

Are there general causal forces in ecology?

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Abstract In this paper, I adopt the view that if general forces or processes can be detected in ecology, then the principles or models that represent them should provide predictions that are approximately correct and, when not, should lead to the sorts of intervening factors that usually make trouble. I argue that Lotka–Volterra principles do not meet this standard; in both their simple “strategic” and their complex “tactical” forms they are not approximately correct of the findings of the laboratory experiments and historical studies most likely to confirm them; nor do they instruct ecologists where to look for likely intervening factors. Evidence drawn from long-term case studies and other available data sets suggests that the populations of predators and their prey are not regulated by an interaction between them but are controlled by transient, contingent, and accidental events that affect each animal and each population individually. This paper argues that the presence of general forces or processes in ecology should be determined by comparing competing models of these forces not just to each other or to a null model but also to case studies that may challenge theoretical approaches with convincing individualistic causal accounts of the phenomena.

Keywords Philosophy of ecology · Lotka–Volterra models · Isle Royale

“There’s been a good ice bridge for the past 10 days.” On February 6, 2014, Rolf Peterson of Michigan State University, who since 1970 has led a study that began in 1959 of the predator-prey dynamics of wolf and moose populations at Isle Royale, a remote wilderness island in Lake Superior, Michigan, e-mailed this good news to

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an NPR science reporter ([Brush 2014](#)). It was considered good news because the ice bridge created the hope that wolves from Canada would migrate again to the island and refresh the population, which had declined to eight or nine adults. Things turned out inauspiciously. Isabelle, a 5-year old female in prime breeding condition, used the perilous ice bridge to travel the other way from the island to the Lake Superior shoreline, where she died a victim of a stray shot from a pellet gun ([Marcotty 2014](#)).

At the beginning of the 20th Century, several moose migrated from Ontario across the frozen waters of Lake Superior to the 210-square-mile Isle Royale, which has been designated a national park because of its relatively pristine or natural character. In the late 1940s, about a dozen wolves crossed the frozen waters to the island and grew to a population of twenty after about a decade. When the study began in 1959, approximately 750 moose and 10 wolves inhabited the island. “The wolf-moose project of Isle Royale, now in its 56th year, is the longest continuous study of any predator-prey system in the world” ([Vucetich and Peterson 2014](#), p. 1).

1 Forces in ecology

This paper explores the question whether there are general ecological forces or processes that help determine and thus explain the abundance and distribution of plants and animals. I shall use predator-prey systems, such as the interaction of moose and wolf at Isle Royale, to analyze this question, because I believe predator-prey interactions exemplify what is meant by an ecological force of a kind that shapes animal populations. I agree with P. H. Ronald and Nickolas Waser that the way to find out whether a general ecological force is at work is not simply to see whether the data support one model or hypothesis better than another. It is also to see whether in view of natural history the causes of phenomena can be credibly traced to the forces a model elaborates. [Ronald and Waser \(2010, p. 70\)](#) have written that the way to identify causal forces in ecology is to explore conceptual “possibilities by challenging multiple working hypotheses with increasing sophisticated knowledge of natural history based on long-term place-based observation and experiment.” I refer to the predator-prey research at Isle Royale, among other examples, because it represents a good opportunity to match a model with a knowledge of natural history.

The question whether there are general forces or processes in ecology—such as between predator and prey populations—is one of the most contentious in the philosophy of that science. This question is often phrased in terms of the possibility of laws in ecology, that is, models or principles that represent general forces. In their bibliography on the question of laws in ecology, [Colyvan and Ginzburg \(2014\)](#) have written, “A great deal of the material on this topic focuses on what laws of nature are and what roles they are supposed to play in scientific theory.” A common starting place, these authors say, is that “laws in science are non-accidental, exceptionless generalisations, which make precise, falsifiable predictions.” Whether or not this starting-point may relevant to physics and sciences reducible to it, philosophers have developed a variety of different views of the concept of a law and of the role it plays in the “special sciences,” such as biology and economics, which are not reducible to physics ([Fodor 1974](#); [Kincaid 1997](#)).

Philosophers of science have suggested ways one might judge the credibility of a model or principle that represents a general force in a special science. Woodward (2003) assimilates the detection of general causal forces in biology to the identification of “factors or conditions such that manipulations or changes in those factors or conditions will produce changes in the outcome being explained” (p. 9). Woodward (2000) elaborates, “A generalization is invariant if it is stable or robust in the sense that it would continue to hold under a relevant class of changes” (p. 197). Later in this paper, I shall use the “law of supply” in economics—the idea that the amount of a good produced varies with its price—as an example of the kind of observed co-variance that helps establish the credibility of a generalization in a “special” science.

Where it is difficult to manipulate one variable while holding others constant, as may be the case in ecology, one would expect the model to be approximately predictive in most cases and when its predictions fail, to lead researchers at least often to the kinds of countervailing powers or intervening variables likely to account for the aberration. As Cartwright (2007) has written, the force in question always makes a systematic difference to the phenomena to which it applies. “The notion of the systematic difference produced by a cause in a given situation is cashed out in the vector addition of its contribution ... to the contribution of the other causes in that situation, i.e., the forces exerted by the other causes” (p. 3).

On this view, a model represents a force or capacity in nature only if it provides a predictive advantage in the sense Cartwright describes, that is, if it succeeds predictively and, when it does not, it makes a systematic difference to the phenomena so that researchers, by consulting the model, can usually identify the other causes which, in addition to the force in question, lead to an explanation of the phenomena. A model that represents a general force will predict the phenomena within a margin of error in most cases to which it *prima facie* applies, and, when it does not, it will instruct the scientist where to look for the distorting or intervening conditions. If the intervening or external factors do all the causal work and if the model does not direct attention to these causes, there is a sufficient reason to doubt its credibility.

It may be useful to give an example of a general principle in population biology that fails to meet the conditions of credibility I have described. In 1798, Thomas Malthus proposed a law-like regularity between the size of the human population and the amount of food it is able to produce. Malthus argued that size of the human population would double every cycle, while the production of food would increase only arithmetically. “The power of population is indefinitely greater than the power in the earth to produce subsistence for man,” Malthus (1798 [1966] Ch. 1, p. 13).

