resource for another. Effective conservation practices should be rooted in these basics of species interactions and community structure. This is how I interpret what our seminar speaker from the National Trust was trying to accomplish.

ACKNOWLEDGMENTS

I want to thank Gail A. McPeck, John W. Fitzpatrick, Fred Lohrer, Douglas Morris, and Per Lundberg for valuable information and comments on previous drafts.

REFERENCES

- Anderson, R.M., and May, R.M. 1980. Infectious diseases and population cycles of forest insects. *Science*, **210**: 658–661.
- Anderson, R.M., and May, R.M. 1981. The population dynamics of microparasites and their invertebrate hosts. *Phil. Trans. R. Soc. B: Biol. Sci.*, **291**: 451–524.
- Armstrong, R.A., and McGehee, R. 1980. Competitive exclusion. *Am. Nat.*, **115**: 151–170.
- Beschta, R.L., and Ripple, W.J. 2012. Berry-producing shrub characteristics following wolf reintroduction in Yellowstone National Park. *Forest Ecol. Manage.*, **276**: 132–138.
- Beschta, R.L., and Ripple, W.J. 2016. Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. *Biol. Conserv.*, **198**: 93–103.
- Bonsall, M.B., and Holt, R.D. 2010. Apparent competition and vector-host interactions. *Isr. J. Ecol. Evol.*, **56**: 393–416.
- Bronstein, J.L. 2015. *Mutualism*. Oxford: Oxford University Press.
- Carpenter, S.R., and Kitchell, J.F. 1993. *The Trophic Cascade in Lakes*. Cambridge: Cambridge University Press.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, **31**: 343–366.
- Chesson, P.L., and Ellner, S. 1989. Invasibility and stochastic boundedness in monotonic competition models. *J. Math. Biol.*, **27**: 117–138.
- Chesson, P.L., and Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.*, **117**: 923–943.
- Clavero, M., Brotons, L., Pons, P., and Sol, D. 2009. Prominent role of invasive species in avian biodiversity loss. *Biol. Conserv.*, **142**: 2043–2049.
- Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M., and Gemmill, N.J. 2005. Are invasive species the drivers of ecological change? *Trends Ecol. Evol.*, **20**: 470–474.
- Dillon, P.J., and Rigler, F.H. 1974. The phosphorus-chlorophyll relationship in lakes. *Limnol. Oceanogr.*, **19**: 767–773.
- Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., and Dickman, C.R. 2016. Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci. USA*, **113**: 11261–11265.
- Edmondson, W.T., and Lehman, J.T. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. *Limnol. Oceanogr.*, **26**: 1–29.
- Elser, J.J., and Carpenter, S.R. 1988. Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment. *Oecologia*, **76**: 148–154.
- Elser, J.J., Marzolf, E.R., and Goldman, C.R. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the fresh-waters of North America: a review and critique of experimental enrichments. *Can. J. Fish. Aquat. Sci.*, **47**: 1468–1477.

- Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H. et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.*, **10**: 1135–1142.
- Estes, J.A., and Palmisano, J.F. 1974. Sea otters: their role in structuring nearshore communities. *Science*, **185**: 1058–1060.
- Estes, J.A., Duggins, D.O., and Rathbun, G.B. 1989. The ecology of extinctions in kelp forest communities. *Conserv. Biol.*, **3**: 252–264.
- Grover, J.P. 1994. Assembly rules for communities of nutrient-limited plants and specialist herbivores. *Am. Nat.*, **143**: 258–282.
- Hall, S.R., Duffy, M.A., and Cáceres, C.E. 2005. Selective predation and productivity jointly drive complex behavior in host-parasite systems. *Am. Nat.*, **165**: 70–81.
- Harper, J.L. 1969. The role of predation in vegetational diversity. *Brookhaven Symp. Biol.*, **22**: 48–62.
- Holt, R.D., and Dobson, A.P. 2006. Extending the principles of community ecology to address the epidemiology of host-pathogen systems. In *Disease Ecology: Community Structure and Pathogen Dynamics* (S.K. Collinge and C. Ray, eds.), pp. 6–27. Oxford: Oxford University Press.
- Holt, R.D., and Pickering, J. 1985. Infectious disease and species coexistence: a model of Lotka-Volterra form. *Am. Nat.*, **126**: 196–211.
- Holt, R.D., Grover, J., and Tilman, D. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.*, **144**: 741–771.
- Hsu, S.-B., Hubbell, S.P., and Waltman, P. 1977. A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM J. Appl. Math.*, **32**: 366–383.
- Hsu, S.-B., Cheng, K.-S., and Hubbell, S.P. 1981. Exploitative competition of microorganisms for two complementary nutrients in continuous cultures. *SIAM J. Appl. Math.*, **41**: 422–444.
- Huisman, J., and Weissing, F.J. 1999. Biodiversity of plankton by species oscillations and chaos. *Nature*, **402**: 407–410.
- Huisman, J., and Weissing, F.J. 2001. Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology*, **82**: 2682–2695.
- Huisman, J., and Weissing, F.J. 2002. Oscillations and chaos generated by competition for interactively essential resources. *Ecol. Res.*, **17**: 175–181.
- Huisman, J., Johansson, A.M., Folmer, E.O., and Weissing, F.J. 2001. Towards a solution of the plankton paradox: the importance of physiology and life history. *Ecol. Lett.*, **4**: 408–411.
- Hutchinson, G.E. 1958. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.*, **22**: 415–427.
- Hutchinson, G.E. 1961. The paradox of the plankton. *Am. Nat.*, **95**: 137–145.
- Inouye, R.S. 1980. Stabilization of a predator-prey equilibrium by the addition of a second “keystone” victim. *Am. Nat.*, **115**: 300–305.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**: 629–637.
- Jiang, J., Moore, J.A.M., Priyadarshi, A., and Classen, A.T. 2017. Plant-mycorrhizal interactions mediate plant community coexistence by altering resource demand. *Ecology*, **98**: 187–197.
- Johnson, C.A. 2021. How mutualisms influence the coexistence of competing species. *Ecology*, 102: e03346 [https://doi.org/10.1002/ecy.3346].
- Johnson, C.A., and Amarasekare, P. 2013. Competition for benefits can promote the persistence of mutualistic interactions. *J. Theor. Biol.*, **328**: 54–64.
- Keeling, M.J., and Rohani, P. 2008. *Modeling Infectious Diseases in Humans and Animals*. Princeton, NJ: Princeton University Press.
- Klausmeier, C.A. 2010. Successional state dynamics: a novel approach to modeling nonequilibrium foodweb dynamics. *J. Theor. Biol.*, **262**: 584–595.
- Kleinhesselink, A.R., and Adler, P.B. 2015. Indirect effects of environmental change in resource competition models. *Am. Nat.*, **186**: 766–776.
- Lapointe, D.A., Atkinson, C.T., and Samuel, M.D. 2012. Ecology and conservation biology of avian malaria. *Ann. NY Acad. Sci.*, **1249**: 211–226.

