The Interaction Between Habitat Conditions, Ecosystem Processes and Terrestrial Biodiversity – a Review

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“Ecology has so long chased after untested thoughts and unconfirmed models with such unimpressive results that we should have learned that models unsupported by data merit little attention”.

R.H. Peters. 1991. *A Critique for Ecology*. p. 300.

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Preface

The national State of the Environment Reporting System is a program for regular, systematic analysis and evaluation of Australia's environment. The first major product of the system, *Australia: State of the Environment 1996*, was released in September 1996. Production of a State of the Environment Report covering the Australian jurisdiction is now a legislative requirement under *the Environment Protection and Biodiversity Conservation Act 1999,* the next report must be prepared by December 2001.

Since the publication of *Australia: State of the Environment 1996* a set of environmental indicators has been developed by technical and scientific experts for each of the seven reporting themes: Human Settlements; Biodiversity; The Atmosphere; The Land; Inland Waters; Estuaries and the Sea (now Coasts and Oceans); and Natural and Cultural Heritage.

The State of the Environment program also included world leading research documented in the Environmental Indicators Series for National State of the Environment Reporting. The theoretical framework and sets of environmental indicators documented in these reports provide the fundamental basis for the collection and analysis of data that will be used for the 2001 Australian State of the Environment Report and beyond.

The 2001 Australian State of the Environment Report will concentrate on trends and changes since the 1996 report, cover new and emerging issues, and will pioneer the use of the environmental indicators on a continental scale.

In conjunction with the second reporting cycle, a new technical paper series has been initiated. The papers in this second series were commissioned to contribute to the preparation of the 2001 national state of the environment report. The scope of the second series of technical papers includes analysis of trends in environmental indicator data, case studies, and reviews of particular issues. All papers in the second technical paper series have been peer reviewed externally.

A list of national State of the Environment Reporting products and on how to obtain them is provided at the back of this paper.

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Abstract

This report reviews and critically assesses the relationship between biodiversity, habitat complexity, habitat quality and ecosystem processes with the aim of identifying surrogate or 'higher-order' indicators of biodiversity.

Debate surrounding the relationship between biological diversity and ecosystem function has been central to community ecology for many decades. Mathematical models have produced inconclusive results showing that more diverse ecosystems can be either more or less stable than simpler ecosystems, depending on the ecosystem under investigation. The relationship between habitat complexity and species diversity has also not been resolved.

There are numerous short-term studies of the effects of disturbance on biodiversity, but very few, if any, long-term studies that can unravel the complexity associated with multiple disturbances and inherent natural variability.

Despite the large amount of literature discussing biodiversity, habitat conditions and ecosystem processes, there is scant empirical data to be able to prove more than simple linkages between specific elements. An emerging trend in thinking involves the idea of biodiversity acting within functional groups as an ‘insurance policy’ or ‘buffer’ against major ecosystem change.

A cautious approach to the implementation of biodiversity indicators for SoE reporting is warranted. Given the lack of rigorous, scientific understanding of linkages between biodiversity and ecosystem function, broad level indicators such as the amount of vegetation cleared may serve a more useful purpose in the short term than more precise measurements of diversity at the species or gene levels.

Summary

In June 1997, the State of Environment (SoE) Reporting Unit of Environment Australia commissioned a team consisting of staff from CSIRO Wildlife and Ecology and the Institute of Wildlife Research at Sydney University to review and critically assess the relationship between biodiversity, habitat complexity, habitat quality and ecosystem processes. A principal aim was to report on the search for surrogate or 'higher-order' indicators of biodiversity.

The literature search yielded approximately 1,700 references that were evaluated for relevance. The final database consisted of approximately 400 references. The focus of the review was terrestrial. Single species autecological studies were generally omitted; the emphasis was placed on studies that considered the interrelationships between more than one species or specifically studied the role of 'diversity' in ecosystems.

Debate surrounding the relationship between biological diversity and ecosystem function has been central to community ecology for many decades, although antecedents of the idea can be traced back to at least the 13th century. The debate is largely centred upon concepts of species redundancy and ecosystem stability, both concepts being characterised by a lack of empirical data and few well-designed field investigations. Mathematical models have produced inconclusive results showing that more diverse ecosystems can be either more or less stable than simpler ecosystems, depending on the ecosystem under investigation.

The relationship between habitat complexity and species diversity has also not been resolved. It has been known for decades that species diversity increases as the size of the sampling area increases: thus, larger areas contain more species. However, the relationship between this pattern and habitat complexity has not been adequately investigated.

There are numerous short-term studies of the effects of disturbance on biodiversity, but very few, if any, long-term studies that can unravel the complexity associated with multiple disturbances and inherent natural variability. Australian studies on the role of pastoral grazing on biodiversity consistently find that the presence of grazing reduces biological diversity, but there is greater ambiguity about the relationship between logging and biodiversity. There is a paucity of studies that examine the effects of multiple fires occurring in the same area over time. There is general agreement among scientists that habitat fragmentation is a major threat to biodiversity. Examples of such mechanisms include gross habitat loss, increased isolation of populations leading to reduced opportunities for recolonisation and increased vulnerability to stochastic events, edge effects, and increased disturbances.

Despite the large amount of literature discussing biodiversity, habitat conditions and ecosystem processes, there is scant empirical data to be able to prove more than simple linkages between specific elements. Essentially there is little known about the

interactions between habitat conditions, ecosystem processes and biodiversity *per se* at all scales and what is known cannot be reliably generalised to other areas. However, an emerging trend in thinking involves the idea of biodiversity acting within functional groups as an 'insurance policy' or 'buffer' against major ecosystem change. The interaction of habitat conditions, ecosystem processes and biodiversity is therefore a two-way process and hence the effects of biodiversity on the environment are just as important as the effects of environment on biodiversity.

It is apparent that the importance of biodiversity cannot be assessed other than in relation to a specified function. In most, if not all cases, this will be in relation to some human use – even if it is only human appreciation of the natural world. However, science cannot determine the existential value of biodiversity *per se* since there is ultimately no end point in ecosystem development. All ecosystems are unique products of 3.5 billion years of evolution and environmental change, and their functionality will change over time irrespective of human inputs. Similarly, certain species will become locally and globally extinct over time as part of the ongoing evolution of life on earth.

A cautious approach to the implementation of biodiversity indicators for SoE reporting is therefore warranted. Given the lack of rigorous, scientific understanding of linkages between biodiversity and ecosystem function, broad level indicators such as the amount of vegetation cleared may serve a more useful purpose in the short term than more precise measurements of diversity at the species or gene levels. That is, an ecosystem-level approach will probably give best results overall for the measurement of the state of biodiversity until more detailed linkages are investigated, if ever. This approach is particularly pertinent at the national level of SoE reporting.

An experimental approach to this issue is crucial if any useful linkages are to be evaluated for SoE reporting. However, any such experiment must be clearly focussed and address specific aspects of ecosystem function that are measurable. Relevant fields that could contribute to and benefit from such scientific inquiry include conservation biology, agriculture, forestry, mining and the field of restoration ecology, where ecosystems are being rehabilitated, recreated or even artificially created. In these instances, structural and functional redundancies are critical issues that must be addressed if the aim of a long-term functioning ecosystem is to be achieved.

An expert workshop was held in March 1998 to review the draft of this manuscript and to develop an experimental approach, if feasible, to the development of surrogate indicators for monitoring the state of Australian biodiversity for national SoE reporting purposes. The way forward in the long term for national SoE reporting may be the integration of data from (i) existing long-term manipulative experiments and on-going management experiments with (ii) new data derived from a series of mensurative experiments conducted within Interim Biogeographic Regionalisation of Australia (IBRA) regions (Thackway and Cresswell 1995).

1 Introduction

1.1 Background

The national system for State of the Environment (SoE) reporting was established by the Commonwealth Government in 1992, and is consistent with Objective 14.2 of the National Strategy for Ecologically Sustainable Development. The purpose of the national SoE reporting system is to compile scientifically credible, up-to-date and consistent information about changes in Australia's environment and, on the basis of rigorous analysis and assessment, to provide an integrated picture of conditions and trends in an understandable way to all Australians.

In 1996, the first Australian SoE report was released (Commonwealth of Australia 1996). This report makes an independent, nation-wide assessment of the state of the environment under seven themes: human settlements; biodiversity; atmosphere; land resources; inland waters; estuaries and the sea; and natural and cultural heritage.

The development of a nationally agreed set of indicators is the next stage in the state of the environment reporting process. It is believed that by systematic monitoring of environmental indicators, trends in the condition of the environment can be identified, and brought succinctly to the attention of decision-makers and policy implementers involved with environmental management.

The development of indicators that accurately portray trends in the status of key environmental values is no easy task for one simple reason. It requires a detailed knowledge of the relationships between indicators and the components of the environment they purport to represent.

As Saunders *et al.* (1998) point out, indicators of biodiversity are poorly developed and information limited compared to the more readily measured indicators of air or water quality. This is compounded by the fact that biodiversity is such a broad term: at its broadest, it encompasses all diversity at the genetic, species and ecosystem levels.

