How to Do Ecology

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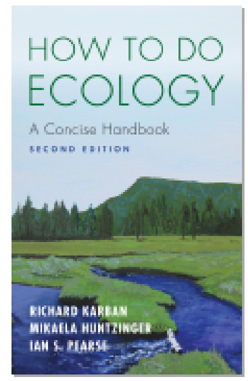

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CHAPTER 2

Posing Questions (or Picking an Approach)

Much of what you can learn about ecology depends on the questions you ask. Your preconceptions and intuition determine the factors that you choose to examine, and these will constrain your results. Ecologists take several different approaches to science, and which approaches you use will constrain the kinds of answers that you'll get. Answers to the questions that you ask then form your view of how the natural world works. Deciding on an approach may sound like a bunch of philosophical nonsense to waste time, but it can have important consequences on everything that follows.

Different Ways to Do Ecology

Ecologists use several different approaches to understand phenomena, which we place in three categories: (1) observations of patterns, (2) manipulative experiments, and (3) model building. As is often the case in ecology, these categories are not mutually exclusive, and each has something to offer.

Observations of Patterns or Natural History

Observations of patterns in natural systems are essential, as they provide us with the players (factors and processes) that may be important. Observations allow us to generate hypotheses and test models. Natural history used to be the mainstay in ecology, but it started to go out of style in the 1960s. Current training in ecology has become less and less based on a background in natural history (Futuyma 1998, Ricklefs 2012). Undergraduate education requires fewer hours of labs than it did in the past because labs are expensive and time-consuming to teach. Traditional courses in the "ologies" (entomology, ornithology, herpetology, etc.) are becoming endangered. Graduate students are pressured to get started on a thesis project before they've spent time poking around in real ecological systems. It doesn't get any easier for professors, who are most "successful" by becoming research administrators. They write grants to fund other people to work with the organisms, allowing themselves more time to write papers, progress reports, and the next grants. The result of all this is that the intuition for our experiments and models comes from the literature, computer models, or the intuition of our major professor. We spend a lot of time refining what everyone already believes is important. This has the danger of making ecology conservative and unexciting.

It is clear to the writers of this book that ecology as a discipline would be improved if we were encouraged to learn more about nature by observing it first and manipulating and modeling it second. Observations are absolutely necessary to provide the insights that make for good experiments and models. For example, experiments usually manipulate only one or a small number of factors because of logistical constraints. The factors that we as experimenters choose to manipulate determine the factors that we will conclude are important. For instance, if we test the hypothesis that competition affects community structure, we are more likely to learn something about competition and less likely to learn something about some other factor (such as facilitation, predation, abiotic factors, genetic structure, and so on) that we did not think to manipulate. Observe your organism or system with as few assumptions as possible and let it suggest ideas to you.

Good intuition is the first requirement for meaningful experiments. The best way to develop that intuition is by observing organisms in the field. Sadly, none of us "has the time" to spend observing nature. Guidance committees and tenure reviewers are not likely to recommend spending precious time in this way. However, observations are absolutely essential for you to generate working hypotheses that are novel yet grounded in reality. Carve out some time to get to know your organisms. If you are too busy with classes and other responsibilities, then reserve two days before you start your experiments to observe your system with no manipulations (or preconceived notions). It often helps to do this with a lab mate or colleague. The opposite is also true; spending a whole day with no other people around and no distractions just looking at your organism can be very instructive as well. Even after you have set up your manipulations, continue to monitor the natural variation in your organisms. This will help you interpret your results and plan better experiments next year. For example, Mikaela's initial project plan for her first research project involved examining the role of fire on butterfly assemblages on forested hillsides. Poking around during her first season revealed that most butterflies were using riparian areas, a habitat that fire ecologists had largely ignored. This led to a second experiment the following year that was far more informative than the original experiment she had planned (Huntzinger 2003).

A field notebook is one tool that may help you make and use observations. It is difficult to remember all the details that you observe. Jot them down in your notebook even if they don't seem particularly relevant to the question you are addressing. Also jot down ideas that you have in the field about your study organism, other organisms it may interact with, general ideas about how ecology works, even unrelated ideas that pop into your head, even if they seem unimportant. It is amazing how valuable some of these observations can be at a later time.

