

# Applied Ecology and Natural Resource Management

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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  $\alpha$ -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  $P \leq 0.05$ , sometimes  $P \leq 0.1$ . 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:

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

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

the decision-making process. Ultimately, management decisions should be made by managers most familiar with individual systems.

#### MAKING MANAGEMENT DECISIONS

Management decisions must be temporally, spatially, and objective specific. Thus, management and conservation are ultimately conducted at the local level. Specific management activities, although presumably based on scientific knowledge, are conducted within the context of relevant social, economic, and political issues (*sensu* Brown and MacLeod 1996).

Clearly stated goals and objectives will facilitate management and allow the selection of appropriate tools to accomplish these goals and objectives (Box 1.3). Conversely, selection of goals or objectives that are poorly defined or quantified may actually impede management. For example, use of the term “ecosystem health” implies that there is an optimal state associated with an ecosystem, and that any other state is abnormal; however, the optimal state of an ecosystem must be defined, and clearly stated quantifiable objectives must be developed to achieve that state. Similarly, “ecosystem integrity” (Wicklum and Davies 1995) and sustainability (Lélé and Norgaard 1996) are not objective, quantifiable properties.

#### **Box 1.3** Applying the appropriate fire regime to meet management goals

Throughout the New World, fire regimes changed dramatically after Anglo settlement in concert with changes in ecosystem structure and function. Many ecosystems formerly characterized by frequent, low-intensity surface fires are now characterized by infrequent, high-intensity fires. Altered fire regimes have contributed to, and have resulted from, changes in ecosystem structure; for example, savannas typified by low-intensity surface fires have been replaced in many areas with dense forests that burn infrequently and at high intensities.

Many managers recognize that periodic fires played an important role in the maintenance of ecosystem structure and function, and that these fires probably contributed to high levels of biological diversity. As a result, precise determination of the presettlement fire regime has become an expensive pursuit of many managers. This exercise often is followed by the large-scale reintroduction of

recurrent fires into areas where they once were common, in an attempt to restore ecosystem structure by restoring the fire regime.

Unfortunately, accurate reconstruction of events that contributed to historical changes in vegetation (including interruption of fire regimes) will not necessarily facilitate contemporary management, and rarely will engender restoration of presettlement conditions. Pervasive and profound changes have occurred in the biological and physical environments during the last century or more (e.g., dominance of many sites by nonnative species, altered levels of livestock grazing, increased atmospheric CO<sub>2</sub> concentrations). As a result, simply reintroducing periodic fires into areas in which fires formerly occurred will not produce ecosystems that closely resemble those found before Anglo settlement; in this case, understanding the past will *not* ensure that we can predict the future, and a detailed understanding of past conditions may impede contemporary management by lending a false sense of security to predictions based on retrospection. Rather, recurrent fires in these “new” systems may enhance the spread of nonnative species and ultimately cause native biological diversity to decline.

As with any management action, reintroduction of fire should be considered carefully in light of clearly stated, measurable goals and objectives. Historic and prehistoric effects of fires serve as poor analogs for present (and near-future) effects, and presettlement fire regimes should not be used to justify contemporary management. Rather, reintroduction of fires should be evaluated in terms of expected benefits and costs to contemporary management of ecosystems.

The use of terms such as “health,” “integrity,” and “sustainability” as descriptors of ecosystems implies that managers or scientists can identify the state that is optimum for the ecosystem (vs. optimum for the production of specific resources) and that the preservation of this state is scientifically justifiable. These terms are not supported by empirical evidence or ecological theory, and should be abandoned in favor of other more explicit descriptors (Wicklum and Davies 1995). Appropriate goals and objectives should be identified on a site-specific basis and linked to ecosystem structures or functions that can be defined and quantified.

Pressing needs for the production of some resources and conservation of others indicate that management decisions cannot be postponed until complete scientific information is available on an issue. In



Figure 1.3 Purple loosestrife is a nonnative perennial plant that was introduced into North America in the early 1800s. By the 1930s, it was well established in wetlands and along drainage ditches in the east. Control of this and other exotic species requires consideration of the impact of potential control agents, as well as the nonnative species itself. Photo by Stephen DeStefano.

addition, management goals often change over time. These two considerations dictate the thoughtful implementation of management actions that do not constrain future management approaches and that are targeted at sustaining or increasing biodiversity (e.g., Burton *et al.* 1992). For example, widespread purposeful introduction of nonnative species illustrates a case of near-sighted management focused on the short-term solution of an acute problem, but which reduces future management options by potentially decreasing biodiversity and altering ecosystem structure and function (Abbott and McPherson 1999). Such narrowly focused management efforts are analogous to drilling a hole in the skull of a patient to relieve a severe headache (Figure 1.3).