A workshop held in 1998 under the auspices of the SoE Reporting Unit of Environment Australia canvassed the possible benefits that may be derived from the development and use of surrogate or higher order indicators of biodiversity. Surrogate indicators could: i) help ameliorate the severe resource constraints that currently operate and will continue to operate on efforts to monitor Australia's rich biodiversity, and ii) help synthesise a wide range of information on ecosystem processes that underpin biodiversity indicators. Such surrogates might also assist in interpreting change in habitat fragmentation with respect to biodiversity, as well as the change in the proportion of major vegetation types covered in conserved areas and the relevance for biodiversity contained within those systems.

The workshop therefore firmly recommended that there should be an assessment of the usefulness of surrogate indicators of biodiversity.

Concurrently, the SoE Reporting Unit had commissioned a review to critically assess the relationship between biodiversity and such concepts as habitat complexity, habitat quality and ecosystem processes to help inform the search for surrogate indicators. A team consisting of staff from CSIRO Wildlife and Ecology and the Institute of Wildlife Research (at Sydney University) was subsequently engaged to conduct the review. There are two major products from this consultancy: a written literature review; and a collation of relevant papers, categorised according to a number of criteria (Appendix 2).

1.2 Scope

After the initial agreed terms of reference for the literature review were evaluated against the potential literature covered under the term "biodiversity", it became apparent that time and cost constraints would not permit the full evaluation of the issue across the entire literature base. The scope of the review was modified to concentrate primarily on Australian literature, with a more limited review of only key international literature. The scope was also limited to terrestrial systems, with limited reference to key marine or freshwater papers. Although this reduces the wider applicability of the review, the existence of key syntheses such as Heywood (1995) meant that the present review could concentrate on more recent developments in the literature and evaluate past international syntheses in relation to the Australian literature.

Although literature that examined biodiversity at a number of levels was reviewed, in most cases species (or recognisable taxonomic units that were used as species analogues by authors) was adopted as the unit in which biodiversity was considered. This is consistent with much of the summary literature to date, such as Groombridge (1992). One major difficulty in undertaking a review of this nature was determining the relative significance of the large number of single species studies in the literature (principally, in the areas of conservation biology, population ecology) compared with the lesser number of multi-species studies (community ecology) or whole-of-systems studies (ecosystem ecology, landscape ecology). Most studies dealt, understandably, only with certain components of biodiversity. The more complex issue of diversity *per se*, which this review had set out to investigate, is only sparingly dealt with in the literature in a quantitative fashion, although many modelling and speculative papers exist on the topic. We therefore restricted our considerations to the effect of habitat conditions and ecosystem processes on biodiversity using species as the response variable. In so doing, we also noted and explored the possibility that environmental variables (e.g. climate, soils, topography, overall vegetation cover and land use) can also play a useful role as a surrogate predictor for biodiversity at a regional scale, especially when correlated with changes in vegetation types.

1.3 Methodology

The Commonwealth Agricultural Bureaux International (CABI) Abstracts and Current Contents databases were searched for relevant literature using the key words biodiversity, habitat complexity, habitat quality and ecosystem processes. Key Australian journals – the *Australian Journal of Ecology*, the *Australian Journal of Botany,* the *Australian Journal of Zoology*, *Proceedings of the Ecological Society of Australia* and *Wildlife Research* (formerly known as the *Australian Journal of Wildlife Research*) – were also searched manually and systematically for relevant references. Other references were obtained from the personal databases of team members, from the reference lists of key papers and on an *ad hoc* basis from other scientists. Australian literature was selected preferentially, but a substantial number of international papers were also included, particularly on topics where the Australian literature was less comprehensive.

This search yielded approximately 1,700 references, consisting of title, key words and, in some cases, abstracts. All were screened for relevance, and the database was eventually reduced to approximately 400 references. Single species studies were generally omitted; the emphasis was placed on studies that considered the interrelationships between more than one species or that specifically studied the role of 'diversity' in ecosystems.

Selected papers were sorted into alphabetical order by author and distributed for review between three members of the team, each of whom was responsible for obtaining a copy of the paper, 'pigeon-holing' it, and incorporating it into the written review. The written review was thus written in three parts; these were then combined and synthesised. Not all references on the database were cited in the written review. Thus, the reference list for the review is not identical to that reproduced in Appendix 2.

The purpose of this report was to provide a review of literature relevant to the relationship between biodiversity, habitat complexity, habitat quality and ecosystem processes. This review subsequently formed the basis of discussion among attendees at a workshop held in 1998 with the aim of developing an experimental approach to the development of surrogate indicators for determining the state of Australia's biota.

2 Towards useful definitions

A foundation of good science, and ecology in particular, is that key processes and terms are clearly defined and measurable. One of the most apparent shortcomings of much of the literature reviewed in this survey is the plethora of factors deemed to fall under the broad umbrellas of biodiversity, habitat complexity, habitat quality and ecosystem processes, as well as confusion about such terms as stability, diversity, resilience and persistence.

Perhaps such confusion is inevitable, given the complexity of the natural world, as well as the diversity of learned institutions and potential applications of such concepts. Yet is seems that ecology is particularly prone to concepts that defy universal and consistent definition (see Peters 1991 for a critique). This is compounded by the reticence of many authors to define such terms as they are applied in their studies.

We discuss here some of the key terms used in this review, highlighting their often ambiguous nature.

2.1 What is Biodiversity?

E.O. Wilson was one of the original popularisers of the term ‘biodiversity’ (Wilson 1992, 1993; 1994) and his definition captures the essence of most views of the notion:

> *“The variety of organisms considered at all levels, from genetic variants belonging to the same species through arrays of species to arrays of genera, families and still higher taxonomic level; includes the variety of ecosystems, which comprise both the communities of organisms within particular habitats and the physical conditions under which they live.”* (Wilson 1992)

Heywood and Baste (1995) initially restate one of the earlier definitions of biological diversity as suggested by Norse and McManus (1980) which has only two major components: “ecological diversity” and “genetic diversity”, the former being a combination of the “species” and “ecosystem” components used by authors. However, they subsequently categorise biodiversity into four components, “ecological”, “genetic”, “organismal” and “cultural”. These various categories are summarised as follows:

Norse and McManus (1980)		Wilson (1992)		(Heywood 1995)
genetic	=	genes	=	genetic
ecological	=	species	=	organismal
(ecological)	=	ecosystems	=	ecological
-	=	-	=	cultural

The problem with these and most other definitions of biodiversity, is that they seem to have simply become a synonym of 'all life' (Williams *et al.* 1996). Hence, it is logically questionable whether any researcher could measure or provide indicators of biodiversity *per se*, as opposed to certain selected components of biodiversity.

Working definitions that specify the units used in its measurement are therefore required. Attempting to overcome this problem, Gaston (1996a) lists different definitions of biological diversity and biodiversity, identifying a series of approaches to biodiversity, its measurement and its potential significance. A key element of all these definitions is that biodiversity as a concept appears to operate over a number of biological levels of organisation as well as at different scales. It is also an interdisciplinary concept, appearing in various guises as a biological concept, a measurable entity and a social/political construct (Gaston 1996a).

However, Ghilarov (1996) provided a more critical evaluation of the history of the concept of biodiversity. He discussed the history of early diversity studies and it is clear that although the term biological diversity (biodiversity) itself first appeared as late as the early to mid 1980s, the basic diversity concept is an old theme in biology. He argues that although the theme of diversity has re-emerged under the semblance of a new discipline called biodiversity, previous diversity studies had already shown by the early 1970s that there was no universal type of distribution of relative abundance that corresponded to all real communities. A deep understanding of underlying mechanisms that yield a given pattern of species abundance has still not been achieved despite much apparent research.

There is therefore some debate within the scientific community as to the utility of the term "biodiversity" and whether it assists or clouds the issue of gene, species and ecosystem conservation. However, the term is currently widely used and has been readily adopted by most of the scientific community, government departments and the general community. This review will analyse a cross section of the wide range of research covered by the term, in an attempt to critically evaluate whether proven links exist between biodiversity *per se*, habitat conditions and ecosystem processes.

2.2 Units of Biodiversity

The existence of multiple levels of organisation within the term biodiversity compounds the problem of measuring it: most workers evaluate only one or two aspects of biodiversity (Gaston 1996c and chapters therein). It is not possible to evaluate all components during one study or even a series of studies, and as discussed previously, biodiversity is commonly broken down into three components; ecosystem, species and genetic. In evaluating the utility and rigour of these we also discuss the potential use of habitat diversity. It must also be kept in mind that, although we regard species as being the effective linchpin for most ecological studies, ultimately it is individuals that are the fundamental units upon which selection acts and the vehicle in which genes are carried through to the next generation. A parallel hierarchy to that discussed above from simpler to more complex ecological interactions may therefore be expressed as:

Individuals Populations Communities

2.2.1 Ecosystem Diversity

Ecosystems are the largest units generally considered in biodiversity, comprising some amalgam of habitats, the species within them and importantly the processes occurring within and between the biotic and abiotic components (Wilcove and Blair 1995; Christensen *et al.* 1996; Noss 1996). It has been suggested recently that ecosystems form an appropriate unit for the management of large natural areas (Christensen *et al.* 1996; Noss 1996). However, the study of ecosystems and their use as management units has been frustrated by the looseness of definitions and the seeming inability to reach consensus on what they are in an operational sense, despite over 60 years of debate since Tansley first introduced the term (Tansley 1935). Tansley explicitly linked the term ‘biome’ with ‘ecosystem’, defining the former as comprising the complex of organisms and the latter the complex of organisms plus all inorganic factors. However, subsequent usage has obscured the meaning of the term, and has since been applied at broad and very fine scales. Additionally, the term “landscape” has become more frequently used in the past decade but it too suffers from some definitional and usage problems.

