ELSEVIER

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 counterintuitive 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.

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. Occa-

sionally, 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

growth, any change that further reduces oxygen availability is expected to destabilize the system, 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 connected. Enriched ecosystems generally display reduced complexity, but we have yet to encounter a case where this simplicity was the result of trophic level destabilization of the kind predicted by Rosenzweig (1971).

Since Rosenzweig proposed that increasing the carrying capacity of a prey species could destabilize a predator–prey pair, a number of experiments have tested this prediction. The first empirical work was performed in the *Didinium–Paramecium* system by Luckinbill (1973) and Veilleux (1979). Both authors showed 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 searching efficiency of the predator and (ii) the availability of prey food (i.e. enrichment) had to be reduced. This second condition is commonly misinterpreted as clear evidence for the paradox of enrichment, as it appears at first glance to be the 'paradox of enrichment in reverse'—the system goes from instability to stability when nutritional inputs are reduced (Harrison, 1995).

More recently, an experiment performed in a *Rotifer-Algae* system by Fussmann et al. (2000) showed that predator extinction resulted from enrichment. Like the Luckinbill and Veilleux experiments, the results of this experiment showed that reducing nutrient input can bring the system from a region of consistent predator extinction to a region of coexistence; unlike these much earlier experiments, the work of Fussman et al. did not demonstrate a region of consistent dual extinction. Nevertheless, these experiments do make a coarse argument in favor of the paradox of enrichment;

increasing nutrient inputs does seem to destabilize the system.

However, *how* this increase in available nutrients destabilizes the system remains unclear. During his experiments, Veilleux showed that adding nutrients to the system not only increased the carrying capacity and growth rate of the prey but also increased the conversion efficiency and searching efficiency of the predator. With so many parameters potentially moving in response to a single manipulation, a variety of competing models (Hassell and Varley, 1969; Beddington, 1975; DeAngelis et al., 1975; Arditi and Ginzburg, 1989) can lay claim to the results of Luckinbill, Veilleux and Fussman et al., and there is no reason to assume that the Rosenzweig model should be considered the superior explanation.

We find it remarkable that extinction has been shown in only three enrichment experiments. In lieu of demonstrating the extinction events predicted by the paradox of enrichment, many researchers have used increasing amplitude of oscillation as a proxy for actual irreversible destabilization. We find this substitution unsatisfactory, because the notable prediction of the paradox of enrichment is the loss of one or more trophic levels, not changes in the oscillation pattern of the system. Marshall and Peters (1989) show that the magnitude of oscillations is greater in eutrophic than oligotrophic lakes, but provide no evidence that greater oscillations can or will translate to extinction of consumers. In order for evidence of the kind presented by Marshall and Peters to be convincing, it would have to be shown that further eutrophication has the potential to lead to *destabilizing* oscillations (i.e. extinction). Ethical and logistical concerns surrounding artificial eutrophication place understandable limitations on manipulations of this sort in natural systems; however, the laboratory—which is free from such limitations—ought to be the ideal environment in which to produce irreversible destabilization. Unfortunately, laboratory microcosm work (Bohannan and Lenski, 1997; Kaunzinger and Morin, 1998; McCauley et al., 1999) also conflates increased amplitude of oscillation with extinction. We wonder why such studies fail to show that massive nutrient inputs do not produce the extinction predicted by the paradox of enrichment.

When ecologists have looked for evidence for the paradox of enrichment in natural and laboratory systems, they often find none (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.

Why do researchers fail to observe this paradox in most experimental or any natural systems? If it is assumed that the paradox of enrichment *could* exist, the logical conclusion is that most of the experimental or natural systems in which it has been sought are not 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 it is assumed that the paradox of enrichment *does not* exist, the logical conclusion is that new models of trophic interactions—ones that do not produce paradoxical destabilization under enrichment—must be sought.

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 mechanisms. The list of these potential mechanisms is long and continues to grow, as it has been shown that the paradox can be effectively eliminated by expanding the model to include: edible/inedible algae (Phillips, 1974; Leibold, 1989; Kretzschmar et al., 1993; Genkai-Kato and Yamamura, 1999); density-dependence of the predator death rate parameter (Gatto, 1991); refuges and immigration (Abrams and Roth, 1994); vulnerable/invulnerable prey (Abrams and Walters, 1996); spatial heterogeneity (Nisbet et al., 1998; Petrovskii et al., 2004); life-history traits that allow consumers to buffer the effects of low prey densities (McCauley et al., 1999) and inducible defenses (Vos et al., 2004).

