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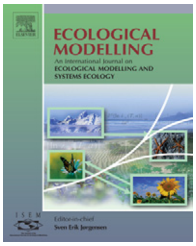

Short communication

Aiming the "unreasonable effectiveness of mathematics" at ecological theory

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ABSTRACT

A good theory is focused without being blurred by extraneous detail or overgenerality. Yet ecological theories frequently fail to achieve this desirable middle ground. Here, we review the reasons for the mismatch between what theorists seek to achieve and what they actually accomplish. In doing so, we argue on pragmatic grounds against mathematical literalism as an appropriate constraint to mathematical constructions: such literalism would allow mathematics to constrain biology when the biology ought to be constraining mathematics. We also suggest a method for differentiating theories with the potential to be "unreasonably effective" from those that are simply overgeneral. Simple axiomatic assumptions about an ecological system should lead to theoretical predictions that can then be compared with existing data. If the theory is so general that data cannot be used to test it, the theory must be made more specific.

1. Introduction

As a language capable of describing patterns, mathematics has unmatched explanatory power (Steiner, 1978; Colyvan, 2001). Mathematical theory's consistent success in the physical sciences inspired Eugene Wigner to celebrate the "unreasonable effectiveness of mathematics" in a famous 1959 lecture (Wigner, 1967). In many so-called exact sciences, mathematics has illuminated natural laws, allowing clear principles to be formulated.

Ecologists differ over whether it is appropriate to emulate these accomplishments: while some believe that "Principles of Ecology" are within our reach (Lawton, 1999; Turchin, 2001; Berryman, 2003; Colyvan and Ginzburg, 2003b), others maintain that the physical sciences provide a poor model for progress in biological fields (O'Hara, 2005). If we are to harness the unreasonable effectiveness of mathematics for ecology's benefit, how should we go about it? What lessons can we learn from the mathematical successes of other scientific fields? What special properties of ecology

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create pitfalls for those attempting to use mathematical approaches?

We maintain here that it is crucial for ecological theories to remain in focus: general enough that their predictions and explanations extend beyond a single data set or system but specific enough that their predictions and explanations do not become trivial (Fig. 1). Although we remain optimistic that mathematics can yield increased understanding in ecology, many current uses of mathematics remain uninformative: theories are either too specific (Fig. 1c) or too general (Fig. 1e). The most useful theories emphasize explanation over description and incorporate a "limit myth" (i.e., they describe a pure situation without extraneous factors, as with the assumption in physics that surfaces are frictionless). Ecological theories commonly do not meet the above criteria. Using our specific knowledge of predator–prey interaction theory, we review the reasons for this misfit and explore the possibilities and problems associated with the use of mathematics. We argue for a specific approach to constraining mathematical constructs in ecology and suggest a set of rules for those who wish to use mathematics to illuminate ecological principles.

2. Laws, postulates, and principles

Newton's competitor Leibnitz developed a conception of gravity similar to but more general than the familiar Newtonian version. Rather than specifying a particular relationship between gravitational force and distance from the sun (as Newton did), Leibnitz suggested that gravitational force declined monotonically with distance. The idea was correct but not useful because it suggested no specific applicable function. The specific function Newton proposed (an inverse square decline in gravitational force with distance) led to the potentially falsifiable prediction of elliptical planetary orbits. This historical example demonstrates that generality is guaranteed to be safe but not practically useful. However uncomfortable it might be to take a risk and postulate a specific relationship, specificity at least has a chance of being useful. Generalities are too imprecise to serve as building blocks for productive theories.

Formulating basic principles for constructing theories necessarily involves striking a balance between generalities, which are safe but potentially useless, and specific statements, which are risky but potentially useful. Theories that are either too general or too specific are unlikely to be useful. Two of us have already described the errors associated with overly specific theories (Ginzburg and Jensen, 2004); here we address the problem of overly general theories.

A statement that will serve as a foundational principle must be precise and informative. We know of only one such unanimously agreed upon principle in ecology: the Malthusian law of exponential growth, a simple statement stressing the multiplicative character of reproduction. It is called a law in most textbooks even though populations cannot grow exponentially for long. It has all the features of a "good" law: it describes what happens in the absence of extraneous factors, establishing a baseline that sets the stage for developing theories aimed at more biologically relevant situations. The similarity of this law to Newton's first law of inertia (uniform motion in the absence of forces) has been observed (Ginzburg, 1986; Turchin, 2001).

