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Integrating ecology and management

Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs 1972). Predicting and maintaining or altering the distribution and abundance of various organisms are the primary goals of natural resource management; hence, the effective management of natural ecosystems depends on ecological knowledge. Paradoxically, management of ecosystems often ignores relevant ecological theory and many ecological investigations are pursued without appropriate consideration of management implications. This paradox has been recognized by several agencies and institutions (e.g., National Science Foundation, U.S. Forest Service, U.S. Fish and Wildlife Service, Bureau of Land Management, Environmental Protection Agency) (Grumbine 1994; Alpert 1995; Keiter 1995; Brunner and Clark 1997) and entire journals are dedicated to the marriage of ecology and management (e.g., *Journal of Applied Ecology, Conservation Biology, Ecological Applications*). Nonetheless, the underlying causes of this ambiguity have not been determined and no clear prescriptions have been offered to resolve the paradox. The fundamental thesis of this book is that ecological principles can, and should, serve as the primary basis for the management of natural ecosystems, including their plant and animal populations.

Some readers will undoubtedly argue that managers are not interested in hearing about ecologists' problems, and vice versa. Although we fear this may be true, we assume that progressive managers and progressive scientists are interested in understanding problems and contributing to their solution. Indeed, progressive managers ought to be scientists, and progressive scientists ought to be able to assume a manager's perspective. As such, effective managers will understand the hurdles faced by research ecologists, and the trade offs associated with the different methods used to address issues of bias, sample size, and so on. Managers and scientists will be more effective if they understand science and management. How better to seek information, interpret scientific literature, evaluate management programs, or influence research than to understand and appreciate ecology and management?

ECOLOGY AS A SCIENCE

As with any human endeavor, the process of science shares many characteristics with "everyday" activities. For example, observations of recurring events – a fundamental attribute of science – are used to infer general patterns in shopping, cooking, and donning clothing: individuals and institutions rely on their observations and previous experience to make decisions about purchasing items, preparing food, and selecting clothing. This discussion, however, focuses on features that are unique to science. It assumes that science is obliged in part to offer explanatory and predictive power about the natural world. An additional assumption is that the scientific method, which includes explicit hypothesis testing, is the most efficient technique for acquiring reliable knowledge. The scientific method should be used to elucidate mechanisms underlying observed patterns; such elucidation is the key to predicting and understanding natural systems (Levin 1992; but see Pickett *et al.* 1994). In other words, we can observe patterns in nature and ask why a pattern occurs, and then design and conduct experiments to try to answer that question. The answer to the question "why" not only gives us insight into the system in which we are interested, but also gives us direction for the manipulation and management of that resource (Gavin 1989, 1991).

From a modern scientific perspective, a hypothesis is a candidate explanation for a pattern observed in nature (Medawar 1984; Matter and Mannan 1989); that is, a hypothesis is a potential reason for the pattern and it should be testable and falsifiable (Popper 1981). Hypothesis testing is a fundamental attribute of science that is absent from virtually all other human activities. Science is a process by which competing hypotheses are examined, tested, and rejected. Failure to falsify a hypothesis with an appropriately designed test is interpreted as confirmatory evidence that the hypothesis is accurate, although it should be recognized that alternative and perhaps as yet unformulated hypotheses could be better explanations.

A hypothesis is not merely a statement likely to be factual, which is then "tested" by observation (McPherson 2001a). If we accept any statement (e.g., one involving a pattern) as a hypothesis, then the scientific method need not be invoked – we can merely look for the pattern. Such statements are not hypotheses (although the term is frequently applied to them); they are more appropriately called predictions. Indeed, if observation is sufficient to develop reliable knowledge, then science has little to offer beyond everyday activities. Much ecological research is terminated after the discovery of a pattern and the cause of the pattern is not determined (Romesburg 1981; Willson 1981). For example, multiple petitions to list the northern goshawk (*Accipiter gentilis atricapillus*) under the Endangered Species Act of 1978 as a Threatened or Endangered Species in the western United States prompted several studies of their nesting habitat (Kennedy 1997; DeStefano 1998). One pattern that emerged from these studies is that goshawks, across a broad geographical range from southeastern Alaska to the Pacific Northwest to the southwestern United States, often build their nests in forest stands with old-growth characteristics, i.e., stands dominated by large trees and dense cover formed by the canopy of these large trees (Daw *et al.* 1998). This pattern has been verified, and the existence of the pattern is useful information for the conservation and management of this species and its nesting habitat. However, because these studies were observational and not experimental, we do not know *why* goshawks nest in forest stands with this kind of structure. Some likely hypotheses include protection offered by old-growth forests against predators, such as great horned owls (*Bubo virginianus*), or unfavorable weather in secondary forests, such as high ambient temperatures during the summer nesting season. An astute naturalist with sufficient time and energy could have detected and described this pattern, but the scientific method (including hypothesis testing) is required to answer the question of *why*. Knowledge of the pattern increases our information base; knowledge of the mechanism underlying the pattern increases our understanding (Figure 1.1).