Generally, these theoretical explanations for the absence of the paradox of enrichment remain untested; some may even be untestable. Those few attempts to empirically confirm some of these increased complexity hypotheses have been unsuccessful (Murdoch et al., 1998), but faith in the paradox of enrichment persists. 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.

Models that incorporate various levels of additional complexity 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 the laboratory, which is sufficiently free from all of these possible complicating factors? Is the lack 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?

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* intuitive. After all, many enriched systems are exceptionally simple, containing relatively few trophic links. Examples of such ecosystems can be found in both aquatic and terrestrial systems, including the aforementioned eutrophic lakes. We do not deny that such a trend exists—we simply do not find credible evidence that Rosenzweig's paradox of enrichment explains this enriched/simple configuration.

2. The enrichment response

The term "trophic cascade" is widely used by an array of ecologists and its meaning varies with context (Ponsard et al., 2000). We will be concerned with only one meaning, the response of the trophic chain to enrichment at the bottom; we refer to this phenomenon as the "enrichment response". As was the case with Rosenzweig's paradox of enrichment paper, a particular theoretical paper has considerably influenced ecological thought about enrichment responses; Oksanen et al. (1981), which expanded upon early work by Fretwell (1977), has been cited well over 500 times. We focus on two theoretical predictions made by Oksanen et al.: (i) noticeable additions in the number of trophic levels as productivity increases and (ii) a curious behavior of the four-level system (Fig. 1a). We believe that both phenomena emerging

Number of Trophic Levels	Response of each trophic level to enrichment			
	1st "Producer"	2nd "Herbivore"	3rd "Primary Carnivore"	4th "Secondary Carnivore"
2	constant	**increase**		
3	**increase**	constant	**increase**	
4	*decrease*	**increase**	constant	**increase**

(a)
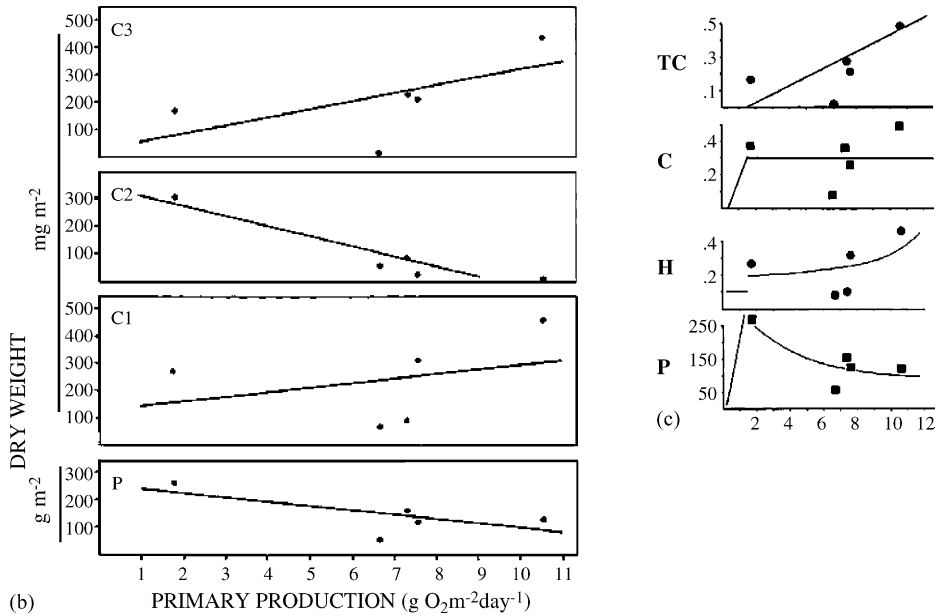
(b)

(c)

Fig. 1. (a) 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 (after Arditi and Ginzburg, 1989). (b) Arruda (1979) explored the relationship between productivity and equilibrial abundance but found significance only in the third-trophic-level (labeled "C2"). (c) The same data, redrawn in Oksanen et al. (1981), suggests that the theoretically-derived predictions presented in the paper are consistent with Arruda's data, despite the non-significant nature of any attempt to fit a three-parameter curve to five data points.

from Oksanen et al. theory contradict available data.

First, we find the idea that the number of trophic levels is a function of overall enrichment problematic. As proposed by Oksanen et al. (1981), new trophic levels are added and producer populations equilibrate at new abundances as enrichment at the bottom increases. At very low levels of enrichment, 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. While this unproven hypothesis seems logically possible, it is at odds with available data: a large-scale review of a wide variety of ecosystems suggests that no relationship exists between primary productivity and the 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? This paradox has yet to be resolved.

