**Paradoxes or Theoretical Failures? The jury is still out**

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**We focus on two paradoxes of ecological theory: the paradox of enrichment and the bottom-up trophic cascade. Both are counterintuitive theoretical predictions that are not supported by empirical evidence. We argue that both enrichment paradoxes are theoretical artifacts and do not exist when theory is corrected.**

We are fascinated with paradoxes. Observations that confirm our intuition – that are consistent with our presumptions – rarely attract our attention. But when something defies this intuition and really surprises us, we are suddenly enthralled. We call these counterintuitive observations "paradoxes", and the pursuit of their resolution has been a key source of innovation in a diversity of scientific fields.

All "paradoxes" are not alike. There are really two kinds of paradoxes confronted by scientists. The classic paradox emerges when empirical observations are at odds with a stated and accepted theory. If observations are reliable, such paradoxes are always resolved by modification of theory. The theory must be changed so that it is consistent with evidence.

A second type of paradox exists when necessary empirical observations are unavailable. In the absence of complete or appropriate data, theory is often employed to yield understanding. Based on our intuition, we build models that we believe will depict reality. These models make predictions about the behavior of systems. Usually, such theories are pretty much self-fulfilling prophecies: we construct a model based on what we believe is occurring within a system, and the model outputs behavior that confirms our intuition about that system. Sometimes, however, theory displays properties that are at odds with our intuition, and we encounter another kind of paradox. Like the paradox emerging from empirical observations, theoretical paradoxes also arise when observations are unexpected. However, it is important to remember that what we are observing is not data, but rather the output of a model. Theories that are inconsistent with intuition comprise a very different kind of paradox than empirical observations that are inconsistent with theory, and need to be dealt with differently.

We contend that paradoxes of both the theoretical and empirical variety are scientifically significant. The comparison of intuition with theory and theory with empirical observation yields progress in scientific understanding, and suggests a logical cycle that we see repeated throughout scientific history: intuition leads to a theory, and that theory is compared with empirical observations. When the properties of a theory contradict our intuition, empirical observations must be made to resolve this paradox. When empirical observations contradict either our original intuition or our resulting theory (or both), our intuition is reconfigured. This cyclic process continually modifies our intuition until intuition, theory, and empirical observations are all harmonized. It is for this reason that theoretical and empirical paradoxes – observations that are

inconsistent with our intuition – should not remain paradoxical. Once a theory proves consistent with empirical observations, our intuition evolves and no longer remains in conflict with observations. The paradox disappears once we achieve understanding by making our intuition and our theory consistent with each other and with empirical observations.

　　　We focus on two theoretical "paradoxes" that have remained 'paradoxical' for extraordinary periods of scientific time: the *paradox of enrichment* and the *bottom-up trophic cascade*. Both make predictions that contradict our intuitive sense of how ecosystems should behave, and have therefore attracted significant attention. Neither, however, has been seriously compared to available data. It is for this reason that these paradoxes, and the theory that underlies them, have remained unquestioned for several decades.

## The paradox of enrichment

　　　This paradox, based on what has become a standard textbook generalization of the Lotka-Volterra-derived model of MacArthur and Rosenzweig (1963), states that when you enrich stable predator-prey systems sufficiently, they begin to cycle (Rosenzweig 1971). In fact, mathematically the emerging structure is a limit cycle. As enrichment proceeds, this cycle brings populations closer and closer to zero. In various interpretations, 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 400 times[1], the Rosenzweig paper (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 despite a glaring lack of empirical evidence in its favor. For reasons not fully comprehensible to us, the paradox of enrichment has achieved the status of an ecological axiom, an assumed property that can only be overturned by proof that it does not exist. Without comparison to empirical observations, the paradoxical theory has become intuition. Theoretical analyses in which the paradox of enrichment is demonstrated continue to be produced in abundance (Yodzis and Innes 1992, Abrams 1993, Boer et al. 2001, Murdoch et al. 2003), and any reasonable 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 we were unable to find support for it. Several commonly-misinterpreted examples merit discussion. The most prevalent cited example of the paradox of enrichment involves the process of lake eutrophication. Additional nutrients added to the system over a short or long period of time can cause a rapid increase in producer biomass, 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

