Erratum

p15 end of INTRODUCTION: add
"theoretical questions and at the same time be of use to managers."

p77. column one, third line from bottom of page: insert hyphen between research and management.

p81. column one, fifteenth line from bottom : insert "management" in place of mamagement".

WHAT IS ECOLOGICAL THEORY AND IS IT OF ANY USE TO MANAGERS?

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INTRODUCTION

A criticism often levelled at much ecological research is that it bears little relevance to real-world problems associated with the management of biological resources (e.g. McKellar 1987; Fig. 1). There appears often to be an unbridgeable gulf between the theoretical constructs of ecology and their actual application. Even within the science of ecology, researchers are seen as being divided into those who deal primarily with mathematical models based on theoretical premises and those who collect field data and attempt to answer "real" problems. Indeed, it has been the case that many field ecologists have little training in mathematics and many theoretical ecologists make little effort to get into the field. However, the distinction between theory and practice is not as clear cut as some would make out.

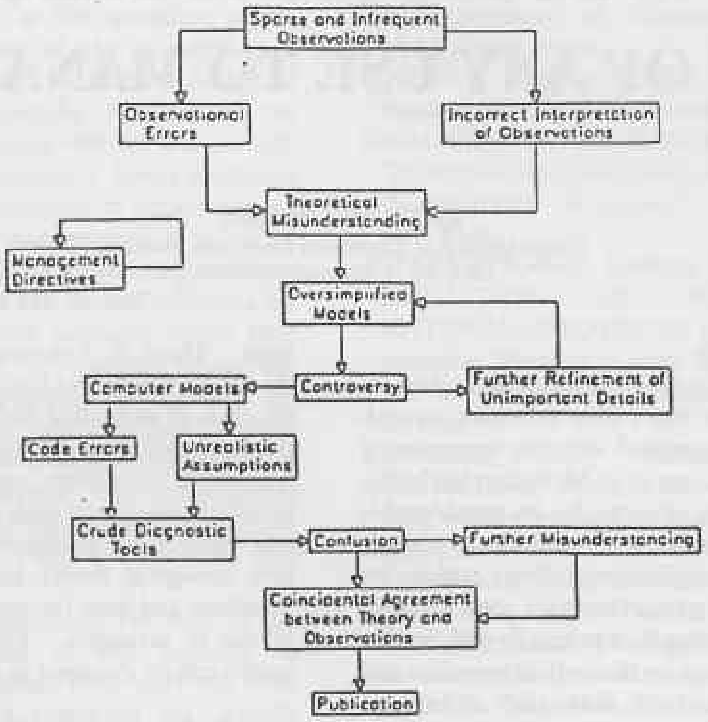
In this paper I want to illustrate that ecological theory is essential to both field ecologists and managers since it underpins everything that they do,. I use "theory" in its broadest sense here, which can be described as a "systematic statement of principles and methods" (Levin 1981), which serves to organize our thoughts and perceptions and aids us in designing our research to be more effective. Thus ecological theory is not simply a collection of mathematical formulae and is not practiced only by theoreticians. Much current ecological theory has been developed from careful field observations by people who are primarily field ecologists. Managers also use ecological theory in almost every management decision they take, even if they do not explicitly recognize that they are doing so. In that respect some aspects of theory have become "second nature" and no longer recognized as theory. It is thus impossible to separate theory and management at this broad level. There is, however, a difference between the broad theoretical basis of ecology and the application of individual ecological theories. In this paper, I will first outline the basic theoretical framework of ecology, and then go on to look at problems associated with particular past and current theoretical arguments. I will then discuss how ecological theory impinges on management questions and how theoretical approaches can be of use to managers. Finally I discuss how research can be designed to address important

THE THEORETICAL FRAMEWORK OF ECOLOGY

Ecology is still a relatively young science and as such does not have a rigid formalized set of theories (e.g. McIntosh 1980). Lawton (1974) commented that "Ecology suffers from a surfeit of fascinating but apparently unrelated observations, superimposed on an acute shortage of general theories". The search for general theories has often been fruitless, and a reason for this lies in the vastness of the subject matter of ecology. Ecology deals with everything from genes to global processes, from arctic tundra to tropical rain forests and from microbes to blue whales. The very diversity of life that ecology sets out to study and explain conspires to thwart any generalities that are put forward. A theory that works in a desert probably will not help much in the intertidal zone.