A second paradoxical behavior emerges when the effects of enrichment on the equilibrial abundance of each trophic level are considered. According to conventional theory, enrichment can cause the abundance of particular trophic levels to either increase, remain constant or decrease. The four-level system yields the greatest insight into this behavior. As shown in Fig. 1a, 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 decreasing abundance with increasing enrichment.

Oksanen et al. (1981) discuss a single purported example of a four-trophic-level system that is consistent with their theoretical predictions. The example, from a study performed by Arruda (1979), appears to show the expected results for the four-trophic-level system shown in Fig. 1a. For several reasons, we remain unconvinced by these results as they are presented. First, there appears to be an error in the transfer of results from Arruda (Fig. 1b) to Oksanen et al. (Fig. 1c); in the third-trophic-level (primary carnivore), the data points appear to shift, changing a clear decrease in equilibrial abundance with increased productivity to an apparent constant abundance. The error changes the meaning of the results: instead of showing the constancy in equilibrial abundance, Arruda's results actually display a significant decrease in abundance in response to enrichment. Such a result cannot be explained by any currently popular theory of predator–prey interaction.

Another concern arises when the significance of the curve fits are considered. All but one of the theoretically-derived curves of Oksanen et al. require at least three parameters to depict mathematically (one for the breakpoint and two for the linear trend). These curves are overlaid on the five Arruda data points (Fig. 1c), giving the impression that data are consistent with predictions. This impression is false, as it is impossible to reliably fit a three-parameter model to only five data points (Ginzburg and Jensen, 2004).

A final worry concerns replication: if Arruda's results truly demonstrate that a four-trophic-level system could be consistent with the theoretical construct

of Oksanen et al., we would expect other researchers to attempt to replicate them using a larger-scale approach more likely to yield statistically significant results. We know of no such replication in over 20 years and therefore question whether Arruda's apparent results resulted from anything more than chance.

In the absence of field data we turn to the results of laboratory microcosm work, much of which claims to produce results consistent with the predictions of Oksanen et al. Two recent examples are by Bohannan and Lenski (1997) and Kaunzinger and Morin (1998). As shown in Fig. 1a, the theoretical predictions of Oksanen et al. suggest that in a simple two-trophic-level system, enrichment should cause no change in prey abundance and an increase in the predator population. What the papers by Bohannan and Lenski and Kaunzinger and Morin show are significant increases in both predator and prey abundance, a result that is inconsistent with the Oksanen et al. predictions. Such results are more consistent with predator-dependent models (Hassell and Varley, 1969; Beddington, 1975; DeAngelis et al., 1975; Arditi and Ginzburg, 1989; Berryman et al., 1995), which predict that in response to enrichment all trophic levels will increase in abundance with differing slopes (the highest levels increase the most, while successively lower levels respond with smaller and smaller increases) (Akcakaya et al., 1995). The smaller-yet-significant increases in prey abundance shown by these experiments demonstrate that the Oksanen et al. theory is at odds with biological observations.

The most compelling empirical argument in favor of Oksanen et al. theory comes from the second experiment of Kaunzinger and Morin (1998). In this three-trophic-level system, they showed that the top predator was consistently excluded from the microcosms with the lowest nutrient inputs. To our knowledge, this experiment remains the only evidence for this prediction of Oksanen et al. While we find these results interesting, we worry that they could arise from a rather large departure from the assumptions of standard predator–prey theory. Like all batch culture systems, the microcosms of Kaunzinger and Morin violate the assumption of continuous nutrient input. We recognize the practical concerns that govern such a violation (and find little solace in the more complex alternative: the continuous system of the chemostat) but we fear that the magnitude of this violation—rather than an underlying mechanism consistent with MacArthur–Rosenzweig

theory—may have produced the extinction of the top predator. The microcosms were refreshed every 4 days; given that in this 4 day span one can get nearly 50 generations of the bacteria that occupy the producer level, we are concerned that starvation between nutrient pulses may be the reason for the elimination of the top predator from the microcosms with the lowest nutrient inputs. The approach of Kaunzinger and Morin was ingenious; we would like to see it replicated with a more frequent (i.e. closer to continuous) input of nutrients.