An excellent way to begin a project is by observing and quantifying a pattern in nature, as we mentioned in chapter 1. Common ecological patterns include changes in a trait of interest that varies over space or time. This could be anything from a trait of individuals (e.g., beak length) to a trait of ecosystems (e.g., primary production or species diversity). Ask questions about it. How variable is the trait? Is there a real pattern to the variation over space or time? For example, are there large differences in primary production from one place to the next? What factors correlate with the variation that you observe? For example, do the differences in diversity follow a latitudinal gradient? What factors covary with this response variable (species diversity)? For example, what factors vary from the poles to the equator that could help to explain the observed pattern in diversity? It is often helpful to represent the pattern as a figure with one variable on the *x* axis and the other on the *y* axis. This representation allows you to get a sense of the pattern—how strong it is and whether the relationship between the two variables appears to be linear. At this point, an experiment can help to determine if the two variables are causally linked. If the relationship appears linear, then an experiment with two levels of the independent (predictor) variable may be appropriate. For example, if the relationship between the number of pollinators and seed set is linear, then an experiment with and without pollinators may be informative. If the relationship is nonlinear (let's say hump-shaped), then an experiment with only two levels (with and without pollinators) will not be as informative as an experiment with many levels of pollinators.

Observations are critical for meaningful experiments; in some cases they even replace experiments as the best way to gain ecological understanding. This is due in part to the unhappy fact that many processes are difficult to manipulate experimentally. Manipulative experiments must often be conducted on small plots and over short periods of time (Diamond 1986). However, important ecological processes often occur at scales that are large or have little replication. These processes may involve organisms that cannot be manipulated for ethical reasons. Other processes are simply hard to manipulate in any realistic way. For example, manipulations involving vertebrate predators are difficult to achieve with any realism. Their home ranges are often larger than the plots available to investigators. Removing predators is often more feasible than adding them, but may be unethical. Observations are often possible in these and other situations when experiments are problematic. Observational experiments still require replication and controls to be most informative (see "Manipulative Experiments" below). We discuss how to analyze observed patterns in chapter 5.

Although it's tempting to extrapolate our results from small-scale experiments to more interesting and realistic processes at larger scales, it is difficult to justify doing so. One partial solution to this dilemma is to observe processes that have occurred over larger spatial and temporal scales and ask whether these observations support our data from modeling and doing experiments at small scales. Such observations are sometimes termed "natural experiments," since the investigator does not randomly assign and impose the treatments (Diamond 1986).

Long-term data sets expand the temporal scale of any experimental or observational study. If you have the opportunity to link your work to a long-term survey, it is worth considering. For example, daily surveys of amphibians have been collected at one pond, Rainbow Bay in South Carolina, since 1978. This record has been useful for understanding the causes of worldwide amphibian declines (Pechmann et al. 1991), the consequences of anthropogenic climate change (Todd et al. 2011), and other ecological issues.

Why are observations less valued than manipulative experiments? Observations can be applied to test hypotheses, but they are poor at establishing causality. This is their main limitation. For example, we can observe that two species do not co-occur as frequently as we would expect. This may suggest that the two are competing. In the early 1970s everyone was "observing competition" of this sort because it made such good theoretical sense. However, the observed lack of co-occurrence could be caused by the two species independently having different habitat preferences that have nothing to do with current competition. Observations alone do not allow the causes of the pattern to be determined, although methods are being developed to infer causal relationships from observational surveys (chapter 5). But while limited in some ways, observations provide natural history intuition at realistic scales so that important factors for manipulative experiments and modeling can be identified.

Manipulative Experiments

Manipulative experiments vary only one thing (or at most a few). The experimenter controls that variable. If the experiment has been set up properly, any responses can be attributed to the manipulation. This approach is very powerful for establishing causality. Treatments, including controls, should be assigned randomly so that they are interspersed (Hurlbert 1984). Statistical tests can then be used to evaluate the likelihood that the observed effect was caused by chance or by the manipulation. These issues will be considered in much more detail throughout this book, particularly later in this chapter and in chapter 4.

Model Building

Modeling is an attempt to generalize, to distill the cogent factors and processes that produce the behaviors, population dynamics, and community patterns that we observe. The strengths of the approach are that the results apply generally to many systems and that the model allows us to identify the workings of the important elements. Mathematical modeling forces us to be explicit about our assumptions and about the ways that we envision the factors (individuals, species, etc.) to be related. Since we often make these assumptions anyway, writing a model almost always focuses our thinking. We all use models to organize our observations, although these are usually verbal generalizations rather than mathematical equations. The act of writing an explicit model forces us to be more precise about the logical progression that produces generalizations. Models also allow us to explore the bounds of the hypothesis. In other words, under what conditions does the hypothesis break down?