The level of prediction possible in ecology is also low compared to other sciences. In chemistry it is possible to say with certainty that if you add compound X to compound Y you get a predictable reaction which produces compound Z. The exact rate of the reaction may vary with temperature, but the result is always the same,

Fig. 1. The way in which managers might sometimes conclude that ecological research is carried out (original by S. Briggs).



and the laws governing the process are well understood. In ecology such a level of predictability is not possible because of interacting species or system components, environmental variability and the general level of complexity confronting the ecologist. Ecologists have spent a long time searching for a theoretical basis for making such predictions, but it may be that more limited theories relevant to particular systems or subsystems will be more productive (e.g. Oster 1981; May 1986).

Ecology has however developed a broad theoretical framework which helps to put some order into the apparent chaos. This relies on a hierarchical arrangement of levels of organization, ranging from the individual organism through populations, communities and ecosystems to landscapes and finally the entire biosphere (Table 1). These different levels of organization have distinct sets of processes which operate mostly at a certain level, and theoretical concepts have been derived for each level. Thus, for instance, at the community level ecologists have developed the concepts of niches and food webs to formalize the interrelations between species in any given assemblage, while the concepts of stability, resilience and succession deal with community change and response to disturbance. These general concepts can be widely applied; niches and food webs can be studied equally well in the desert or intertidal zone. Concepts such as population growth and regulation, succession and hydrologic cycles are also central to management decisions. It is impossible to manage a species without some consideration of its population processes.

A potential problem involved in the transferring of ecological concepts to management is that ecological and managerial units do not always coincide, especially at larger scales (Table 1). It may be relatively easy to define an individual population and treat it as a management unit. However, nature reserve boundaries seldom follow natural community or ecosystem boundaries (e.g. Newmark 1985; Schonewald-Cox & Bayless 1986) and landscape and regional units are often the responsibility of several different authorities. There is an increasing awareness of the need to

Table 1. Ecology: A Theoretical Framework

Organisational level	Key concepts and processes	Corresponding management level
Individual	Energy balance Physiological and behavioural responses	? Species reintroduction
Population	Population growth and regulation. Density dependence/ independence. Species interactions. Coevolution Population genetics	Species-oriented management
Community	Environmental gradients, ecotones. Niche theory Diversity, food webs Stability & resilience Succession	Reserve Management
Ecosystem |	Energy flow Trophic levels Biogeochemical cycles	Reserve management
Landscape | Regional	Geomorphologic processes Hydrologic cycles Connectivity Island Biogeography climatic patterns	Catchment, Regional, Multi-authority Management
Global	Biomes Greenhouse effect Acid rain Global climate etc.	National/ international

manage natural systems as ecological units which may cut across several legal and political boundaries (e.g. the Murray Catchment in eastern Australia). The idea of landscape level "networks" is also gaining support (e.g. Forman & Baudry 1984; Noss & Harris 1986). This involves the integration of smaller land-use units (e.g. reserves, farmland, road verges, etc.) into a larger integrated unit. The application of such ideas often requires cooperation between several management authorities.

CAN THEORY HELP MANAGEMENT?

The theoretical framework of ecology given in Table 1 is imbedded in all aspects of research and management of natural systems. However, some more detailed theoretical aspects may apparently be of little day-to-day use to managers. In this section I outline some of the areas where particular ecological theories have been applied successfully to management situations.

Perhaps the most successful application of theory has been in harvesting situations. The concept of maximum sustainable yield has been applied widely, especially in forestry and fisheries. Forestry, in fact, embodies many aspects of ecological theory and some of plant ecology's most robust concepts have come from forestry (e.g. the -3/2 law for self-thinning; Westoby 1984). Theory has helped explain the dramatic drop in fish stocks which has often occurred following increased fishing pressure. The concept of multiple stable states for populations (e.g. May 1977) predicts that increases in harvesting rates can lead to a sudden switch from a relatively high stable population size to a much lower level. This

Fig. 2. Figure from Shimwell (1971) illustrating hydroseral succession. The succession is inferred from the vegetation zonation. The pollen profile on the left is hypothetical - actual analyses by Walker (1970) indicated that the supposed sequence was incorrect.