The literature on top predator removal experiments has generated considerable confusion. A series of experiments has shown consistently that the abundances of lower trophic levels can be dramatically affected by the removal or addition of a top predator. Often, the results of these removal experiments look superficially like the predicted results of enrichment described by Oksanen et al. For example, Shapiro and Wright (1984) showed that the elimination of planktivorous fish resulted in a reduction in the steady-state abundance of phytoplankton. Viewed without consideration of causality, this transition from a system with three-trophic-levels to a system with only two resembles the predicted difference between the three- and two-level systems shown in Fig. 1a. When causality is considered, the resemblance is rendered meaningless: the fact that predator removal produces results that are similar to those predicted under enrichment does not show that these predictions are confirmed in actual trophic systems. When it comes to the results of predator removal experiments, many other models of predation (including the ratio-dependent extreme) make predictions identical to those of the traditional prey-dependent form (H.R. Akcakaya, pers. comm.). Because model predictions in this area do not differ, these experiments do not allow us to distinguish between various predation models. While we do not question the importance of these studies for understanding the effect of predators on lower trophic levels (so-called "top-down" effects), we hasten to point out that experiments of this kind have no relevance to the question of whether or not enrichment responses follow the pattern predicted by Oksanen et al.

Evidence from a variety of ecosystems suggests that comparable communities, varying 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; Ware and Thomson, 2005). Both intuition and evidence suggest that enrichment causes increases in the overall abundance of all trophic levels.

3. Origins of the paradox: how the field got this far astray

Both the paradox of enrichment and the enrichment response emerge as the result of the same assumption about consumer-resource systems. The vertical predator isocline, a consequence of linking trophic levels with a prey-dependent (i.e. Lotka–Volterra) functional response, is the theoretical construction which produces these enrichment phenomena. Under prey-dependence, the functional response of the predator depends on the abundance of prey, not 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 (Arditi and Akcakaya, 1990; Jost and Ellner, 2000; Jost and Arditi, 2001; Skalski and Gilliam, 2001; Vucetich et al., 2002; Schenk et al., 2005). Under predator-dependent models, such as that of Beddington–DeAngelis (Beddington, 1975; DeAngelis et al., 1975), as interference increases so too does the carrying capacity at which destabilization occurs (Huisman and DeBoer, 1997). 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 hasn't the prey-dependent axiom been widely questioned?". The paradox of enrichment and the enrichment response both emerge because of the assumption of a purely prey-dependent functional response. For many authors (Abrams, 1994; King and Shaffer, 2001; Murdoch et al., 2003), this construction is beyond question—prey-dependence is the only logical form and need not be confirmed by empirical inquiry.

3.1. The fallacy of instantism

The unquestioned acceptance of prey-dependence is often justified by a simple but dangerous assumption about the nature of the differential equations employed in modeling predator–prey interactions. When a population is modeled by considering its change over time, dN/dt, exactly what dt means needs to be defined. Of course by using differential equations, mathematically it is assumed that change occurs continuously and instantaneously and therefore dt represents an infinitely small time step. The question is: should mathematical constructions be taken literally? In using instantaneous equations, should theorists be constrained 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).

Instantism has been used to argue that only the prey-dependent functional response can be logically nested within predation models. As the argument goes, 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 times steps larger than an instant are considered. Murdoch et al. (2003) effectively summarize the instantist argument in favor of prey-dependence, noting:

… 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 this instantist view, the only natural functional response to use in continuous-time models is the prey-dependent form. We question this assertion and point out that predator interference has been successfully incorporated into differential equations that model only instantaneous interaction (Beddington, 1975; DeAngelis et al., 1975).

We also feel that the instantist view is fallacious. We can conceive of few if any organismal processes that literally occur in instantaneous time. Organismal behaviors are by and large discrete in nature and for

this reason differential equations cannot be considered or used as literal depictions of biological processes. At best, differential equations are apt metaphors and so any consideration of which metaphor (time scale) to employ should be based on comparison of their relative utility, not on their conformation to instantist orthodoxy.

It also 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 the instantaneous conversion of food into offspring (if for no other reason than that reproduction is commonly a discrete process). Given that consumption is instantaneous and reproduction is discrete, the correct mathematical formalism should be 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 and validity of the instantist argument.

3.2. 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, those that 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 *Escherichia coli*, humans, or *Daphnia* are continuous: they reproduce at any time without a specified frequency. The authors consider differential equations the correct abstraction for continuous species and difference equations the correct abstraction for discrete species.

We find such a literalist projection of the mathematical construct into biology very restrictive and unreasonable. Depending on the time scale appropriate to the particular case, the same species can be described by both constructs. Darwinian natural selection is a prime example. It does not matter whether a geometric series (discrete) or exponential growth (continuous) is

invoked to deduce the idea of natural selection from Malthusian law. The law is just a caricature that captures the necessary properties of the process in either form.