Several biologists in the last century applied this principle—or this “power of population”—to predict the massive die-off of humanity due to starvation and with it the collapse of civilization. In an article published in 1970, for example, Stanford biologist Paul Ehrlich (1970) argued that global food shortages would cause four billion people to starve to death between 1980 and 1989, 65 million of them in the United States. In a 1970 textbook co-authored with his wife Anne, Ehrlich suggested that laws “could be written to make bearing a third child illegal and that would require an abortion to terminate all such pregnancies” (Ehrlich and Ehrlich 1990, p. 274). Hardin (1968), also a biologist, deployed Malthusian logic in an influential argument for coercive birth control.

The Malthusian model failed at prediction. Food production per capita has steadily increased, for example, by 12 % between 1990 and 2010 (Barrett 2010). The deeper problem is that the model directed attention not toward but away from the causes, such as the demographic transition, the empowerment of women, urbanization, contraception, and so on, that account for the size of the human population, and away from the reasons such as oppression and civil war that cause famine. Sen (1984) has written that with such “misleading variables as food output per unit of population, the Malthusian approach profoundly misspecifies the problems facing the poor of the world.” Sen commented that the Malthusian model, by so thoroughly mistaking the causes of famine, led to “policies that actually killed millions of people” (p. 524).

2 Internal and external forces

The question whether ecological forces help explain ecological facts recalls the pre-war debate over whether these facts are driven (1) by the “internal” dynamics of a community, especially predator-prey relations, competition, and density-dependence (i.e., the idea that as a population increases in size it crowds itself out of needed resources it therefore declines or oscillates in predictable ways) or (2) by “external” factors such as weather, invasive species, and diseases (Nicholson 1933; Andrewartha and Birch 1954; for review see Turchin 2003). One way to understand the internal vs. external debate is to assume that ecological systems or communities exist as units with boundaries, however drawn. Forces are “external” if they impinge upon the system or community from outside its boundary. They are internal otherwise.

A second very different way to understand the internal vs. external distinction is to distinguish those causal factors that serve as variables in a model from those that do not. Mathematically-minded ecologists have displayed a large number of variants on Lotka–Volterra equations to include many variables not represented in simple models (Ginzburg and Colyvan 2004). In other words, what counts as internal to the system will depend on the model. No matter how embracive a model may be, however, it will not take into account many contingent, accidental, or individualistic factors. If those who study the natural histories of populations, communities, or ecosystems are able to explain phenomena in terms of individualistic and path-dependent factors, while they can find no way to discover them by applying the general or theoretical model, one may ask how general forces, if they exist, can be detected in ecology.

Particularly perplexing is the question whether and how theoretical models in ecology should include, control for, or exclude the influence of human activity on study populations. For example, in an impressive study of the population dynamics of wolves in Minnesota, where they prey principally on deer, Fuller (1989) found, “Despite legal protection, 80 % of identified wolf mortality was human-caused (30 % shot, 12 % snared, 11 % hit by vehicles, 6 % killed by government trappers, and 21 % killed by humans in some undetermined manner); 10 % of the wolves that died were killed by other wolves” (p. 5). It is unclear how predator-prey population equations would apply to cases where the mortality of the predator is driven largely by human activity. In this paper, I do not contend that internal processes or forces—such as predator-prey relationships—have no influence on the abundance and distribution of populations. I argue that external forces (however construed) so overwhelm internal ones that one

is not be able to tell the extent to which internal forces, such as the predator-prey relation, are relevant to population dynamics. I restrict the conclusions of this paper to those systems or sites, like Isle Royale, the natural history of which has been studied.

Whether the same is true *mutatis mutandis* of generalizations applied at the community level, as Lawton (1999) has argued, goes well beyond the scope of this paper. Yet I believe that the example of Lotka–Volterra equations may serve to illustrate how mathematical models or generalizations that represent general forces in ecology should stand up to sophisticated knowledge of natural history based on long-term place-based observation and experiment. It would otherwise not be possible to tell whether these forces, or the models that represent them, do explain phenomena or are merely figments of the mathematical imagination.

As Colyvan and Ginzburg (2003) have pointed out, general laws about the structure and workings of nature have exceptions, need not make precise predictions, and often rely for their application on a lot of background information. This is true especially of the “special” sciences, such as biology and economics, which are not reducible to physics. But even in the “special” sciences, one would expect that predictions based on general laws or forces are approximately true most of the time and otherwise usually are able to show clear, demonstrable, and useful relevance to empirical discovery. They would then be more credible than the Malthusian model.

I believe that if there are general forces in ecology, then in representative circumstances these forces (or the models associated with them) should at least approximately predict events or lead ecologists to those intervening or distorting factors which are likely to make trouble. Lotka–Volterra models do make predictions, for example, that populations will oscillate in various ways or dampen toward an equilibrium. If predator and prey populations at a given site, as studied by natural historians and other empiricists, vary independently for individualistic reasons, then it is fair to ask how a Lotka–Volterra model helps explain the phenomena. If the force in question matters less than a myriad of other causes discovered by natural historians without benefit of the model, or in spite of it, as in the Malthusian case, this would be a reason to reject the model.

If the predictions a model makes, e.g., oscillations of some kind, are not observed, one may expect the model to help researchers identify the disturbing factors that make the difference. If the model or general principle does not do even that, if like the Malthusian model of human population growth it collapses into implausibility when challenged by knowledge obtained by the study of natural history, the problem is not that the law has exceptions, introduces *ceteris paribus* clauses, provisos, and the like. The problem is that the principle along with all its *ceteris paribus* conditions, provisos, and theoretical apparatus and qualifications, fails to be informative.

