



Where Newton might have taken ecology

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Abstract

A dilemma in ecology: Ecologists aspire to build a discipline to both understand the natural world and to provide society with tools to make responsible decisions about the environment. For both of these purposes, most sciences have, at their core, a set of empirical generalizations that predict the behaviour of important properties of nature (e.g., Newton's laws of mechanics, Mendeleev's periodic table, Mendel's genetics). Ecological science, in contrast, has favoured studies to understand processes (competition, population regulation, etc. – i.e., independent variables) rather than models that predict attributes of nature (dependent variables). Classical reductionist scientific training emphasizes studies of mechanisms under controlled experimental conditions. Yet, inferences about nature from experiments are nearly always unjustifiable extrapolations beyond the experimental conditions. Mechanisms that are statistically detectable in experimental systems may contribute very little to the variation of nature. Studies of ecological processes in isolation may contribute to “expert understanding,” but experts have been shown to be poor predictors of the behaviour of natural systems.

A proposed solution: The more relevant, often neglected question is: what factors can statistically account for the observed variance of nature? A more Newtonian approach to ecology would: (a) first, specify the properties of nature (i.e., dependent variables) whose variance is of concern; (b) develop models that statistically capture the variance of those properties in nature; (c) demonstrate that those models can predict independent data; and, only last, (d) experimentally test hypotheses about processes that could give rise to the predictable patterns in nature.

Why it matters: Successful disciplines identify specific goals and measure progress toward those goals. Predictive accuracy of properties of nature is a measure of that progress in ecology. Predictive accuracy is the objective evidence of understanding. It is the most useful tool that science can offer society.

KEYWORDS

ecology, macroecology, philosophy, prediction, progress, science

1 | WHITHER GOETH ECOLOGY?

In 2015, the President of the Ecological Society of America (ESA) wrote about the future of the discipline (Inouye, 2015). On one hand, the discipline aspires to be a basic science: “The science of ecology is about relationships—among organisms and habitats, on all scales—and how

they provide information that helps us better understand our world.” The discipline also aspires to provide tools to deal with anthropogenic perturbations of nature. Ecologists are typically interested in both goals: roughly three-quarters of the grant proposals for basic research in evolution and ecology funded by the Natural Sciences and Engineering Research Council of Canada (NSERC, 2018) are presented

as being relevant to specific contemporary environmental issues (D. J. Currie, unpublished). According to Inouye (2015), “We enter a time when society is armed with the scientific knowledge and ability to make responsible decisions.”

But how effectively has the academic discipline of ecology armed society with useful tools? Inouye (2015) argues that “basic research on organism and environment interactions has had far-reaching impacts on legislation.” Yet, the examples he cites are from ecological work and legislation in the 1960s and 1970s. Peters (1991, Chap. 1) presented evidence that “[basic] ecology is sometimes a weak science in need of harsh critical scrutiny.” Other ecologists have expressed similar views (Keddy & Weiher, 1999; Pickett, Kolasa, & Jones, 1994; Saaranen, 1980). The view from outside the discipline is also discouraging: in a sample of 10 Canadian university environmental engineering programs (which presumably focus on responsible decisions), none requires an ecology course, although some require courses in molecular biology or microbiology. Apparently, academic ecology has not provided tools that environmental engineers find useful.

I submit, paraphrasing Platt (1964), that certain methods of ecological thinking are more likely than others to produce tools useful to society.

2 | HOW ECOLOGY PROCEEDS

Scientists, including ecologists, are trained to ask how processes work. How do fish survive hypoxia? How does resource availability affect organisms’ growth? Is light composed of particles or waves? Reductionist questions such as these are often best addressed in small-scale, controlled experiments. Ask an undergraduate how to test an ecological hypothesis, and s/he will almost certainly suggest an experimental manipulation because that is what s/he has been taught. The frequentist statistics that s/he studied were designed to analyse data from experimental agricultural plots. The literature s/he read often phrased environmental issues as experimental manipulations: what are the consequences of climate changes (Lubchenco et al., 1991), or of habitat fragmentation (Haddad et al., 2015), or of plastics in the ocean? These questions all focus on *independent* variables.

Yet, society is typically more concerned about variation in properties of natural systems – that is, dependent variables – such as productivity, or ecosystem functions such as pollination, or species’ ranges, or contaminant levels in biota, or species’ abundances. Ecologists are unanimous that, for any of these properties of natural systems, many processes act simultaneously, pushing and pulling in different directions (Figure 1 shows a mind-boggling example). Few

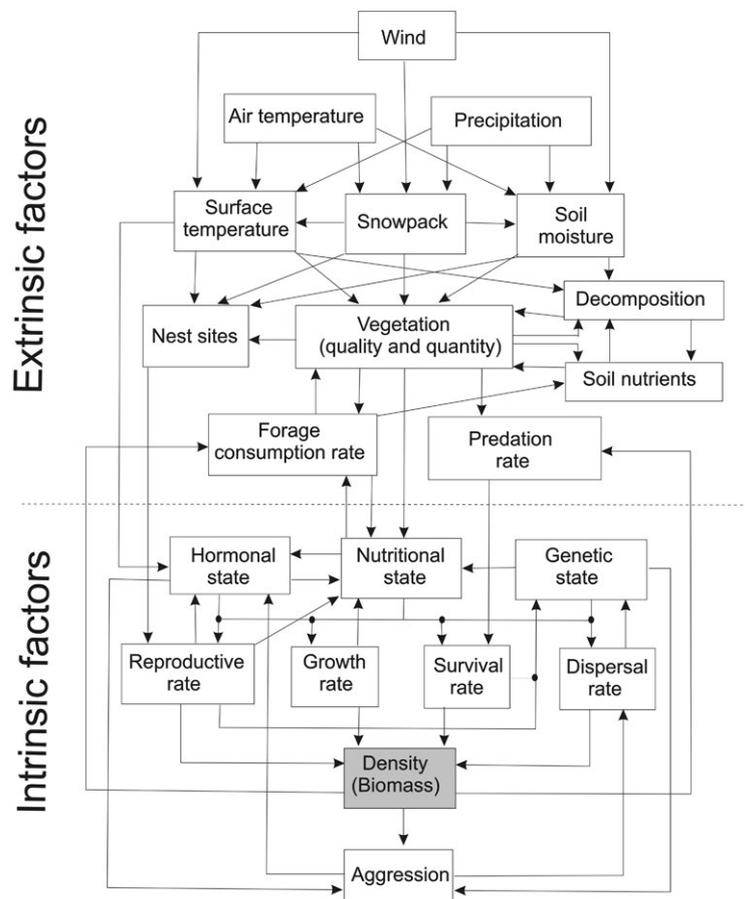


FIGURE 1 Part of the International Tundra Biome program and the International Biological Program sought to explain the cyclic population fluctuations of lemmings (the main herbivore) at Barrow Alaska (the shaded box, i.e., the dependent variable). This figure, adapted from figure 10–15 in Batzli, White, Maclean, Pitelka, & Collier (1980) and figure 1.6 in Chitty (1996), summarizes the “Relationships among factors influencing lemming population density”