Some researchers have questioned the use of null hypothesis testing as a valid approach in science. The crux of the argument is aimed primarily at: (1) the development of trivial or "strawman" null hypotheses that we know a priori will be false; and (2) the selection of an arbitrary α-level or P-value, such as 0.05 (Box 1.1). We encourage readers to peruse and consider the voluminous and growing literature on this topic (e.g., Harlow *et al.* 1997; Cherry 1998; Johnson 1999; Anderson *et al.* 2000). Researchers such as Burnham and Anderson (1998) argue that we should attempt to estimate the magnitude of differences between or among experimental groups (an *estimation problem*) and then decide if these differences are large enough to justify inclusion in a model (a *model selection problem*). Inference would thus be based on multiple model

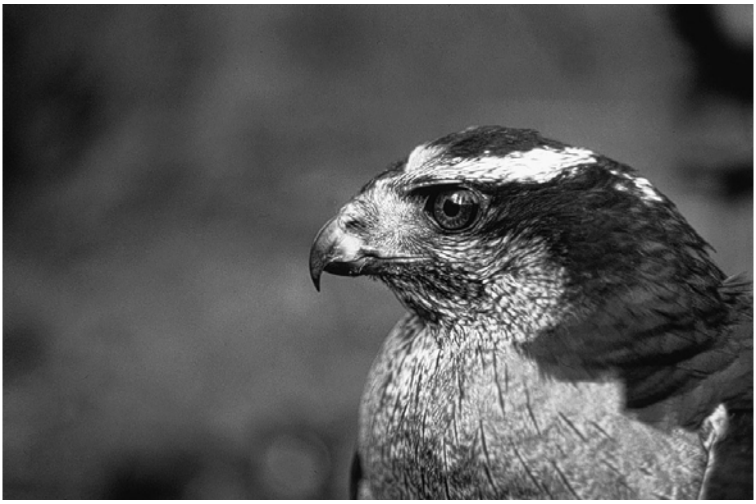

Figure 1.1 Northern goshawks are often found nesting in stands of older trees, possibly because of the protection offered from predators or weather. Photo by Stephen DeStefano.

building and would use information theoretic techniques, such as Akaike's Information Criterion (AIC) (Burnham and Anderson 1998), as an objective means of selecting models from which to derive estimates and variances of parameters of interest (Box 1.2). In addition, statistical hypothesis testing can, and should, go beyond simple tests of significance at a predetermined *P*-value, especially when the probability of rejecting the null hypothesis is high. For example, to test the null hypothesis that annual survival rates for male and female mule deer do not differ is to establish a "strawman" hypothesis (D. R. Anderson, personal communication; Harlow *et al.* 1997). Enough is known about the demography of deer to realize that the annual survival of adult females differs from adult males. Thus, rejecting this null hypothesis does not advance our knowledge. In this and many other cases, it is time to advance beyond a simple rejection of the null hypothesis and to seek accurate and precise estimates of parameters of interest (e.g., survival) that will indicate *what* and *how different* the survival rates are for these age-and-sex cohorts. Another approach is to design an experiment rather than an observational study, and to craft more interesting hypotheses: for example, does application of a drug against avian cholera improve survival in snow geese? In this case, determining *how different* would be important, but even a simple rejection of the null hypothesis would be interesting and informative.

Box 1.1 Null model hypothesis testing

The testing of null hypotheses has been a major approach used by ecologists to examine questions about natural systems (Cherry 1998; Anderson *et al.* 2000). Simply stated, null hypotheses are phrased so that the primary question of interest is that there is no difference between two or more populations or among treatment and control groups. The researcher then hopes to find that there is indeed a difference at some prescribed probability level – often $P \leqslant 0.05$, sometimes $P \leqslant 0.1$. Criticism of the null hypothesis approach has existed in some scientific fields for a while, but is relatively new to ecology. Recent criticism of null hypothesis testing and the reporting of *P*-values in ecology has ranged from suggested overuse and abuse to absolute frivolity and nonsensicality, and null hypotheses have been termed strawman hypotheses (i.e., a statement that the scientist knows from the onset is not true) by some authors. Opponents to null hypothesis testing also complain that this approach often confuses the interpretation of data, adds very little to the advancement of knowledge, and is not even a part of the scientific method (Cherry 1998; Johnson 1999; Anderson *et al.* 2000).

