THE ECOLOGY OF PLACE

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Cover sheet for Chapter 13: Case Studies and Ecological Understanding

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CHAPTER 13 CASE STUDIES AND ECOLOGICAL UNDERSTANDING

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Abstract

Does ecology develop as a science mainly inductively, through case studies that lead to theory? Or does it develop deductively by abstract mathematical theory that is then analyzed empirically? Since philosophers of science have long discredited empirical induction, how does ecology really develop? Are case studies just a pleasant outdoor way of "stamp collecting" to validate mathematical theory? I identify 15 major conceptual advances made in ecology during the last 50 years, and attempt to judge what contributions mathematical theory and empirical studies have made to these major advances. Four of the advances could be classed as having arisen primarily from theoretical work, and I have judged 10 to be primarily empirical in origin. One advance arose from a nearly equal combination of both approaches. Mathematical theory in ecology has described a complex world during the last 40 years, but we have too few empirical evaluations of whether the theoretical world now in place is built on sand or rock. Empirical case studies firmly rooted in place have led to valuable ecological theory whose test is that it is useful for natural resource management. Case studies will continue to enrich ecological theory and practice for the near future.

> *Errors using inadequate data are much less than those using no data at all.*
>
> —Charles Babbage (1792–1871)

Introduction

All ecologists, politicians, and business people are in favor of progress, and view time's arrow as pointing in the direction of progress. Anyone who dares to say that we are not making progress in an area, as Peters (1991) did for ecology, is condemned for writing "an essay written by a dreadfully earnest, but ill-informed, poorly read undergraduate" (Lawton 1991). But in every science progress is uneven, reversals occur and are quickly buried and forgotten. The question we need to raise concerns the rate of progress, and whether there are any shortcuts we can follow to speed it up.

The recipe for progress in science is fairly simple: find a problem, designate multiple alternative hypotheses, and test them by searching for evidence that contradicts the predictions of each hypothesis. But as every practicing scientist knows, applying this recipe is complicated by a whole set of decisions and assumptions that are typically unstated in the resulting scientific papers. Among the first of these decisions is the question of place: Where shall I carry out this research? But the location or place of the research carries with it a whole array of assumptions and additional decisions that are rarely considered explicitly. In the first part of this chapter I explore some of these assumptions and decisions with respect to ecological science, and discuss in particular how we might move from site-specific studies to general knowledge. In the second part of this chapter I discuss ecological advances and the role of place-based research in producing progress in ecological understanding.

I will not here discuss evolutionary ecology and its handmaids, physiological ecology and behavioral ecology. These areas have made great advances in recent years because they deal with relatively simple problems with solutions that are known because of evolutionary theory. These areas work in what Kuhn (1970) has called normal science, filling in important gaps in understanding while guided by well-established theory. The rest of ecology, mechanistic ecology, does not have the luxury of an established theory like evolution by natural selection, and so it is much harder to do. This does not mean that mechanistic ecology ignores microevolutionary changes in populations, as there are many examples of how both population and community interactions have changed because of microevolution (Carroll et al. 2007). But if you wish to know why a population stops growing, or why the composition of a community is changing rapidly, the theory of evolution will not tell you a priori which mechanistic processes you should investigate. There is no "optimal foraging theory" for population dynamics or plant succession. It is for this reason that mechanistic ecology is much more difficult than physiological or behavioral ecology.

Assumptions Underpinning Ecological Studies

All good ecology is founded on a detailed knowledge of the natural history of the organisms being studied. The vagaries of species natural history are a challenge to the field ecologist trying to understand natural systems as much as they are a menace to modelers who assume that the world is simple and, if not linear, at least organized in a few simple patterns. I begin with the often unstated background supposition that we have good natural history information on the systems under study. The great progress that ecology has made in the last century rests firmly on this foundation of natural history.

The following is a list of assumptions and decisions that are implicit or explicit in every ecological study. In most published papers you will find little discussion of these assumptions, and in bringing them forward here I am trying to make more explicit the logical skeleton of ecological progress.