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[1] ISI Web of Knowledge, ISI:A1960WJ59900005, November 2003.

water. It is this reduction in dissolved oxygen that can cause the subsequent loss of consumers from higher trophic levels. While eutrophication does involve enrichment, its results are not paradoxical. We expect a system where the influx of oxygen is limited to be severely destabilized by any change that further reduces oxygen availability, particularly at trophic levels occupied by consumers. Clearly the only connection to consumption present in the phenomenon of eutrophication is the fact that consumers require oxygen. Other than this trivial similarity, eutrophication bears no resemblance to the predator-prey phenomenon described by Rosenzweig. We are puzzled by the fact that many ecologists still believe that eutrophication and the paradox of enrichment are in any way connected. Other enriched ecosystems also display reduced complexity, but we have yet to encounter a case where this simplicity was the result of the trophic level destabilization predicted by Rosenzweig (1971).

A second example cited as evidence in favor of the paradox of enrichment is the empirical work in the *Didinium-Paramecium* system done by Luckinbill (1973) and Veilleux (1979). Both authors were attempting to show that the system of Gause (1934) could be modified to produce coexistence of predator and prey. They found that two modifications to the system were required to prevent the predator from consuming all of the prey: (i) the interaction rate of predator and prey within the system had to be reduced by the addition of methyl cellulose, which serves to thicken the medium and presumably reduces the attack rate of the predator; and (ii) the availability of prey food (i.e. enrichment) had to be reduced. This second condition is commonly misinterpreted as evidence for the paradox of enrichment, as it appears initially to be the 'paradox of enrichment in reverse'— the system goes from instability to stability when nutritional inputs are reduced. What MacArthur-Rosenzweig theory fails to account for is the intermediate results of the Luckinbill experiment. Before reducing enrichment, Luckinbill reduced interaction, producing consistent predator extinction. Then, by reducing food available to prey, he was able to produce coexistence. Figure 1 shows that this sequence of system behaviors is difficult to account for under MacArthur-Rosenzweig theory.

Not only is empirical evidence in favor of the paradox of enrichment lacking, but the literature contains a large number of failed attempts to produce or observe the phenomenon (Walters et al. 1987, McCauley et al. 1988, Watson and McCauley 1988, Leibold 1989, McCauley and Murdoch 1990, Watson et al. 1992, Persson et al. 1993, Mazumder 1994). Obviously negative results receive less attention than positive ones, but we are surprised by just how minimal the impact of these results has been.

So why don't we see this paradox in natural or experimental systems? If we assume that the paradox of enrichment *could* exist, we must conclude that none of the experimental or natural systems in which it has been sought is sufficiently simple. In other words, experimental conditions did not meet the theoretical assumptions and this is why experiments failed to demonstrate the paradox. Alternatively, if we assume that the paradox of enrichment *does not* exist, we must conclude that new models of trophic interactions – ones that do not produce paradoxical destabilization under enrichment – must be sought out.