Differences of opinion surface when theorists describe the ecological processes that lead to deviations from exponential behavior. Here, we consider as examples sets of principles proposed by Berryman (2003) and postulates suggested by Turchin (2001). Although there is nothing erroneous in either set, both suffer from a substantial degree of overgenerality that might render them unsuitable to serve as the foundation for effective theory. The problem with overly general statements is that they are trivially correct but do not lead to predictions specific enough to be checked against evidence.

An example from each of the two sets serves to demonstrate the risk in being too general. Turchin (2001) suggests generalizing the biomass conversion postulate (Ginzburg, 1998) to make it a more general inequality rather than an equality. In its original, specific form the postulate suggests that the rate of consumer reproduction is a function of its consumption rate. Such a rule imposes a particular symmetry on predator–prey theories, forcing a linkage between the so-called functional and numerical responses. Turchin suggests a more general one-sided inequality: a consumer cannot derive more from what is consumed than the consumed resource contains. Theories positing this more general assumption have excessive flexibility, since they are not constrained by the conversion postulate that the specific statement requires. It is hard to disagree with a more general statement if one agrees with a special case. Nonetheless, from a practical point of view, the specific formulation is more useful in constructing theories because it places a reasonable and reasonably precise biological constraint on theoretical constructions.

Berryman (1999) suggested a set of principles substantially similar to Turchin's. He later articulated the general view (Berryman et al., 2002) that ecology, like physics, may not need its own laws since both disciplines are subject to general system theory, which describes interactions and feedbacks in any dynamical system. But such a claim is problematic. While system theory could be used to describe elements of ecology or physics, it would do so in such general terms as to provide little practical foundation. We would like to know, for instance, how fast gravitational force declines with distance or how predator consumption and reproduction rates relate to one another. These specifics make theoretical physics different from theoretical ecology; that both involve "interactions" containing "feedback" is true but not sufficiently informative.

Although we are hesitant to advance examples from outside our area of expertise, we can suggest contexts in which the perspective we offer here might be useful. In reviewing the last several years of 'Ecological Modelling' in search of safe, overly general models, we found a potential candidate in a community ecology model (Salles et al., 2006). In addition, we identified a pair of relevant methodological discussions, one dealing with systems ecology modelling (Schizas and Stamou, 2007) and the other with individual-based modelling (Aumann, 2007).

A qualitative perspective on a four-species community by Salles et al. (2006) does little more than confirm that the authors developed a model whose outcomes coincide with the limited number of observed real world outcomes. While such a finding represents an important – and necessary –