1. A problem has been identified

This is a key step that is rarely discussed. A problem is typically a question, or an issue that needs attention. Problems may be local and specific or general. Local problems may be specific as to place as well as time, and if they are so constrained, they normally are of interest to applied ecologists for practical management matters, but are of little wider interest. General problems are a key to broader scientific progress, and so ecologists should strive to address them to maximize progress. The conceptual basis underpinning a study is an important identifier of a general problem. Applied ecologists can often address what appear to be local problems in ways that contribute to the definition and solution of general problems. A solution to a general problem is what we call a general principle.

General ecological problems can be recognized only if there is sufficient background information from natural history studies to know that an issue is broadly applicable. There is also no easy way to know whether a general problem will be of wide or narrow interest. For example, the general problem of whether biotic communities are controlled from the top down by predation or from the bottom up by nutrients is a central issue of the present time, and of broad interest (see Estes, chapter 8; Peckarsky et al., chapter 9). The answer to this question is critical for legislative controls on polluting nutrients (Schindler 1988) as well as for basic fisheries management (Walters and Martell 2004). The top-down/bottom-up issue will always be a general one for ecologists to analyze because some systems will show top-down controls and others bottom-up controls, so the answer will be case-specific. The level of generality of the answer will not be “all systems are top-down,” but only some lower level of generality, such as “Insectivorous bird communities are controlled bottom-up.” It is only after the fact that problems are recognized as general, and science is littered with approaches that once appeared to be of great general interest but did not develop. The converse is also true: problems originally thought to be local have at times blossomed into more general issues of wide relevance.

<!figure 13.1 should go approx here!>

The typical pattern in the evolution of general problems is illustrated in figure 13.1. A problem is recognized, such as: What are the factors that control primary production in lakes? From prior knowledge (e.g., agricultural research) or data from a set of prior studies, a series of hypotheses is set up. A hypothesis that has a reasonable amount of support is what we refer to as a general principle. One can view these hypotheses as “straw men” in the sense that many variables affect any ecological process, and all explanations should be multifactorial. But it is not very useful at this stage to say that many factors are involved and that the issue is complex. Ecologists should introduce complexity only when necessary. Often it is useful to view a hypothesis as answering a practical question: What variable might I change as a manager to make the largest impact on the selected process? Ecologists should sort out the large effects before they worry about the small effects. Large effects may arise from interactions between factors that by themselves are thought to be of small importance. Good natural history is a vital ingredient here because it helps us to make educated guesses about what factors might be capable of producing large effects.

It is nearly universal that once a hypothesis is stated and some data are found that are consistent with the suggested explanation, someone will find a contrary example. For example, although most freshwater lakes are phosphorous-limited, some are micronutrient-limited (e.g., by molybdenum; Goldman 1967; see also Elser et al. 2007). The question then resolves into one of how often the original suggestion is correct and how often it is incorrect, and one or another set of hypotheses should be supported. Although statisticians may be happy with a hypothesis that 87% of temperate lakes are phosphorous-limited, ecologists would prefer to define two (or more) categories of lakes in relation to the factors limiting primary production. We do this in order to produce some form of predictability for the occasion when we are faced with a new lake: are there criteria by which we can judge which factors might be limiting this particular lake? Can we establish criteria that allow near-absolute predictability? Some might argue for a statistical cutoff, such as 80% correct predictability, at which point we should be content with the generalization. But the general approach of rigorous science is to concentrate on those cases in which the prediction fails, so that by explaining contrary instances we can strengthen the generalization. Clearly, though, we cannot investigate all the lakes in the world to achieve complete predictability, so this takes us back to the problem of place.

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2. The statistical population has been delimited

Ecologists often drive statisticians to distraction. We assume that place does not matter, so that, for example, if we wish to study the predator/prey dynamics of aphids and ladybird beetles on cabbage, we can do it anywhere that cabbage is grown. This is a gigantic assumption, but a necessary one in the early stages of an investigation in which we must assume simplicity until there is evidence against it. This assumption about the irrelevance of the place or location where we do our studies is often coupled with the assumption of time irrelevance, so we make the joint assumption that our findings are independent of time and space. Statisticians try to capture these assumptions in the idea of a “statistical population.”