The resulting perception of ecosystems as ‘shifting, unfocused landscapes’ has led to valid criticisms of their uncritical use in management and ecology (Wilcove and Blair 1995). The major problem with ecosystems and their use as a unit of measure for biodiversity is the lack of consensus over an operational definition for ecosystems themselves, let alone a unit of measurement for quantifying them. The notion that the arbitrariness and absence of apparent spatial boundaries is actually a strength of the ecosystem concept (Noss 1996) seems nebulous if ecosystems are to be used in the description, quantification and assessment of biodiversity.

Functional approaches to the assessment of ecosystems seem to simply involve operational definitions of ecosystems such as the habitat surrounding it. Reducing the definition of ecosystems to the description of a particular area containing certain organisms, such as ‘a physical habitat with an associated assemblage of interacting organisms’ (Noss 1996) renders the definition no longer appropriate for a sweeping notion encompassing fundamental ecosystem processes and services (Begon *et al.* 1996).

Peters (1991) astutely pointed out that ecologists require clear and precise operational definitions of concepts, entities and process to undertake research successfully. If the ecosystem simply becomes a habitat, no longer incorporating processes as well as biotic constituents, it is the responsibility of biologists to describe it as such. Unfortunately, habitat diversity is often mistaken for ecosystem diversity in discussions of biodiversity. Faith (1997) identified a lack of ‘system’ in most usages of the term ecosystem, describing substantial inconsistency among popularly accepted definitions of the term (see Figure 1 in Faith 1997) in which a variety of elements were incorporated.

2.2.2 Habitat Diversity

Habitats can be defined as areas that provide the resource requirements for a discrete phase of a plant or animal's life (Southwood 1981). Implicit in most definitions of habitat is location in space – a 'place'. Andrewartha and Birch (1984) provide a broader context to potential influences on the survival and reproduction and hence distribution and abundance of organisms via their theory of environment with direct (the Centrum) and indirect (the Web) influences on an organism. This is a concept that goes beyond a simple notion of 'habitat'. However in practice, their physical structure and their constituent vegetative species, especially with respect to dominant species within them often define habitats (Caley and Schluter 1997). Estimates of habitat diversity are often considered as a foundation of area-based management, although again it is often very difficult to assess habitats quantitatively.

It is often difficult to define boundaries for habitats and there are clear problems in defining when one habitat becomes another (Christensen *et al.* 1996). The classification of areas over coarse spatial scales using dominant vegetation can be very effective (e.g. Benson and Howell 1994), although the distinctions between habitats can often be blurred and more often than not are scaled over gradients (Budiansky 1995).

The key problem in evaluating and using habitats as measures of diversity lies in the complex and variable nature of habitats (Budiansky 1995). Despite the best efforts of numerous landscape ecologists (e.g. Christensen *et al.* 1996), the use of habitats as units for assessing biodiversity causes many of the same problems that some ecologists find with ecosystems.

2.2.3 Species Diversity

In terms of readily measurable field entities and as units of evolution, species are the fundamental unit of organisation in ecology. They are essential for the evaluation of ecological and evolutionary patterns and process as well as generally being considered the most appropriate units for the management and conservation of natural areas (Spellerberg 1996; but see Moritz 1994). Although species concepts vary and despite the well known difficulties of applying biological species concepts (e.g. Spellerberg 1996; Williams *et al.* 1996; Lee 1997), the use of species as measures of biodiversity is less open to conjecture than are the other possible units of measurement (Wilcove and Blair 1995). Although operational definitions of morphospecies in ecology can be effective (Oliver and Beattie 1992; 1996, but see criticism by Goldstein 1997); expert taxonomists successfully distinguish between species consistently over long time scales despite problems with synonymy (May and Nee 1995) and fine description (O'Hara 1994).

The relative ease, with which different species can be recognised, the functional roles identified for many species and the effectiveness of species as units of management appear to make them ideal units for the measurement of biodiversity. Conserving species across their range is also likely to conserve genetic diversity within these species too, although many issues involving genetic diversity remain to be resolved (Mallet 1996; Brown *et al.* 1997).

Species diversity is also a conventionally accepted measure of diversity. There are effective ways to assess the composition of assemblages using species (or potentially surrogates of species) as units of distinction (e.g. Clarke 1993), and to consider the relative phylogenetic similarity between groups of interest, using species or higher taxonomic distinctions (Williams *et al.* 1996; Lee 1997).

Measuring biodiversity using species diversity involves a complex combination of values such as species richness, species composition and taxonomic range (Gaston 1996c; Williams *et al.* 1996). Species richness alone, as a measure of biodiversity, has been used in several experimental studies investigating the functional significance of biodiversity on 'ecosystem processes' (Naeem *et al.* 1994; Tilman *et al.* 1996). The approach has been criticised as being inappropriate (Beck 1998) because it does not account for differences between component species. Species richness alone is consequently a poor measure of diversity, although it must be recognised that biologists have historically assessed species diversity in more complex ways (Ghilarov 1996).

2.2.4 Genetic Diversity

Genetic diversity is clearly an important component of biodiversity (Gaston 1996c, Mallet 1996): the 'fine scale' level of biodiversity is measured in the variety of expressed genes or characters among organisms (Williams *et al.* 1996). However, as a basic unit for measuring and assessing biodiversity it has previously been dismissed as too difficult and costly to use (Moritz 1994).

The conservation of genetic diversity can be considered a subset of the notion of conserving species diversity by conserving species across their range. This would alleviate apparent problems with fine taxonomic distinction (Mallet 1996), notwithstanding the clear need to incorporate studies of genetic variation in key species as part of overall strategies (Baur *et al.* 1996).

2.3 What is Habitat Complexity?

Pimm (1984), in his review on the effect of complexity and stability on ecosystems, defined ‘complexity’ solely on the basis of characteristics of species (richness, connectance, interaction strength and evenness) in the ecosystem. He also identified the fact that the abundance and diversity of definitions of ‘complexity’ had led to a great deal of confusion in previous reviews of this subject. The same can be said for previous syntheses of work examining the role of habitat complexity on biodiversity.

Habitat complexity is often considered a synonym for habitat heterogeneity. However, habitat heterogeneity refers to spatial or temporal change across a landscape, whereas habitat complexity refers more to the level or strength of interaction between a species and its environment. In essence, habitat heterogeneity is synonymous with habitat diversity.

For the purposes of this study, habitat complexity is defined with respect to the species or assemblages using the habitat. Care must be taken to recognise that different degrees of habitat complexity in these circumstances will be relative rather than absolute. Hence, the search for generalisations about the role of habitat complexity will be restricted, as many of the experimental studies purporting to examine the role of complexity and its effects on biodiversity can rarely be generalised (Beck 1997).

2.4 What is Habitat Quality?

The issue of habitat quality can be approached through an examination of anthropogenic and natural disturbances: these may affect the suitability (in one sense a synonym of quality) of habitat for particular species, or suites of species. The search for general characters defining the quality of a habitat is confounded by the fact that habitats should be defined in a species-specific manner.

Habitat quality can be related directly to the responses of species to changes in any of the abiotic and biotic factors deemed to affect individuals or populations. These factors may range from local, fine-scale factors (e.g. the presence of a tree hollow for an arboreal mammal: Smith and Lindenmeyer 1988, Lindenmeyer 1995) to the fragmentation of previously large, continuous areas (e.g. arboreal mammals in north-eastern Australia: Pahl *et al.* 1988; see Saunders *et al.* 1991 for a general review). The State of the Environment Report (Commonwealth of Australia 1996) and Saunders *et al.* (1998) describe many factors that may affect the overall quality of a habitat.

Key agents of habitat disturbance include fire, pollution from various toxic substances, water supplementation, fragmentation, and land use activities such as forestry, mining and agriculture. Biogeographic characters (e.g. size and shape of habitat, relative isolation, and amount of ‘edge’ adjoining hostile habitat) are also likely to play a major role in influencing the quality of habitats at coarser scales. As is the overall general composition of the habitat with respect to major abiotic (e.g. temperature, rainfall, fertility and slope) and biotic (e.g. vegetation) factors.

There is an extensive literature on the effect of disturbance on habitats, and it was beyond the scope of this project to review all of this literature. We present here a pertinent sample of the available literature, having focused particularly on the effects of disturbance on habitat structure, which in turn, may be a possible surrogate indicator for habitat complexity.

2.5 What are Ecosystem Processes?

There is an apparent confusion in the scientific literature regarding the use of the terms “ecological” processes and “ecosystem” processes, and unfortunately these terms have been used interchangeably. “Ecological” processes are thought by some to only encompass biological interactions (e.g. predation, pollination and so on) (Gaston 1996c). However, the distinction between “ecological” processes and “ecosystem” processes is actually not clear-cut since fundamental “ecosystem” processes are often defined by the literature in terms of abiotic characters (such as changes in soil characteristics or nutrient turnover), which in turn may be driven by biotic interactions (e.g. decomposition, respiration)

Overall, the effects of these processes on biodiversity are often poorly understood, primarily because of the difficulty of manipulating these factors over coarse spatial scales.

In reviewing the literature, we have therefore grouped together papers dealing with either “ecological” and/or “ecosystem” processes, since these terms appear to be too inconsistently used in the literature. We believe that the most appropriate term to use is “ecosystem” processes, rather than “ecological’ processes.