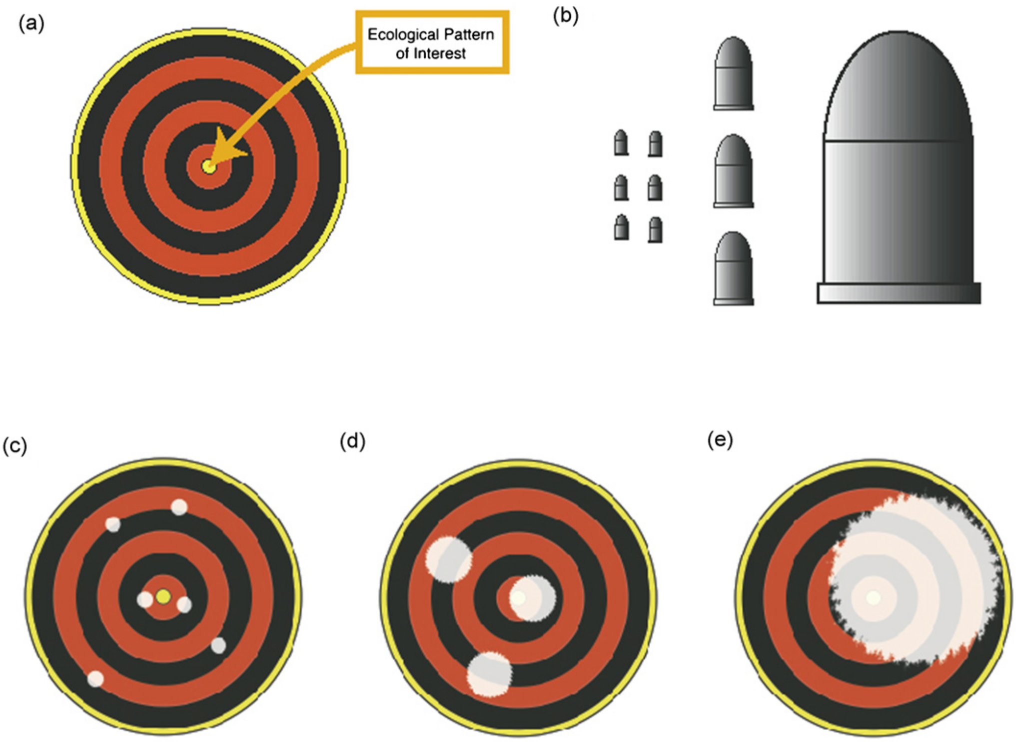

Fig. 1 – Maintaining the balance between specificity and generality in ecological theories. (a) Ecological theorists "target" particular ecological patterns or phenomena. Resulting theories can either "hit the bullseye" (i.e., capture the phenomenon perfectly) or strike some distance from the target. (b) Theories are like artillery shells of varying caliber: not all can strike a particular target with equal accuracy. Overly specific theories are like small caliber rounds, while overly general theories are like large caliber rounds. More specific theories always outnumber general theories; at the extreme, the most general theory encompasses all possible specific theories. (c) If an overly specific theory is used to approach a particular ecological phenomenon, the chance of it capturing the phenomenon correctly is very small, even as multiple competing theories are employed. (d) A theory that correctly balances specificity and generality has the potential to properly capture the ecological phenomenon. Notice that being of the "right caliber" does not guarantee that a theory will be "on target": some theories may contain the correct level of specificity but still fail to capture the ecological phenomenon of interest. (e) Overly general theories may capture the phenomenon but encompass so many other possible ecological patterns as to be of little practical use. In order to maintain some confidence in a theory, we need to believe that it could be wrong; overly general theories have the undesirable quality of being "correct" over too large a range of possible ecological phenomena.

preliminary achievement, the result's generality is not very informative. Of course, examples of appropriate model generality are typical of 'Ecological Modelling'. Rather than focus attention on a diverse range of such efforts, we thought it might be more useful to point out a particular recent perspective on modelling methodology that is consistent with our analysis. To that end, we suggest Aumann (2007), which articulates a general approach to developing simulations while grounding that methodology in appropriately specific work on species–habitat interactions.

We would also point out that the current paper provides a potentially useful perspective for a variety of modelling enterprises. In addressing the manner in which systems ecology modelling appropriately addresses physiochemical or biological phenomena, Schizas and Stamou (2007) face the central methodological issue of interest to us: what level of model generality is sufficient and what level is excessive? While we would not presume to answer that question for them, we hope that the current discussion might provide a useful perspective.

In our own work we certainly try to be clear and specific about our assumptions in developing simple, testable theories (Ginzburg and Colyvan, 2004). This self-imposed discipline forces us away from the safety of generality and into the riskier territory of specific prediction. We accept the resulting risk in the hope that our approach will give us a chance to make progress.

3. Assumption selection and generality

Mathematical theories are based upon axiomatic assumptions. In ecology, assumptions usually follow from intuition about the way in which biological systems function. An important contribution of ecological theorists is to explain how particular sets of assumptions lead to theoretical predictions. The resulting theoretical predictions aid in assessing the quality of particular assumptions and models by allowing for comparison between model predictions and empirical observations. Selecting appropriate assumptions to underlie a model is crucial, because the behavior of more complex models can vary drastically under different assumptions.

Modern predator–prey theory is built upon the foundation laid by Lotka (1925) and Volterra (1926) and is generally formulated on the basis of a Rosenzweig and MacArthur (1963) model. Inherent to this family of models is the assumption of prey dependence: the per capita consumption rate of the predator is a function of prey abundance and does not depend on predator abundance. Two mathematical discoveries – the paradox of enrichment (PoE) and the enrichment response (ER) – illuminated key predictions of this model (Rosenzweig, 1971; Oksanen et al., 1981).

The PoE predicts that a simple obligate predator–prey system might be destabilized by increases in the carrying capacity of the basal trophic level. As such, the PoE remains the chief mechanism by which traditional predator–prey models explain dual extinction of predator and prey owing to overconsumption. Although most ecology textbooks feature the PoE, it enjoys almost no experimental support in either laboratory or natural systems (Arditi and Berryman, 1991; Jensen and Ginzburg, 2005). Although the general ecological community may not be attuned to this problem, the community of theoretical ecologists is acutely aware of the discrepancy and has exerted significant effort to explain why the PoE is rarely (if ever) observed (Jensen and Ginzburg, 2005).

