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Paradoxes or theoretical failures? The jury is still out

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Abstract

We focus on two paradoxes of ecological theory: the paradox of enrichment and the enrichment response. Both are counter-intuitive theoretical predictions that have received little empirical support. We argue that both enrichment paradoxes could be theoretical artifacts and suggest that further experimental work is necessary to determine whether these paradoxes deserve their current status as ecological axioms.

Keywords: Paradox of enrichment; Trophic cascades; Intuition; Prey-dependence; Predator-dependence; Ratio-dependence; Instantism

Observations that confirm intuition—that are consistent with presumptions—rarely attract attention. But when observations defy intuition in a surprising manner, they attract scientific interest. Counterintuitive observations are labeled "paradoxes" and the pursuit of their resolution has been a key source of scientific innovation.

The classic paradox emerges when empirical observations are at odds with a stated and accepted theory. If observations are reliable, such empirical paradoxes must be resolved by modifying the theory so that it is consistent with evidence.

In the absence of complete or appropriate data, theory is often employed to yield understanding. Usually, such theories are self-fulfilling prophecies: a model is constructed based on logical assumptions, and the model outputs behavior that confirms intuition. Occasionally, theoretical predictions prove to be inconsistent with intuition. Such theoretical paradoxes can only be resolved by comparison to appropriate data.

We contend that paradoxes of both the theoretical and empirical varieties are important. The comparison of intuition with theory and theory with empirical observations yields progress in understanding and suggests a logical cycle that has been repeated throughout history: intuition leads to a theory and that theory is compared with empirical observations. When the properties of a theory contradict intuition, empirical observations must be made to resolve the paradox. When empirical observations contradict prevailing intuition or a prevailing theory (or both), intuition is reconfigured. This cyclic process continually modifies intuition until intuition, theory and empirical observations are harmonized.

Theoretical and empirical paradoxes should not remain paradoxical. Once a theory proves consistent with empirical observations, intuition evolves and no

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longer remains in conflict with observations. The paradox disappears once intuition, theory and empirical observations are made mutually consistent.

We focus on two theoretical paradoxes in ecology that have remained paradoxical for a substantial period of time: the *paradox of enrichment* and the *enrichment response*. Both make predictions that contradict an intuitive sense of how ecosystems should behave and both have therefore attracted significant attention. Neither, however, has been appropriately assessed in light of available data. It is for this reason that these paradoxes, and the theory that underlies them, have remained unquestioned for several decades.

1. The paradox of enrichment

This paradox, based on what has become a standard textbook generalization of the Lotka–Volterra-derived model of Rosenzweig and MacArthur (1963), states that when the prey carrying capacity of a stable predator–prey system is increased sufficiently, the system begins to cycle (Rosenzweig, 1971). In fact, mathematically, the emerging structure is a limit cycle. As prey carrying capacity is increased further, this cycle brings one or both populations closer and closer to zero. As conventionally interpreted, when the limit cycle is sufficiently large, one of the species can go extinct. If the prey species goes, predator extinction will follow; if the predator species goes, a trophic level is lost. Cited over 450 times, Rosenzweig (1971) has captured the imagination of countless ecologists and is upheld as a classic example of an ecological paradox.

While we find Rosenzweig's (1971) theoretical work innovative and important, the manner in which it has been handled since publication by the field of ecology is somewhat unnerving. Notwithstanding a few notable exceptions (Arditi and Berryman, 1991), the paradox of enrichment has been widely accepted based on very little empirical evidence. For reasons we find difficult to comprehend, the paradox of enrichment quickly achieved the status of an ecological axiom, an assumed property that can only be overturned by proof that it does not exist. Without substantial comparison to empirical observations, the paradoxical theory *became accepted intuition*.

In particular, the community of theoretical ecologists has enthusiastically embraced the paradox of enrichment. This unjustified enthusiasm is epitomized by the manner in which the word "paradox" has come to be interpreted in the phrase "paradox of enrichment". For Rosenzweig, the "paradox" was that enrichment—intuitively perceived as beneficial—had the potential to destabilize an ecosystem. In more recent use, ecologists speak of "resolving" or finding "a solution to" the paradox of enrichment (Jansen, 1995; Genkai-Kato and Yamamura, 1999; Petrovskii et al., 2004; Vos et al., 2004): the "paradox" is that actual systems do not behave as accepted models predict they should. Even authors who are aware of this transformed meaning are forced to invent new terminology to precisely refer to the phenomena: our favorite is the "enigma known as Rosenzweig's paradox of enrichment" (Petrovskii et al., 2004).

The paradox of enrichment continues to exert a strong influence on theoretical work (Yodzis and Innes, 1992; Abrams, 1993; Huisman and DeBoer, 1997; Boer et al., 2001; Murdoch et al., 2003) and any student of ecology will have to search heartily for a textbook that does not present the paradox of enrichment as biological fact. We have reviewed the literature on experimental attempts to demonstrate the paradox of enrichment and found a disturbingly small number of studies in favor of the phenomenon. The majority of the empirical work that is suggestive of the paradox of enrichment has been done within the last decade; at least two decades passed before this theoretical prediction was exposed to experimental testing. We contend that the need for experimental verification of the phenomenon is far from exhausted.

What evidence is there for the paradox of enrichment? Several commonly-misinterpreted examples, as well as several experiments that begin to answer the question "does the paradox of enrichment exist?", merit discussion.

A commonly suggested example of the paradox of enrichment is the process of lake eutrophication. Enrichment of aquatic systems does appear to increase the carrying capacity of producers, producing a bloom that covers the lake. This bloom deprives the lake bottom of light, increasing aerobic decomposition and lowering the oxygen content of the water. It is this reduction in dissolved oxygen—not trophic destabilization—that can cause the subsequent loss of top predators.

While eutrophication does involve enrichment, its results are not paradoxical. If oxygen availability limits