**Figure 1:** Alternative explanations of the Luckinbill (1973) experiment interpreted in MacArthur-Rosenzweig space. In **(a)**, recreating the conditions of Gause (1934) produces a limit cycle that causes consistent dual extinction. High interaction rate, interpreted as high predator attack rate, causes the vertical predator isocline to lie far to the left of the prey isocline 'hump'. The trajectory theoretically cycles indefinitely, but in practice is interpreted as leading to dual extinction. In **(b)**, adding methyl cellulose reduces the attack rate of the predator, pushing the predator isocline to the right. In order for predator extinction to occur, this isocline must move beyond the $N=K$ point. When prey food supply is reduced in **(c)**, predator extinction should also result. This prediction is contradicted by the Luckinbill experimental results, which instead produced coexistence. An alternative explanation of the effects of adding methyl cellulose is shown in **(d)**, where the reduction of predator attack rate is interpreted as less severe. In order to account for the consistent predator extinction produced by Luckinbill (1973), the limit cycle must widen vertically. To our knowledge, such a change in the shape of a limit cycle has never been demonstrated. If such a limit cycle were to exist, reduction in prey food supply (i.e. the 'paradox of enrichment in reverse') would lead to coexistence as shown in **(e)**. *Key to symbols*: red circles denote initial predator/prey abundances, yellow circles indicate equilibrial abundances.
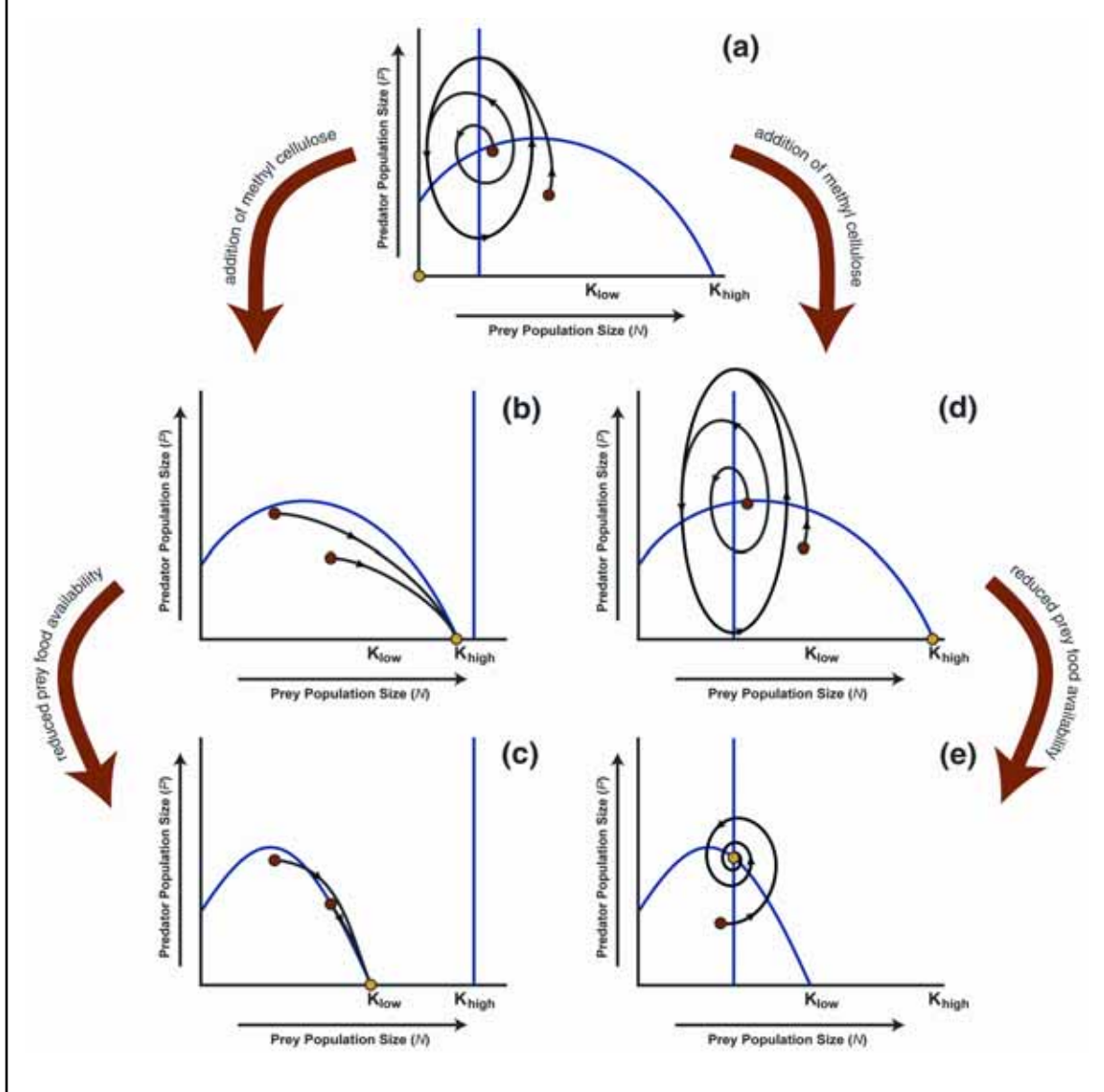