There is also apparent confusion in the literature over the terms “process” and “function”, which are also used somewhat interchangeably. Once again, we have been forced by this inconsistency to group together literature using either term or both terms in order to conduct our analyses. Nevertheless, we regard “processes” to be operational at a lower level in the hierarchy than “function”. According to Hamblin (1998), ecosystem function is, first and foremost, characterised by the ability of soils to break down plant and animal remains and to liberate carbon dioxide, nutrients and water (i.e. the aggregation of processes). Examples of ecosystem processes addressed in this review include nitrogen mineralisation and decomposition rates.

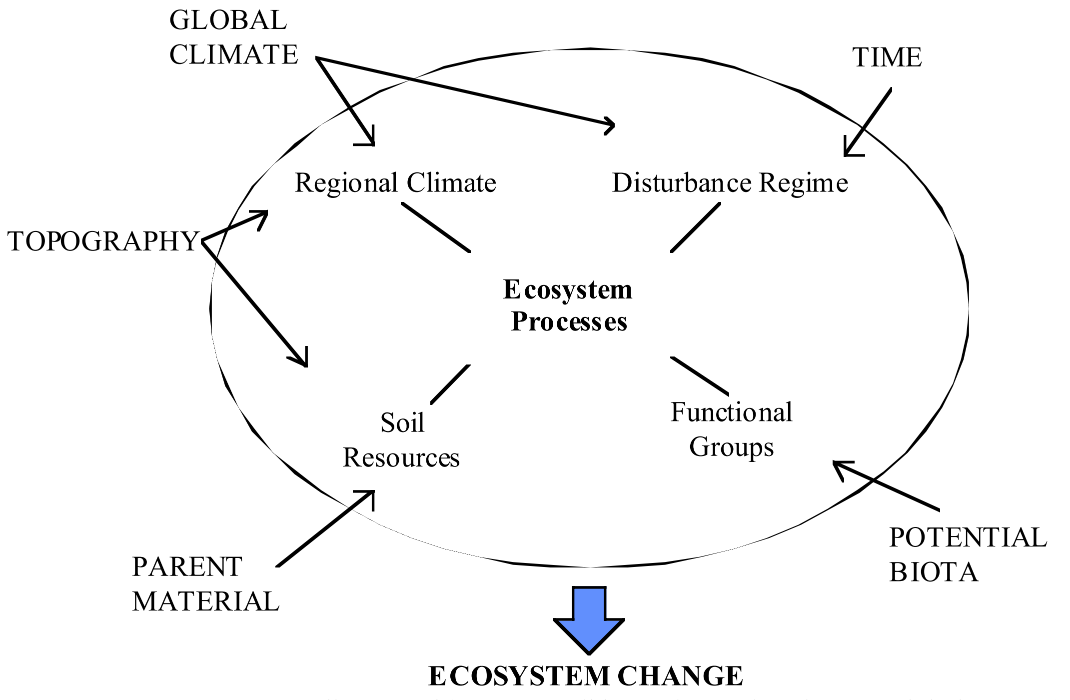
Chapin *et al.* (1996) presented a framework for defining ecosystem processes that sustain natural ecosystems, and which they argue is applicable to the sustainability of managed ecosystems (Figure 1). They defined a sustainable ecosystem as one that:

> *“…over the normal cycle of disturbance events, maintains its characteristic diversity of major functional groups, productivity and rates of biogeochemical cycling”.*

They suggested that the current species composition and structure of any ecosystem and its pattern of successional development are transitory assemblages that are not sustainable indefinitely, and that few ecosystems are sustainable longer than a few tens of thousands of years. Natural disturbances and successional processes occur at local scales but a characteristic vegetation pattern is usually maintained at the landscape scale. They extended the framework of Jenny (1941) who suggested that five independent state factors (parent material, climate, topography, potential biota and time) determined soil and ecosystem properties by characterising each ecosystem by four dynamic elements or interactive controls (local climate, soil resource, functional groups of organisms and disturbance regime). These both control and respond to ecosystem characteristics. For example, while climatic changes have caused massive ecosystem changes, the productivity and vertical structure of vegetation, in turn, govern microclimatic factors like water and temperature gradients and hence, influence regional climate through energy and water exchange with the atmosphere.

On the basis of Chapin *et al.*'s analysis, any indicator of ecosystem change would need to integrate measures of area, condition, biota, disturbance and global factors such as climate.

Figure 1: The relationship between state factors and ecosystem processes.



After Chapin *et al*, 1996.

2.6 The Question of Scale

The breeding habitat of most species is not uniformly distributed over space; rather it occurs as discrete habitat patches (Fahrig and Paloheimo 1988). Populations exhibit patchiness at multiple spatial scales, with dispersal between patches a continuum from complete isolation to panmixia (random mating between conspecifics) (Burkey 1995). Spatial heterogeneity may be important for overall population survival (Roff 1974) and abundance (Hanski 1985), and can determine the persistence of interacting species (Levin 1974).

There are scaling differences between different organisms in both space and time (Weins 1989, Lawton 1996). Over a coarse scale, rates of endemism in small animals, for example millipedes, are high (Enghoff and Baez 1993) and migration rates generally increase with increasing body size (Nieminen 1996). Insects generally require a smaller area for survival than vertebrates, but many insect species use different habitats in different life stages and thus, need a large area to complete their lifecycle (Janzen 1987). Thus the effects of habitat conditions may become apparent to different organisms at different scales (Weins 1989).

Observations of patterns at one scale do not necessarily apply to other scales (Wiens 1989, Levin 1992). For instance, field manipulation experiments may yield patterns that are relevant to a different spatial and temporal scale from those on which habitat fragmentation has its main effect (Lawton 1996). Predator-prey interactions (Karieva 1987) and edge effects (Ingham and Samways 1996) have been studied in fine-scale plots, but very few manipulative experiments have operated on a scale relevant to habitat fragmentation or island biogeography (but see the classic work of Simberloff and Wilson 1969). Recent experiments, such as that of forest fragmentation by Margules *et al.* (1994) are helping to address this imbalance. Correlative or mensurative approaches (which are inductive) may be more relevant than manipulative experiments (which are deductive) in examining coarse-scale, long-term processes. This is because manipulative experiments are more readily amenable to investigations of fine-scale and short-term processes, which makes it difficult to integrate studies of mechanisms operating at ecological and evolutionary timescales (e.g. succession) into them (Gaston and Williams 1996).

The value of scientific research is extremely limited if there is little or no additional emphasis placed on estimating the predictive value of any findings with respect to local, regional and continental scale, and the confidence with which those predictions can be made. The need to generate findings that can be generalised to various terrestrial systems, using a diverse range of taxa considered at several scales (spatial and temporal) of observation is paramount to the development of meaningful and effective surrogate indicators for biodiversity. This underscores the essential nature of reviews, such as this one, in undertaking a critical evaluation of the large body of scientific research and theory that currently pertains to biodiversity, ecosystem processes and habitat conditions

Ecologists have studied patterns of species richness and diversity for some time, and through the literature, have often stated general principles and descriptions of processes underlying species richness and diversity (e.g. Begon *et al.* 1996, Gaston 1996b, Ghilarov 1996). However, many of these mechanisms are still currently poorly understood and there is little evidence that processes observed at one scale or in one system can be generalised to other scales or systems (e.g. Gaston 1996a, Beck 1997). This is most notable in the lack of emphasis given to soil biology, in comparison to vertebrates and plants, in studies of diversity and functioning in terrestrial ecosystems (Wardle and Giller 1997, Ohtonen *et al.* 1997). Even when there are well-accepted general principles describing some aspects of habitat conditions on biodiversity, the application of these to understanding the amelioration of anthropogenic impacts is often unclear (Simberloff 1988).

2.7 Some General Comments on the Literature

In this review it was our original intention to sort evidence by the scale at which it was collected. However, as the review progressed it became apparent that a large part of the literature was of such a general, broad-scale nature that such a sorting would have been impractical. Nevertheless, the issue of scale is taken up at various points throughout the text.

Willson (1996) summarised some of the problems with past studies concerning the relationship between biodiversity and ecosystem processes. These were:

1) the assumption of an equilibrium situation;
2) a unifactorial focus;
3) too typological without emphasis on variation in time and space;
4) too limited in temporal and spatial scope, restricted to a single study site or a short time span;
5) neglect of evolutionary aspects of ecology; and
6) substitution of correlation for explanation.

It should also be stressed that many field experiments in ecology are poorly designed, often with little or no attempt at replication or control treatments. Although it is arguable whether true replication can ever be achieved in the field, it is nonetheless a critical part of experimental design that needs to be addressed. Willson (1996) suggested that in order to gain an understanding of biodiversity and ecosystem processes, a focus was needed on process, function and interaction together.

Many studies reviewed in this survey make claims about the role of biodiversity on ecosystem processes but, in fact, biodiversity *per se* is not examined and, if it is, it is rarely the only variable being manipulated (Beck 1998). Of the few experiments that do examine the role of biodiversity on ecosystem processes, little effort is made to test the predictions of various hypotheses that may describe relationships between biodiversity and ecosystem processes (Johnson *et al.* 1996).