ecologists would dispute that the large-scale behaviour of whole systems may bear little relationship to underlying small-scale processes (e.g., Dyzinski & Tilman, 2007; Taubert et al., 2018).

In this light, users of ecological research (e.g., environmental engineers, or framers of environmental legislation, or cottage owners who are concerned about algae in their lakes) care little about processes that *may* act in nature. They probably have little interest in competition, or population regulation or habitat fragmentation. Rather, they care about properties of natural systems and the ability to predict and to manipulate them. In this view, the first task of ecological science is to identify what properties of nature are important to society, and then to identify what Popper (1990) called the “propensities” of nature: the tendency of particular outcomes to be related, with measurable probabilities, to specified “generating conditions.” In ecology (as in epidemiology), these propensities will usually initially be expressed as correlations.

Experiments rarely address propensities. First, the scales usually do not match. The systems and questions that motivate ecological investigations are generally very large, whereas experiments are generally only possible at much smaller scales. If one wants to make inferences about natural ecological systems, then one must sample the variability of those systems. Second, experiments are designed to manipulate some variables while controlling others. Statistical inferences are limited to systems subject to the same controls. Consequently, inferences about nature from experiments are nearly always gross extrapolations beyond the conditions in the experiment. Ecological experiments most often suggest post hoc explanations of nature, as opposed to explicit predictions with confidence limits.

Consider, for example, the classic study of predation in the intertidal zone by Paine (1966). The motivating hypothesis was quite general (p. 65): “Local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species.” Paine experimentally removed predators from an 8 m × 2 m stretch of shoreline in Washington State. He concluded that (p. 73): “Where predators capable of preventing monopolies are missing, or are experimentally removed, the systems become less diverse.” Paine’s conclusion is stated as a propensity, yet it is based on short-term changes at a single site. Menge (1992) subsequently noted that Paine’s results “provided an explanation for some of [the] patterns” of organisms’ abundance in Washington, but they failed to predict the patterns of abundance at two intertidal sites in near-by Oregon. Would Paine’s conclusion also be true in a case where the predator is naturally absent, rather than removed, or if some other predator had been removed? No inference about any other system is possible. Rather, Paine’s experiments provided a *narrative* about a specific experimental system, not improved ability to predict the behaviour of intertidal systems in general.

Similarly, the review of trophic cascades in terrestrial systems by Schmitz, Hamback, and Beckerman (2000) asked whether studies reported any detectable effect of experimental removal of carnivores on “some plant variable.” They did not ask to what extent variation

among natural systems in a specific variable (e.g., plant biomass) is related to the presence/absence of carnivores (cf. Currie, Dilworth-Christie, & Chapleau, 1999). Predicting states of nature was not the goal. This illustrates, I believe, why environmental engineers find little need for ecology.

Consider, now, an alternative approach.

3 | ENVIABLE PHYSICS

Physics is sometimes seen as enviable because it is quantitative, experimentally rigorous, and reductionist. For me, the physics that beginning scientists learn is enviably successful for other reasons. First, physicists identified a set of properties of nature whose variation they considered important. They then provided simple empirical generalizations (“laws”) that predict much of the macro-behaviour of those properties: for example, displacement of fluids (Archimedes’ principle), movement of macroscopic bodies (Newton’s laws of mechanics, Hooke’s law), pressure of gasses (Boyle’s law), magnetism (Faraday’s law), etc. Once those empirical “laws” were developed, non-experts could usefully apply them to a host of practical problems (e.g., dropping projectiles on specified locations, generating electricity, remotely transmitting information).

Physics is not alone in this respect: most sciences have similarly developed empirical patterns that summarize the basic behaviour of their systems (Table 1). For example, Mendeleev (and others) realized that, if chemical elements are arranged in order of increasing atomic weight, their properties show predictable patterns. That ordered list (i.e., the periodic table) predicted the existence of elements not yet discovered. Importantly, these predictions came decades before knowledge of atomic structure (Gribbin, 2002).

In biology, Mendel observed statistically predictable outcomes from genetic crosses. Textbooks of genetics and of applied genetic counselling begin with Mendel’s empiricisms. Epidemiology also begins with statistical associations. Empirical generalizations form the basis of evidence-based clinical practice (treatment X does, or does not, produce the desired outcome, e.g., Canadian Task Force on Preventive Health Care, 2016; Glynn, Murphy, Smith, Schroeder, & Fahey, 2010).

Lawton (1999) famously questioned whether there are general laws in ecology. Avoiding the issue of what constitutes a law, there are, at minimum, many strong empirical generalizations in ecology. Examples include the regular distribution of the numbers of individuals among species (Preston, 1962), the species–area relationship (MacArthur & Wilson, 1967), the relationships between metabolic rates and body mass (Peters, 1983), or the relationship between biomes’ geographic distributions and climate (Whittaker, 1970). For other examples, see Brown, Gillooly, Allen, Savage, and West, (2004), Connor and McCoy (1979), Currie (1991), Dillon and Rigler (1974), Hubbell (2001) and Taylor (1961). Linquist, Gregory, Elliott, and Saylor (2016) reviewed 240 meta-analyses in ecology, 84% of which identified “resilient generalizations”—statistical patterns that applied across a range of different systems and conditions.