Simberloff (2004, p. 788) describes the difference between general forces and individualistic causes in terms of “the distinction between nomothetic knowledge, which is the goal of most natural sciences and consists of general laws about the structure and workings of nature, and idiographic knowledge, which characterizes historical sciences and consists of depicting singular events in a coherent narrative focusing heavily on unique aspects of particular phenomena.” If general forces in ecology or the models that represent them make a systematic difference to the phenomena, they will allow the kind of invariance under manipulation Woodward describes or they

will be approximately predictive much of the time and, when not, they will usually identify or lead empirical research to the distorting factors. If a principle or model fails in these respects, one would then have to consider the possibility that—however well it may be analogized in a formal way to principles or models in physics (Colyvan and Ginzburg 2010)—it is of no empirical relevance to ecology. More generally, one would consider the possibility that ecology succeeds as an idiographic not a nomothetic science.

3 Strategic versus tactical models

How much general predictive capacity should we expect of principles, such as are expressed in Lotka–Volterra models, if they are relevant to ecology? In a well-known essay published in 1966, Richard Levins describes a tradeoff any model must make between three competing objectives: realism, generality, and precision. Levins argued that biological phenomena are so complex and contingent that models to deal with them have evolved to emphasize either mathematical precision, generality in their potential application to many places or populations, or realism in the sense of being accurate or offering the kind of predictive advantage I have described. Levins added that models may be improved on any of these three dimensions, but that it is not possible to maximize generality, precision, and realism at the same time.

Evans et al. (2013) have drawn a number of distinctions that help us to understand the extent to which fidelity to experience (realism, predictive capacity) matters in assessing the credibility of models that represent general forces or processes in ecology. These authors following Holling (1966) distinguish “between strategic models, which are as simple as possible to reveal potential explanatory generalities, and tactical models, which are more complex because they are designed to predict the dynamics of specific systems” (p. 578).

Evans et al. (2013) describe Lotka–Volterra models as strategic rather than as tactical. “They will not be useful at predicting the behaviour of specific systems and, thus, cannot be empirically tested against data from a particular system” (p. 581). These authors continue, “Very general models with only one or two causal factors will not have an especially good fit to any particular system. ... [T]hey potentially inform about phenomena that exist in many systems, but may not necessarily make good predictions about any individual system” (p. 580, citing Matthewson and Weisberg 2008).

If strategic models, such as are illustrated by the family of Lotka–Volterra models, “cannot be empirically tested against data from a particular system,” how do they “potentially inform about phenomena”? To answer this question one may ask why Evans and coauthors believe these models cannot be tested against data from a particular system. The reason, apparently, is that they test badly. That models consistently yield poor predictions in all specific cases, however, does not mean they cannot be tested in those cases. They simply do poorly. To be informative, these models, I believe, in their provisos, *ceteris paribus* clauses, and background conditions should lead researchers most or much of the time to the causal factors that account for the predictive failure. In a later section, “Stone Soup,” I will consider how simple models may be used to initiate research even if they do not add informational sustenance to it.

4 Economics and ecology: a comparison

Strategic or simple models in economics differ from those in ecology in the following way. The science of economics provides examples of simple or strategic models, such as the law of demand and the law of supply, that when tested in specific cases generally yield approximately accurate predictions and, through a well understood and limited number of provisos or *ceteris paribus* conditions suggested by the background theory, usually, but not always, point to the reasons for discrepancies. In other words, strategic models in economics are both general and realistic in Levin's sense, although they will not always (in fact, rarely) be exact or precise, and will occasionally fail because of the influence of forces exogenous to the theory. In contrast, strategic models in ecology, to quote Evans and coauthors again, "will not be useful at predicting the behaviour of specific systems." In other words, they are not at all realistic. Because they are such predictive flops these authors resort to the euphemism that they "cannot be empirically tested against data from a particular system."

According to Mill (1995) [1848], the force that economics theorizes is the desire to accumulate wealth. Mill wrote of political economy,

It does not treat of the whole of man's nature as modified by the social state, nor of the whole conduct of man in society. It is concerned with him solely as a being who desires to possess wealth, and who is capable of judging of the comparative efficacy of means for obtaining that end. It predicts only such of the phenomena of the social state as take place in consequence of the pursuit of wealth.

Mill believed that economics is an "inexact science" in the sense that Hausman (1992) has explained. According to Hausman, economics counts as an "inexact" science (but as a science nevertheless) because its predictions are true only within a margin of error. This is because there are always other forces at work beside the desire for wealth but these will exert only a small effect on the relevant phenomena, for example, on prices. When the predictions are not approximately correct, the reason can usually be found within the theory itself and thus in the manageable number of *ceteris paribus* and other provisos associated with the model. In highly exceptional cases, the relevant phenomena, such as the price of a good, will be determined not approximately by the force economic models represent (the desire to increase one's wealth) but by a truly external or exogenous shock. The pursuit of wealth is only one force or motive among many that determine human behavior, of course, but according to Mill it is a strong enough force in relation to others that strategic models based on it are largely predictive and, when not, economists are often led by the model and well-known *ceteris paribus* conditions, except in very unusual circumstances, to discover the distorting forces or causes.

The "law of supply" illustrates the point. Nearly all production is done with the idea of making a profit and thus is responsive to the price signal. When the price of a good increases, more of it will be produced. A fall in price will result in a fall in production. While this seems generally to hold, the textbook theory lists reasons for a few exceptions. As I write, Saudi Arabia instead of producing less petroleum in response to dramatic price declines, announced it will produce as much or more, thereby pushing prices down still further. Why this anomaly? The theory behind the

law of supply, at the Economics 101 level, adds the proviso that in pursuit of greater wealth in the longer term, a major producer may force down prices in the short term to drive out competition, in order to raise prices later. An economist might then predict that if one looked at the internal documents at the Saudi Oil Ministry one would find evidence of this design. According to the *Economist* (2014), the Saudis have been open about their desire to maintain their market share to drive out new producers such as in the United States. Sometimes forces do intervene from entirely outside the theory—for example, the 1973 embargo of oil by Arab petroleum exporting companies to protest the involvement of the United States in the Yom Kippur War. These cases are truly exceptional.