Statisticians request that one should define the particular unit of study for which one is trying to make some conclusion the “statistical population.” I have not found a single ecological paper that defines the statistical units to which the study is supposed to apply, except in the very general sense that a given study is being done in the rocky intertidal zone, or in the boreal forest, or on a particular island. We do this deliberately because we do not know the extent of application of any conclusions we make in ecology. When in doubt, apply your results to the entire universe of the rocky intertidal zone or the boreal forest. This type of global generalization can be defended as a conjecture that is designed for further testing and subsequent revision. Critics may argue that such broad conclusions are too simplistic, but such a criticism ignores Ockham's razor and the need to embrace simplicity and introduce complexity only when needed. But the issue of defining a statistical population brings us back to asking how a particular site is chosen for a particular study.

Where most of the highly influential ecological field studies have been carried out is almost an accident of history. The presence of field stations, people in particular universities, the location of protected areas, and arrangements of travel all combine to determine where a field study is carried out. A pure statistician would be horrified at such a lack of random sampling, and we are in the anomalous intellectual position of basing our most important ecological contributions on non-random sampling. But of course this is not a problem if you can make the assumption that no matter where you have carried out a particular investigation, you will get the same result. This rescue of generality can be done only if one views the ecological world as invariant in its properties and dynamics over space and time. This is a critical assumption. System dynamics may be invariant over space, but not over time.

There are now good studies that show how the assumption of time invariance is incorrect. Grant and Grant (chapter 6) illustrate this difficulty with two episodes of natural selection on Darwin's finches. Range managers have faced the same problem by not recognizing multiple stable states, so that removing cattle grazing does not necessarily reset the system to its initial conditions (van de Koppel et al. 1997). We need to be aware of the assumption of time invariance, and it may be a mistake to assume that, if a particular study was done from 1970 to 1980, the same results would have been observed from 1995 to 2005.

The assumption of spatial invariance, as Pulliam and Waser discuss (chapter 4), has never been popular in ecology because the abundance of resources, predators, and diseases are well known to vary spatially. Much of modern ecology has focused on trying to explain spatial variation in processes. Plant ecologists discarded the Clementsian monoclimax view of ecological communities and replaced it with the continuum concept of a community (Austin and Smith 1989, Crawley 1997). Animal ecologists recognized keystone species, which showed that a single species could have major community consequences (Paine et al., chapter 11). The exact dynamics of a community may be greatly affected by the species present, their interaction strengths, and their relative abundances. We do not yet know how much variation can occur in community composition before new rules or principles come into play.

The result is that we almost never specify a statistical population in any ecological research program, and we issue a vague statement of the generality of our findings without defining the units to which it should apply. This is not a problem in experimental design if we can repeat our findings in another ecosystem to test their generality. The key to generality is to predict correctly what we will find when we study another ecological system in another place. For the present, ecologists should retain a dose of humility by continually testing the limits of generality of their ideas rather than believing that they have found scientific laws.

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3. Random sampling is applied

In the chosen area of study, we now observe or apply some treatments to obtain the data that will test an array of alternative hypotheses. In the case of observational experiments the sample units are defined by nature, and our job in random sampling is to locate them, number them, and select those for treatment at random. For manipulative experiments we define the sample units and apply a similar random selection of them for each treatment. Most ecological field experiments have a small number of replicates, and Hurlbert (1984) has discussed what can happen if treatments are defined randomly. All our control or experimental plots may end up, for example, on north-facing slopes. Hurlbert recommended maintaining an interspersion of treatments so that both treatments and controls are spread spatially around the study zone.

<!table 13.1 should go approx here!>

Consequently a good biologist almost never follows the instructions from the pure statistician for three reasons. First, they may not be practical. The major reason such random assignments may not be practical is that transportation to the sites may limit choices. Not everyone can access field sites by helicopter, and roads typically determine which study units can be used (table 13.1). Second, places for study may need to be in a protected nature reserve or an area in which the private owner welcomes ecologists to use his or her land. Since nature reserves in particular are often put in landscapes that cannot be used economically for agriculture or farming, there is an immediate bias in the location of our experimental units. Third, field stations or other sites where research has been carried out in the past have a legacy of information that draws ecologists to them for very good reasons (Aigner and Kohler, chapter 16; Billick, chapter 17), although this compounds the nonrandomness of choice of field sites.

The consequence of these problems is the practical advice to randomize when possible on a local scale, and to hope that generality can emerge from nonrandom sampling on a regional or global scale.