TABLE 1 Examples, from a variety of fields, of empirical generalizations that capture the broad behaviour of important state variables

Planetary motions	Kepler's laws
Motion on earth	Newton's mechanics
Properties of elements	Mendeleev's periodic table
Behaviour of gasses	Boyle's law
Hydrology: fluid flow	D'Arcy's law, Stoke's law
Light transmission	Beer–Lambert law
Genetic crosses	Mendel's laws
Molecular biology: information coding and transmission	Genetic code Central dogma of molecular biology
Economics	Law of supply and demand Hotelling's rule, Wagner's law
Epidemiology	Cholera cases and the Broad St. well; smoking and lung cancer, etc.
Pharmacology	Beta blockers and a variety of conditions
Medicine	Clinical practice guidelines, for example, Cochrane reviews

Yet, I am unaware of any attempt to identify and codify the basic set of empirical relationships that predict the general behaviour of ecological systems (with some exceptions, cited above), either as the organizing principles of the academic discipline, or as guidelines of applied best practice. Instead, introductory ecology textbooks are catalogues of concepts and processes that *may* be relevant in at least some situations in nature (e.g., evolution, competition, predation, food webs, succession, etc.). The Ecology Curricular Framework Initiative of the Ecological Society of America (undated) proposes that the “basic modes of ecological inquiry [are] description, comparison, experimentation and modeling.” Identifying the predictable patterns of nature does not figure in the list. Nor have I ever seen an ecology text that begins with the empirical patterns of life, and then shows how the properties of ecological systems follow from them. In contrast, I *have* seen extremely influential research works do so: for example, Preston (1962), MacArthur and Wilson (1967, p. 8 ff.), Hubbell (2001, p. 116) or Brown et al. (2004).

4 | WHAT DARWIN AND NEWTON SAW ON THE “ENTANGLED BANK”

Consider what Darwin (1859) and Newton (1730) saw when they looked at nature. The “Entangled Bank” in the final paragraph of

Darwin's *On the Origin of Species* is iconic, but a less cited passage in *the Origin* (Chap. 3) summarizes Darwin's view: “Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins!” Darwin focuses on the innumerable individual actions and reactions, rather than “definite laws.” Textbook definitions of ecology typically follow Darwin: ecology is the study of “the relations of organisms to one another and to their surroundings” (Ricklefs & Miller, 1999). Little wonder that the goal of ecology is often portrayed as being to dissect and understand the complicated workings of nature (Chitty, 1996; Paine, 2010), and to develop narratives about them (Allen, Tainter, Pires, & Hoekstra, 2001).

Contrast this with the view proposed by Isaac Newton: “To tell us that every Species of Thing is endow'd with an occult specifick Quality by which it acts and produces manifest Effects, is to tell us nothing: But to derive two or three general Principles of Motion from Phaenomena, and afterward to tell us how the Properties and Actions of all corporeal Things follow from those manifest Principles, would be a very great step in Philosophy, though the Causes of those Principles were not yet discover'd: And therefore I scruple not to propose the Principles of Motion above-mention'd, they being of very general Extent, and leave their Causes to be found out [later]” (Newton, 1730).

In the ecological context, the “occult specifick Qualit[ies]” to which Newton refers are the tangles on Darwin's bank: the “action[s] and reaction[s]” among the “innumerable plants and animals.” Instead of focusing on tangles, Newton would have us focus on general patterns (“two or three general Principles”) from which state variables (“Properties”) can be predicted (“follow”) for “all corporeal things.”

5 | A NEWTONIAN METHOD IN ECOLOGY

Instead of focusing on interactions among organisms (i.e., *processes*, *independent variables*), Andrewartha and Birch (1954) (also Krebs, 2009) defined ecology as the study of the distribution and abundance of organisms (i.e., *dependent variables*). This definition defines both the objects of study—state variables *in nature*—and a straightforward measure of success: how well do observations of nature correspond to predictions? The variables or processes that need to be in our models are the ones that improve predictive ability in nature.

Risking hubris, allow me to propose a more Newtonian model of ecological investigation, with the goal of identifying “two or three general principles.”

1. First, identify the ecological state variables Y_i of natural systems whose variation would be useful to predict. These variables may include biomass, productivity, species richness, carbon storage, geographic ranges, species' abundances, species' reproductive success, etc.

2. Look for the “propensities” (Popper, 1990) in that variation: what distinguishes cases (places, times) where Y_i is high from cases where Y_i is low? Initially, this often means testing the correlations between Y_i and hypothesized drivers (X_1, X_2, \dots). Then, model $Y_i = f(X_1, X_2, \dots) + \varepsilon$, where ε is residual error. Popper (1990) suggests that, in natural situations, Y is likely to be influenced to different degrees by many variables; however, the bulk of the variation in Y —its propensity—may be related to a manageable small number of variables X_i . For example, the path of a comet through the solar system is influenced by the gravitational attraction of every other object in the solar system. Yet, the trajectory—the propensity—depends primarily on the gravitational attraction of the sun. The attraction of planets, asteroids, etc. is summed up in the error term.

When $Y_i = f(X_1, X_2, \dots) + \varepsilon$ results from fitting a statistical model to data, the resulting model represents an inductively generated hypothesis, *not* a hypothesis test. One may also generate hypotheses/models by other means, for example, based on speculation or on understanding of processes that may operate. In either case, the goal is the same: to produce a model from which predictions can be deduced.

3. Test whether the model $Y_i = f(X_1, X_2, \dots)$ can accurately predict Y_i in independent data sets, for example, at a different time, in a different geographic area, for a different set of species (or a different comet), under a different management regime, etc. This is not the same as using bootstrapped subsets of the original data. Bootstrapping within a data set assesses model fit, not predictive ability; see Fourcade, Besnard, and Secondi (2018). Bootstrapping is not the same as predicting outside the calibration data set.
4. If a model passes test 3, then test whether $Y_i = f(X_1, X_2, \dots)$ describes a causal link. Manipulate X_1, X_2, \dots , and observe whether Y_i changes in the manner predicted by the model. To predict the variation of Y_i in nature, this will often mean relying upon “natural experiments” in which X_1, X_2, \dots change for reasons not controlled by the scientist.
5. Once it has been demonstrated that there is a predictive pattern and a causal link, then propose and test hypotheses about mechanisms that could give rise to the pattern. This is where “understanding” can actually be demonstrated and quantified.