Like all sciences, ecology is characterized by periodic dramatic changes in concepts. Progressive managers will want to be apprised of these paradigm shifts. For example, the Clementsian model of vegetation dynamics (Clements 1916; Dyksterhuis 1949) still serves as the basis for the classification and management of most public lands, despite the fact that the more appropriate state-and-transition model (Westoby *et al.* 1989) was adopted by ecologists over a decade ago. The delay in adopting the state-and-transition model by land managers probably stems, at least in



part, from the absence of an analytical technique to quantify state conditions and transition probabilities (Joyce 1992). The state-and-transition model is described in Chapter 4.

#### PURSUING RELEVANT ECOLOGICAL KNOWLEDGE

Although descriptive studies are necessary and important for describing ecosystem structure and identifying hypotheses, reliance on this research approach severely constrains the ability of ecology to solve managerial problems. In addition, the poor predictive power of ecology (Peters 1991) indicates that our knowledge of ecosystem function is severely limited (Stanley 1995). An inability to understand ecosystem function and unjustified reliance on descriptive research are among the most important obstacles that prevent ecology from making significant progress toward solving environmental problems and from being a predictive science. Many ecologists (e.g., Hairston 1989; Keddy 1989; Gurevitch and Collins 1994; McPherson and Weltzin 2000) have concluded that field-based manipulative experiments represent a logical approach for future research.

Ecologists can make the greatest contribution to management and conservation by addressing questions that are relevant to resource management and by focusing their research activities at the appropriate temporal and spatial scales (Allen *et al.* 1984). We suggest that these scales are temporally intermediate (i.e., years to decades) and spatially local (e.g., square kilometers), depending on the questions posed and the species of concern. Of course, contemporary ecological research should be conducted within the context of the longer temporal scales and greater spatial scales at which policy decisions are made. For example, experimental research on climate-vegetation interactions should be conducted within individual ecosystems for periods of a few years, but the research should be couched within patterns and processes observed at regional to global spatial scales and decadal to centennial temporal scales. In other words, the context for ecological experiments should be provided by a variety of sources, including observations, management issues (McPherson and Weltzin 2000), long-term databases (Likens 1989; Risser 1991), cross-system comparisons (Cole *et al.* 1991), and large-scale manipulations (Likens 1985; Carpenter *et al.* 1995; Carpenter 1996) (Figure 1.4).

Results of most ecological studies are likely to be highly site specific (Keddy 1989; Tilman 1990) and it is infeasible to conduct experiments in each type of soil and vegetation or for an animal species in every portion



Figure 1.4 Documenting the potential change in geographical distribution of sugar maples and other trees due to global warming requires ecologists to think at large spatial and temporal scales. Photo by Stephen DeStefano.

of its geographical range (Hunter 1989). Therefore, experiments should be designed to have maximum possible generality to other systems (Keddy 1989). For example, the pattern under investigation should be widespread (e.g., shifts in physiognomy), selected species should be “representative” of other species (of similar life form), the factors manipulated in experiments should have broad generality (biomass), experiments should be arranged along naturally occurring gradients (soil moisture, elevation), and experiments should be conducted at spatial (community) and temporal (annual or decadal) scales appropriate to the management of communities.

Ecological experiments need not be conducted at small spatial scales. For example, ecosystem-level experiments (i.e., relatively large-scale manipulation of ecosystems) represent an important, often-overlooked

technique that can be used to increase predictive power and credibility in ecology. Ecosystem-level experiments may be used to bridge gaps between small-scale experiments and uncontrolled observations, including “natural” experiments. However, they are difficult to implement and interpret (Carpenter *et al.* 1995; Lawton 1995): they require knowledge of species’ natural histories, natural disturbances, and considerable foresight and planning. Fortunately, ecology has generated considerable information about the natural history of dominant species and natural disturbances in many ecosystems. Similarly, foresight and planning should not be limiting factors in scientific research. Time and money will continue to be in short supply, but this situation will grow more serious if ecology does not establish itself as a source of reliable knowledge about environmental management (Peters 1991; Underwood 1995).

In addition to posing questions that are relevant to resource management and that investigate mechanisms, scientists should be concerned with the development of research questions that are tractable. Asking why certain species are present at a particular place and time forces the investigator to rely on correlation. In contrast, asking why species are *not* present (e.g., in locations that appear suitable) forces the investigator to search for constraints, and therefore mechanisms (e.g., DeStefano and McCloskey 1997). Although Harper (1977, 1982) presented a compelling case for tractable, mechanistic research focused on applied ecological issues two decades ago, the underwhelming response by ecologists indicates that his message bears repeating.

#### SUMMARY

Management decisions must be temporally, spatially, and objective specific, so that management and conservation are ultimately conducted at the local level. Appropriate management can be prescribed only after goals and objectives are clearly defined. After goals and objectives are identified, ecological principles can be used as a foundation for the progressive, effective management of natural resources. Managers of natural resources must be able to distinguish candidate explanations from tested hypotheses, and therefore distinguish between conjecture and reliable knowledge. Ecologists can contribute to management efforts by addressing tractable questions that are relevant to resource management, and by focusing their research activities at appropriate temporal and spatial scales. The following chapters illustrate that the science of ecology can be linked with the management of natural resources in ways that are conducive to the improvement of both endeavors.