4. Transient dynamics are not dominant

The time scale of ecological system responses is assumed to lie within the time frame of our studies. Thus, if we manipulate vole or lemming populations that have several generations per year, we assume that our manipulations will be effective within a year. But what if fast variables like vole numbers interact with slow variables like soil nutrient dynamics or climate change?

The time lags in system response that are inherent in transient dynamics can be found only by longer-term studies (e.g., Grant and Grant, chapter 6), and at present we are guided in these matters only by our intuition, which is based on natural history knowledge and process-based (i.e., mechanistic) models that can explore our assumptions about system dynamics. Process-based models are a vital component of our search for generality because they can become general principles waiting for further testing (e.g., see King and Schaffer 2001; Pulliam and Waser, chapter 4). The important limitation of process-based models is to determine how much structure is essential to understanding the system of study. Too much detail leaves empirical scientists with little ability to discern which factors are more important, and too little detail leaves out biological factors that are critical.

5. The predictions being tested follow from the hypotheses

Ecological hypotheses typically are less clearly structured logically than might be desirable. In particular the background assumptions that are necessary to support deductions from a particular hypothesis are rarely stated, with the net result that there is a somewhat tenuous connection between hypotheses and predictions. The only remedy for this problem is to demand more rigor in specifying the unstated assumptions that accompany every study.

6. The relevant variables have been identified

Another difficulty at this stage is that the set of alternative hypotheses proposed as explanations of the identified problem may not include the correct explanation. For example, the three alternative hypotheses for freshwater lakes—that primary production is limited by nitrogen, phosphorus, or carbon—may all be wrong if a lake's production is limited by micronutrients such as molybdenum. There is no simple way out of this problem, except to identify as wide an array of possible explanations as current knowledge will permit, and to recognize always that in the future a new hypothesis may arise that we had not considered.

By diversifying one's observations at a variety of places, we can minimize the probability of failing to see and include a relevant variable. Diversifying means carrying out similar studies in several different places. This is one of the strongest recommendations that one can make about ecological science: we should systematically diversify our observations in different places to help identify relevant variables. If we have missed an important variable, it will be picked up when management actions flow from our ecological findings, because those actions will not achieve their predicted results. Practical management can be used as the touchstone of ecological ideas and as a valuable test for missing variables. This will occur only when management actions have a firm foundation in ecological ideas and—if management actions fail—when time and money are made available to find the source of the failure. Ignoring failures of predictions is a sure way to reduce progress in scientific understanding (Popper 1963).

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Ecological Advances

The past century has seen an enormous growth in ecological knowledge, and I will attempt to identify some of the key ideas that have emerged during this interval. The central problems of ecological science are to decipher the reasons for the distribution and abundance of organisms (Krebs 2009), and within this broad umbrella I recognize four key areas of advance. All of these areas have advanced because of multiple studies with many different empirical approaches, whether they be experimental, observational, field-based, or laboratory-based.

1. The limitation of geographical distributions

This is one of the oldest areas of research in ecology, interfacing with biogeography, which began developing insights in the eighteenth century. Advances in our understanding of the factors limiting geographic ranges have resulted from the recognition that answers are scale-dependent. A forest herb studied at the scale of 1 m^2 may be limited in distribution by competition from other plants, at a scale of 1 ha by the feeding habits of its herbivores, at a scale of 1 km^2 by the vagaries of seed dispersal, and at the scale of continents by its evolutionary origins in relation to continental drift. All these scales bring the concept of *place* into strong focus because we have to specify exactly which place we are studying. This was pointed out by Forman (1964), but the whole issue of scale-dependence in ecological analysis has only slowly developed. Recent advances in understanding range limitations have built on the basic hypothesis that, aside from dispersal limitation and human translocations, climate is the master factor limiting geographical ranges, and climate change is a process that will test this hypothesis. Data showing range changes that have accompanied global warming help to advance the need for action on climate change (Parmesan and Yohe 2003).

Botanists have been at the forefront in analyzing the factors limiting distributions within the geographic range. The classic studies of sand dune succession on the shores of Lake Michigan by Cowles (1899), and the more recent work by Daubenmire (1954, 1956) stand out as major advances. The seminal work of Connell (1961) on barnacle distribution in the Scottish rocky intertidal zone is another classic case of mechanistic hypotheses applied to the problem of geographic distributions.