To use an artistic metaphor, we feel that literalist theorists are attempting something akin to photorealism. 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, information adequate to 'paint' photorealistic pictures in ecology is not available. Imposing a strict literalist constraint only serves to guarantee that the resulting image will be distorted and non-sensical; in essence, a high-resolution image must be reconstructed from a very small subset of data 'pixels'. Such an approach will only work if: (i) the domain of the image that one aims to depict is very small (i.e. a specific, non-generalizable model is produced); or (ii) there is data sufficient to 'paint' a complete image. It seems clear to us that the former case is the best portrayal that photo-realist theorists 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 interpreting 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 particular forms of predator-dependence that emerge most prominently in time steps that are larger than instantaneous. Certainly, inclusion of such mechanisms violates literalist rules, but the resulting metaphors often work (Arditi and Akcakaya, 1990; Akcakaya, 1992; Ginzburg and Akcakaya, 1992; Akcakaya et al., 1995; Jost and Ellner, 2000; Ponsard et al., 2000; Jost and Arditi, 2001; Skalski and Gilliam, 2001; Vucetich et al., 2002; Schenk et al., 2005). 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 the resulting 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 models portray levels of detail which far outweigh the complexity of the simple questions that are asked (Ginzburg and Jensen, 2004). In relaxing literalist constraints, we hope to make theoretical work more practical and tractable—the goal is to 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 alternative.

3.3. 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, to assess their validity these models must be exposed to empirical tests. Fig. 2 suggests two out of many possible paths that such an inquiry might take. Once relevant data can be brought to bear on a theoretical paradox, data re-informs either intuition (Fig. 2b and c), theory (Fig. 2d and 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, a particular theory has been accepted without empirical confirmation, leading to unjustified alteration of intuition on a massive scale. In what seems to us a bizarre turn of events, an entire field has come to embrace a theory based not on data but on the beauty of theory itself.

In this sense, perhaps the work of theorists like Rosenzweig and Oksanen et al. is too good. The simple mathematical elegance of their theoretical discoveries, 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.
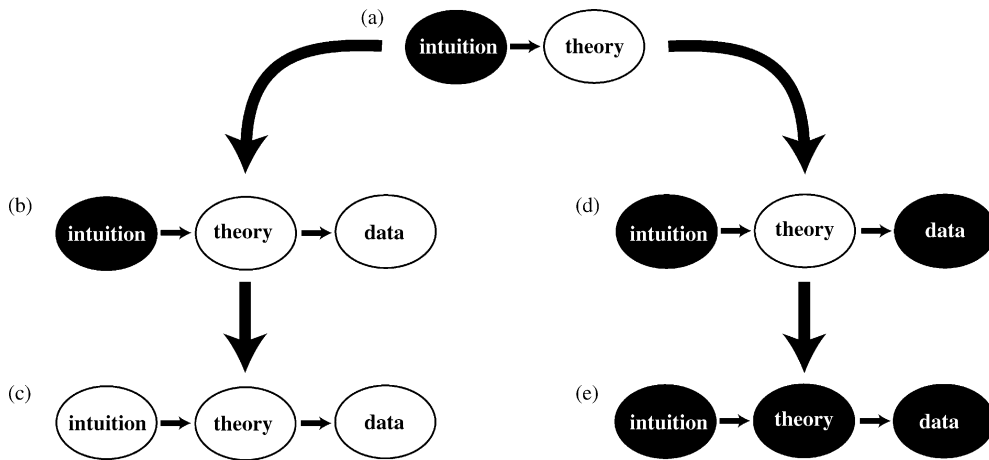
Fig. 2. Theoretical paradoxes and their resolution by comparison with data (matching shades signify agreement; mismatching shades signify disagreement). (a) A paradox emerges when intuition and theoretical predictions disagree and can only be resolved when the theory is compared with appropriate data. (b) In one scenario, data agrees with theory. (c) When theory and data are in agreement, intuition is informed by data and thereby altered, making intuition, 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.

4. The potential hazards of blind faith

Continuing unwarranted acceptance of the paradox of enrichment and the enrichment response phenomena presents ecology with 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 the management strategies based on them will 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 strategy has the potential to result in the mismanagement of an ecological system. The costs associated with such errors on an applied scale are much higher than those associated with theoretical reconsideration.

One need only look at the number of papers explaining away the empirical absence of these enrichment phenomena to begin to realize how much effort may have been wasted on upholding these paradoxes. Even though the occasional pursuit of dead-ends is a vital part of scientific exploration, we suggest that the ben-

efits associated with upholding these paradoxes may have been exhausted.

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