With respect to the phenomena of economics, such as prices, self-interest or the desire for wealth is a governing force that makes a systematic difference and leads empiricists to detect the reasons for most apparent anomalies. With respect to the phenomena of biology, at least in terms of the example of Lotka–Volterra equations, does the force in question, e.g., predation, similarly make a systematic difference and lead researchers to countervailing or distorting conditions?

In a well-known analogy to the study of the tides, Mill argues that the force of self-interest is strong enough to make the study of it, i.e., economics, credible as a science, even if an inexact one. In the *System of Logic* (1963 [1843], VI. 2), Mill wrote on the “Science of Human Nature.”

No one doubts that Tidology. . . is really a science. As much of the phenomena as depends on the attraction of the sun and moon. . . may be foretold with certainty; and the far greater part of the phenomena depends on these causes. But circumstances of a local or casual nature, such as the configuration of the bottom of the ocean, the degree of confinement from shores, the direction of the wind, &c., influence in many or in all places the height and time of the tide. . . General laws may be laid down respecting the tides; predictions may be founded on those laws, and the result will in the main. . . correspond to the predictions. And this is, or ought to be meant by those who speak of sciences which are not exact sciences.

Mill argues in this context that the pursuit of wealth functions as a “greater” cause of human activity as the moon functions as a “greater” cause in the movements of the tides. These “greater causes, those on which the principal part of the phenomena depends, are within the reach of observation and measurement.” As Mill put this point, “inasmuch as other, perhaps many other causes, separately insignificant in their effects, co-operate or conflict in many or in all cases with those greater causes, the effect, accordingly, presents more or less of aberration from what would be produced by the greater causes alone.”

Reflecting on the relevance to ecology of Mill’s analogy, Lange (2005, p. 398) has observed that because simple or strategic models “omit the negligible influences, they are only approximately true” (citing Colyvan and Ginzburg 2003). Using a similar phrase, Simon (1963, p. 230) has written of economics that “if the conditions of the real world approximate sufficiently well the assumptions of an ideal type [i.e., a simple or strategic model], the derivations from these assumptions will be approximately correct.” Simon suggested that the context will determine how correct “approximately

correct” must be, that is, when predictive failure “is beyond the limits of our tolerance.” Plainly, if the model gets the sign or direction of change wrong, this will exceed our tolerance. What more may be required for a model to count as “approximately correct” beyond that it predicts the sign or direction of change?

Simon argued that in many sciences the statistical notion of “significance” is misused to support the view that a theory is “approximately correct” if its predictions are better than those of a null model or those that could be derived by chance. He wrote (p. 231):

The word “significant” has been appropriated by the statisticians to mean “unlikely to have arisen by chance.” Now, in testing extreme hypotheses—ideal-types we do not primarily want to know whether there are deviations of observation from theory which are “significant” in this sense. It is far more important to know whether they are significant in the sense that the approximation of theory to reality is beyond the limits of our tolerance.

Consider the statement that an increase in price is followed by an increase in supply. One may want to test the theory in terms of more quantitative measures, e.g., to ask by how many units will production increase in response to each dollar increase in price? Simon suggested that the question whether deviations of theory from reality at this finer scale of analysis exceed the limits of our tolerance will depend on many factors, for example, the purposes we have in mind, the background empirical knowledge we bring to bear, and the ability of the theory to predict quantitative not just directional change. Empirical research, such as at Isle Royale, that allows one to expose theoretical assumptions to empirical critique will also influence one’s sense of which derivations from theoretical assumptions one may accept as “approximately correct” and which lie “beyond the limits of our tolerance.”

Commenting on Mill’s passage on tidology, [Lange \(2005, p. 398\)](#) helpfully remarks that to argue that general ecological forces or laws do not exist “is to argue that where ecological phenomena are concerned, there is no distinction to be drawn between the ‘greater causes’ and a host of petty, local, idiosyncratic influences that must be ascertained on a case-by-case basis.” On this view, what counts as a “greater” or as “lesser” depends on the local conditions at any moment and the distinction is otherwise arbitrary. This is a somewhat stronger thesis than I have presented here. I do not dismiss the possibility that the kinds of general forces ecologists theorize may operate in some way in the background. I have argued that their influence is so overwhelmed by contingent historical events that they are too weak to be detected at least in all cases that have been studied. Explanation depends far more on the identification of contingent historical events than on the extrapolation of theoretical assumptions.

This weaker thesis opens the possibility that future empirical research may produce results more in line with theoretical projections. I do not see why contingent or “external” forces that influence small populations—disease, weather, starvation, parasites, etc.—would not similarly operate on large populations, but it is logically possible that models may do better with large predator-prey populations studied over long time periods than with the relatively small populations so far studied. This must remain mere speculation, however, in the absence of a great deal of long-term empiri-

cal ecological research and of natural historians who want to dedicate their careers to this particular task (for discussion see [Salt 1983](#)).

I doubt there are a sufficient number of natural historians among professional ecologists to provide empirical studies that might detect the action of general forces in ecology. Natural historians, who might have pursued this kind of empirical research over the past 50 years, were largely driven out of the academy after the 1960s, when mathematicians, statisticians, physicists, chemists, and theoreticians from other sciences, many of whom brought their models with them, populated academic departments promising to make ecology a hard, mathematical science in response to the ecological crisis ([Greene 1986](#); [Pyle 2001](#); [Futuyma 1998](#); [Wilcove and Eisner 2000](#); [Schmidly 2005](#); and many others). If theoreticians have dominated the ecological establishment for 50 years, they cannot cite the absence of natural historians from their ranks as a reason that empirical evidence for their models has not materialized. This would be too much like the man who, having killed his parents, pled for mercy because he was an orphan.