The vast amount of theoretical effort in this area has been directed at the former explanation, producing a rich body of work showing that the paradox of enrichment can

in theory be eliminated by any number of complicating factors. Multiple species embedded into each trophic level will effectively eliminate the 'paradox'. Models including edible/inedible algae (Phillips 1974, Leibold 1989, Kretzschmar et al. 1993, Genkai-Kato and Yamamura 1999) and vulnerable/invulnerable prey (Abrams and Walters 1996) both show that multiple-species models do not demonstrate destabilization under enrichment. Refuges and immigration have also been shown to remove the destabilizing effects of enrichment (Abrams and Roth 1994). In addition, spatial heterogeneity has been shown as a potential source of trophic stabilization (Nisbet et al. 1998). Attempts to empirically confirm some of these 'increased complexity' hypotheses have been unsuccessful (Murdoch et al. 1998), but faith in the paradox of enrichment remains strong. Theorists continue to provide models built upon MacArthur-Rosenzweig theory, confident that the proper complicating factors can be identified so that the conspicuous absence of the paradox of enrichment can be satisfactorily explained.

One problem with models that incorporate various levels of additional complexity is that they are difficult to falsify. With this additional complexity (and the associated addition of parameters) the danger of overfitting increases, and authors risk drawing invalid conclusions (Ginzburg and Jensen 2004). Algae species do differ in their edibility, some prey may be more vulnerable than others, and spatial heterogeneity and/or refuges are bound to be present in most natural systems. But we wonder: is there no system, in nature or in the laboratory, which is free from all of these possible complicating factors? Is the total absence of evidence for the paradox of enrichment an indication that – despite an underlying Lotka-Volterra mechanism – no system will ever abide by the assumptions of MacArthur-Rosenzweig dynamics?

Based on the available data, it is clear that there is no evidence supporting the paradox of enrichment. So why have ecologists stood so loyally beside this as-yet-unsubstantiated theory? One explanation returns to the question of intuition. Perhaps, contrary to the implied meaning of Rosenzweig's nomenclature, the idea that enriched systems contain fewer trophic levels is more intuitive than assumed. After all, many enriched systems are exceptionally simple, containing fewer trophic links. Examples of such ecosystems can be found in both aquatic and terrestrial systems, including the aforementioned eutrophied lakes. We do not deny that such a trend exists – we simply do not find credible evidence that this enriched/simple configuration is the direct result of trophic interaction factors.


**The bottom-up trophic cascade**

The term "trophic cascade" is widely used by an array of ecologists, and its meaning varies with the context in which it is employed. We will be concerned with only one meaning, the response of the trophic chain to enrichment at the bottom. According to established theory, as enrichment at the bottom increases new trophic levels are added and producer populations equilibrate at either higher or lower abundances (Fretwell 1977, Oksanen et al. 1981). At very low nutrient levels, no consumer exists. As enrichment increases slightly, a primary consumer species can be sustained, but at abundances too low to support a secondary consumer species. Further trophic levels are added only as ecosystem enrichment occurs. Two paradoxical consequences of this theory are: (i)

noticeable additions in the number of trophic levels as productivity increases; and (ii) a curious behavior of the four-level system (Figure 2). When there are four levels overall the abundance of primary producers has to decline with enrichment. This decline has yet to be demonstrated empirically (Ginzburg and Akcakaya 1992, Akcakaya et al. 1995).

So where is the counterintuitive behavior that makes the bottom-up trophic cascade a 'paradox'? We see two phenomena emerging from this theory that seem to contradict both intuition and available data. First, the idea that the number of trophic levels is a function of overall enrichment seems problematic. A large-scale review of a wide variety of ecosystems suggests that there is no relationship between primary productivity and number of trophic levels (Cohen et al. 1990). For us, this observed pattern is the true paradox: why should the number of trophic levels be independent of primary productivity? A second paradoxical behavior emerges when we consider the effects of enrichment on the equilibrial abundance of each trophic level. The four-level system yields the greatest insight into this behavior. As shown in Figure 2, enrichment of a four-level system causes the top (secondary) carnivore to increase in abundance, while the primary carnivore remains fixed in abundance. Herbivores increase, while producers decrease in abundance. No intuitive explanation can account for this strange pattern. Not surprisingly, most discussions of this phenomenon are limited to the more palatable three-level system, which does not suffer from this prediction of decrease.