Models can be general or specific; both kinds are usually constructed of mathematical statements. General models allow us to formulate the logical links between variables. Specific models involve measured parameters from actual organisms and allow us to make detailed predictions (e.g., how much harvesting can a population sustain?).

Successful models can let us develop new hypotheses about how nature works or about how to manage ecological systems. For example, theoretical models predicted that apparent competition should be common in nature (Holt 1977). In apparent competition, two species at the same trophic level appear to be competing, while in fact one species is actually causing shared predators to become more abundant, which depresses the other species (fig. 1). Partly as a result of these modeling results, Holt and others have looked for this phenomenon in nature, and it is indeed widespread (reviewed by Holt and Lawton 1994). Models have also proven useful in designing conservation and management strategies. For example, a detailed demographic model of declining loggerhead turtles indicated that populations were less sensitive to changes in mortality of eggs and hatchlings and more sensitive to changes in mortality of older individuals than conservation ecologists had previously realized (Crouse et al. 1987). This result prompted changes in efforts to protect turtle populations, which have improved their prospects for survival (Finkbeiner et al. 2011).

In addition to helping us develop new hypotheses, models can tell us where to look for the patterns in nature. For example, Darwin observed many finches with different morphologies and life histories on his visit to the Galapagos. But he didn't record which morphologies were found on which islands. He didn't see this information as relevant at the time because he had not yet generated a model of differentiation and speciation.

Models can make logical connections easier to see. Often the consequences or results are well known and very visible but the processes that caused those results are difficult

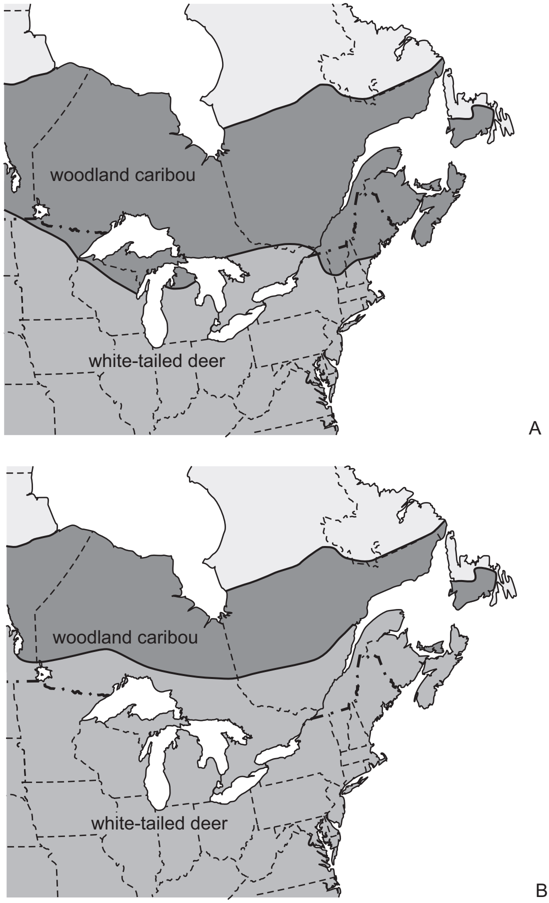
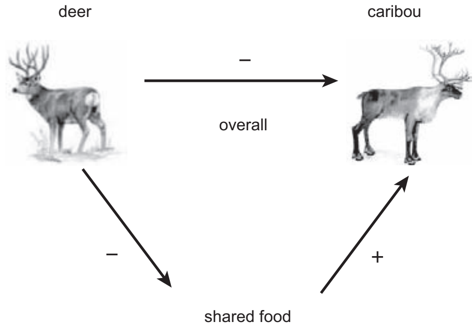


FIGURE 1. Apparent competition between white-tailed deer and caribou (Bergerud and Mercer 1989). A. Caribou historically lived in New England, Atlantic Canada, and the northern Great Lakes states (redrawn from a Wildlands League caribou range map). B. Since European colonization, records show deer expanding their range into these areas and replacing caribou (redrawn from Thomas and Gray 2002). Numerous efforts to reestablish caribou into areas where they could contact deer have failed. C. The conventional hypothesis for the declines in caribou involved competition for food