The recognition of the problem of invasive species has been another achievement of this branch of ecology. The general topic of invasions is not new (Elton 1957), but the details of how particular species have wreaked havoc in ecosystems after deliberate or accidental introductions have led ecologists toward insights on introductions now synthesized in the "enemy release hypothesis" (Keane and Crawley 2002). The spread of the zebra mussel (*Dreissena polymorpha*) in North America (Johnson et al. 2006) and the spread of the cane toad in Australia (Sutherst *et al*. 1995) are good case studies of invasive species expanding their geographic ranges after introduction.

Island biogeographic theory was a bold attempt by MacArthur and Wilson (1967) to tie the loose empirical data on island distribution patterns to a conceptual theory centered on dispersal. As such it was a major conceptual advance, moving from empirical patterns to an elegant theory that had significant ramifications for further research on island populations, metapopulations, and conservation biology (Brown and Lomolino 2000). Its weakness was in fact part of the reason for its success: it dealt only with the numbers of species and did not specify the details of which exact species would occur where—the details that are important for practical conservation decisions.

Macroecology attempts to describe large-scale patterns in the distribution and abundance of species, often adopting as its measure of place a whole country or continent. One of the early insights of the field of macroecology was that the sizes of distributional ranges were correlated positively with abundance, albeit with considerable scatter (Maurer and Taper 2002). This insight has tied together studies of distribution and abundance at large spatial scales. The macroecological search for patterns has been one way of collating many separate studies on different ecosystems in an attempt to generalize over individual place studies. The limitation has been that the patterns recognized are statistical generalizations rather than mechanistic explanations; hence, they are of limited predictive power for management purposes.

2. Population regulation and limitation

The problem of population regulation was already well discussed by the 1950s but three major advances have marked its maturation. Mathematical models of populations were greatly elaborated in the 1960s and 1970s with the recognition of how complex population dynamics like chaos could result from simple assumptions. Ricker (1954) first pointed this out; the mathematics was elegantly described by Maynard Smith (1968) and then fully elaborated by Robert May (1974). A second major advance has been the array of detailed studies on single-species populations that has made the issue of regulation more complex but more biologically interesting (Sibly et al. 2003). A good example is the importance of seasonal migration in the determination of population size in wildebeest (Fryxell et al. 1988).

The practical application of population dynamics theory to conservation made a third major advance when Caughley (1994) described the declining population paradigm and applied ideas of population limitation to the practical issue of threatened and endangered species. This coincided with an elaboration of the Leslie matrix approach to population projections, and the development of elasticity and sensitivity analysis for population changes (Caswell 2001). These mathematical advances have proven most useful in the analysis of problems in both pure and applied ecology. Life-history theory has adopted matrix methods as an important tool, and conservation options can be explored with these same methods to determine the best management actions to use for species recovery.

3. Community trophic dynamics

The approach to understanding community dynamics developed originally from analyses of energy flow through communities, beginning with Lindeman (1942) and carried forward by Odum (1968). These ideas were picked up in an influential paper by Hairston, Smith, and Slobodkin (1967), who pointed out that energy and material flows could be regulated—what we now call "top-down" by predators or "bottom-up" by nutrients and food items (Menge and Sutherland 1987, Hunter and Price 1992). These ideas were an extension of concepts used in population dynamics to determine which regulating factors dominated in stopping population increase, and they led to the important idea of indirect effects on community interactions (Holt 1977;, Menge 1995; Paine et al., chapter 11).

A second important development in thinking about community dynamics has been the replacement of equilibrium community dynamics with nonequilibrium dynamics (DeAngelis 1987). This arose in part because disturbances were found to prevent communities from ever achieving a state of equilibrium, and by the 1980s ecological concepts of succession (Connell and Slatyer 1977) and nutrient cycling (Bormann and Likens 1967, Vitousek 2004) had expanded their theoretical formulations to include nonequilibrium dynamics. The classic case here is that of coral reefs, formerly considered the paradigm of equilibrial communities until the detailed data of Connell et al. (1997) showed clearly that they were nonequilibrial systems.