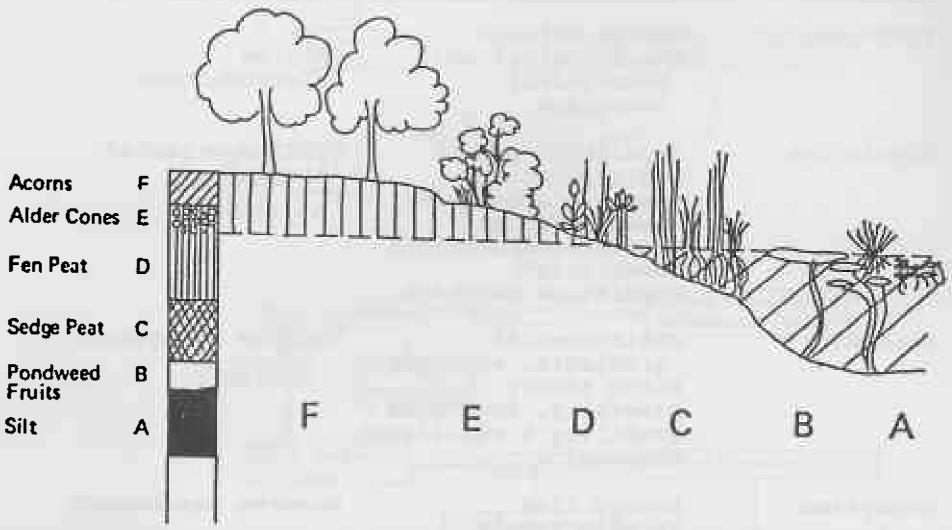


Figure 34. Hydroseral succession and the zonation around a lake. A, zone of floating aquatics; B, rooted acquatics; C, reedswamp; D, sedgemarsh; E, fen-carr; F, mixed mesophytic woodland.

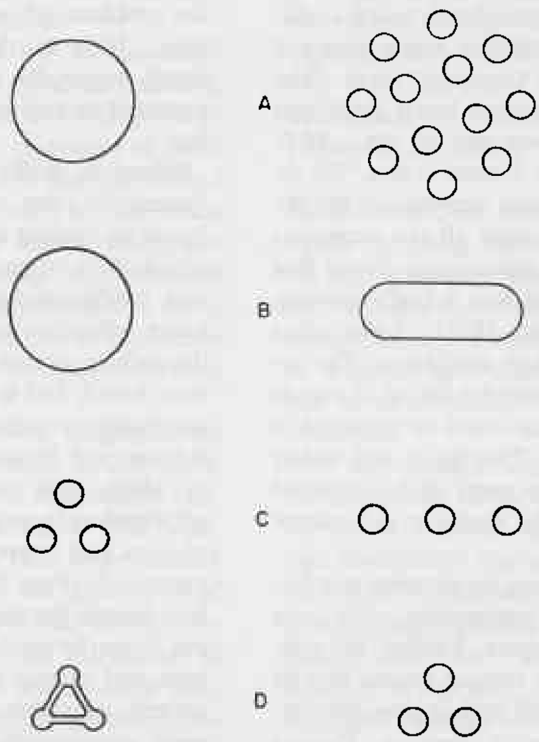
concept is now implicit in the development of more rational fishing policies. The concept of multiple stable states has also been used to explain periodic outbreaks of pests such as spruce budworm in Canada (e.g. May 1977; Moss et al. 1982), and to develop more rational use of herbicides.

A theoretical analysis of the Antarctic ocean ecosystem is also leading to an understanding of changes brought about by whaling and is central to the development of an ecologically sound policy on krill harvesting (May et al. 1979; Laws 1985). The history of whaling has been one of a total rejection of the maximum sustainable yield idea in favour of "mining" for maximum immediate profit (Cherfas 1986) with the result that the bigger whales suffered dramatic population declines. An analysis of the Antarctic food web indicates that the decline in krill consumption due to reduced numbers of large whales has been compensated for by an increase in consumption by smaller whales, seals and birds. An argument for krill harvesting by humans has been that it would simply mop up the surplus not utilized by the larger whales, but it seems likely that this surplus is largely illusory. Any increase in harvesting may therefore affect the rate of population growth of the now rare larger whales. Without an understanding of food-web interactions such problems could go unnoticed - it should be noted, however, that a huge amount of empirical data was also needed to reach these conclusions.

PROBLEMS IN ECOLOGICAL THEORY

Although the theoretical framework in Table 1 can be applied widely and the previous section has indicated that theoretical considerations can be helpful in management, there is still much debate over many more detailed ecological concepts and the relative value of different theoretical approaches. This debate makes the application of theory difficult: how can a manager take theoretical aspects into account when the theorists are bickering amongst themselves about which theories are correct? Discussion in science is, of course, healthy and necessary, but much of the theoretical discussion in ecology often has little obvious relevance outside the seminar room. Johnson & Bossert (1980) suggest that managers find theoretical approaches "faddish, speculative

Fig. 3· "The geometrical rules of design of natural preserves, based on current biogeographic theory", from Wilson & Willis (1975). The configurations on the left are assumed to be superior to those on the right.



and lacking in sustance; in other words not practical" and also "cannot use methods which are new and consequently potentially controversial".