- Law, R., and Morton, R.D. 1993. Alternative permanent states of ecological communities. *Ecology*, **74**: 1347–1361.
- Law, R., and Morton, R.D. 1996. Permanence and the assembly of ecological communities. *Ecology*, **77**: 762–775.
- Leibold, M.A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.*, **134**: 922–949.
- Leibold, M.A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. *Am. Nat.*, **147**: 784–812.
- Letten, A.D., Ke, P.-J., and Fukami, T. 2017. Linking modern coexistence theory and contemporary niche theory. *Ecol. Monogr.*, **87**: 161–177.
- Levin, S.A. 1970. Community equilibria and stability, and the extension of the competitive exclusion principle. *Am. Nat.*, **104**: 413–423.
- Li, L., and Chesson, P. 2016. The effects of dynamical rates on species coexistence in a variable environment: the paradox of the plankton revisited. *Am. Nat.*, **188**: E46–58.
- Linders, T.E.W., Schaffner, U., Eschen, R., Abebe, A., Choge, S.K., Nigatu, L. et al. 2019. Direct and indirect effects of invasive species: biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. *J. Ecol.*, **107**: 2660–2672.
- Litchman, E., Klausmeier, C.A., and Bossard, P. 2004. Phytoplankton nutrient competition under dynamic light regimes. *Limnol. Oceanogr.*, **49**: 1457–1462.
- MacArthur, R. 1969. Species packing, and what interspecies competition minimizes. *Proc. Natl. Acad. Sci. USA*, **64**: 1369–1371.
- MacArthur, R.H. 1972. *Geographical Ecology*. Princeton, NJ: Princeton University Press.
- McPeck, M.A. 1996. Trade-offs, food web structure, and the coexistence of habitat specialists and generalists. *Am. Nat.*, **148**: S124–138.
- McPeck, M.A. 2014. Keystone and intraguild predation, intraspecific density dependence, and a guild of coexisting consumers. *Am. Nat.*, **183**: E1–16.
- McPeck, M.A. 2019. Mechanisms influencing the coexistence of multiple consumers and multiple resources: resource and apparent competition. *Ecol. Monogr.*, **89**: e01328 [<https://doi.org/10.1002/ecm.1328>].
- McPeck, M.A. 2022. *Coexistence in Ecology: A Mechanistic Perspective*. Princeton, NJ: Princeton University Press.
- Revilla, T.A., and Křivan, V. 2016. Pollinator foraging adaptation and coexistence of competing plants. *PLoS One*, **11**: e0160076 [<https://doi.org/10.1371/journal.pone.0160076>].
- Revilla, T.A., and Křivan, V. 2018. Competition, trait-mediated facilitation, and the structure of plant-pollinator communities. *J. Theor. Biol.*, **440**: 42–57.
- Ripple, W.J., and Beschta, R.L. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biol. Conserv.*, **145**: 205–213.
- Ripple, W.J., Beschta, R.L., and Painter, L.E. 2015. Trophic cascades from wolves to alders in Yellowstone. *Forest Ecol. Manage.*, **354**: 254–260.
- Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes. *Science*, **195**: 260–262.
- Schindler, D.W., Fee, E.J., and Ruzyczynski, T. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in Experimental Lakes Area and in similar lakes. *J. Fish. Res. Bd. Can.*, **35**: 190–196.
- Shantz, A.A., Ladd, M.C., and Burkepille, D.E. 2020. Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. *Ecol. Monogr.*, **90**: e01403 [<https://doi.org/10.1002/ecm.1403>].
- Smith, V.H., Foster, B.L., Grover, J.P., Holt, R.D., Leibold, M.A., and deNoyelles, F., Jr. 2005. Phytoplankton species richness scales consistently from laboratory microcosms to the world's oceans. *Proc. Natl. Acad. Sci. USA*, **102**: 4393–4396.
- Tilman, D. 1977. Resource competition between plankton algae: an experimental and theoretical approach. *Ecology*, **58**: 338–348.

- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.
- Titman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science*, **192**: 463–465.
- Turelli, M. 1981. Niche overlap and invasion of competitors in random environments. I. Models without demographic stochasticity. *Theor. Popul. Biol.*, **20**: 1–56.
- van Riper, C., III, van Riper, S.G., Goff, M.L., and Laird, M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.*, **56**: 327–344.
- Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Memoria della Reale Accademia Nazionale dei Lincei*, **6**: 31–113.
- Warner, R.E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor*, **70**: 101–120.
- Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., McMinds, R., Payet, J.P. et al. 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat. Commun.*, **7**: 11833 [<https://doi.org/10.1038/ncomms11833>].
- Zhang, Y., Cheng, L., Li, K.Y., Zhang, L., Cai, Y.J., Wang, X.L. et al. 2019. Nutrient enrichment homogenizes taxonomic and functional diversity of benthic macroinvertebrate assemblages in shallow lakes. *Limnol. Oceanogr.*, **64**: 1047–1058.