5 Lotka–Volterra as a foundational theory in ecology

“It was in the late 1960s that I began a study of the moose and their wilderness at Isle Royale,” ecologist ([Botkin 1990](#), p. 30) has written, “with the idea that here was a place where we could come to understand how a balance of nature might be achieved...” A balance or constant correlation between predator and prey populations had been described in a set of equations derived from the work of Alfred Lotka and (independently) Vito Volterra early in the 20th Century. Variants of these equations have been thought to govern the dynamics of biological systems in which a population of a predator interacts with the population of its prey. According to Botkin (p. 36), the Lotka–Volterra equations provided a fundamental mathematical model on which “theory in ecology, from the origin of this science until the 1970s, relied”

The Lotka–Volterra equations treat all members of each population as the same; they do not distinguish, for example, between male and female, young and old. The equations predict that predator and prey populations will oscillate cyclically in relation to each other, either in regular patterns, perhaps dampening to constancy, or if out of phase, like a see-saw, with the ups of one correlating with the downs of another. Each population, in other words, will control the population the other in predictable and patterned ways. “It is worth repeating,” according to [Botkin \(1990, p. 38\)](#), “that with the Lotka–Volterra equations, two kinds of stability are possible: unending constant oscillations or dampened oscillations that lead to a fixed simple equilibrium.”

Ecologists who sought to provide general mathematical foundations for their discipline found in the Lotka–Volterra equations an example of how strategic assumptions about forces may advance ecology as a formal and mathematical science. As one theorist wrote in 1980, “Volterra’s work was a tour de force, in which he demonstrated with relatively simple mathematical models how the predator-prey interaction itself could lead to cyclical behavior. His usage of mathematics was in the best sense: as a deductive tool to explore the consequences of particular assumptions [T]he true legacy of Volterra is in the innovative use of mathematics to crystalize biological ideas and to allow insights otherwise impossible” ([Levin 1980](#), p. 423).

While Volterra did demonstrate “with relatively simple mathematical models how the predator-prey interaction itself could lead to cyclical behavior,” he did not show that the interaction ever does lead to cyclical behavior. In the same way, Malthus was able to use relatively simple mathematical models to show that population growth would lead to mass starvation—a boom-and-bust cycle for human population. Both kinds of models have been used extensively in resource management in spite of the absence of empirical confirmation of them. Of the Lotka–Volterra model, [Botkin \(1990, p. 48\)](#) has written,

Even two-species laboratory populations fail to support the theory, and long-term records of predator-prey populations in the wild show cycles that are not similar to those predicted by the theory, with huge variations in amplitude and periodicities of different length. In spite of the absence of agreement between theory and fact, the theory was used in science as a basis for resource management.

In the absence of observed simple oscillations, theoretical ecologists have sought to “save” the phenomena (one might think of equants and epicycles by analogy) by developing complicated tactical models of predator-prey cycles to show that different patterns can be derived from different assumptions, for example, about the relative importance of predator density, prey density, the ratio between them, and so on. [Arditi and Ginzburg \(2012\)](#) classify “the various models as prey dependent, predator dependent, and ratio dependent” (p. 8; see also 1989). Other authors identify nine ([Jost et al. 2005](#)) and fifteen ([Vucetich et al. 2002](#)) different kinds of tactical predator-prey models. [Hanski \(1991, p. 141\)](#) wrote of predator-prey dynamics that “a formidable tower . . . of models has been constructed by adding all sorts of conceivable, and often quite a few inconceivable, modifications to previous, simpler and in some sense more fundamental assumptions.”

[Weisberg and Reisman \(2008\)](#) make a related point. “To determine whether a theoretical result actually depends on core features of the models . . . , theorists have developed the technique of robustness analysis, the examination of multiple models looking for common predictions” (p. 106). As I interpret this statement, the idea is to climb through the “formidable tower” of Lotka–Volterra models to see which predictions are associated with many or most of them. The robustness of a prediction, on this view, lies in its grounding in many models, that is, its grounding in lots of theory. All this leaves open or ignores the question of its grounding, if any, in fact.

[Weisberg and Reisman \(2008\)](#) have written that the Lotka–Volterra model of predation “can account for oscillation and other periodic dynamics of populations in which there is no external stimulation, such as in unchanging environments” (p. 108). This describes what happens in unchanging environments to populations that are unaffected by anything but each other. The question remains what this has to do with populations found in nature, which do change and are subject to external causes. However “robust” the grounding of a prediction in theory, predator and prey population dynamics may result not from a “greater” cause but a host of petty, local, idiosyncratic, and contingent influences to be ascertained on a case-by-case basis.

If the force described in Lotka–Volterra models can be shown to represent a “greater” cause then it should yield accurate predictions or at least provide a predictive advantage in the way I have described. The advantage must be displayed in a

relation to empirical findings. The question is not whether a model fits the data better than another model or than a null model. The question is whether a strategic model is approximately predictive of the data, and when it is not, if it leads the ecologist to the kinds of intervening factors that are likely to explain the difference.

It is true that if one takes a quite flexible approach to modeling, one often can accommodate recalcitrant data by adding additional dynamics to a model. One can “save” the phenomena by retrofitting the model or from a smorgasbord of tactical models, each deploying different assumptions, by choosing the one that seems to fit best. To be general, however, the principles that model a force have to be approximately correct or provide a predictive advantage in many cases; they cannot be cherry-picked for each data set. They have to be approximately correct in a number of different environments. If a model is not approximately correct, if it fails to help empiricists make sense of the natural history of a place, it is hardly an argument for it that other models or null models fare even worse. It is more plausible to suppose that the explanation of phenomena in ecology is idiographic not nomothetic, i.e., it does not follow a priori assumptions.

6 Isle Royale: an example

The moose-wolf interaction at Isle Royale constitutes an almost ideal natural experiment in which to test predator-prey mechanisms. As [Sergio et al. \(2014, p. 1236\)](#) have written, the 59-year history of research at Isle Royale constitutes one of a few “landmark studies capable of integrating top predators as ecosystem components and structuring agents.”

The chronology of the Isle Royale study, however, does not suggest that any predator-prey model would predict the relative sizes of wolf and moose populations observed over more than five decades. Researchers have attributed changes in these populations to accidental, contingent, ephemeral, extemporaneous, external, haphazard, idiosyncratic, one-off, and particular events that affect each animal in its own way. The principal investigators who led the Isle Royale study describe an 80 percent decline of the wolf population in the early 1980s due to an outbreak of canine parvovirus. Shortly afterwards the population of moose also crashed (also about an 80 percent decline) “due to the combined effects of a severe winter, a tick outbreak, and a catastrophic food shortage. Most recently, it was learned that of all the factors affecting short-term fluctuations in moose abundance, wolves are the least important; whereas climatic factors, such as summer heat and winter severity, are far more significant” ([Nelson et al. 2011, p. 32](#)).