Evidence from a variety of ecosystems suggests that comparable communities, differing in nutrient input level, differ only in overall abundances at each trophic level, and show none of the paradoxical behaviors predicted by accepted theory (Ginzburg and Akcakaya 1992, Akcakaya et al. 1995). Both intuition and evidence suggest that enrichment causes increases in the overall abundance of all trophic levels. As with the paradox of enrichment, multispecies explanations have been forwarded to why data do not conform to established theory.

**Figure 2:** Response of trophic levels to enrichment in the MacArthur-Rosenzweig predator-prey system. As enrichment occurs, primary productivity increases; however, abundances of producers, herbivores, and/or carnivores do not always respond to productivity.

| Number of Trophic Levels | Response of each trophic level to enrichment | | | |
|:---:|:---:|:---:|:---:|:---:|
| | Producer | Herbivore | Primary Carnivore | Secondary Carnivore |
| **2** | constant | **increase** | | |
| **3** | **increase** | constant | **increase** | |
| **4** | *decrease* | **increase** | constant | **increase** |

(after Arditi and Ginzburg 1989)

Unlike the paradox of enrichment, the origin of the bottom-up trophic cascade cannot be traced to a single, highly-influential paper. However, we see one probable progenitor in the classic 'why the world is green' paper of Hairston, Smith, and Slobodkin (1960). The HSS paper argued that carnivores in a three-level trophic system could effectively keep herbivore abundances low (even when resources increase in availability), allowing larger producer abundances. Notice that this prediction, at an initial glance, bears striking similarity to the predictions for a three-level enriched MacArthur-Rosenzweig system (Figure 2). The mechanisms explaining these superficially-similar patterns, however, are quite dissimilar. We believe that this misunderstanding may account for the unwarranted acceptance of bottom-up trophic cascade predictions.

## Origins of the paradox: how we got this far astray

Both the paradox of enrichment and the bottom-up trophic cascade emerge as the result of the same assumption about consumer-resource systems. The reason extinction due to enrichment occurs in theory is the presence of a vertical predator isocline, a consequence of linking trophic levels with a prey-dependent (i.e. Lotka-Volterra) functional response. Under prey dependence, the functional response of the predator depends on the amount of food, and does not depend on the abundance of consumers. This assumption has been questioned (Abrams and Ginzburg 2000), but remains a prominent component of most predator-prey models. Predator dependence seems to be more of a common case than an exception (Skalski and Gilliam 2001). Ratio dependence, an extreme form of predator dependence, emerges at the opposite end of the spectrum from prey dependence (Arditi and Ginzburg 1989). At this opposite extreme, the paradox of enrichment is theoretically absent (Arditi and Berryman 1991).

So, when we ask "why have these enrichment paradoxes remained unquestioned for so long?", we are really asking the question: "why is prey-dependence assumed to be axiomatic?". The paradox of enrichment and the bottom-up trophic cascade both emerge because of the assumption of a purely prey-dependent functional response. For many authors (Abrams 1994, Murdoch et al. 2003), this construction is beyond question – prey dependence is absolute truth, and need not be confirmed by empirical inquiry.

### The fallacy of instantism

The acceptance of prey-dependence without question follows from a simple but dangerous assumption about the nature of the differential equations employed in modeling predator-prey interactions. When we model a population by considering its change over time, $dN/dt$, we need to define exactly what our $dt$ really means. Of course by using differential equations, mathematically we assume that change occurs continuously and instantaneously and therefore $dt$ represents an infinitely small time step. The question is: should we take our mathematical constructions literally? In using instantaneous equations, should we constrain ourselves to considering only processes which transpire in an instant? Many theorists answer 'yes' to these questions, and constrain their instantaneous models to capturing instantaneous phenomena; we call such mathematical formalism *instantism* (Ginzburg and Colyvan 2004).