Theory is often developed with little or no data, leading to what Slobodkin (1974) has termed "ecological nonsense with mathematical certainty". A further problem is that "Theoretical ecology has only too often developed models without sufficient regard for the basic natural history of the organisms being studied" (Wangersky 1970). Such theory is the happy hunting ground of much pointless ecological debate. In other cases, theory is developed from a particular system and extrapolated to all other situations, where it is of dubious relevance. Many arguments in ecology are between researchers who study totally different organisms. It should not come as too much of a surprise to find that the population or community processes of copepods and birds are different in some respects. Further confusion arises from concepts which are proposed and become enshrined in the ecological literature and textbooks without being rigorously tested.

An example of this is the classical "hydrosere" first proposed by Clements (1928). Observed zonations of plant communities around in-filling lakes or ponds were interpreted as representing a successional sequence; i.e. starting from open water and developing through reedswamp to fen-carr and finally oak woodland (Fig. 2). This developmental sequence has been used in many textbooks as a classic example of succession (e.g. Shimwell 1971). It is now a classic example of the pitfalls of inferring temporal sequences from spatial patterns. Walker (1970) carried out detailed pollen analytical work and was able to show that vegetation development in in-filling lakes was not unidirectional and that the end point of the hydrosere was likely to be bog, not woodland. Although adjacent, the oak woodland was never part of the same successional sequence. It should be noted, however, that there are other excellent studies of succession which have stood the test of time much better (e.g. vegetation development behind retreating glaciers; Crocker & Major 1955).

The whole conceptual framework for succession has also undergone radical change in the past 20 years, with a move away from the original ideas of the community as a "superorganism" and of climatic climaxes (Clements 1928; see Miles 1979). However, old ideas die hard, and it is difficult to find a modern textbook which does not include major sections on Clements' ideas. The persistence of Clementsian ideas had a significant effect on how research was carried out. M.B. Davis suggested that in the United States, "We do not know what the virgin vegetation of the pioneer days was like because all the ecologists were so busy looking for non-existing climax that they forgot to record what was actually growing there" (quoted in Colinvaux 1973). Later ideas have also stayed beyond their usefulness. For example, Odum (1969) produced a list of 24 trends in ecosystem properties that could be expected in the course of succession. This list is still widely quoted despite the fact that many of the expected trends are now known to be wrong or at least not general.

Theoretical misconceptions, or theories put forward without adequate supporting data can present problems for managers. Further, the relative youth of ecology as a science means that its theoretical framework is still evolving and the emphasis of debate is constantly changing. Factors not considered important (or not considered at all) 20 years ago now occupy a central place in much research. An example of this with important management implications can be found in the Australian arid zone. Ross (1969) put forward an outline for an "integrated ecology of arid Australia" and listed the major components of the system. Nowhere in the paper was fire mentioned, and yet now fire is considered one of the major influences in the arid zone (e.g. Saxon 1984; Griffin & Freidel 1985).

This example is symptomatic of a more general change in the way natural systems are viewed. Traditional concepts are often based on the assumption of equilibrium, and in fact many current models still contain this assumption, if only because it makes the mathematics easier. But is is becoming clear that real systems often have non-equilibrium dynamics, and this dramatically alters the management approach required (e.g. White & Bratton 1980; Mooney 1984; Lewin 1986).

ISLAND BIOGEOGRAPHY AND CONSERVATION

Few areas of ecology openly admit to having a "theory", but island biogeography is one, and island biogeographic theory has been applied to the problems of nature reserve design and selection. It is worthwhile exploring this in some detail, especially since this is an area of great potential interchange between theory and practice.

Wilson & Willis (1975) produced a series of "geometric rules of design of natural preserves, based on current biogeographic theory" (Fig 3) in which they suggested that certain sizes, shapes and configurations of reserves would result in lower extinction rates. It should be noted that the authors provided no data on which their rules were based, and in fact their hypotheses had been previously rejected for publication in both Science and Bioscience (Willis 1984). The book in which their work was published was later criticized as "a most frustrating volume in its lack of data and supporting evidence for hypotheses presented" (Peet 1976). Despite the rather shaky foundations for the ideas, Wilson & Willis (1975) put them forward as recommendations to planners and managers of natural parks and other natural preserves, and these recommendations were subsequently adopted by IUCN (1980) as guidelines for reserve selection. Considerable debate has followed on the use of island biogeographic theory in conservation (reviewed by Soule' & Simberloff 1986; Boecklen 1986), but its incorporation into the World Conservation Strategy led Simberloff & Abele (1984) to conclude that "a theory, even a partially discredited one, can impress non-experts".