Biodiversity has become a focal point for much research effort, as an extension of the older problem of what controls species diversity in communities (Connell and Orias 1964). In a 1955 theoretical exercise Robert MacArthur raised the issue of how species diversity affected community stability, and this triggered a discursive series of studies on the role of biodiversity in plant and animal communities (Loreau 2000, Worm and Duffy 2003). As the capstone concept of conservation biology, biodiversity has brought the taxonomy of earth's organisms to our attention and stimulated much research and analysis of how it contributes to human welfare through ecosystem services (Costanza et al. 1997).

4. Ecosystem dynamics

The recognition of ecosystem services has pushed ecology to the forefront in an attempt to prevent the degradation of the earth's biological systems. Paul Ehrlich coined the idea in 1983 (Ehrlich and Mooney 1983) in an attempt to analyze why humans should be concerned about extinctions. The focus on ecosystem processes has gained renewed energy from the spreading concern about climate change and its impact on natural and human-dominated ecosystems. At present this is the touchstone for ecologists to push their concerns about environmental degradation. The difficulty has been in getting some ecological measurements of ecosystem services, and much effort is now going into the economic evaluation of these services, unfortunately while we know little about their ecology and how they are affected by human actions (Daily 1997).

Landscape ecology emerged in the 1980s as part of a recognition that conservation could not be limited to national parks if we were to preserve large, charismatic species (Newmark 1985). As part of a recognition that ecological studies were typically done at very small scales while fundamental ecosystem problems occur at large scales (Kareiva and Andersen 1988; see also Curtin, chapter 12), ecologists began to consider the landscape context of their analyses. Fragmentation of ecological communities was the earliest recognition of landscape issues, and this evolved into theoretical and practical analyses of the consequences of populations and communities being distributed on habitat islands (Gill 1978, Hanski 1998). Flows between ecosystems are also critically important in landscape function (Anderson and Polis 1998; Estes, chapter 8), and fragmentation has consequences at all levels of integration in ecology.

Landscape ecology begins with the assumption that ecological processes are affected by the landscape configuration. While this is a reasonable premise, it will be correct only at certain spatial scales, and for some organisms or processes it may not be correct at all. Because of the difficulty of manipulating large areas, landscape ecology has either used microcosms to investigate questions of configuration (e.g., Huffaker 1958) or used spatial modeling to investigate the possible impact of different habitat configurations (Levey et al. 2005). Since most models are likely to be wildly wrong in their predictions, there is an urgent need to test these scenarios in the real world. And since much microcosm work has been completely misleading when applied to natural systems (Carpenter 1996), another caution about the perceived advances in landscape ecological understanding is in order. While microcosms can be useful for investigations of simple population- or community-level questions, they are less useful for investigating problems in open systems containing many species in typical landscapes. But on the positive side, the importance of landscape is suspected by many experienced ecologists, even though the detailed data are not in—and landscape ecology shouts to ecologists to consider place as being central to understanding ecological processes.

The concept of metapopulation dynamics is closely connected with landscape ecology, although in a population context it is usually thought of as being associated with dispersal between patches. Place as a spatial location has a critical importance in metapopulation dynamics, as in all of landscape ecology, because it is the configuration of each place or habitat in relation to others that can drive the ecological processes.

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The Role of Case Studies

Ecology operates as a dialectic between modelers and theoreticians, who push generality in which place has no position, and place-based empiricists, who study particular problems in particular places and try to understand the processes involved. The dialectic is slow to operate. Alfred Lotka and Vito Volterra produced models of competitive interactions and predator/prey relationships in the 1920s before there was virtually any detailed study of competitive or predatory systems, or any data available. Only later were the limitations of these models recognized, as detailed laboratory and field studies were carried out in various places around the world from 1950 onward. In an ideal world, theoretical and empirical approaches would merge as model → data → revised model → more data in continuous synergistic feedback loops. We may be in an ideal world 200 years from now, if we adopt the development of chemistry and physics development as a guide, but at the present time the prospect of grand synthetic models recedes at the speed of light, partly

because exceptions to general principles are continually being found (as is illustrated in figure 13.1).

I argue in this chapter that progress in ecology is limited by the great divide between theoretical research and empirical research that focuses on understanding the workings of real ecosystems in the field. The divide occurs not because theoretical and empirical domains are nonoverlapping. After all, theory includes abstract conceptual models as well as mathematical formulations, theoreticians do live in the real world and get ideas from it, and empiricists typically have some general mental or verbal model of their system of study. Instead, the divide occurs because theoretical and empirical approaches are rarely integrated in ecological research. Anyone who reads the journals *Theoretical Population Biology* and *Ecological Monographs* will clearly understand this lack of integration.