Alternatives to the testing of null hypotheses and the reporting of *P*-values tend to focus on the estimation of parameters of interest and their associated measures of variability. The use of confidence interval estimation or Bayesian inference have been suggested as superior approaches (Cherry 1996). Possibly the most compelling alternative is the use of information theoretic approaches, which use model building and selection, coupled with intimate knowledge of the biological system of interest, to estimate parameters and their variances (Burnham and Anderson 1998). The questions then focus on the values of parameters of interest, confidence in the estimates, and how estimates vary among the populations of interest. Before any of these approaches are practiced, however, the establishment of clear questions and research hypotheses, rather than null hypotheses, is essential.

These arguments against the use of *statistical hypotheses* are compelling and important, but are different, in our view, from the development of *research hypotheses* and the testing of these hypotheses in an *experimental framework*. It is the latter that we suggest is fundamental

Box 1.2 Model selection and inference

Inference from models can take many forms, some of which are misleading. For example, collection of large amounts of data as fodder for multivariate models without a clear purpose can lead to spurious results (Rexstad *et al.* 1988; Anderson *et al.* 2001). A relatively new wave of model selection and inference, however, is based on information theoretic approaches. Burnham and Anderson (1998:1) describe this as "making valid inferences from scientific data when a meaningful analysis depends on a model." This approach is based on the concept that the data, no matter how large the data set, will only support limited inference. Thus, a proper model has: (1) the full support of the data, (2) enough parameters to avoid bias, and (3) not too many parameters (so that precision is not lost). The latter two criteria combine to form the "Principle of Parsimony" (Burnham and Anderson 1992): a trade off between the extremes of underfitting (not enough parameters) and overfitting (too many parameters) the model, given a set of a priori alternative models for the analysis of a given data set.

One objective method of evaluating a related set of models is "Akaike's Information Criterion" (AIC), based on the pioneering work of mathematician Hirotugu Akaike (Parzen *et al.* 1998). A simplified version of the AIC equation can be written as:

$$\mathrm{AIC} = \mathrm{DEV} + 2K,$$

where DEV is deviance and K is the number of parameters in the model. As more parameters (structure) are added to the model, the fit will improve. If model selection were based only on this criterion, one would end up always selecting the model with the most possible parameters, which usually results in overfitting, especially with complex data sets. The second component, K, is the number of parameters in the model and serves as a "penalty" in which the penalty increases as the number of parameters increase. AIC thus strikes a balance between overfitting and underfitting. Many software packages now compute AIC. In very general terms, the model with the lowest AIC value is the "best" model, although other approaches such as model averaging can be applied.

The development of models within this protocol depends on the a priori knowledge of both ecologists and analysts working together, rather than the blind use of packaged computer programs. Information theoretic approaches allow for the flexibility to develop a related set of models, based on empirical data, and to select among or weight those models based on objective criteria. Parameters of interest, such as survival rates or abundance, and their related measures of variance can be computed under a unified framework, thereby giving the researcher confidence that these estimates were determined in an objective manner.

to advancing our knowledge of ecological processes and our ability to apply that knowledge to management problems.

Use of sophisticated technological (e.g., microscopes) or methodological (e.g., statistical) tools does not imply that hypothesis testing is involved, if these tools are used merely to detect a pattern. Pattern recognition (i.e., assessment of statements likely to be factual) often involves significant technological innovation. In contrast, hypothesis testing is a scientific activity that need not involve state-of-the-art technology.

TESTING ECOLOGICAL HYPOTHESES

Some ecologists (exemplified by Peters 1991) have suggested that ecology makes the greatest contribution to solving management problems by developing predictive relationships based on correlations. This view suggests that ecologists should describe as many patterns as possible, without seeking to determine underlying mechanisms. An even more extreme view is described by Weiner (1995), who observed that considerable ecological research is conducted with no regard to determining patterns *or* testing hypotheses. In contrast to these phenomenological viewpoints, most ecologists subscribe to a central tenet of modern philosophy of science: determining the mechanisms underlying observed patterns is fundamental to understanding and predicting ecosystem response, and therefore is necessary for improving management (e.g., Simberloff 1983; Hairston 1989; Keddy 1989; Matter and Mannan 1989; Campbell *et al.* 1991; Levin 1992; Gurevitch and Collins 1994; Weiner 1995; McPherson and Weltzin 2000; McPherson 2001a; but see also Pickett *et al.* 1994).

Since hypotheses are merely candidate explanations for observed patterns, they should be tested. Experimentation (i.e., artificial application of treatment conditions followed by monitoring) is an efficient and appropriate means for testing hypotheses about ecological phenomena; it is also often the only means for doing so (Simberloff 1983; Campbell *et al.* 1991). Experimentation is necessary for disentangling important driving variables which may be correlated strongly with other factors under investigation (Gurevitch and Collins 1994). Identification of the underlying mechanisms of vegetation change enables scientists to predict vegetation responses to changes in variables that may be "driving" or directing the system, such as water, temperature, or soil nutrients. Similarly, understanding the ultimate factors that underlie animal populations will allow wildlife managers to focus limited resources on areas that will likely be most useful in the recovery and management of the population. An appropriately implemented experimental approach yields levels of certainty that are the most useful to resource managers (McPherson and Weltzin 2000).