Details of Wilson & Willis' scheme have also been adopted elsewhere. For instance, the Conservation Strategy for Western Australia states that "Conservation corridors are important for the maintenance of representative systems of flora and fauna, especially in regard to migratory fauna" (SCSWA). This certainly represents a useful guiding principle, but it is only really a working hypothesis and the actual database on which it rests is very small (e.g. Forman & Baudry 1984; Dendy 1987). Many authors have suggested that corridors must be important for wildlife (e.g. Saunders 1986; Bridgewater 1987), and they certainly have a useful function in other ways such as providing windbreaks. Current research in the W.A. wheatbelt by D.A. Saunders and co-workers is now producing the first good evidence that vegetation corridors are used by wildlife to move between reserves. Much more work needs to be carried out on how animals perceive and utilise corridors before we can assess whether management strategies are being successful.

Recent debate has centred on the so-called SLOSS problem (single large or several small?), which deals with the contention that a single large reserve is generally preferable to groups of small ones. The general assumption is that this should be so if all else is equal, but clearly all else rarely is equal and there are many factors which can confound the area effect (Soule' & Simberloff 1986). The SLOSS debate has generated a lot of heat in the ecological literature and is apparently far from being resolved (e.g. Murphy & Wilcox 1986; Lahti & Ranta 1986).

Recent attempts to use island biogeographic theory in conservation management have found it of less use than basic ecological information (e.g. Kitchener et al. 1980; Lahti & Ranta 1985; Zimmerman & Bierragaard 1986). The latter authors are particularly scathing about the application of island biogeographic theory to conservation; "Our results ... lead us to conclude that calculation of reserve sizes based solely on species-area data can never be more than uninspired guessing. Intuitive guessing about characteristics of a faunal reserve made by the field biologists involved would probably achieve better conservation results. If the impressive brainpower and effort used in repeated vain attempts to extract conservation strategy from biogeographic theory were instead devoted to autecological research, how much better would conservation be served?". It is interesting to note a recent paper on the selection of a conservation reserve network in SW Queensland (Purdie et al. 1986). This subject would appear to be a prime candidate for the application of island biogeographic theory, but it is not referred to once in the paper. Reserve selection was instead carried out on the basis of field assessment of conservation value.

The case of island biogeographic theory has all the ingredients which tend to make managers suspicious of ecological theory, i.e. wide acceptance of a theory based on assumption rather than data, continued argument as to its validity, and the diversion of resources from more directly "useful" research. Nevertheless, the proposition that island biogeography can be applied to conservation has generated a lot of research and useful debate on the important characteristics of nature reserves. It has provided a hypothesis to be tested and modified, on the basis that you have to start somewhere. It can thus be regarded as providing useful guiding principles until the ideas are refined on the basis of further data. This highlights the need for researchers to make sure that they point out the limitations of current theory, and for managers to be kept informed of recent developments.

RELEVANCE TO MANAGEMENT

The foregoing discussion of problems involved with ecological theory serves to indicate that the transfer of theoretical considerations to management problems is not easy. I now go on to consider how ecological theory and research can be more effectively applied to management problems.

To the ecologist everything is possible, within the constraints of the natural system. The biological world presents limitless scope for research, and researchers can spend their entire lives flitting about in this sea of research questions, constantly coming up with new problems and new research directions. The manager's view of the world is, of necessity, more restricted because factors other than the biological system have to be involved (Fig. 4). In the terminology of decision analysis (Norton & Walker 1985; Fig 5) the managers' perceptions of ecological problems are different from the researchers because they are constrained by more factors. The options available to managers are restricted by practical feasibility, environmental acceptability, economic desirability and, in many cases, political advantage. These different factors may only have a small area of overlap or may not overlap at all, in which case conflicts arise. Successful co-operation between managers and researchers requires that the researcher recognises these additional constraints and that the managers point out the most appropriate options. This does not mean, however, that all research should be concentrated on the small overlap area since advances in technology can alter the practical and economic feasibility and changing attitudes can alter environmental and/or political acceptability. A function of research therefore is to indicate possible expansion of the range of options open to managers.