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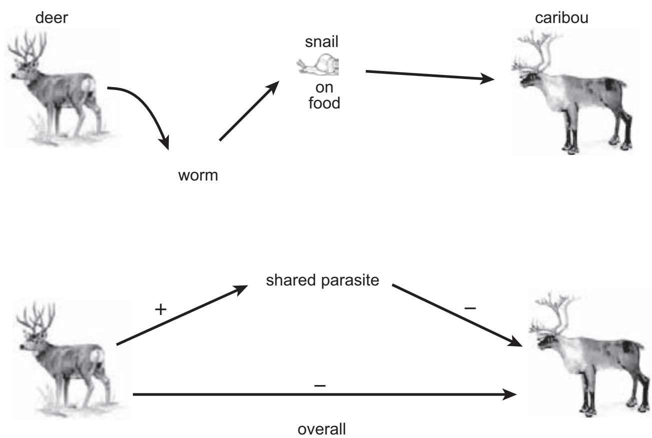

D

resources. More deer meant less food for caribou (shown as a negative effect of deer on shared food). This explanation has not been supported by data, and one current hypothesis involves mortality to caribou caused by a shared parasite, a meningeal worm. D. White-tailed deer are the usual host for the worm, and they are far more tolerant of infection than are moose, mule deer, and, especially, caribou. Caribou get the worms by ingesting snails and other gastropods that adhere to their food. The gastropods are an intermediate host for the worms.

to assess. Models can force us to consider alternative mechanisms when the currently favored explanation does not produce the “right result” in our modeling effort. For example, John Maron and Susan Harrison (1997) were faced with trying to explain why high densities of tussock moth caterpillars were tightly aggregated. They knew from a caging experiment that the moths could survive outside of the aggregation, although in nature the moths were restricted to the aggregation area. Spatial models suggested that very patchy distributions could arise within a homogeneous habitat if predation was strong and the dispersal distance of the moth was limited. As a result of these model predictions, they looked for predation, a previously unexamined explanation, and found that it was indeed operating.

Models of all sorts have been used to test ecological hypotheses. If a model has been constructed that includes particular ecological mechanisms, it is possible to ask whether the model fits actual data. If the fit is good, people may argue that the ecological mechanisms included in the model are probably operating. However, this reasoning uses correlation to support the implicit hypothesis that the mechanisms that provide a good fit are the ones that caused the patterns in the data. Such arguments rarely acknowledge that other mechanisms could also produce good fits to the data and may be the actual causal factors in nature. Models can be very useful as long as you don’t over-interpret them.

It is unfortunate that modeling and natural history often attract different people with different skills and little appreciation for each other’s approach. However, many of the most successful ecologists have been individuals who have been able to bridge these two approaches.

Why Ecologists Like Experiments So Much (Or Why We Couldn't Call This Book *The Tao of Ecology*)

The Tao is an ancient Chinese term that refers to the streamlike flow of nature. Like a stream, the Tao moves gently, seeking the path of least resistance and finding its way around, without disturbing or destroying. A Tao of Ecology might entail noninvasive and nondestructive observations of entire systems to understand who the players are and how they interact with one another. We find the Tao to be an appealing image in general and one that could be applied to ecology (see book cover). However, nothing could be farther from the approach that most ecologists currently employ. In this section, we explain why ecologists like to manipulate their systems so much.

In recent decades, ecology has come to rely on manipulative experiments. The investigator disturbs the system and observes what effect the disturbance has. This experimental approach has the advantage of providing more reliable information about cause and effect than do more passive methods of study. Understanding cause and effect is critical, powerful, and much more difficult than it sounds.

Consider the inferences that can be drawn based on observations versus those based on experiments. Observations provide us with a chance to discover many correlations; however, correlations provide limited insight into cause-and-effect relationships. One version of the old adage says that correlation does not imply causation. Bill Shipley (2000) points out that this is incorrect. Correlation almost always *implies* causation, but by itself, cannot *resolve* which of the two correlated variables might have *caused* the other. Let us give two examples, the first from one of our life experiences and the other from the ecological literature.