As an example, consider cultural eutrophication of freshwaters in the 1960s–1970s (Valentyne, 1974). High phytoplankton biomass in some waters led to anoxia, fish kills, foul smells, etc. The state variable of concern in this case (step 1) was phytoplankton (or sometimes cyanobacterial) biomass, the abundance of which varied greatly among water bodies, and through time within water bodies. It was hypothesized that phytoplankton biomass may depend upon nutrient availability. To test this hypothesis (step 2), Dillon and Rigler (1974) sampled a set of lakes in southern Ontario, Canada, among which chlorophyll concentration varied widely. They found that summer chlorophyll concentration in lakes correlated very strongly with spring total phosphorus concentration (Figure 2). They tested the ability of the Ontario relationship to predict chlorophyll concentrations in independent

data. First, they found that the Ontario statistical relationship accurately predicted chlorophyll concentration in a set of Japanese lakes (step 3). Importantly, (step 4) the model also predicted temporal changes of chlorophyll in Lake Washington when phosphorus loading to the lake changed. Subsequently, David Schindler and colleagues experimentally manipulated the independent variable (phosphorus) in a natural lake (Schindler & Fee, 1974). P fertilization led to the predicted increase in phytoplankton biomass. This body of evidence led to legislation restricting phosphorus levels in wastewater (Valentyne, 1974). Further, the empirical chlorophyll–phosphorus relationship of Dillon and Rigler (1974) was used to predict the effect of cottage construction around lakes, based on the amount of phosphorus leakage from domestic septic systems (Dillon, 1975). Although there were many subsequent experimental studies (step 5) of the mechanisms of P cycling (e.g., Currie & Kalff, 1984; Wen, Vezina, & Peters, 1994), few did much to improve the ability to predict and manage the consequences of eutrophication.

Consider a second, more recent example that reversed the order of operations, with perverse effect. Habitat fragmentation is often portrayed as a serious threat to biodiversity (Fourcade et al., 2018; Tilman et al., 2017) (step 1). Experiments (step 5) have clearly shown that species diversity can be lost from isolated habitat patches (Haddad et al., 2017; Laurance et al., 2011). Fletcher et al. (2018) tell the reader that, “Decades of advances in metapopulation and meta-community theory show clearly that effects of habitat fragmentation can increase extinction rates and decrease colonization rates, leading to reduced likelihood of population persistence and lower diversity.” However, the state variable that usually concerns people is diversity within some managed area (e.g., parks, municipalities, countries), rather than diversity within individual experimental habitat patches, or in theoretical models. So, do areas (landscapes) with greater habitat fragmentation have fewer species than landscapes with equal amounts of habitat, but concentrated in larger patches? In a meta-analysis of 118 landscape-level studies, Fahrig (2017) did not find systematic negative effects of fragmentation, after accounting for total habitat amount (step 2). Nor did De Camargo, Boucher-Lalonde, and Currie (2018) when they examined bird species in 991 landscapes across southern Ontario (Canada). In other words, the mechanisms studied in experimental systems did not predict the propensities of nature (step 5 came before 2, 3 and 4). Fletcher et al. (2018) argued that the mechanisms are well understood; Fahrig’s (2017) data must be wrong. Yet, there is a simpler possibility: that mechanisms isolated in model systems are not necessarily the main drivers of natural variation in nature. There is no logical reason to infer that they must be.

I suggest that, if ecologists wish to “arm [society] with the scientific knowledge and ability to make responsible decisions” (Inouye, 2015), then the propensity of natural systems (e.g., no tendency for more fragmented systems to have lower diversity) provides a predictive tool. It remains to be shown whether experimental observations of negative effects of fragmentation (Haddad et al., 2017) can measurably improve predictive ability in natural systems.