Note that, in this context, research is assumed to be problem-orientated, and this is taken as a pre-

Fig. 4. Differences in perceptions of options available between researchers and managers.

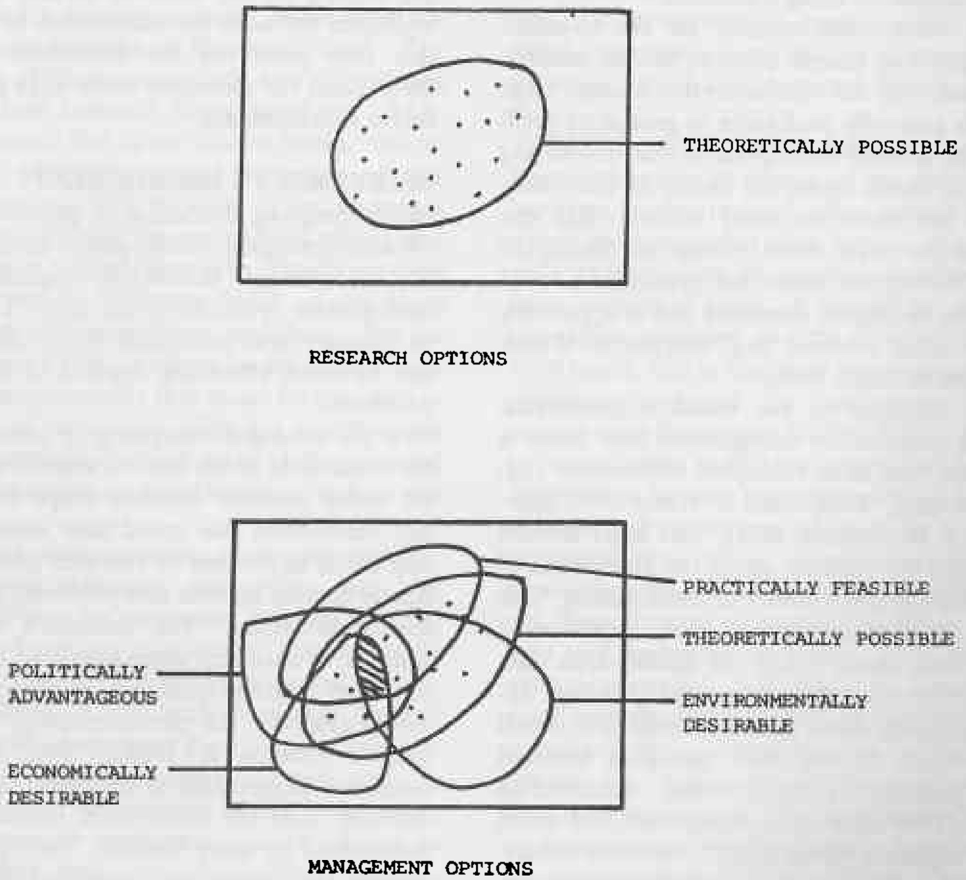
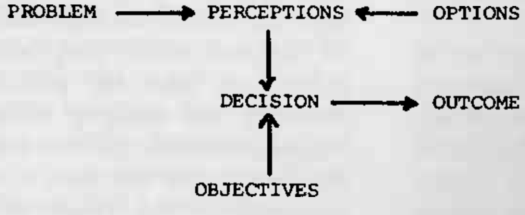


Fig. 5. A decision analysis approach illustrates the relationships between perceptions, options and the decision making process.



requisite for relevance to management. While this approach is valid where management does involve dealing with specific "problems" (e.g. pest control), problem definition becomes harder in more general conservation management. Problems to be dealt with range from fairly specific topics such as the maintenance of particular species or populations through to the maintenance of biotic/genetic diversity. Relevant research problems thus include a wide range of questions which fall into three main categories:

1.What's there?
2.What's it doing?
3.How do we manage it?

These three questions can be thought of as an idealised sequence for a research program - i.e. a series of surveys and sampling programs followed by more detailed population, community or ecosystem studies which lead to management prescriptions. Questions 1 and 2 could be thought of as non-applied compared with question 3, but in reality the distinction is not so clear, simply because you need some knowledge of 1 and 2 before you can answer 3.