If we assume that we are literally modeling changes of a population over instantaneous time, the prey-dependent functional response is the only one we can choose. This is because in an infinitely small time step, predators cannot interfere with each other – they can only respond to the instantaneous abundance of prey. Interference is a factor that only emerges when we consider times steps larger than an instant. Murdoch *et al.* (2003) effectively summarize the instantist argument in favor of prey-dependence:

> … ratio dependence sometimes emerges in a natural way in a discrete-time framework… We do not believe that it makes ecological sense, however, to insert ratio-dependent functional responses into continuous time models which, by their nature, describe instantaneous rates… (p. 103)

Under the instantist view, the only "natural" functional response to use in continuous-time models is the prey-dependent form.

We feel that the instantist view is fallacious. We can conceive of few if any organismal processes that literally occur in instantaneous time. Organisms are by and large discrete in nature, and for this reason differential equations cannot be considered as literal depictions of biological processes. At best differential equations are apt metaphors, and so our consideration of which ones to employ should be based on their relative utility, not on their conformation to instantist orthodoxy.

It should be noted that the instantists are not fully consistent. While one might legitimately argue that consumption occurs instantaneously, it is much more difficult to justify literally instantaneous conversion of food into offspring (if for no other reason, that birthing viable offspring is an undeniably discrete process). Given that consumption is instantaneous and reproduction is discrete, the 'correct' mathematical formalism that should be applied is an integro-difference equation. Such equations may be more 'realistic', but this realism comes at great cost – integro-difference equations are difficult to interpret analytically. That theorists who uphold the prey-dependent axiom usually do not use these cumbersome equations calls into question the consistency of the instantist argument.

*Literalism in using mathematical constructs*

Instantism, as described above, is a special case of a larger problem which can be termed *literalism* in applying mathematical constructs to biology. A good example is partitioning of actual biological species into discrete and continuous categories, an approach endorsed by Murdoch et al. (2003). Discrete species are, in their judgment, ones which reproduce every spring, for instance. Whether these species are iteroparous or semelparous does not matter: as long as reproduction is periodic, they are discrete. Other species, like *E. coli*, humans, or *Daphnia* are continuous: they reproduce at any time without a specified frequency. The authors attribute differential equations as a correct abstraction for continuous species and difference equations for the discrete species.

We find such a literalist projection of the mathematical construct into biology very restrictive and unreasonable. Depending on the time scale that works in the particular case, the same species can be described by both constructs. Darwinian theory of natural selection is a prime example. Is it the geometric series (discrete) or exponential growth (continuous) that we have to invoke to deduce the idea of natural selection from

Malthusian law? Obviously, it does not matter. The law is just a caricature of reality which captures the necessary properties of the process.

To use an artistic metaphor, we feel that literalist theorists are attempting to be photorealists. If data were abundant and perfect, it might be reasonable to impose a literalist aesthetic and require that all 'images' of ecological phenomena be photorealistic. Unfortunately, because data are so limited and often imperfect, we do not possess information adequate to 'paint' photorealistic pictures in ecology. Imposing a strict literalist constraint only serves to guarantee that our image will be distorted and non-sensical; we are in essence trying to reconstruct a high-resolution image from a very small subset of data 'pixels'. Such an approach will only work if: (i) the domain of the image that we wish to depict is very small (i.e. we produce a specific, non-generalizable model); or (ii) if we have data sufficient to 'paint' a complete image. It seems clear to us that the former case is the best portrayal that we can hope for (considering the limited nature of existing data), and that such portrayals do little to advance the field.

We consider good theoretical work to be akin to impressionism. Rather than interpret our mathematical constructions as literal depictions, we see them as metaphors for more complex underlying details. It is for this reason that we allow our models to relax some of the literalist constraints in pursuit of a more valuable albeit imperfect impression. For instance, we utilize differential equations, but allow for mechanisms such as predator dependence that can only emerge in time steps that are larger than instantaneous. Certainly inclusion of such mechanisms violates literalist rules, but the resulting metaphor often works (Akcakaya 1992, Ginzburg and Akcakaya 1992, Akcakaya et al. 1995, Jost and Ellner 2000, Jost and Arditi 2001, Skalski and Gilliam 2001, Vucetich et al. 2002). What results is an image that is less sharp but more meaningful. It is our judgment that this approach will achieve more with less – theorists will construct more valuable pictures out of the limited available data.