According to the [Isle Royale Research Project Websites](#), “By 1980, the study in its 22nd year, the moose population had tripled from its original size and then declined to half its maximum size. During that time, wolves more than doubled to fifty.” The website report continues, “In 1980 the wolf population crashed when humans inadvertently introduced a disease, canine parvovirus. In 1996, the moose population collapsed during the most severe winter on record and an unexpected outbreak of moose ticks. In the late 1990s ... a wolf immigrated to the island from Canada. In response, the wolf population generally increased throughout the early 21st century, despite declining moose abundance.” The website acknowledges, “The most important events in the history of

Isle Royale wolves and moose have been essentially unpredictable events—disease, tick outbreaks, severe winters, and immigrant wolves.” That wolves bring down mostly senescent moose too old to breed suggests another reason to believe that predation by wolves has little effect on the population of moose (Montgomery et al. 2014).

The problem is not just that Lotka–Volterra models fail to be predictive in contexts, such as Isle Royale, where one would expect them to work. The problem is not simply that they often get the sign of change wrong. The deeper problem is that these models give no clue about how to explain the discrepancies. They leave one ignorant about the causes that matter. Because of external or contingent factors, “wolves seemed to have relatively little impact on moose abundance” (Nelson et al. 2011, p. 32).

A 50 % decline of the wolf population at Isle Royale between 2011 and 2013 illustrates the many kinds of factors that drive the relative sizes of predator-prey populations. The 2013–2014 annual project report records sadly, “Late in 2011, just 2–3 months prior to the 2012 mating season, the alpha male of Chippewa Harbor Pack drowned in a flooded mine shaft along with two other wolves.” The alpha male had sired several pups in previous years and “likely would have continued to do so, possibly preventing much of the recent decline in Isle Royale’s wolf population (from 16 wolves in 2011 to eight in 2013).” The decline in wolves followed an increase in moose. The mine shaft incident “appears to have become more important than previously appreciated” (Vucetich and Peterson 2014, pp. 5–6).

Consider a different example. In 1995–1996, about thirty wolves were introduced into Yellowstone National Park to control the burgeoning population of elk (Bangs and Fritts 1996). At the time theoretical models suggested that the introduction would cause the number of elk to decrease between 5 percent and 30 percent and then stabilize or oscillate in that vicinity (Boyce 2000). Empirical evidence has not supported theoretical expectations.

Studies have shown that wolf predation has “little biological significance with respect to elk population trajectory. These results suggest that the effects of wolf predation on elk populations differ substantially over relatively small spatial scales, depending on a complex suite of interacting factors” (Garrott et al. 2005, p. 1245). “Elk are the primary prey of wolves in Yellowstone; so far, wolves have not significantly affected the elk population anywhere in the park” (Smith et al. 2003, p. 334).

7 Do hare eat lynx?

The Hudson Bay Company of Canada kept records of the number the pelts of hare and of lynx it bought from hunters in northern Canada between about 1848 and 1910. Egbert R. Leigh, Jr., in 1968, published a 60-page mathematical analyses of these data, plotting the numbers of hare against the numbers of lynx (as represented by the number of their pelts purchased). Leigh was unable to see any pattern or meaning in the oscillations. He concluded his study with the remark, “I find the whole oscillation most mysterious” (Leigh 1968, p. 61).

The oscillations of lynx and hare as derived from the data are mystifying. According to one commentator, “Unlike the classical theory which predicts the peak density of the predator to follow that of the prey, the peak volume of the hare pelt on average follows

that of the lynx” (Deng 2013, p. 2). In 1973, Michael Gilpin applied a sophisticated model to the data.

Since my model has greater flexibility than the Lotka–Volterra model and permits, for instance, stable limit cycle oscillations, I felt that it might fit the data better. But the regression fit was equally poor. In fact, it was worse than poor; it was impossibly bad. The signs of the interspecies coupling constants were reversed. Mathematically, the hare was the predator (Gilpin 1973, p. 728).

Other ecologists and mathematicians have remarked on the problem of opacity in the hare-lynx data. In a text on mathematical biology, Nicholas Britten (2012) commented that the oscillations observed between the predator and prey populations “are far from the regular oscillations predicted by Lotka–Volterra, and indeed occasionally move clockwise rather than counter-clockwise—suggesting that it is the hares that are eating the lynx” (p. 58).

What can explain the difference between what the data show and what a model predicts? Biologists have ventured many conjectures. Maybe hunters, driven by relative prices, put more effort into bagging one animal rather than the other in different years (Weinstein 1977). Maybe the lynx caught a disease—a possibility Gilpin suggests. Parasites are known to kill in some years a lot of hare in the study region (Keith et al. 1985). Hunting and trapping practices of the Cree-Ojibwa may have made a difference (Winterhalder 1980). The weather, particularly the depth of the snow, affects different animals differently (Stenseth et al. 1997). Sunspots are highly correlated with the number of hare (Sinclair and Gosline 1997). Likewise food shortages (Bryant 1981). There are fires.

Several species—not just lynx—prey on hare; and lynx might pounce on squirrels if they are abundant (Stenseth et al. 1997). Evolutionary change can make a difference (Cortez and Weitz 2014; Abrams and Matsuda 1997). “Climate change has been implicated as playing a leading role in the recent moose declines in Minnesota” (Mech and Fieberg 2014, p. 1143). Then there is immigration and emigration. Hall (1988; see also Finerty 1980) reviews many intervening factors and notes evidence “that the hares on Anticosti Island in the Gulf of Saint Lawrence go through cycles similar to hares on the mainland, but there are no lynx on Anticosti Island” (p. 19).