In contrast to the majority of ecologists, most managers of ecosystems do not understand the importance of experiments in determining mechanisms. In the absence of experimental research, managers and policy-makers must rely on the results of descriptive studies. Unfortunately, these studies often produce conflicting interpretations of underlying mechanisms and are plagued by weak inference (Platt 1964): descriptive studies (including "natural" experiments, *sensu* Diamond 1986) are forced to infer mechanism based on pattern. They are, therefore, poorly suited for determining the underlying mechanisms or causes of patterns because there is no test involved (Popper 1981; Keddy 1989). Even rigorous, long-term monitoring is incapable of revealing causes of change in plant or animal populations because the many factors that potentially contribute to shifts in species composition are confounded (e.g., Wondzell and Ludwig 1995).

Examples of "natural" experiments abound in the ecological literature, but results of these studies should be interpreted judiciously. For example, researchers have routinely compared recently burned (or grazed) areas with adjacent unburned (ungrazed) areas and concluded that observed differences in species composition were the direct result of the disturbance under study. Before reaching this conclusion, it is appropriate to ask why one area burned while the other did not. Preburn differences in productivity, fuel continuity, fuel moisture content, plant phenology, topography, or edaphic factors may have caused the observed fire pattern. Since these factors influence, and are influenced by, species composition, they cannot be ruled out as candidate explanations for postfire differences in species composition (Figure 1.2).

Figure 1.2 Many environmental variables, such as fuel loads, available moisture, and plant phenology, can influence how a fire burns on the landscape. Photo by Guy R. McPherson.

LIMITS TO THE APPLICATION OF ECOLOGY

Considerable research has investigated the structure and function of wildland ecosystems. This research has been instrumental in determining the biogeographical, biogeochemical, environmental, and physiological patterns that characterize these ecosystems. In addition, research has elucidated some of the underlying mechanisms that control patterns of species distribution and abundance. Most importantly, however, research to date has identified many tentative explanations (i.e., hypotheses) for observed ecological phenomena. Many of these hypotheses have not been tested explicitly, which has limited the ability of ecology, as a discipline, to foresee or help solve managerial problems (Underwood 1995). The contribution of science to management is further constrained by the lack of conceptual unity within ecology and the disparity in the goals of science and management.

The unique characteristics of each ecosystem impose significant constraints on the development of parsimonious concepts, principles, and theories. Lack of conceptual unity is widely recognized in ecology (Keddy 1989; Peters 1991; Pickett *et al.* 1994; Likens 1998) and natural resource management (Underwood 1995; Hobbs 1998). The paucity of unifying principles imposes an important dichotomy on science and management: on the one hand, general concepts, which science should strive to attain, have little utility for site-specific management; on the other hand, detailed understanding of a particular system, which is required for effective management, makes little contribution to ecological theory. This disparity in goals is a significant obstacle to relevant discourse between science and management.

In addition, scaling issues may constrain the utility of some scientific approaches (Peterson and Parker 1998). For example, it may be infeasible to evaluate the response to vegetation manipulation of rare or wide-ranging species (e.g., masked bobwhite quail (*Colinus virginianus ridgwayi*), grizzly bear (*Ursus arctos*)). In contrast, common species with small home ranges (e.g, most small mammals) are abundant at relevant spatial and temporal scales and are, therefore, amenable to description and experimentation.

LINKING SCIENCE AND MANAGEMENT

Ecologists have generally failed to conduct experiments relevant to managers (Underwood 1995), and managerial agencies often resist criticisms of performance or suggestions for improvement (Longood and Simmel 1972; Ward and Kassebaum 1972; Underwood 1995). In addition, management agencies often desire immediate answers to management questions, while most ecologists recognize that long-term studies are required to address many questions. These factors have contributed to poorly developed, and sometimes adversarial, relationships between managers and scientists. To address this problem, scientists should be proactive, rather than reactive, with respect to resource management issues, and managers should be familiar with scientific principles. These ideas are developed in further detail in Chapter 5.

Interestingly, some scientists believe that there is insufficient ecological knowledge to make recommendations about the management of natural resources, whereas others believe that ecologists are uniquely qualified to make these recommendations. Of course, decisions about natural resources must be made – the demands of an increasingly large and diverse society necessitate effective management – so it seems appropriate to apply relevant ecological knowledge to these decisions. However, ecologists generally have no expertise in the political, sociological, or managerial aspects of resource management, and they are rarely affected directly by decisions about land management. Thus, ecologists are not necessarily accountable or responsible land stewards. Conversely, managers are ultimately accountable and responsible for their actions, so they should exploit relevant ecological information as one component of