Although there are other empirical ecological approaches that we can recognize, I emphasize place-based, process-oriented field approaches because I think the contributions of these alternatives to ecological knowledge that has practical utility are scarcely visible at the present time. Laboratory microcosm studies can certainly be place-based and process-oriented, but they are a poor and often misleading guide to what happens in natural ecosystems. Macroecology is a recent high-level approach to recognizing and studying large-scale empirical patterns, similar to the pattern analysis often used in plant ecology. I consider both of these approaches empirical because they are ultimately reducible to sets of data obtained from studies in particular places—but their utility is compromised by the separation of data from a real ecological context.

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If we accept the empirical/theoretical dichotomy, we can ask which of these approaches has been more important for progress in ecological understanding. My vote goes with Shrader-Frechette and McCoy (1993) who emphasized the key role that case studies should play in the development of ecological theory. As table 13.2 illustrates, most of the major advances in ecological science over the last 50 years have come from the place-focused, empirical side of ecology, and while we could construct a similar table for major advances in mathematical ecological theory, we would be unable to determine whether any of that theory was applicable to the real world. This dichotomy between mathematical theory and empiricism in ecology was recognized by Fretwell (1972), but the years have not reduced the gap, in spite of heroic efforts. Theory advances at lightning speed because it does not have to deal with place, while empirical ecology moves slowly, always constrained by place and time, enriching our understanding of how the natural world operates but at the same time burying us in its complexity. We should all rejoice that there is so much left to do in empirical ecology. My recommendation is for ecologists to push place-based empirical research to the fore in an effort to test all the accumulated theory that sits idle in the absence of good field data.

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Table 1. Experimental manipulations in the Kluane Boreal Forest Ecosystem Project and the decisions that led to their site placement. Each experimental unit was 1 km^2. This example illustrates some of the reasons randomization cannot be achieved in field ecology. Similar forested habitat was the first constraint on area selection, and access in summer and winter was the secondary determinant of location, followed by the need to spread treatments over the 350 km^2 study area. Details are given in Krebs et al. (2001).

Experimental unit	Treatment	Reasons for location
Fertilizer 1	55 tons of commercial fertilizer added aerially each year	Along Alaska Highway at north end of study area, 3 km from airstrip used for aircraft loading fertilizer
Fertilizer 2	55 tons of commercial fertilizer added aerially each year	Along Alaska Highway near north end of study area, 6 km from airstrip, separated from other treatments by at least 1 km
Food addition 1	Commercial rabbit chow fed year round	Access by ATV in summer and minimum 1 km spacing from electric fence treatment
Food addition 2	Commercial rabbit chow fed year round	At extreme southern end of study area with ATV access and 3 km from Control 3
Electric fence	Exclude mammal predators	Along Alaska Highway, access by heavy equipment, relatively flat area
Electric fence and food addition	Exclude mammal predators and add rabbit chow food	Near Alaska Highway, access by heavy equipment, one side of fence already cleared for old pipeline, relatively flat area
Control 1	None	Along Alaska Highway, spaced 1 km from manipulated areas and 10 km from Control 2
Control 2	None	Along Alaska Highway, spaced 5 km from Control 3 and 7 km from nearest treatment site
Control 3	None	Near southern end of study area accessed by old gravel road

Table 2. Major advances in ecological understanding during the past 50 years and the source of the advance classified as theoretical or empirical, place-based research. The references are meant to illustrate the point, not to be comprehensive. This classification is clearly only my opinion and can be considered as a hypothesis rather than a fact. Theoretical advances arise deductively from a set of assumptions connected via a mathematical model, while empirical advances often arise inductively and are rarely rigorously formulated.