Most explanations for the absence of the PoE begin with the assumption that the phenomenon could exist. This assumption is equivalent to establishing prey dependence as an axiom. With the Rosenzweig–MacArthur model as a basis, additional terms are added to depict ecological phenomena that, if present in experimental systems, might explain the failure to observe the PoE. These phenomena represent an array of possible ecological scenarios including the presence of: (i) multiple prey species varying in edibility (Phillips, 1974; Leibold, 1989; Kretzschmar et al., 1993; Abrams and Walters, 1996; Genkai-Kato and Yamamura, 1999); (ii) density dependence of the predator death rate parameter (Gatto, 1991); (iii) refuges and immigration (Abrams and Roth, 1994); (iv) spatial heterogeneity (Nisbet et al., 1998; Petrovskii et al., 2004); (v) life-history traits that enable consumers to buffer the effects of low prey densities (McCauley et al., 1999); and (vi) prey possessing inducible defenses (Vos et al., 2004).

We contend that at the most fundamental level ecology ought to utilize mathematics in exactly this manner. A simple axiomatic assumption (e.g., prey dependence) about an ecological system should lead to theoretical predictions that can then be compared with existing data. If the data contradict those predictions, theory must be modified. Where we depart from most ecological theorists is at this last step: deciding how theory should be modified.

Although their specific mechanisms vary, all explanations outlined above for the absence of the PoE posit an additional causative mechanism. As such, they run the risk of being too specific (Fig. 1c); it seems unlikely that any one of the suggested factors could be influential in all systems, and so any explanation of why the PoE cannot be observed is liable to be specific to the system in question. One way to address this problem would be to construct a massive model that incorporates the potential for all conceivable mechanisms; yet while such a model would be applicable to all systems, its extreme generality would prevent it from being useful (Fig. 1e).

We wonder why a more obvious step has not been taken: if basic theory can only explain existing data via formulations that are either too specific or too general, perhaps basic theory needs to be revised. Specifically, we wonder why the prey-dependent assumption has not been replaced with a different assumption: predator dependence. Predator dependence, which can come in a variety of forms (Leslie, 1948; Hassell and Varley, 1969; Beddington, 1975; DeAngelis et al., 1975; Arditi and Ginzburg, 1989; Jensen et al., 2007), dampens or completely removes the effect of enrichment on stability (Huisman and DeBoer, 1997) without invoking overly specific or overly general model formulations.

The enrichment response (ER) also illuminates the effects of increasing carrying capacity but considers these effects over food chains of varying lengths. As with the PoE, a preponderance of empirical evidence does not support the existence of ER (Jensen and Ginzburg, 2005), and the results of laboratory and natural experiments are more consistent with predator-dependent models of trophic chain enrichment (Arditi and Saiah, 1992; Bohannan and Lenski, 1997; Kaunzinger and Morin, 1998). Not surprisingly, many theorists have also turned to increased-complexity explanations in attempting to preserve the prey-dependent assumption in spite of its poor predictive power.

4. Pragmatism

The validity of the principles underlying a theory determines whether or not it will be effective in predicting actual ecological outcomes. Unfortunately, inspecting these principles directly might only reveal internal logical inconsistencies without indicating a given theory's usefulness. A simple pragmatic rule (i.e., check the consequences of the model against data) remains most reliable. Such a comparison is not as simple as it might seem, as the danger of overfitting covered in our previous review (Ginzburg and Jensen, 2004) represents only one of many hurdles that must be overcome.

Theories never work perfectly; each incorporates, to use a famous expression of Quine's (Quine, 1976, 1980, 1995), a "limit myth" (a description and consideration of a pure situation that ignores extraneous factors—for example, a body falling in the absence of air resistance or the interaction of a single predator species with a single prey species in the absence of any others). To illustrate this idea, we use the example of the tension between the two limit myths of predation theory (prey dependence and ratio dependence), which is described in Abrams and Ginzburg (2000). Qualitatively, two main arguments favor a ratio-dependent limit: the absence of the paradox of enrichment and the equilibrial behavior of trophic chains in response to increased basal productivity (Arditi and Berryman, 1991; Ginzburg and Akçakaya, 1992; Akçakaya et al., 1995). Both have been reviewed above and can be explained within the framework of a more traditional prey-dependent limit myth if the model includes additional complexity. Since complex predator–prey webs are the norm in nature, few opportunities are available to test the predictions of simple models (i.e., those that depict obligate predator–prey pairs). One approach to adjudicating the debate between prey- and ratio-dependent explanations is to directly measure functional responses. Doing so most commonly reveals predator dependence (a more general intermediate situation between the two limit myths), although pure ratio-dependence is also an occasional result (Skalski and Gilliam, 2001). The question we wish to ask is not which of the two extremes is correct, because we know that both are wrong. Instead, we wish to determine which of the two simplified views is more useful if we have to make a practical judgment today, before all the details of the intermediate mechanism are fully understood. Pragmatism dictates that we temporarily adopt the ratio-dependent myth, because it produces a rough, qualitatively correct outcome based on a simple model. Direct measurements of functional responses reject prey dependence more frequently than they do ratio dependence (Jost, 1998; Jost and Ellner, 2000; Jost and Arditi, 2001; Skalski and Gilliam, 2001).