Any number of factors exogenous to a model seem more strongly to influence the number of hare and of lynx than do factors internal to the model. No mathematical model of predator-prey dynamics, moreover, offers a clue about which external factors affected the lynx and hare. No model leads ecologists to the confounding variables and suggests a way to put them together in an explanatory narrative. It seems that the principal use of predator-prey models may be to create more predator-prey models (it would be interesting to know if tactical variants of strategic models in ecology increase at an arithmetic, geometrical, or exponential rate). The intervening contingencies have to be discovered *ad hoc* and may differ week to week and site to site. If no detectable “greater” force governs lynx-hare interactions, what is a mathematical theorist to do? It may be time to summon the strange attractor. According to Schaffer (1984, p. 805) “the [lynx-hare] cycle was governed by a strange attractor.”

In 1954 Andrewartha and Birch wrote that the Lotka–Volterra competition model is “so unreal as to hold practically no interest for a biologist” (p. 411; see also Smith

1952; Pielou 1981; Hall 1988). Levandowsky (1976) wrote of Lotka–Volterra models, “Few ecologists are interested now in these misleading equations, but mathematicians apparently dote on them and are always trying to foist them on us—a classic case of the drunkard who loses his watch in the dark but looks for it under the lamp post because that’s where the light is” (p. 418).

This critique, however venerable and constant, often falls on deaf ears. Theoreticians today as much as ever engage each other in mathematical a priori modeling exercises without looking over their shoulders for empirical evidence (for examples, see Zhou et al. 2013; Loreau and Mazancourt 2013; Massarelli et al. 2013). Arditi and Ginzburg (2012, p. 14) expressed a concern that “theoretical ecology has developed as a more or less closed discipline, with theoretical predictions often taking the status of facts.” Other experts agree. “It would be a vast understatement to say that prey-dependent models based on Lotka–Volterra dynamics are the entrenched, majority view, for they are the foundation of most of the scientific literature on predation over the past century. Never mind that... no serious student of predation believes the model suitably depicts the real world” (Peterson 2013, p. 142). Botkin (1990, p. 41) has opined that “since physicists and mathematicians had the highest status among scientists, and since what physicists and mathematicians generally said was generally right, field ecologists tended to regard ... Lotka–Volterra equations as true ... on the basis of authority.”

8 Is there empirical evidence for Lotka–Volterra models in ecology?

“Predator–prey theory forms a cornerstone of ecology and drives much of population, community, and conservation biology” (Hebblewhite 2013, p. 511; citing Arditi and Ginzburg 2012). One might then expect that predator–prey theory rests on a considerable amount of empirical evidence. As far as I have been able to learn, it does not. White (2013) states this view in the title of a paper: “Experimental and Observational Evidence Reveals that Predators in Natural Environments Do Not Regulate their Prey: They Are Passengers, Not Drivers.”

Even laboratory attempts to confirm the Lotka–Volterra model fail. Gause (1934) conducted experiments that tried to produce in the laboratory the cycles predicted by Lotka–Volterra predator–prey equations. “However, instead of the desired coexistence, the most frequent result was that the populations (*Paramecium* sp. preyed upon by *Didinium nasutum*) went extinct either immediately or after a couple of oscillations” (Jost et al. 1999, p. 30). According to Lawler (2001, p. 239), Gause “was able to prolong the co-existence of the pair” only by ad hoc methods, for example “by adding a special refuge for *Paramecium* (oat sediment) or by adding one immigrant predator and prey every three days.” He cooked the experiments, but he still could not get the results he wanted.

In subsequent years, other investigators tried and failed to design in the laboratory experiments that would yield the results of the sorts that Lotka–Volterra models might predict (e.g., Luckinbill 1973; Veilleux 1979). According to Christopher Jon Jenson (2007, p. 13), “Each of these empiricists had a clear goal: to see if simple experimental systems could replicate the behavior of contemporary theory.” The purpose of these experiments, in other words, was not to *test* but to *implement* one or another Lotka–Volterra model. Confronted with a conflict in the laboratory between theoretic-

cal predictions and empirical results, Gause and those who followed him modified the conditions of the experiment to try to force an outcome that supported the theory. “This approach of adding to contemporary theory rather than questioning its fundamental validity would continue: Gause et al. (1936) and Flanders (1948) added prey refuges and Huffaker (1958) added physical complexity to achieve experimental coexistence” (Jenson, p. 4).

I have searched through the literature in vain to find a single case study that lends persuasive empirical support to a strategic Lotka–Volterra model. Hebblewhite (2013) collected data on wolf and elk populations in Banff National Park taken from 1985 to 2007. The data Hebblewhite presents (p. 516) do not look at all like constant or dampened oscillations leading to equilibrium such as those a strategic or simple Lotka–Volterra model predicts. If one assumes that the simple or strategic Lotka–Volterra model is approximately correct, one can “test for support for prey-, ratio, or predator dependent functional and numeric responses of wolf killing rate to elk density” (Hebblewhite 2013, p. 511). In other words, one can see which tactical model is the least implausible with respect to a particular data set. This would not show that predator and prey populations influence each other in a significant way but only that, if one assumes that they do, then one may be motivated to search through the formidable tower of conceivable (and in some cases inconceivable) tactical models to find the one that deviates the least from the empirical findings in a particular case. Even if predation is never a strong term in structuring animal populations, in other words, one can construct a tactical model—think of epicycles by analogy—that is less out of whack with the phenomena than other models for a given data set. This is a statistical trick, however, and does not detect the existence of “greater causes” in ecology.

In a comprehensive review of Lotka–Volterra models in ecology, Arditi and Ginzburg (2012, p. 48) have written, “It is hard to imagine a better example of a natural predator-prey system involving big mammals than wolves and moose in the Isle Royale National Park. It provides an almost perfect ‘natural experiment’ which is also the longest-running large mammal predator-prey study on earth.” Yet this case history offers no support for a predator-prey model.