This can be illustrated by a hypothetical problem concerned with managing a hypothetical animal (Fig 6). To establish the requirement and/or priority for management, surveys are conducted to determine the animal's current range and status. More detailed studies are then required to determine its life history characteristics, population dynamics and habitat requirements. These in turn require some information on interactions with competing species and predators, the population dynamics of its food organisms and the dynamics of its habitat. This then requires information on the vegetation dynamics of its habitat and processes such as succession, nutrient cycling and so on. Management decisions can, and usually have to, be made at any stage in this investigative hierarchy, but decisions can be made with more confidence as more information becomes available. Note that the theoretical concepts discussed earlier (Table 1) are prominent amongst the information required for management. Note also that the information required concerns processes rather than entities - i.e. the processes of predation, competition, succession, nutrient dynamics have to be quantified, and it is through manipulation of these processes that the management of the organism will proceed. Thus although the organism itself was the initial object of management, it is the manipulation of basic ecological processes which has to be achieved. This has been argued previously by Main (1981), and must underlie any management decisions. The dynamic nature of natural systems must also be recognised - natural change has to be recognised and dealt with (e.g. White & Bratton 1980; Lewin 1986). Vegetation succession, changes in animal population sizes and the impacts of infrequent events such as storms or floods are examples of factors which have to be considered in management - natural systems are rarely static entities.

STRATEGIC VERSUS OPERATIONAL RESEARCH

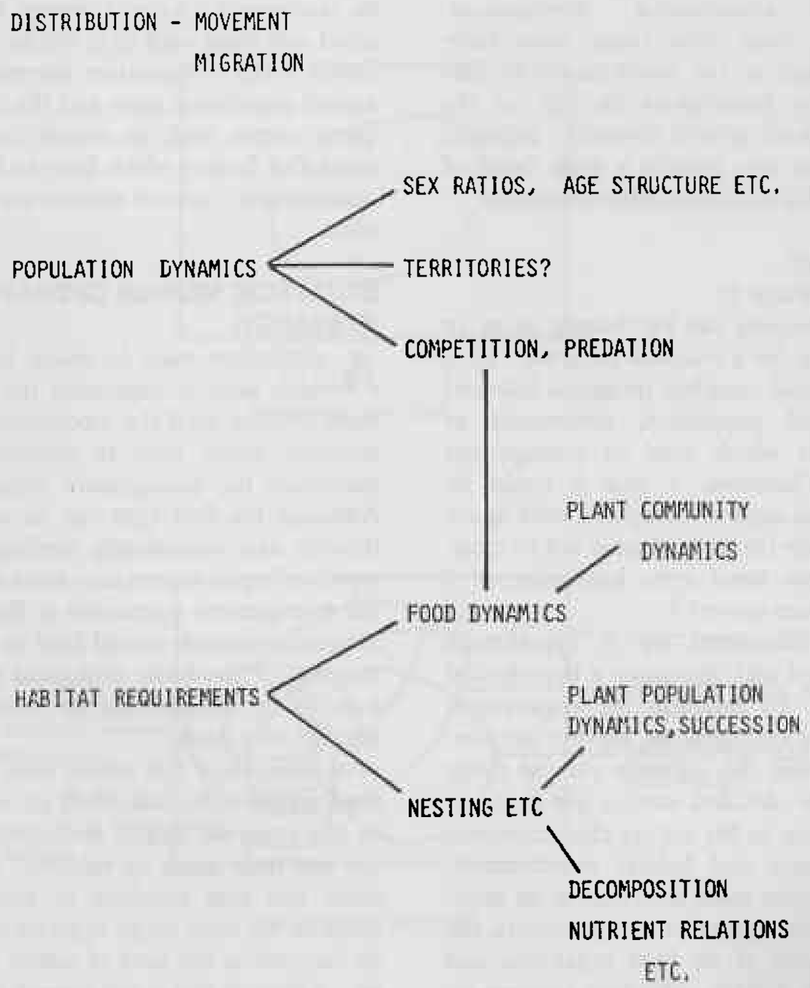
A distinction must be made between research which aims at improving the actual management process itself (i.e. operational research) and research which aims to provide more general guidelines for management (strategic research). Although the first type can be considered more directly and immediately applicable, the second type is of equal importance since it can help channel management operations in the best direction. Strategic research should lead to a better understanding of the basic ecological processes which have to be manipulated to achieve the desired management goals.

An example of this comes from recent work on road verges in the wheatbelt (Arnold et al. 1986). In this study we looked at the status of road verges and their usage by wildlife. A finding of the study was that numbers of small insectiverous birds in the road verge vegetation increased with an increase in the area of native vegetation nearby. Although this study provides no information on the management of road verges per se (i.e. how to control weeds, regenerate trees, etc - "operational"), it does indicate that management effort should perhaps be concentrated on relatively short verges connecting large area of bush, compared with longer, more isolated verges.