Our observation is that the literature is dominated by speculation and debate, but is relatively data-poor: for example, our pigeon-holing of data shows that of the 450 papers in the database, approximately 15% had an experimental basis, 10% were theoretical, and 55% were reviews. (The remaining 20% were categorised as ‘modelling’, ‘survey’ or ‘observational’). It is enlightening to quote at length from Mooney *et al.* (1995) who summarise the global literature to that date and provide the following conclusions regarding the links between biodiversity and ecosystem functioning:

> From: ***What are the influences of genetic diversity on ecosystem functioning?***
>
> *“There is very little information on whether the genetic similarity of populations influences ecosystem functioning”.*
>
> From: ***What are the influences of species diversity on ecosystem functioning?***
>
> *“Compensatory overlap is thus suggested to provide “insurance” in the sense that key functions are more likely to continue despite changes that result in the loss of some species. There is some evidence for this prediction, but it is a very difficult phenomenon to demonstrate. There is no evidence that contradicts the predictions. This is an area where further research is needed.”*
>
> From: ***Summary***
>
> *“The main consequence of diversity at all levels seems to lie in the degree of adaptive insurance it provides for the maintenance of ecosystem processes against environmental variation and/or stress.”*

Thus, after this analysis and synthesis of the literature up until 1995, all that could be said of biodiversity *per se* was that it *seemed* to act as an insurance policy against major ecosystem change. However, while the concept of biodiversity acting as a buffer against loss of ecosystem functioning is intuitively appealing, this concept has yet to be experimentally tested and has not yet been adequately formulated as a testable hypothesis.

‘Biodiversity’ is an all-encompassing term and it is therefore not surprising that relatively few experimental papers directly related to the role of ‘biodiversity’ in ecosystems were uncovered by the literature search. It should also be remembered that reviews – such as this one, it is hoped – are an important part of the process by which the many fragments of scientific knowledge are drawn together. Nevertheless, the lack of experimental data hampers any attempt to draw general conclusions about the role of diversity in ecosystems and to determine the feasibility of surrogate indicators of trends in biodiversity.

3 The relationship between diversity and ecosystem function

3.1 *The Role of Diversity in Ecosystem Function*

There has been considerable conjecture about the role that biodiversity plays in the functioning of ecosystems. That many species are involved in such functioning is not questioned: rather, the debate focuses on the importance of diversity *per se*. If diversity declines, will the functioning of the ecosystem be affected?

Wardle *et al.* (1997) noted three theories for how species richness may affect ecosystem function:

- the **species redundancy hypothesis**, which predicts that beyond a critical (probably low) diversity, most species are functionally redundant;
- the **ecosystem rivet hypothesis**, in which all species are potentially important to ecosystem functioning – thus, the capacity of the ecosystem to deal with environmental fluctuations declines progressively as species are lost (the name derives from the analogy with the rivets on an aeroplane: some redundancy is built in, but the loss of rivets makes the plane increasingly more vulnerable to a calamitous event); and
- the **idiosyncratic hypothesis**, in which diversity changes ecosystem function but not in predictable directions.

A fourth potential hypothesis can be added to these: the **insurance policy hypothesis**, that a diversity of species aids the stability of a system, particularly in the face of unusual, extreme events as well as human-induced perturbations. It should be noted that there is considerable overlap between components of each hypothesis as they are currently formulated.

Debate on the role of diversity in ecosystem functioning has been heightened by attempts to establish whether the current extinction “crisis” (Pimm *et al.* 1995) will affect life-sustaining processes. Yet on the basis of this review, it appears that our understanding of the relationship remains minimal and supported by few data. Indeed, much of the literature consists of reviews of minimal datasets, and statements about the role of diversity in ecosystem functioning are, necessarily, imprecise and cautious.

For example, Giller (1996) provided a global review of soil biota diversity and their role in ecosystem processes but noted little data on the role of diversity *per se* in such processes. He reported that the impact of indirect or direct human activities on soil ecosystems ‘*more often than not seems to lead to reduced biodiversity of soil communities*’, although the long term effects of this on important ‘ecosystem services’ ‘*remain to be seen*’. Hendrix (1996) using the Nearctic earthworm fauna of southern USA as a case study examined this issue. In one example, a single species of earthworm appeared to perform adequately a number of ecosystem functions in an agricultural soil, including the incorporation of plant residues, reduction of soil surface crusting, increased aggregate stability, water infiltration and seedling emergence in agricultural soils. He concluded that:

> *"More diverse earthworm communities under similar conditions might do little more to influence these processes".*

A component of the literature investigates the relationship between ecosystem functioning and 'functional groups', which are typically species exploiting a common pool of resources (Terbough and Robinson 1986). This reduces the apparent complexity of an ecosystem and allows the comparison of communities with little species overlap (Andersen 1997b). However, Hobbs *et al.* (1995a) argued that the concept of functional groups still needed to be addressed:

> *"It is yet to be seen whether sensible functional groupings can be created to incorporate some or all of the various aspects of ecosystem function and/or adaptive responses to environmental variables ..."*

The functions of particular trophic groups may be many, varied and complex. Huntly (1995), for example, examined the influence of primary consumer species on ecosystem processes. She reported that moderate grazing frequently produced more productive communities, while high grazing can result in conversion to a much less productive system. Herbivores influence ecosystem processes by processing biomass and returning fractions of it as faeces, frass, urine or other excretions. They can also affect the way in which plants of a particular species function and interact with other species or abiotic components of their environment. The effects of herbivores may be manifested through landscape-level dynamics. Huntly (1995) used the example of migratory grazers _ elk and bison – in Yellowstone National Park. These grazers not only graze uplands:

> *"... but also alter the form and phenology of the dominant riparian vegetation, particularly willows and cottonwoods. The balance of nutrient flows among these system components should be very important in determining the net effects of consumers on the long-term productivity of the ecosystem they depend on and influence".*

According to Huntly (1995), herbivores may also influence ecosystem processes by physically moving soil and other materials and by trampling, clipping, scraping or cutting plants. In North America, beavers dam rivers, while even small invertebrates such as scarab beetle larvae can move substantial amounts of soil. Population fluctuations of herbivores may also have lasting effects on ecosystem functioning by causing significant shifts in plant species composition.

3.2 Are Some Species Redundant?

The classification of species into functional groups leads, perhaps inevitably, to conjecture about levels of 'redundancy' within such groups: if many species of any given functional group perform more-or-less the same task, it may be that the loss of one or a few species will have no impact on ecosystem function.

Walker (1992) argued that in terms of ecosystem function, some species are more important than others are:

> *"At one extreme, some [species] are determinants, or 'drivers', of the ecosystem of which they form a part. At the other extreme are those that are 'passengers'. Removing the former causes a cascade effect, but loss of the passengers leads to little change in the rest of the ecosystem".*

He advocated a four-step procedure by which ecosystem function analysis could be used to develop conservation strategies. The first step is to identify the rate-limiting or otherwise relatively important processes in the system of concern, coupled with the development of appropriate corresponding functional classifications of the biota. That is,

> *"... the objective should be to try to further subdivide the species in a guild on the basis of nontrivial functional attributes... If this cannot be done and there are still several different species in the group, then ... there is some ecological redundancy within the guild concerned".*

The second step is to determine the number of species within each guild. Guilds with only one or a few species would be considered vulnerable and '*constitute an obvious, immediate conservation focus*'. The third set involves a further examination of species within a guild to identify species that are functionally redundant. The fourth step is to examine how a change in abundance of a functional group would affect ecosystem and community processes, and how such a change would influence the net effect on the biota.

Walker admitted that little is known about the degree of functional redundancy in ecosystems, and there are other problems with his approach. One such problem is:

> *"... the time scale on which function is considered. The separate significance of a particular species may only become apparent under particular environmental conditions ..."*

Interestingly, there is a large body of work that actually pre-dates the current interest in biodiversity and ecological redundancy, and Walker's formulation of the hypothesis. For example, Main (1982) discussed rare species and their potential importance. He suggested that in an extant ecosystem, the common species perform the bulk of ecosystem function, but that under different environmental circumstances the status of currently abundant and rare species may be reversed. Thus, rare species, along with other components of biodiversity, form an ‘insurance policy’ against change, that is, the more species in more functional groups the better.

Similarly, some manipulative work investigating this theme had been undertaken in North American deserts. Brown (1986) reviewed the role of vertebrates in desert ecosystems in southwestern North America, identifying the important types of desert vertebrates and classifying them into functional groups. In a series of experiments in the Sonoran and Chihuahuan Deserts, some or all species of granivorous rodents and ants were removed and supplemental feed was added to large plots. For example, removal of rodents resulted in substantial increases in the number of colonies of granivorous ants, but reciprocal removal of ants resulted in less pronounced increases in the density of seed-eating rodents. Overall, different kinds of seed-eating vertebrates respond differently to experimental manipulations but, in general, vertebrate granivores tend to increase consumption and thus compensate at least partially for increased food availability. In terms of plant response, large-seeded plants increased in density to dominate the annual plant community when rodents were removed.

At a broader scale, Whitford (1986) reviewed decomposition and nutrient cycling in deserts in North America. Unlike temperate systems, decomposition of leaf litter in deserts is not correlated with precipitation. However, if soil fauna is experimentally eliminated, decomposition then becomes a function of precipitation. Similarly, the turnover of buried litter also appears to be independent of rainfall. Once again, when microarthropods were experimentally eliminated, decomposition became a function of precipitation. Generalisations can be made from a variety of studies indicating that regulation of the rate of buried litter-root decomposition by microarthropods is indirect and that all groups of soil organisms are important even if their role appears to be indirect.