The end of grad school was a time of reckoning for Rick. The only car he had ever owned, a Chevy Vega, was clearly falling apart, although he pretended not to notice. His girlfriend convinced him that since he had a job lined up on the other side of the country, and he would soon actually have a salary, he should abandon his grad-student lifestyle and buy another car before heading west. Red has always been his favorite color, so naturally he was interested in a red car. However, his girlfriend had seen a graph on the front page of *USA Today* indicating that red cars are involved in more accidents per mile than cars of other colors. Concerned about their safety, she argued for another color. Statistics don't lie, and red cars are more dangerous than other cars. Her working hypothesis had the cause and effect as "red causes danger":

Red ⟶ Danger

Rick was unsuccessful in convincing her that more dangerous (sexy?) people chose red cars in the first place and that getting a more boring color would do little to help them:

Danger ⟶ Red

In the end, Rick bought a gray car but drives a red one now (when a bicycle won't do). As this book goes to press he has luckily escaped being in any automobile accidents.

This example may seem silly, and unlikely to happen to scientists (Rick's girlfriend was a social worker). We can assure you that we have seen it repeated many times by ecologists who infer causal links from correlations. For example, Tom White made the insightful observations that outbreaks of herbivorous psyllid insects were associated with physiological stress to their host plants and these outbreaks followed unusually wet winters plus unusually dry summers (White 1969):

unusual weather ——— physiological stress ——— psyllid outbreaks

He argued that plant physiological stress increased the availability of limiting nitrogen to the psyllids he studied and to many other herbivores (White 1984, 2008). So essentially he hypothesized a causal connection between these correlated factors:

weather → stress → increased N → herbivore outbreaks

However, the actual causal links could be different. For instance:

weather → herbivore outbreaks → stress → increased N

Or perhaps weather influences some other factor that then causes herbivore outbreaks, without involving the host plant:

weather → plant stress
↘ reduced predation → herbivore outbreaks

Without manipulative experiments, it is difficult to establish which of these causal hypotheses are valid and important. However, if microenvironmental conditions, physiological stress, available nitrogen, herbivore numbers, and predator numbers can all be manipulated, it will be relatively easy to determine which of these factors cause changes in which others. In the end, White's intuition got him fairly close to the truth. A review of experimental studies suggests that herbivores, especially the sap feeders that White studied, are negatively affected by continuous drought stress, but that intermittent bouts of plant stress and recovery promote herbivore populations (Huberty and Denno 2004).

Replicated manipulative experiments have the potential to provide more definitive evidence about causality, but unfortunately many ecological problems are not amenable to experimentation. New techniques are being developed that can provide inference about causal relationships from observational data (Shipley 2000, Grace 2006). These techniques involve directed graphs (the diagrams with arrows shown above). Once we have specified a causal path or directed graph, we can predict which pairs of variables will be correlated and which pairs will be independent of one another. These techniques allow us to build models that estimate the probability of causation from correlations in the data. We can then discard causal models that don't fit our observations.

These methods are not difficult to use, but are much less well known than inferential statistics such as analysis of variance (see chapter 4). This correlational approach is most useful when one model matches the observed patterns more accurately than alternative models, which is often not the case in ecology. The jury is still out on how often and severely the assumptions will limit the applicability of these new methods. We will return to directed graphs in chapter 5.

In summary, ecologists love manipulative experiments because we love understanding causality. Regardless of your philosophical persuasion on this issue, the truth remains that it is easier to publish experimental work than work relying on observations and correlations. Observations can address patterns at larger scales than experiments, but if you have a choice between observations and experiments to ask the same question, experiments are more powerful and convincing. However, not all experiments are created equal. Experiments are only as good as the intuition that stimulated the experimenter to manipulate the few factors that he or she has chosen. Experiments are limited by this initial intuition and by problems of scale and realism. In addition, natural history observations can provide the intuition to design meaningful experiments and provide information over larger areas and longer time frames than an experimenter can handle with manipulations. Another approach, modeling, can provide generality, suggest results when experiments are impossible, project into the future, and stimulate testable predictions.

Whenever possible, you should integrate several of these approaches to pose and answer ecological questions. One approach can make up for the weaknesses of another. The best of modern ecology combines observations, models, and manipulative experiments to arrive at more complete explanations than any single approach could provide. You are after the best cohesive story you can put together.