THEORY AND MANAGEMENT - WHERE TO NEXT?

In this paper I have tried to outline both the necessity to consider ecological theory in management and also the problems involved in doing so. There is a basic requirement to deal with fundamental ecological processes if conservation management is to succeed. This requirement has to be viewed in the light of other constraints, but failure to meet it will result in the subsequent

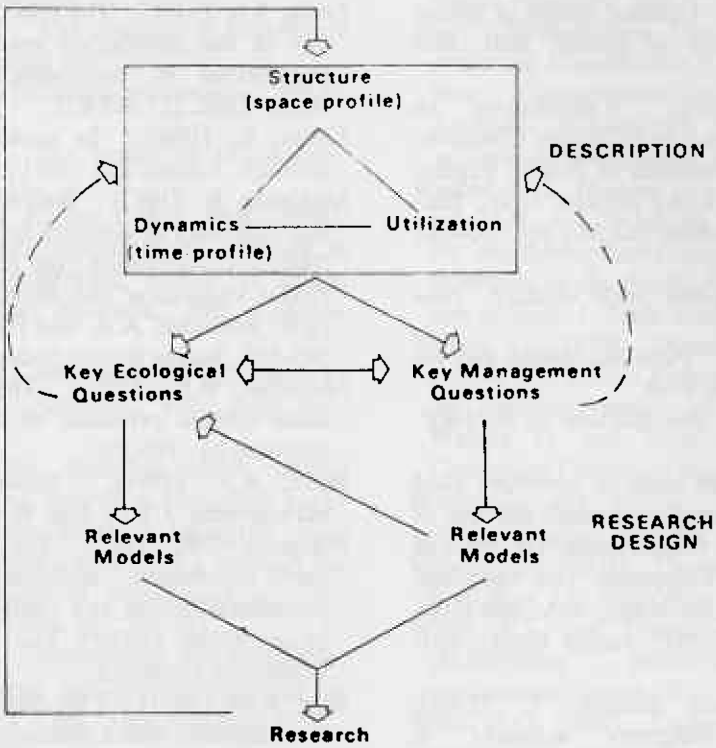
Fig. 6. Information required for adequate management of a target species.



failure to meet the goals of conservation. Thus ecological concepts such as succession, nutrient dynamics and so on should have a central place in management decision. Most management decisions are based on ecological theory, even if the manager does not realise it because the principles are so deeply ingrained. However, managers must also realise that current theoretical development may have major impacts on their activities. The relevance of detailed ecological theory may be difficult for the manager to assess. I suggest that ecologists need to point out clearly the empirical base on which their ideas are founded. A major problem at the moment is that it is very difficult for the non-expert to assess the status of a "theory" - i.e. is it just a good idea or has it been rigorously checked against the real world? In general it seems that there is no substitute for good empirical data for the formulation of either theory or management decisions.

There is a need for greater cooperation between researchers and managers so that theoretical developments can go hand in hand with practical requirements (e.g. Hopkins & Saunders 1987). Walker et al. (1978) suggested an approach in which key ecological questions and key management questions are formulated in parallel so that research can be designed accordingly (Fig. 7). They also suggest that "Research effort would be carried out simultaneously at a fundamental research and management-oriented level. The two are interconnected and the development of each

Fig. 7. Suggested procedure for an ecosystem study (from Walker et al. 1978).



should influence the other". This therefore represents an extremely interactive process, with theoreticians, field ecologists and managers all having an input to the formulation of research programs. To complete the picture, Figure 7 should be extended to include further arrows from research through to management and monitoring, with a feed back loop leading to further questions and models. There are problems associated with this scheme; for instance, the timescale of fundamental research is often much greater than that for applied research. Applied research is also often much more productive if some of the basic work has already been done. However, we now rarely have the luxury of separating basic and applied research completely, and they should at least be considered in an integrated framework. Researchers should also be able to take advantage of management operations for the provision of ready-made experiments, while cooperation from managers could allow the design of large scale experiments which would otherwise be impossible (e.g. the Wog Wog experiment; Margules 1985). This then leads to the development of research programs which collect empirical data which is useful to managers and at the same time aids in the development or testing of ecological theory. Closer contact between researchers and managers should improve communication and make for easier transfer of information and ideas. Such active cooperation between researchers and managers should lead to increased awareness of each other's problems and proccupations and should ensure more effective research and more successful application of ecological theory.

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