While we understand why many theorists impose a literalist constraint (they honestly believe that their models are more 'accurate' that way), we call for models that are far too rough to depend on such delicate detail. Taken to its logical extreme, literalist thinking often requires that we model levels of complexity which far outweigh the complexity of the simple problems that we strive to answer (Ginzburg and Jensen 2004). In relaxing literalist constraints, we hope to make theoretical work more practical and tractable – we can actually produce rough but meaningful models in a world constrained by limited data. In this sense, we see the metaphorical approach to modeling as being far more realistic than the literalist approach.

*Theories as limit myths*

Theoretical conditions are never exactly satisfied in experiments. The ball rolling on the plane stops instead of rolling uniformly because of friction. Does this observation mean that the laws of inertia are invalid? No, of course it does not. The way that we convince ourselves is by looking at a sequence of planes with decreasing friction. We notice that the ball stops further on a smoother surface and conclude that if the surface were perfect, the ball would never decelerate and stop. All theoretical constructs are thus limit myths (Quine 1976, 1980, 1995, Colyvan and Ginzburg 2003, Ginzburg and Colyvan 2004). To determine a limit myth from simply the wrong idea we therefore require that a demonstration of a sequence of experiments approaching the theoretical

prediction is presented. Without such a sequence, chances are that a theory is just plain wrong.

In the case of the paradox of enrichment, we would like to see at least instability emerging with enrichment, possibly a cycle or two which may dampen instead of oscillating for very long. We would like to see a clear description of the experimental imperfections (whatever is equivalent to 'friction' in the example above) which in a sequence are suggestive of the validity of the theory at the limit. In spite of an honest effort, we were unable to find this required support in the literature. Both paradoxes are consequences of the prey dependent assumption in describing the coupling across trophic levels. Both have no field or laboratory evidence as support. By support we mean here, just as above, a degree of concordance, steps toward the limit myth, not necessarily conformation to the ideal. Unless further empirical work can substantiate the validity of the prey-dependent limit myth, other limit myths depicting trophic interactions will have to be considered.

The question is: when do we continue to stick to a simple principle (viewed as 'fundamental' by many) that requires complex constructions? Would it not be better to replace the underlying principle and keep it simple? We doubt that we can seriously affect a predator-prey theoretical tradition with 80 years of history, a tradition that is deeply embedded in all the textbooks. It is our hope, however, that a reasonable alternative proposal which is much more intuitive, produces no paradoxes, and is roughly supported by the evidence is seriously considered.

*Intuition, evidence, and math*

Theoretical paradoxes can only provide a starting point for further inquiry. While it may be interesting when verbal or mathematical models suggest paradoxical behaviors, these models must be exposed to empirical tests before their validity can be assessed. Figure 3 suggests two of several paths that such an inquiry might take. Once relevant data can be brought to bear on a theoretical paradox, data reinforces either our intuition (Figure 3(b)(c)), our theory (Figure 3(d)(e)), or both. When relevant data are absent, the paradox remains. Neither intuition nor theory can be assumed correct when data is absent or incomplete.

The prevailing acceptance of enrichment paradoxes violates this tenet of empirical science. Data in favor of existing theory is either weak or completely absent, and in some cases data are in agreement with alternative theories (Akcakaya et al. 1995). For some reason, theory has been accepted without empirical confirmation, leading to unjustified alteration of intuition on a massive scale. In what seems from the outside a bizarre turn of events, an entire field has come to embrace a theory based not on data but on theory itself.

In this sense, perhaps the work of theorists like Rosenzweig is too good. The simple mathematical elegance of his theoretical 'discovery', mistakenly associated with unrelated phenomena, has lulled many ecologists into complacent acceptance. Mathematical 'discoveries' were confused with empirical discoveries. In order to return to a more regular path of inquiry, these enrichment phenomena and the underlying prey-dependent functional response that drives them must be subjected to proper empirical testing.