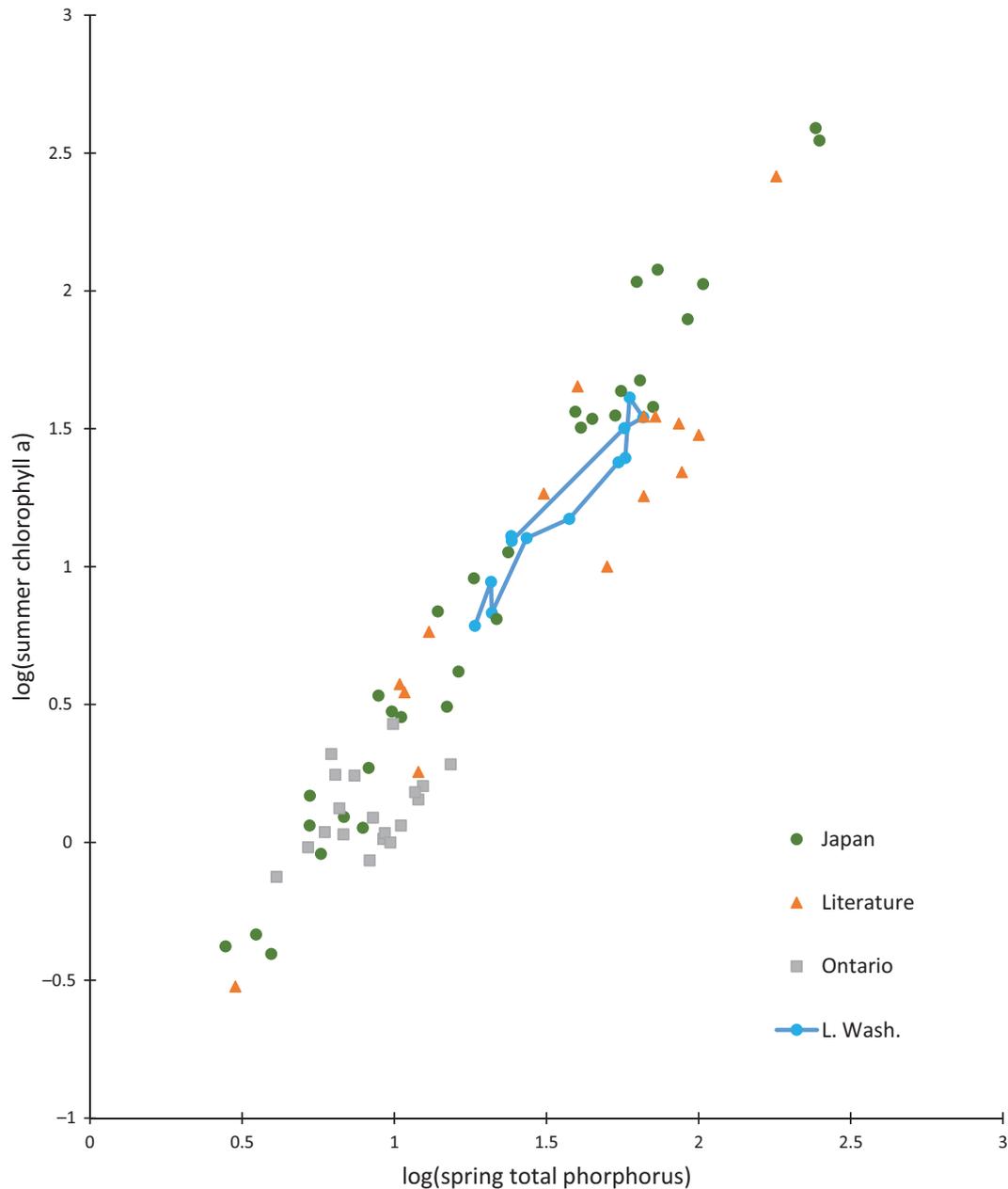


FIGURE 2 The relationship between summer-time chlorophyll a concentration and spring-time total phosphorus concentration (TP), measured in several sets of lakes: one set in Japan, another in southern Ontario, Canada, a third in lakes drawn from the literature, and finally, in Lake Washington from 1957 to 1971. Data are from Dillon and Rigler (1974). TP in Lake Washington increased from 24.2 to 65.7 mg/m between 1957 and 1963, and then decreased to 18.4 mg/m by 1971. The chlorophyll–phosphorus relationship is congruent among geographic regions, and it remained consistent through time when phosphorus changed in Lake Washington [Colour figure can be viewed at wileyonlinelibrary.com]

6 | BUT WHAT ABOUT UNDERSTANDING?

By now, some readers will be bristling: empirical patterns are just correlations; I want to understand how nature works. Paine (2010) wrote, “Detailed natural history coupled to experimental ecology has provided a rich harvest of insights into how natural communities in all ecosystems function, insights that cannot be gleaned from macroecological analyses.” “Correlations, however striking, are no substitute for experimental evidence” (Chitty, 1996, p. 39).

Moreover, “Observational studies ... have often magnified ... controversy because inference from nonmanipulative studies is limited to correlation ...” (Haddad et al., 2015).

Of course scientists want to understand! Yet, the history of science is riddled with “understanding” that subsequently proved to be incorrect. Galileo’s contemporaries understood that the Earth does not move: scripture and the Pope told them so. For centuries, physicians understood that human health depends upon the balance of the corporeal humors: black bile, yellow bile, phlegm and blood.

Many geologists first rejected continental drift because they knew of no natural process that could cause it (Gribbin, 2002). Velikovsky (1950, 1955) understood that phenomena ranging from glacial erratics to the Biblical parting of the Red Sea were due to fragments of Venus that passed close to the Earth.

But, “understanding” is a personal psychological state with no confidence limits. How do you know that you understand? The only concrete answer to that question that I have ever found is: predictive ability. Scientists develop hypotheses or models that *predict* properties of the systems that interest them. Those predictions permit hypothesis tests (Houlahan, 2016; Marquet et al., 2014; Peters, 1983; Platt, 1964; Popper, 1958; Rigler, 1982). But more than that, “Predictive power [is] the strongest evidence that the natural sciences have an objective grip on reality” (Gottfried & Wilson, 1997). Predictions with confidence intervals are what permit evidence-based management of nature (e.g., Dillon, 1975). One may “understand” why airplanes can fly, or why CaCO_3 is a good antacid; one can relate a coherent narrative about those things. However, in the end, successful prediction is the evidence that that understanding is real: the narratives derive from models that survived further tests.

One might object: isn’t “expert opinion” based on understanding acquired through long experience? Figure 1 presents the opinion of a team of experts (Batzli et al., 1980) about the factors that determine lemming abundance at Barrow, Alaska. Yet, the authors conclude that, “it does not seem that any single extrinsic or intrinsic factor can explain the population dynamics of lemmings. Rather, lemming populations respond to a number of factors that act and interact concurrently to determine the amplitude of fluctuations.” Chitty (1996) argued that the decades of research on lemmings had “provided a rich harvest of insights into how natural communities ... function,” but he goes on to say that that understanding did not answer the original question: what controls lemming population dynamics (p. 206)?

Empirical studies of “experts” in many domains—university admissions, clinical pathology, financial investment, sports, weather forecasting—consistently find that measurable outcomes (e.g., financial returns) based on expert opinion are little better than outcomes from less skilled peers, or from simple statistical models (Camerer & Johnson, 1991). Expert understanding is clearly useful in formulating plausible hypotheses, but in the end, “Prediction is the only way to demonstrate scientific understanding” (Houlahan, 2016).

7 | AND WHAT OF MECHANISM?

Newton (above) did not “scruple... to propose the Principles of Motion above-mention’d,... and leave their Causes to be found out [later]” (Newton, 1730). First, predictive patterns. Then, hypotheses about the processes that generate the patterns.

Unquestionably, mechanisms are useful when they improve the ability to predict the phenomenon of interest, and/or other phenomena. During a cholera outbreak in London in 1854, Dr John Snow associated incidences of cholera with proximity to

the Broad Street water well. Based on this statistical association, Snow persuaded local authorities to remove the well handle. New infections near the well subsided (Burke, 1985). This provided a means to control cholera decades before Louis Pasteur’s germ theory of disease suggested a mechanism. However, building on Pasteur’s work on microbes, Robert Koch was able to associate several diseases (including cholera) with bacterial infections (Lippi & Gotuzzo, 2014). Knowing the mechanism underlying cholera was very useful because it made important *new* predictions: for example, boiling water contaminated with cholera could kill the bacteria and make the water safe to drink. The mechanisms came after the correlations.