Work on aquatic systems has also been undertaken. Odum (1990) commented on a study by Schindler (1990) which set out to test a number of predictions by introducing perturbations (nutrient enrichment and acidification) to whole lakes. One prediction not verified was that ecosystems are able to maintain metabolic homeostasis even when there are changes in community organisation such as declines in species diversity and an increase in the dominance of a few species, a decrease in lifespans of species, or an increase in nutrient throughflow. One observation from the experiment that Odum thought noteworthy was that the greatest damage to food webs in the perturbed lakes:

> *“… appeared to occur when species were eliminated that had no functional analog in the lake (low redundancy) _ ”*

Odum also noted that functional attributes of an ecosystem recovered more rapidly than structural attributes (such as species diversity) after stress was removed or reduced.

Majer (1992) cited two examples suggesting that an ecosystem function could still be performed when species were lost from a system. One of these involved the introduction of the pathogenic organism *Phytophthora cinnamomi* to the Jarrah forest of Western Australia. Reduced plant cover in affected areas leads to a more severe microclimate at ground level, resulting in a reduction in the densities 'and no doubt diversity' of the soil and litter fauna (Majer 1992). Yet a study cited by Majer found that decomposing Jarrah leaves lost more mass in the diseased than in the healthy forest. He concluded that this was:

> *"... an example of one ecological function, decomposition, being maintained when the abundance and diversity of agents which are normally associated with this activity are reduced".*

Main (1992) again put forward the argument that the role of diversity in an ecosystem is to provide a pool of organisms from which functional substitutes can be found following the loss of species that previously fulfilled the role. Thus, while substitutes are present, the loss of diversity may not cause a loss in function. The author suggested, however, that the large number of extinctions and range contractions seen in the Mediterranean climatic zone of Australia in recent years:

> *"... has massively reduced the capacity of ecosystems to engage in species substitution to fill essential roles, as probably successfully happened following the extinction of the megafauna".*

Hobbs (1992b) commented that of all the papers presented in Hobbs (1992a) – the subject of which was biodiversity in Mediterranean ecosystems in Australia – only one cited an example of actual data on the issue of 'diversity versus function'. This example (Springett 1976, cited by Lambeck 1992) compared soil microarthropod diversity and abundance and litter decomposition in natural woodland and plantations of *Pinus pinaster* of three ages. According to Hobbs (1992b), data from the study suggested that:

> *"... a certain minimum number of species may be required for full ecosystem function, but the addition of more species may have little further effect on function (or rates thereof), except as insurance against disturbance and change _ ."*

In a largely anecdotal account, Sokolov (1994) looked at the effect of mammal extinctions or reductions on ecosystems. He cited the decline of whales in marine ecosystems and beavers and sable in Russia, concluding that no particular changes in ecosystem function were recorded. In the case of the beaver and sable, the numbers of which recovered to almost original levels, '*no changes in the ecosystems were noted*'. However, the speculation was made well after the extinction of these species and as such, no real assessment of impact can be made under these circumstances.

Effectively, Walker's 1992 formulation of the ecological redundancy hypothesis started a new round of debate and speculation (see Blake 1993, Gitay *et al.* 1996, Ghilarov 1997), but also coincided with some degree of new experimentation. In his 1994 review, Woodward (1994) posed the question: how many species are required for a functional ecosystem? His answer was:

> *"In general, it may be concluded that it is not regularly possible to quantify the number of species which make up a functional ecosystem. However, if the species complement is not at a maximum which the ecosystem can include, then the dynamic richness is reduced. This reduced richness then lays the ecosystem open to invasion and disruption".*

Interestingly, Walker (1995), while still advocating the utility of the ecological redundancy concept and arguing for its usefulness, somewhat re-formulated the concept to emphasise that ecosystem resilience is strengthened if there are multiple species occupying roles in each functionally important group. Hence, the idea of biodiversity being a form of 'insurance policy' against change was now subtly integrated with the ecological redundancy concept. The integration of what are effectively minimum and maximum set concepts regarding biodiversity and its importance for ecosystem function reflects the way that the scientific debate evolved over the period between Walker's two papers. It also highlights the fact that this idea had been proposed but effectively overlooked for at least 10 years prior to that more recent debate (see Main 1982 above).

Frost *et al.* (1995) examined what they called complementarity in ecosystem function. This occurs when '*ecosystem processes are maintained at constant levels despite stresses that induce shifts in the populations driving those processes*'. They presented results from the experimental acidification of a lake. The lake had two basins that were divided by a curtain; one basin was acidified in stages over a six-year period and the other was not manipulated. They then measured the biomass of all common zooplankton species. They found that there were major declines in some taxa during the earliest acidification stage, and more declines with further acidification. On the other hand, some taxa increased during each treatment stage. The authors reported little evidence of a difference between basins until the stage of lowest pH was reached and they concluded:

> *"Thus, the function of the zooplankton community represented by its total biomass was much less sensitive to acidification than community structure".*

They found that for each zooplankton group (rotifers, cladocerans and copepods), a single species was identified that increased from a minor fraction to a substantial portion of a group's biomass as acidification progressed. They conjectured that the increase of these species, which was critical to the maintenance of ecosystem functioning, appeared to be a compensatory response:

> *"... due possibly to a relaxation of interspecific competition for resources, triggered by the loss of other species with acidification".*

The authors concluded that compensation in response to environmental stress would be difficult to predict.

Also studying aquatic systems, Pace *et al.* (1995) conducted an experiment to evaluate population variability in response to whole-lake food web manipulation. They found that their ecosystem manipulations (which involved the introduction or elimination of certain fish species) '*demonstrated that increased variability of populations [i.e.*

population size] is one consequence of ecosystem manipulations'. They also found that the zooplankton communities in the lakes they studied '*were highly redundant in the sense that many species feed on the same or similar resources, and all species regenerate nutrients that limit the growth of phytoplankton*'. They concluded that studies seeking to understand how change affects the structure and function of ecosystems require '*better integration of population studies within the framework of ecosystem questions*'.

In relation to soil ecosystems, Kennedy (1995) pointed out that by one estimate, only 1–10 per cent of the Earth's microbial species had been identified, leaving a vast portion of that biota unknown and unstudied. Thus, while soil microbial communities are often characterised as having considerable functional redundancy, it is impossible to quantify this redundancy since most microbial species and their specific functional attributes are not known.

Allen *et al.* (1995) proposed several reasons why there might be little ecological redundancy among mycorrhizal fungal species. For example, many such species have:

> *"... highly diverse combinations of specific functions _ Extinction of these species could cause measurable* (sic) *changes in the local flora, probably even where several species of AM [arbuscular mycorrhizal] fungi coexist".*

The authors cited earlier work in sagebrush ecosystems in Nevada, USA, which provided evidence of seasonality in plant response to a relatively low number of arbuscular mycorrhizal fungal species. Specifically, one species (*Acaulospora elegans*) aided plant growth in summer while others aided growth in spring or autumn. Thus:

> *"... for the functioning of mycorrhizae from the plant's point of view, the fungi are likely to be dissimilar in ways we have not even begun to examine".*

Bruns (1995) proposed two sets of models to explain the high diversity of ectomycorrhizal fungi that can even occur in small monoculture forests. The first is based on resource partitioning: the idea that competitive exclusion is prevented because species are using different resources or are partitioning use of limited resources in some way. According to Bruns, this would predict that diversity:

> *"... is functionally significant to efficiency or stability of the ecosystem".*

The second is based on the effect of disturbance on competitive interactions. Competitive exclusion is avoided:

> *"... not by partitioning of resources, but because the system never reaches equilibrium".*

Bruns concluded that '*an understanding of the natural history of individual species is pivotal to understanding the functional significance of species diversity*'. Such an understanding, he suggested, might increase as the techniques for studying ectomycorrhizal fungi advance.

Vinton and Burke (1995) examined the importance of plant species and plant cover on nutrient cycling in shortgrass steppe of northeastern Colorado. They found that soils under plants had consistently higher carbon and nitrogen mineralisation rates and, in some cases, higher total and microbial C and N levels than soils without plant cover. The identity of the species was less important than plant presence:

> *"... although plant species may have differential local effects on soils, it is the presence, and not so much the identity, of the plant occupying a given space that may be most important to plot level estimates of soil properties in this semi-arid grassland".*

They suggest that this phenomenon may occur because:

> *"1) plant presence is discontinuous and 2) decomposition and nutrient availability are primarily limited by water, not by plant species-mediated characteristics such as litter quality".*

In an Australian context, Hobbs *et al.* (1995b) reviewed the role of biodiversity in ecosystem function in the Mediterranean-type ecosystems of southwestern Australia. They noted that disturbances such as fire can induce shifts in species composition and they considered the implications of this for the role of biodiversity in ecosystem function:

> *"The open question is how reversible the changes are – do species that miss out one time round have another chance next time, or are they lost to the system? To some extent this brings in the question of whether ecosystems can have multiple alternative states, with transitions between states determined by particular combinations of climatic and disturbance events _ This question is in many ways central to the debate on the role of diversity in ecosystem function. If multiple states are possible, then not only the diversity of species in particular states needs to be considered, but also the total pool of species involved in all possible states. The maintenance of ecosystem function may depend not so much on the retention of all species per se, but on the role of these species in the retention of the capability for particular states to develop in response to particular environmental and/or disturbance cues."*

Hobbs *et al.* (1995b) noted that from the late Pleistocene through the whole of the Holocene, environmental change and species extinctions were occurring. In particular, the megafauna through that period would have been capable of causing considerable disturbance, from canopy destruction to soil disturbance, and affecting the structural composition of post-disturbance regeneration. They suggested that the continued high diversity of the region following the loss of the megafauna would indicate that the ecosystems continued to function as before, 'presumably following a series of substitutions as species became extinct'. However, they went on to state:

> *"The present composition of the biota gives few clues as to how ecosystems were reorganised as a consequence of the extinctions, especially following the loss of the megafauna, which must have led to significant changes in both the structure and function of vegetation".*

The authors conjectured that as the megafauna were lost, the surviving species must have reorganised into new assemblages and ecosystems. This may have resulted in significant changes in ecosystem function; alternatively, functioning ecosystems may have persisted, albeit in a different form.