**Figure 3:** Theoretical paradoxes and their resolution by comparison with data (matching colors signify agreement; mismatching colors signify disagreement) **(a)** A paradox emerges when intuition and theoretical predictions disagree, and can only be resolved when the theory is compared with appropriate data. **(b)** In one scenario, data agrees with theory **(c)** When theory and data are in agreement, our intuition is informed by data and thereby altered, making our intuition, our theory, and available data consistent. **(d)** In the alternative scenario, data disagrees with theory. **(e)** If theory is inconsistent with data, theory is informed by data and thereby altered until a theory that is suitably agreeable with data can be identified. If this theory is consistent with previous intuition, intuition need not be altered.
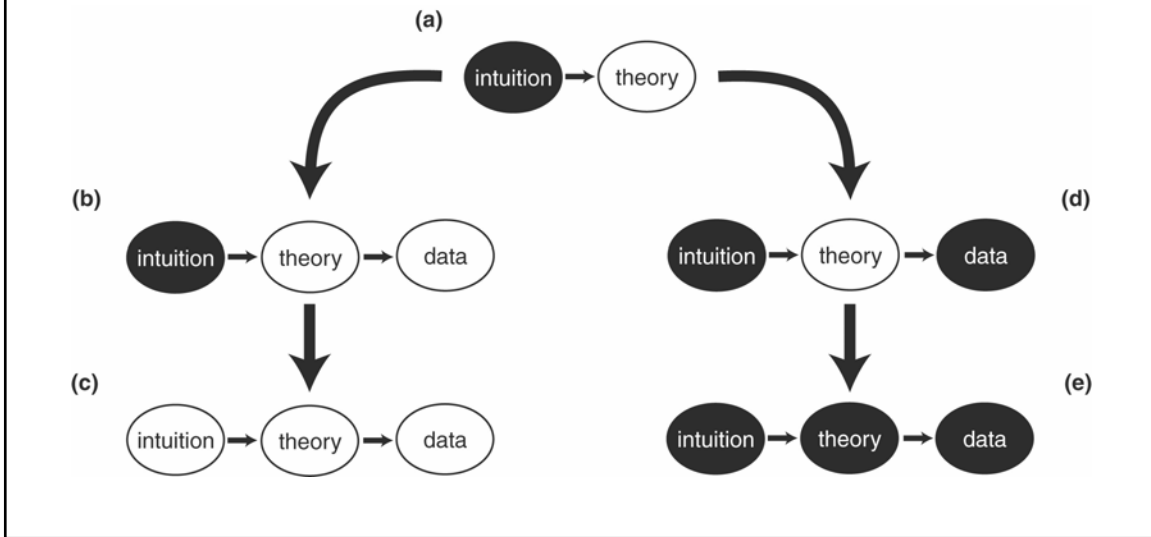


## The potential hazards of blind faith

Continuing unwarranted acceptance of the paradox of enrichment and the bottom-up trophic cascade phenomena presents for the field of ecology problems beyond the theoretical. Applied ecologists, taking cues from colleagues who provide basic theory, include enrichment paradoxes in their models (DeFeo and Rinaldi 1997, Choi and Patten 2001). If these enrichment phenomena are as unsubstantiated as they appear to be, many of these management strategies are doomed to fail. As the demand for more applied use of theory increases, selection against incorrect theories will increase (Ginzburg and Jensen 2004). However, this selection process has intrinsic costs: every poorly-informed management strategy has the potential to result in the destabilization of a critical ecological system. A more balanced view of enrichment paradoxes and the theory that underlies them may prevent the management disasters we believe would eventually undermine faith in these enrichment phenomena. The costs associated with coming to these realizations on an applied scale are much higher than those associated with theoretical reconsideration.

Both theorists and empiricists, assured by their predecessors that enrichment paradoxes are real, will continue to embrace these questionable phenomena. One need only look at the number of papers produced explaining away the absence of these phenomena to begin to realize how much effort may have been wasted on upholding these paradoxes. We recognize that the occasional pursuit of dead-ends is a vital part of scientific exploration. We suggest that the benefits associated with upholding these

paradoxes may have been exhausted. It is time to consider other theories of trophic interaction.

**Acknowledgements**

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