Moreover, mechanisms, however elegant, do not necessarily increase predictive capacity. They may even be a distraction. Consider the R^* theory of interspecific competition (Tilman, 1988). Tilman began by telling the reader that “the central goal of ecology is to understand the causes of the patterns that we observe in the natural world” (p. 3), and that “pattern in ecology is caused by the constraints of the physical and biotic environment and by the trade-offs that organisms face in dealing with these constraints.” Tilman developed an elegant theory that predicts the outcome of interspecific competition, based on which species can reduce the availability of a limiting nutrient to the lowest level (R^*). A massive 11 + year study was subsequently carried out at Cedar Creek to test the theory. Reviewing the Cedar Creek results, Dybzinski and Tilman (2007) concluded that R^* theory accurately predicted the outcome of competition between isolated pairs of species. “However,” they continued, “only a few of our paired species coexisted under our experimentally imposed conditions (homogeneous soils, high seeding densities, minimal disturbance, regular water, and low herbivory levels), [whereas many species coexist under natural conditions], suggesting that other coexistence mechanisms help generate the diversity observed in natural communities.” Tilman’s R^* theory contributed to the understanding of trade-offs in isolated competitive interactions, but those isolated interactions did not improve predictability of species assemblages in nature.

I am not suggesting that this work was futile. Rather, my point is that these studies invested great resources to study mechanisms before identifying a predictive pattern in nature. Knowing those mechanisms has not demonstrably improved predictions of nature. Nor has it obviously “armed [society] with the scientific knowledge and ability to make responsible decisions” (Inouye, 2015).

8 | CONCERNS ABOUT CORRELATIONS

The method I propose above relies initially upon observation and correlation. The reason is simple: except in rare studies in which experiments sample the relevant variation of nature (e.g., Borer et al., 2014; Harpole et al., 2016), inference cannot be made from experiments to variation in nature. Inference about nature is nearly always an extrapolation beyond the conditions of the experiment. Statistical significance in an experiment does not imply importance in nature.

Yet correlational studies are toxic to some scientists because correlation does not imply causation (see the quotes that begin section 6, above). The subtitle of Krebs (2009) textbook of ecology is "The *experimental* study of distribution and abundance" (my emphasis).

While correlations have clear limitations (below), correlations also have essential roles in science. First, they may suggest hypotheses (Rigler, 1982). For example, the variation in algal biomass among lakes is strongly correlated with the variation in total phosphorus (Dillon & Rigler, 1974). Why? Perhaps because phosphorus limits algal growth (Likens, 1972). Note that this is a *hypothesis* generated by *induction*. It is *not* an inference (by deduction) of causation, based on a correlation.

Second, correlations provide explicanda: things that subsequent theory must predict. For example, why does species richness vary with area (MacArthur & Wilson, 1967; Preston, 1962)? Why does population density scale in proportion to mass to the $\frac{3}{4}$ power (Enquist & Niklas, 2001)? Why is geographic variation in species richness strongly correlated with climate (Currie et al., 2004)?

Third, when hypothesized mechanisms make predictions about expected patterns in nature, observed correlations can be used to test them. Correlation may not imply causation, but causation almost always implies a statistical association. If Figure 1 is regarded as a hypothesis, each of the arrows predicts a correlation. The species–energy hypothesis (Hutchinson, 1959) predicts strong correlations not only between latitudinal gradients of species richness and climate, but also between the density of individuals and climate (Currie et al., 2004). Metabolic theory predicts an inverse linear relationship between the logarithm of species richness and temperature over geographic gradients (Allen, Brown, & Gillooly, 2002). When Algar, Kerr, and Currie (2007) failed to observe that predicted correlation, it was *prima facie* evidence to reject the hypothesis of Allen et al. (2002). Tests based on correlations are every bit as legitimate as experimental tests, or even more so: they test hypotheses about mechanisms in the natural systems we actually care about.

Correlational studies are weakest when they present observed correlations as "support" for (or evidence of) a particular mechanism. A famous example was Diamond's (1975) inference of competitive exclusion from the distributions of birds among islands. This inference provoked a pointed (and salutary) debate about how else the same patterns might arise (Connor & Simberloff, 1979; Connor, Collins, & Simberloff, 2013; Diamond & Gilpin, 1982). Much more could be said on this point.

In sum, to dismiss correlative studies because they do not imply causation (Paine, 2010) is to ignore the other critically important roles of correlation in science.

9 | CONCLUSIONS

My remarks above apply equally to both basic and applied ecology. It is true that basic science begins with description, and description

need not be predictive. There is unquestionably a place in ecology for basic description of how particular ecological systems work. Yet basic science routinely aims at generality. Although Paine (1966) studied only a single intertidal site, he presented his conclusions in terms that suggest broad applicability. Dybzinski and Tilman (2007) surely did not think that R^* theory applies exclusively to the plant species included in the Cedar Creek study. General conclusions, be they in basic or applied science, require general predictive ability.

The most successful disciplines have used a method resembling "deliberate practice" (Ericsson, 2008, 2017): that is, identifying a specific goal, and measuring progress toward it. How well predictions about the properties of natural systems agree with observation provides a measure of progress in ecology. Testable predictions are what make science useful to society. Ecological science has largely failed to do this. Ecology could improve its predictive power by first identifying general, predictive empirical relationships in nature (exploiting the strengths of macroecology), and then by testing for mechanisms (exploiting the strengths of experimental ecology). Experimental studies of mechanisms would be most useful when they target improved prediction of nature, rather than improved understanding.