If the Isle Royale natural experiment in Michigan is one leg of the empirical support for Lotka–Volterra theorizing, the lynx-hare interaction in Canada is the other. Turchin (2003, p. 346) has written, “The time series of lynx fur return statistics is the most famous example of oscillatory dynamics in ecology, discussed in every ecological textbook I know of, and is probably the most analyzed data set in ecology.” While it is possible to tour the formidable tower of possible tactical models to find one that fits the data better than others (as Turchin does), the simple models fail to be realistic, the tactical models fail to be general, and the assumption that predation is a “greater force” in population dynamics is not shown. This may be the reason that theoretical ecologists have emphasized the mathematical precision and sophistication of their models, as if this were evidence of their credibility.

The data are not alone; they have to be contextualized in terms of a thousand possible effects of a thousand possible causes operating on each individual organism at any moment. Once one allows external or “lesser” causes into the picture, they may crowd out the “greater” causes assumed by the model (Strong 1982, p. 245) as they plainly do at Isle Royale. In economic science, as Mill explained, the force of self-interest

is so strong that models based on it are quite predictive within a margin of error at least most of the time. The models test reasonably well when used predictively and they lead historians of economics to explanations of past events in part by applying the simple model and in part pointing to the typical reasons for discrepancies.

[Coleridge](#) (1818, p. 179) referred to the what he called the “notorious fact” that zoology was “weighed down and crushed, as it were, by the inordinate number and manifoldness of facts and phenomena apparently separate, without evincing the least promise of systematizing itself by any inward combination, any vital interdependence of its parts.” Darwin helped to systemize zoology, but a huge theoretical effort, lasting almost a century, to detect empirically unifying concepts and theories in ecology has failed. As [Bromley](#) (2012) has pointed out, “Ecologists seem to have succumbed to the warning of the German philosopher Georg Christoph Lichtenberg, who noticed, ‘Delight at having understood a very abstract and obscure system leads most people to believe in the truth of what it demonstrates.’”

Theoreticians must engage not only with each other but also with naturalists. But natural historians have been chased out of the profession of ecology ([Wilcove and Eisner 2000](#)). There is no one to tell mathematicians about mine shafts. There remains only a dwindling number of naturalists to vet a large number of theorists. That is why I believe that the theoretical enterprise in ecology, at least insofar as it concerns predator-prey modeling, is now completely hopeless.

“To the theoretician, models are a part of the real world. In studying the logical consequences of assumptions, the theoretician is discovering, not inventing, and is spiritually akin to the natural historian” ([Levin 1981](#), p. 866). I do not think this is at all right. The forces postulated by theoretical models in ecology, often drawn from other sciences ([Simberloff 1980](#)), are not detected in the natural world, at least in view of the examples I have discussed. The theoretical enterprise in ecology is carried on independently of empirical research; ecologists often complain that it has replaced it ([Van Valen and Pitelka 1974](#)). According to [Sagarin and Pauchard \(2012\)](#), the study of natural history has “fallen from favor in academe.” Sagarin and Pauchard add: “The danger is that bad assumptions can be measurable and precise, esthetically pleasing and apparently useful, but the hypotheses may be irrelevant to the natural world and/or make the right predictions for the wrong reasons” (p. xii).

9 Stone soup

The relation between ecological theory and natural history might be understood by an analogy to the familiar folk tale of stone soup. In the well-known story, hungry newcomers to a village persuade the locals to give them food. They do this by setting up over a fire a large cooking pot in which they boil a stone. When the villagers inquire what they are doing, the strangers reply that they are preparing a magnificent stone soup for everyone to enjoy. All they need is a missing ingredient to improve its flavor. One villager provides carrots, another brings potatoes, another mutton; each time the cooks ask the townspeople for just another garnish to make it right. Eventually, all enjoy a delicious and nourishing repast.

In their textbook in ecology, [Pickett et al. \(2007, p. 138\)](#) ask, “What must be added to the Lotka–Volterra models to make them better reflect natural processes?” One should

consider the reply: “Everything.” Immigration. Emigration. Parasites. Pathogens. Weather. Fire. Sunspots. Social structure. Sex ratios. Age. Cultural and economic factors in human populations. Inbreeding. Availability of vegetation. Mineshafts. Everything must be added to ecological models if one is to understand ecological facts. Another way to put this is that the models themselves contribute nothing. They do not appear even to offer guidance ecologists can use in a particular case to look among a thousand possible intervening or external causal factors for those that are most likely to confound the postulated Lotka–Volterra force, mechanism, or effect.

In the same way, theorists like the hungry entrepreneurs new to the town (indeed many theorists immigrated into ecology from other sciences) may ask empiricists to supply the missing ingredients that will, along with the theory, allow a satisfying causal explanation of the phenomena, for example, the number of wolf and moose at Isle Royale. It is unclear whether the theory makes any more of a contribution to the explanation than the stone makes to the soup.

10 Should more wolves be brought to isle royale?

On May 8, 2013, the three lead researchers at Isle Royale project, John A. Vucetich, Rolf O. Peterson, and Michael P. Nelson, published an op-ed piece in the *New York Times*. They wrote, “The National Park Service is expected to decide this fall whether to save the Isle Royale wolves—a decision that will test our ideas about wilderness and our relationship with nature.” They added, “With the number of wolves reduced to little more than a handful, they face the prospect of extinction.” These authors explain the irony implicit in human actions to bring new wolves into Isle Royale which, as a wilderness area, is supposed to be free of human influence (Vucetich et al. 2013).

Nevertheless, these lead researchers in the study of wolves and moose believe that “the National Park Service should initiate a genetic rescue by introducing new wolves to the island.”

The history of the study of moose and wolf at Isle Royale is praiseworthy for its intellectual honesty, its commitment, its willingness to go where the facts rather than the theory take it, and its concern for the values the public cherishes in its relation to the natural world. One of the saddest consequences of the extinction of the wolf at Isle Royale would be the fate of the research project itself. Vucetich et al. (2012, p. 134) candidly make this point. “Allowing wolves to be excluded from Isle Royale would cause the end of moose-wolf research.” They add that “without wolves the Isle Royale wolf–moose project would be in no position to effectively compete for funding from the US National Science Foundation, the loss of which would be the death of the project. ... There is little reason to think that the longest study of any predator–prey system in the world would survive the loss of wolves from Isle Royale.”

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