We make the choice to follow our philosophy of risk-taking by being specific with basic assumptions fully understanding the risk. We believe that, of the two extremes, ratio dependence is preferable. The more general intermediate choice would be even better, but it requires at least another parameter. There is typically so little data that using one more parameter leads to overfitting—a potentially serious problem since we can barely find data for the simpler extreme cases (Jost, 1998).

There is safety in making no judgment at all, a not uncommon ivory-towerish behavior. But while no academic jobs will be gained or lost as a result of this choice, numerous practical judgments on ecosystem management depend on it. Ecological theory is likely to have practical applications with potentially important consequences. We suggest that it is preferable to use theory in combination with available data to advance ecological understanding now even though in doing so we may risk making occasional errors.

5. Applying appropriate constraint to mathematical constructions

Biology should constrain our mathematical constructions. While mathematics provides an incredibly vast set of possible equations, logic dictates that only a small subset of these equations can represent a given ecological phenomenon. A large number of constructions, while mathematically sound, should be excluded based on their inconsistency with biology. While most ecologists would agree with such a principle, deciding how best to put it into practice remains a contentious issue. Among ecological theorists, a number of constraints have been forwarded; most proposed theories obey some constraints but rarely all. We consider two proposed constraints on predator–prey theories: (i) instantaneous processes and (ii) biomass conversion.

Many ecological theorists believe that continuous equations should be used only in models of instantaneous processes (Murdoch et al., 2003). Models that include processes interpretable as being strictly instantaneous are called “mechanistic”, while those that do not are derided as “phenomenological”. We call this formalism the “fallacy of instantism” and consider it a particular example of mathematical literalism (Jensen et al., 2007). We reject the use of mathematical literalism to constrain mathematical constructions on simple grounds: literalism allows mathematics to constrain biology when biology ought to be constraining mathematics. Proponents of instantism and other forms of literalism fail to appreciate the metaphorical nature of models (Hilborn and Mangel, 1997) and unnecessarily exclude models with potentially great explanatory power.

The biomass conversion principle described above allows ecology to logically constrain mathematics. For a set of predator–prey equations to obey the principle, a predator’s numerical response must be a function of its functional response (Ginzburg, 1998). In biological terms, reproduction must be a function of consumption. While such constraint will strike most ecologists as reasonable, a number of popular models violate the biomass conversion principle (Turchin, 2003).

Applying either too much or too little constraint to our mathematical constructions produces the same undesirable result: because we end up choosing from an incomplete or over-complete list of models, we greatly increase our risk of missing the most reasonable mathematical construction. While the application of logical constraints provides an important first step in avoiding this pitfall, we contend that the best means of determining which constraints should be excluded is to devise and perform experiments that explore contrasting model predictions.

6. Conclusion

Ecologists face a difficult task in assessing the vast array of available models. Some shortcomings can be readily apparent. For instance, the degree of overfitting can be measured fairly easily by comparing available data with the number of parameters in a given theory (Colyvan and Ginzburg, 2003a; Ginzburg and Jensen, 2004). Other potential shortcomings are less easily quantifiable, including (i) determining the appropriate degree of literalism to use in interpreting mathematical concepts in service of ecology, (ii) identifying the point at which a theory becomes too general to be useful, and (iii) assessing the extent to which a theory enjoys empirical support. Nonetheless, selecting the correct intermediate level of abstraction to increase theory effectiveness is not simply a matter of personal aesthetic preference. As we have demonstrated, some elements of that selection process can be logically addressed to separate “unreasonably effective” theories from those that are simply unreasonable. We conclude that an ecological theory that is in focus with evidence will have to be rough and approximate. Recognizing that such a state of affairs exists is potentially helpful rather than problematic, however. As we face an ever-increasing number of ecological crises, social demand will be for crude, imperfect descriptions of ecological phenomena now rather than more detailed, complex understanding later.

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