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REFERENCES

- Algar, A. C., Kerr, J. T., & Currie, D. J. (2007). A test of metabolic theory as the mechanism underlying broad-scale species richness gradients. *Global Ecology and Biogeography*, 16, 170–178. <https://doi.org/10.1111/j.1466-8238.2006.00275.x>
- Allen, A. P., Brown, J. H., & Gillooly, J. F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297, 1545–1548. <https://doi.org/10.1126/science.1072380>
- Allen, T. F. H., Tainter, J. A., Pires, J. C., & Hoekstra, T. W. (2001). Dragnet ecology—"Just the facts, ma'am": The privilege of science in a post-modern world. *BioScience*, 51, 475–485. [https://doi.org/10.1641/0006-3568\(2001\)051\[0475:DEJTFM\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0475:DEJTFM]2.0.CO;2)

- Andrewartha, H. G., & Birch, L. C. (1954). *The distribution and abundance of animals*. Chicago, IL: University of Chicago Press.
- Batzli, G. O., White, R. G., Maclean, S. F. J., Pitelka, F. A., & Collier, B. D. (1980). The herbivore-based trophic system. In J. Brown, P. C. Miller, L. L. Tieszen & F.L. Bunnell (Eds.), *An Arctic ecosystem: The coastal Tundra at barrow Alaska. US/IBP Synthesis Series 12* (pp. 335–410). Stroudsburg, PA: Dowden, Hutchinson and Ross.
- Borer, E. T., Harpole, W. S., Adler, P. B., Lind, E. M., Orrock, J. L., Seabloom, E. W., & Smith, M. D. (2014). Finding generality in ecology: A model for globally distributed experiments. *Methods in Ecology and Evolution*, 5, 65–73. <https://doi.org/10.1111/2041-210X.12125>
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. <https://doi.org/10.1890/03-9000>
- Burke, J. (1985). *The day the universe changed*. London, UK: British Broadcasting Corporation.
- Camerer, C. F., & Johnson, E. J. (1991). The process-performance paradox in expert judgment: How can the experts know so much and predict so badly? In K. A. Ericsson, & J. Smith (Eds.), *Towards a general theory of expertise: Prospects and limits* (pp. 195–217). Cambridge, UK: Cambridge University Press.
- Canadian Task Force on Preventive Health Care. (2016). Recommendations on screening for colorectal cancer in primary care. *Canadian Medical Association Journal*, 188, 340–348.
- Chitty, D. (1996). *Do lemmings commit suicide? Beautiful hypotheses and ugly facts*. New York, NY: Oxford University Press.
- Connor, E. F., Collins, M. D., & Simberloff, D. (2013). The checkered history of checkerboard distributions. *Ecology*, 94, 2403–2414. <https://doi.org/10.1890/12-1471.1>
- Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *The American Naturalist*, 113, 791–832. <https://doi.org/10.1086/283438>
- Connor, E. F., & Simberloff, D. (1979). The assembly of species communities: Chance or competition? *Ecology*, 60, 1132–1140. <https://doi.org/10.2307/1936961>
- Currie, D. J. (1991). Energy and large scale patterns of animal and plant species richness. *The American Naturalist*, 137, 27–49. <https://doi.org/10.1086/285144>
- Currie, D. J., Dilworth-Christie, P., & Chapleau, F. (1999). Assessing the strength of top-down influences on plankton abundance in unmanipulated lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 427–436. <https://doi.org/10.1139/f98-190>
- Currie, D. J., & Kalf, J. (1984). A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. *Limnology and Oceanography*, 29, 298–310.
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., ... Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134. <https://doi.org/10.1111/j.1461-0248.2004.00671.x>
- Darwin, C. (1859). *On the origin of species by means of natural selection, of the preservation of favoured races in the struggle for life*. London, UK: John Murray.
- De Camargo, R. X., Boucher-Lalonde, V., & Currie, D. J. (2018). At the landscape level, birds respond strongly to habitat amount but weakly to fragmentation. *Diversity and Distributions*, 24, 629–639. <https://doi.org/10.1111/ddi.12706>
- Diamond, J. M. (1975). Assembly of species communities. In M. L. Cody & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–444). Cambridge, MA: Belknap.
- Diamond, J. M., & Gilpin, M. E. (1982). Examination of the “Null” model of Connor and Simberloff for species co-occurrences on islands. *Oecologia*, 52, 64–74. <https://doi.org/10.1007/BF00349013>
- Dillon, P. J. (1975). *A manual for calculating the capacity of a lake for development*. Toronto, Canada: Ontario Ministry of the Environment.
- Dillon, P. J., & Rigler, F. H. (1974). The phosphorus-chlorophyll relationship in lakes. *Limnology and Oceanography*, 19, 767–773.
- Dybziński, R., & Tilman, D. (2007). Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *The American Naturalist*, 170, 305–318.
- Ecology Curricular Framework Initiative of the Ecological Society of America. (undated). Four-dimensional ecology education framework | 4DEE. Accessed 24 October, 2018. <https://www.esa.org/4DEE/>
- Enquist, B. J., & Niklas, K. J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, 410, 655–660. <https://doi.org/10.1038/35070500>
- Ericsson, K. A. (2008). Deliberate practice and acquisition of expert performance: A general overview. *Academic Emergency Medicine*, 15, 988–994. <https://doi.org/10.1111/j.1553-2712.2008.00227.x>
- Ericsson, K. A. (2017). Expertise and individual differences: The search for the structure and acquisition of experts’ superior performance. *Wiley Interdisciplinary Reviews-Cognitive Science*, 8, 6. <https://doi.org/10.1002/wcs.1382>
- Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48, 1–23.
- Fletcher, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., ... Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological Conservation*, 226, 9–15. <https://doi.org/10.1016/j.biocon.2018.07.022>
- Fourcade, Y., Besnard, A. G., & Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, 27, 245–256. <https://doi.org/10.1111/geb.12684>
- Glynn, L. G., Murphy, A. W., Smith, S. M., Schroeder, K., & Fahey, T. (2010). Interventions used to improve control of blood pressure in patients with hypertension. *Cochrane Database of Systematic Reviews*, 17(3), CD005182. <https://doi.org/10.1002/14651858.CD005182.pub4>
- Gottfried, K., & Wilson, K. G. (1997). Science as a cultural construct. *Nature*, 386, 545–547. <https://doi.org/10.1038/386545a0>
- Gribbin, J. (2002). *Science: A history*. London, UK: Penguin Books.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances*, 1, 9. <https://doi.org/10.1126/sciadv.1500052>
- Haddad, N. M., Gonzalez, A., Brudvig, L. A., Burt, M. A., Levey, D. J., & Damschen, E. I. (2017). Experimental evidence does not support the habitat amount hypothesis. *Ecography*, 40, 48–55. <https://doi.org/10.1111/ecog.02535>
- Harpole, W. S., Sullivan, L. L., Lind, E. M., Firns, J., Adler, P. B., Borer, E. T., ... Wrang, P. D. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537, 93–96. <https://doi.org/10.1038/nature19324>
- Houlahan, J. E., McKinney, S. T., Anderson, T. M., & McGill, B. J. (2016). The priority of prediction in ecological understanding. *Oikos*, 126, 1–7. <https://doi.org/10.1111/oik.03726>
- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. NJ: Princeton University Press.
- Hutchinson, G. E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *The American Naturalist*, 93, 145–159.
- Inouye, D. W. (2015). The next century of ecology. *Science*, 349(6248), 565–565. <https://doi.org/10.1126/science.aab1685>
- Keddy, P., & Weiher, E. (1999). Introduction: The scope and goals of research on assembly rules. In E. Weiher & P. Keddy (Eds.), *Ecological assembly rules: Perspectives, advances, retreats* (pp. 1–20). UK: Cambridge University Press.
- Krebs, C. J. (2009). *Ecology: the experimental analysis of distribution and abundance* (6th ed.). San Francisco, CA: Pearson Benjamin Cummings.
- Laurance, W. F., Camargo, J. L. C., Luizão, R. C. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., ... Lovejoy, T. E. (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, 144, 56–67. <https://doi.org/10.1016/j.biocon.2010.09.021>