Whitford (1996) reviewed the importance of soil biota diversity in arid ecosystems, hypothesising that soil stability and long term productivity are dependent upon the integrity of the soil biota. There was evidence to suggest that the functionally active fraction of the total soil biota varied considerably over time as a function of soil water content and temperature. There were also very limited data (from an experiment using fungi in the Chihuahuan desert) suggesting that:

> *"... complete species assemblages are necessary for the efficient decomposition processes in arid ecosystems but are not essential for the process to occur".*

The author cited a study in which, as the decomposition process proceeded:

> *"... the microfaunal community became more complex, with a succession of taxa joining the soil biotic assemblage involved in the process".*

The author also noted that the diversity of soil pore size influenced the diversity of soil biota, since this affected their ability to move through the soil. Since organisms moving through different sized pores may have access to different parts of the soil and, in the case of predators, to different sized prey, size diversity within functional groups might play a role in ecosystem function (Whitford 1996).

Whitford (1996) suggested that a combination of relatively low diversity in arid zone ecosystems and the fact that many species are operating close to their tolerance limits affected the composition of the functional fraction of the soil biota. He concluded that:

> *"... while the redundancy hypothesis may hold for highly-evolved, high-diversity ecosystems which are environmentally stable and favourable for biological activity, it is less likely to apply to arid and semi-arid ecosystems".*

Medina (1996) suggested that rare species in tropical savanna ecosystems occupy '*empty spaces in the community*' that can be occupied on a more or less permanent basis, '*making these rare species also characteristic of the primary-producer functional group in these savannas*'. The fact that species can become established in a community means that there are resources that are not being utilised by the dominant species. If this is the case, then:

> *"... the relationship between diversity and resource capture is straightforward: in a stable community of primary producers, reduction of diversity, represented by complete elimination of one or several species, will necessarily result in resource waste"* Medina (1996).

Medina presented evidence from a variety of studies showing that trees and grasses in tropical savannas modified their nutritional environment to varying degrees which were not identical even between species similar in habit and phenology. For example:

> *"... the amount of nitrogen accumulated in the herbaceous biomass is much larger under the African leguminous species* Acacia tortilis *than under* Adansonia *and in nearby open grasslands....."*

Sarmiento (1996) discussed the relationship between plant biodiversity in tropical savannas and water availability, listing the responses to water stress by various functional groups. For example, deciduous tree species responded by shedding their foliage during the dry season; evergreen trees managed to access sufficient water throughout the year; and perennial grasses decreased transpiration rates during the dry season. Within these groups, however, the author noted important differences between species. Evergreen trees, for example, differed in their daily patterns of stomatal conductance and transpiratory fluxes and some of them severely restricted water losses during the midday hours. The author concluded that:

> *"… the functional diversity of savannas allows for only minor floristic changes. 'Redundant' species within each functional group are not entirely equivalent, and hence they have different tolerances to environmental pulsation. Therefore, changing conditions may result in a certain degree of floristic replacement, without major changes in the functioning of the system. This means that savannas should be more stable in functional than in floristic terms. Only major changes in the top levels of the hierarchy of environmental determinants [e.g. plant-available moisture, plant-available nutrients, fire and herbivory] conceivably lead to functional changes and eventually to the complete replacement of the savanna ecosystem".*

The 'redundancy' versus 'insurance' issue in relation to biodiversity and ecosystem functioning was taken up by Lawton *et al.* (1996). They suggested that even if high species richness does not always play a significant role in maintaining ecosystem processes under a 'normal' set of conditions, those conditions might change so that they do not suit the dominant species. In such a situation, species hitherto 'redundant' may show compensatory changes in abundance and act to maintain ecosystem processes. In other words, today's ancient relic could be tomorrow's pioneer.

In a detailed study, Lawton *et al.* (1996) surveyed soils for nematodes and termites at five sites in 'near-primary' tropical rainforest near Mbalmayo in Cameroon and speculated about the relationship between species richness and ecosystem function. Most of the 204 species of nematode sampled were rare: less than half were represented by three or more individuals, and just less than two thirds by two or more individuals. There were 127 specimens of the most common species, while the ten most common species made up only 39.4% of the total number of individuals; 76 species were represented by a single specimen. Based on morphology, taxonomy and gut contents, the authors assigned the nematodes to six trophic (or functional) groups: plant feeders (60 species), fungal feeders (11 species), bacterial feeders (71 species), predators (33 species), unicellular prokaryote feeders (2 species) and omnivores (26 species), with one species unclassified.

Additionally, 78 species in 51 genera of termites were sampled and in two consecutive years, the top 10% of species (in biomass terms) contributed disproportionately to the total biomass (96% in year one and 69% in year two). This implies that most species were rare and have very low biomass (ie. in year one the 27 least abundant species made up 4% of the biomass, in year two the least abundant species made up 31% of the biomass). The authors assigned the termites to functional groups using ecological and morphological criteria, namely soil-feeders (18 species in year one, 24 species in year two), soil-wood interface feeders (four and six species), wood-feeders (seven and eleven species) and wood/litter foragers (one species in both years).

The authors found that the biomass of termites per unit area is between ten and 300 times that of the nematodes and is concentrated in relatively fewer species. They stated that:

> *"When considering the effect of disturbance on ecosystem processes, the resilience of these dominant species is likely to be of prime interest".*

According to the authors, the dominant species of termites are nearly all large-bodied soil-feeders that build (or colonise as secondary occupants) substantial mounds or nests, with large numbers of individuals per colony. The less dominant species generally form either small colonies occupying pockets of existing mounds as secondaries, or live in small diffuse nest systems within the soil. They speculate that:

> *"Given the apparent requirement for possession of large epigeal mounds for numerical dominance, it seems unlikely that removal of the dominant termites would allow other species within the assemblage to take up their ecosystem functions as replacements. In other words there may be rather little redundancy built into this component of the soil food web".*

The authors also discuss the role of termites and nematodes in ecosystem processes. Both contribute to the production of CO_2 and methane. Nematodes play a key role in mineralisation, while termites '*must have a vital role in mineralising organic matter that might otherwise be immobilised in the soil*'. However, the importance of termites and nematodes as ecosystem 'control mechanisms' is not known. For example:

> *"Not enough data exist for the Mbalmayo sites to tell whether the species that are most dominant in termite assemblages are also the most important for these control functions [e.g. the mineralisation of organic matter], nor again, whether it matters whether these functions are carried out by a few, or by many species".*

The authors further suggest that '*one obvious, but highly speculative conclusion*' is that there is considerable redundancy built into the main functional groups of nematodes and termites. The paper concludes with the statement that experimental manipulation of species richness would help resolve the issue, but this would be '*extremely difficult to do with soil animals in an instructive way in the field*'. Hence the survey gathered sufficient data to place species in functional groups but was unable to test potential redundancy in these groups.

Although it focuses on marine systems, a study by Clarke and Warwick (1998) used multivariate analysis to quantify structural redundancy in macrobenthic communities. They used 5 years of data from the Bay of Morlaix, France in relation to an oil spill and 12 years of data from two stations from coastal Northumberland, England. Subsets of the assemblages were assessed to investigate whether the multivariate response pattern closely matched that of the whole community. The number of subsets of species extracted corresponds to the structural redundancy of the system. In both examples, both the number of subsets and the number of species within each subset were similar. Each subset also encompassed a wide taxonomic and functional spread. However, the authors stress that the link between structural redundancy and functional redundancy and the potential for functional compensation are difficult to make from such observational experiments, and that only species removal experiments can really test functional redundancy and functional compensation.

Some authors in relation to the redundancy debate have also explored the role of 'keystone' species (sensu Paine 1969a and 1969b). Keystone species may be defined as those that play a critical role in the maintenance of ecosystem structure or functioning; the loss of such species may cause a major disruption to such structure or functioning. However, Mill *et al.* (1993) actually advocate the dropping of the term ‘keystone’ species due to the lack of data addressing both the range of interaction strengths within communities and the generality of trends across communities. They suggest that the concept has only been useful in demonstrating that some species have particularly strong interactions only under certain conditions. Hence, ‘keystone’ species may only operate as such over a particular time or place and that other species could have similar importance under changed conditions. Hurlbert (1997) concurs with Mill *et al.* (1993), and suggests that rather than an either/or dichotomy between keystone and non-keystone species, the general functional importance of a species in terms of changes in productivity across all species should be calculated instead (see Hurlbert 1971 and 1997).