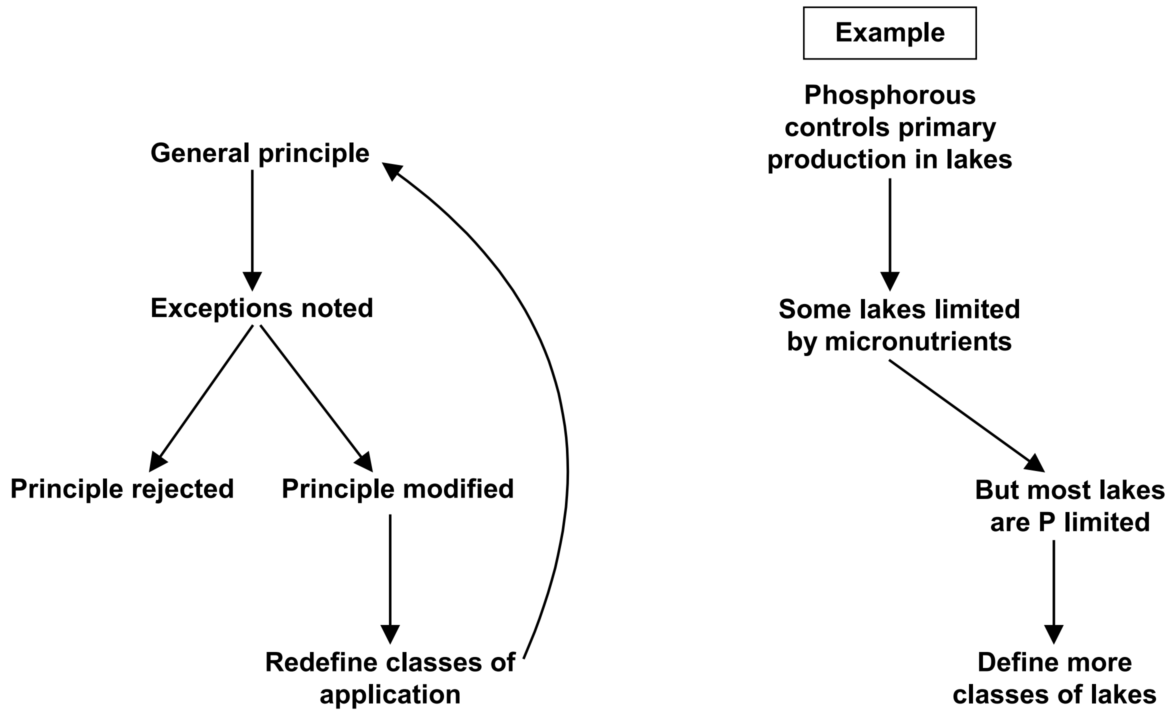
Advance	Source	Reference
Factors limiting ranges depend on scale	empirical	Forman (1964)
Many range limits are set by climate	empirical	Parmesan and Yohe (2003)
Invasive species disrupt ecosystems	empirical	Elton (1958)
Distribution and abundance are correlated	empirical	Brown (1984)
Simple population mathematics can lead to fluctuations or chaos	theoretical	May (1974)
Population regulation can be analyzed quantitatively	empirical	Sibly et al. (2003)
Conservation problems can be solved with the declining population paradigm	empirical	Caughley (1994)
Communities can be controlled top-down or bottom-up	empirical	Menge and Sutherland (1987)
Indirect effects between species can affect community structure	theoretical	Holt (1977)
Communities may show nonequilibrium dynamics	theoretical	Chesson and Chase (1986)
Island species pools are a balance of immigration and extinction	theoretical	MacArthur and Wilson (1967)

Species diversity affects community stability	theoretical and empirical	Elton (1958) and MacArthur (1965)
Ecosystem services are essential for human life on earth	empirical	Daily (1997)
Landscape processes affect population and community dynamics	empirical	Lidicker (1995)
Dispersal determines metapopulation dynamics	empirical	Harrison (1991)

FIGURE LEGENDS

Figure 1. A schematic illustration of how generality is treated in ecological research. A simplified example from the controversy over the nutrients responsible for eutrophication in temperate freshwater lakes (Schindler 1977) is used to illustrate the progression from very general principles to more specific principles that are invariant. Statistical principles such as “primary productivity in 72% of freshwater lakes are controlled by phosphorus” are not very useful for management, and we try to reach universal principles (although we may never achieve this ideal).

Figure 1.


General principle
Exceptions noted
Principle rejected
Principle modified
Redefine classes of application
Example
Phosphorous controls primary production in lakes
Some lakes limited by micronutrients
But most lakes are P limited
Define more classes of lakes