- Lawton, J. H. (1999). Are there general laws in ecology? *Oikos*, 84, 177–192. <https://doi.org/10.2307/3546712>
- Likens, G. E. (1972). *Nutrients and eutrophication: The limiting-nutrient controversy*. Lawrence, KS: Allen Press.
- Linquist, S., Gregory, R., Elliott, T. A., & Saylor, B. (2016). Yes! There are resilient generalizations (or "laws") in ecology. *Quarterly Review of Biology*, 91, 119–131. <https://doi.org/10.1086/686809>
- Lippi, D., & Gotuzzo, E. (2014). The greatest steps towards the discovery of *Vibrio cholerae*. *Clinical Microbiology and Infection*, 20, 191–195. <https://doi.org/10.1111/1469-0691.12390>
- Lubchenco, J., Olson, A. M., Brubaker, L. B., Carpenter, S. R., Holland, M. M., Hubbell, S. P., ... Risser, P. G. (1991). The sustainable biosphere initiative – an ecological research agenda – a report from the Ecological Society of America. *Ecology*, 72, 371–412. <https://doi.org/10.2307/2937183>
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. NJ: Princeton University Press.
- Marquet, P. A., Allen, A. P., Brown, J. H., Dunne, J. A., Enquist, B. J., Gillooly, J. F., ... West, G. B. (2014). On theory in ecology. *BioScience*, 64, 701–710. <https://doi.org/10.1093/biosci/biu098>
- Menge, B. A. (1992). Community regulation: Under what conditions are bottom-up factors important on rocky shores? *Ecology*, 73, 755–765. <https://doi.org/10.2307/1940155>
- Newton, I. (1730). *Opticks*. London, UK: William Innys.
- NSERC. (2018). *Awards database*. Accessed 24 October, 2018. Retrieved from http://www.nserc-crsng.gc.ca/ase-oro/index_eng.asp
- Paine, R. T. (1966). Foodweb complexity and species diversity. *The American Naturalist*, 100, 65–75. <https://doi.org/10.1086/282400>
- Paine, R. T. (2010). Macroecology: Does it ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? *The American Naturalist*, 176, 385–393. <https://doi.org/10.1086/656273>
- Peters, R. H. (1983). *The ecological implications of body size*. UK: Cambridge University Press.
- Peters, R. H. (1991). *A critique for ecology*. UK: Cambridge University Press.
- Pickett, S. T. A., Kolasa, J., & Jones, C. G. (1994). *Ecological understanding: The nature of theory and the theory of nature*. New York, NY: Academic Press.
- Platt, J. R. (1964). Strong inference. *Science*, 146, 347–353.
- Popper, K. R. (1958). *The logic of scientific discovery*. New York, NY: Harper.
- Popper, K. R. (1990). *A world of propensities*. Bristol, UK: Thoemmes.
- Preston, F. W. (1962). The canonical distribution of commonness and rarity: Part I. *Ecology*, 43, 185–215. <https://doi.org/10.2307/1931976>
- Ricklefs, R. E., & Miller, G. L. (1999). *Ecology (Fourth Edition)*. New York, NY: W. H. Freeman and Company.
- Rigler, F. H. (1982). Recognition of the possible: An advantage of empiricism in ecology. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 1323–1331. <https://doi.org/10.1139/f82-177>
- Saaranen, E. (1980). *Conceptual issues in ecology*. Dordrecht, Netherlands: D. Reigdel Publishing.
- Schindler, D. W., & Fee, E. J. (1974). Experimental lakes area: Whole-lake experiments in eutrophication. *Journal of the Fisheries Research Board of Canada*, 31, 937–953. <https://doi.org/10.1139/f74-110>
- Schmitz, O. J., Hamback, P. A., & Beckerman, A. P. (2000). Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. *The American Naturalist*, 155, 141–153. <https://doi.org/10.1086/303311>
- Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., Rödig, E., ... Huth, A. (2018). Global patterns of tropical forest fragmentation. *Nature*, 554, 519–522. <https://doi.org/10.1038/nature25508>
- Taylor, L. R. (1961). Aggregation, variance, and the mean. *Nature*, 189, 732–735. <https://doi.org/10.1038/189732a0>
- Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities*. NJ: Princeton University Press.
- Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, 546, 73–81. <https://doi.org/10.1038/nature22900>
- Valentyne, J. R. (1974). *The algal bowl: lakes and man*. Ottawa, Canada: Department of the Environment, Fisheries and Marine Service.
- Velikovsky, I. (1950). *Worlds in collision*. Garden City, NY: Doubleday.
- Velikovsky, I. (1955). *Earth in upheaval*. London, UK: Abacus.
- Wen, Y. H., Vezina, A., & Peters, R. H. (1994). Phosphorus fluxes in limnetic cladocerans—coupling of allometry and compartmental analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 1055–1064. <https://doi.org/10.1139/f94-105>
- Whittaker, R. H. (1970). *Communities and ecosystems*. New York, NY: Macmillan Publishing.

BIOSKETCH

DAVID J. CURRIE is interested in the predictable properties of the distribution of life on earth (when he is thinking as a scientist) and the beautiful intricacies of nature (when he is not).

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