For example, subterranean termites in the Chihuahuan Desert are thought to be ‘keystone’ taxa because of their importance in the decomposition of organic matter (Whitford 1986): physical weathering and activity of fungi and bacteria was estimated to account for only 4% mass lost from dung pats during the growing season. Termites are also thought to be ‘keystone’ taxa in relation to higher trophic levels: they make up a significant fraction of the diets of lizards and have also been shown to influence hydrological characteristics of soils.

In an Australian context, Eby (1991) summarised the small amount of information regarding the role of Grey-headed flying foxes as dispersers of rainforest seeds and as pollinators of *Eucalyptus* and other myrtaceous species. Because of their large foraging range and ability to shift camp when fruit or nectar resources become available elsewhere, these animals can distribute genetic material, both as propagules and as pollen over very large distances. Hence, they could be pivotal (effectively keystone) species for the reproduction of eucalypts, and thus the maintenance of rainforest remnants and regeneration processes.

However, in a similar vein to Mill *et al.* (1993), Beare *et al.* (1995) questioned what they called the ‘redundancy–keystone dualism’ in the context of soil biota. They suggested that while redundancy in a single function might be common to many soil biota:

> *“... the suite of functions attributable to any one species is unlikely to be redundant. Furthermore, functionally similar organisms often have different environmental tolerances, physiological requirements and microhabitat preferences ... As such, they are likely to play quite different roles in the soil system”.*

The authors also suggested that the concept of keystone species tended to disregard the importance of biotic interactions in regulating ecosystem function and they examined the literature related to the complexity and specificity of soil biotic interactions. They concluded that the interactions of both above-ground and below-ground biodiversity was critical to the development and maintenance of the diverse mosaic of resource patches and microsites in soils. They labelled the species assemblages occupying the distinct resource and refuge types (such as leaf litter types, faecal pellets, macropores and aggregates) that comprised such patches as ‘unit communities’. Aggregated unit communities (i.e. ‘metacommunities’), in turn, would usually contain more species (and presumably greater functional) diversity than any single unit community. Some biological interactions will cross different spatial and temporal scales, serving to increase or decrease environmental heterogeneity by altering the patch mosaic.

> *“As a result of these complex interactions, diversity at one hierarchical level (e.g. plant, macrofauna communities) within an ecosystem may influence the diversity of both structure (e.g. species, functional groups) and function (e.g. lignin degradation, N immobilisation, denitrification) at other hierarchical levels (e.g. detritusphere, rhizosphere, aggregatusphere). It is through this influence that biodiversity may contribute most significantly to the functioning of soil ecosystems”.*

The authors concluded that advances in the understanding of the significance of biodiversity to biogeochemical cycling ‘*will come from taking a broader view of biodiversity*’, from the level of individual organisms to the influence of biodiversity at one spatio-temporal scale on the diversity of structure and function at other levels of organisation.

3.3 Does Diversity Beget Stability?

The redundancy debate discussed above appears to have effectively been a re formulation of particular issues surrounding the larger and still unresolved debate on the concept of diversity and stability. A subset of the diversity-stability hypothesis is also the question of whether diversity increases system productivity, since a greater number of species may be able to exploit a wider range of available resources.

Pimm (1991) pointed out that discourse on the relationship between diversity and stability has been clouded by a confusion of definitions. Ecologists have used stability to mean:

1) that an ecosystem was stable in the mathematical sense, i.e. that the variables all return to equilibrium conditions after displacement;
2) resilience: defined as how fast a variable that has been displaced from equilibrium returns to equilibrium;
3) persistence, which is how long a variable lasts before it is changed to a new value;

4) resistance, which measures the consequences when a variable is permanently changed; and
5) variability, which is the degree to which a variable varies over time.

Given this, Pimm commented:

> *"... no wonder there was so little agreement ... Rarely did two ecologists look at the same question, although when empirical and theoretical ecologists did look at the same relationships between complexity and stability there was remarkably good agreement"*

The following excerpt from Margalef (1969) illustrates the fuzziness that surrounds the diversity-stability issue:

> *"All the facets of the problem of stability of ecosystems are pervaded by history. Nothing is gained by imagining a system subjected to hypothetical changes; the fact is that anything that has passed through a succession or temporal set of selective filters can be called stable, and it can be complex or simple, variable or almost constant. If the capacity to return from a far different state is never needed or realised, the system cannot prove itself stable, but neither is it possible to declare it unstable. Such systems often show a striking stability in taxonomic composition. With this reasoning, the whole notion of stability appears hopelessly confused".*

At face value, at least, it would seem that the problem of defining stability, let alone measuring it, would render the concept of little practical use. Yet it continues to be discussed in the literature, partly because the current high rate of species loss has led to fears of widespread ecosystem collapse. We review the extensive literature on this topic because of its implications for the possible role of parameters of ecosystem function, ecosystem productivity or ecosystem 'leakiness' in the development of surrogate biodiversity indicators for SoE reporting.

Although a popular area of investigation over the recent past, the idea that increasing diversity might increase productivity and/or stability is not new. McIntosh (1985) quotes from St. Thomas Aquinas (1225 AD – 1274 AD):

> *"It is better to have a multiplicity of species than a multiplicity of individuals of one species".*

Many years later, Charles Darwin (1859) wrote that:

> *"It has been experimentally proved, that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can be raised in the latter than in the former case".*

He suggested the existence of a 'balance' in complex natural systems when he wrote:

> *"... and so onwards in ever-increasing circles of complexity. Not that under nature the relations [between organisms] will ever be as simple as this. Battle within battle must be*

> *continually recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains for long periods of time uniform, though assuredly the merest trifle would give the victory to one organic being over another".*

Indeed the concept of diversity and stability does not differ fundamentally from even more ancient, yet still popular, views on the supposed 'balance of nature', as implied by Darwin. While the idea of a 'balance of nature' would be readily dismissed by most modern day ecologists, the idea still appears to re-surface regularly under other guises such as the concepts of 'dynamic equilibrium' or 'steady state'. (Egerton 1973 provides a historical perspective on the concept of a 'balance of nature').

At the other end of the diversity spectrum, Slobodkin and Sanders (1969) considered that species-poor environments could be categorised as follows:

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> 1) *'new' environments, in which the number of species is in the process of increasing;*
> 2) *'severe' environments, which may become completely abiotic with relatively slight environmental change, and*
> 3) *'unpredictable' environments, in which the variances of environmental properties around their mean values are relatively high and unpredictable both spatially and temporally." [references omitted]*

The authors reasoned that in general it was easier for species to migrate from a non-predictable to a predictable environment than the reverse:

> *"This we believe explains why, at a steady state, species diversity is greater in higher predictability areas".*

The authors drew a distinction between short-term stability and long-term predictability, where 'short-term' was defined as time periods of not more than one to five generations, and 'long-term' as higher orders of magnitude. They suggested an interaction between environmental constancy and the degree to which resources limit organisms and the diversity of natural communities. Because of this:

> *"... short-term stability in normally unpredictable environments often results in a reduction of their already low species diversity, in contrast to long-term predictability, which _ increases diversity".*

Thus, the authors claimed that contradictory experimental results regarding the relationship between diversity and stability were often confounded by 'the time factor which has not been clearly brought into focus'.

May examined the diversity-stability question using mathematical modelling techniques in his widely cited 1973 monograph (May 1973). He concluded that while '*Empirical evidence does not yet permit a decisive answer as to whether trophic richness and complexity promote population stability in the real world*', mathematical models implied that '*increased multi-species trophic complexity makes for lowered stability*'. He suggested that while complexity may not beget stability, '*it could be that stability* <u>permits</u> *complexity*' [emphasis added]. The popularity of the linked concept of diversity - stability therefore appeared to decline during the later 1970's.

However, according to Kareiva (1996), May's (1973) monograph was misinterpreted as the final word on diversity_ stability, causing scientists to abandon experiments aimed at contrasting the properties of diverse communities with those of simple communities.

Fortunately, not all researchers mistakenly thought that the issue had been settled. Pimm and Lawton (1977) used a mathematical approach to address the issue of why food-chains rarely consist of more than four or five trophic levels. They argued that the number of levels was constrained not by ecological energetics (as was widely believed) but by population dynamics. Taking a mathematical approach, they calculated the effect of food-chain length and complexity on stability and 'return time' (the time taken for a food-chain to return to equilibrium after disturbance), concluding that stability decreased and 'return time' increased with increasing complexity and number of trophic levels.

McNaughton (1977) diverged from the trend of using mathematics to debunk the diversity-stability hypothesis when he reported results of his experiment in the Serengeti-Mara ecosystem in Tanzania and Kenya. It assessed the relationship between stability and diversity of grasslands in response to rainfall, grazing and the addition of fertiliser. The level of instability was measured by fluctuations in green biomass.

McNaughton found that the plant community of a successionally older and more diverse ecosystem was functionally more stable than a younger and less diverse plant community after undergoing a nutrient perturbation. The application of fertilisation had no effect on diversity of the younger field, but there was a significant reduction in diversity in the older field. There was no change in richness: the diversity change was caused by greater equitability among the same number of species. According to McNaughton:

> *"This confirms the hypothesis: compensations among co-occurring species stabilised an aggregate community functional property in the more diverse community".*

Similarly, the more diverse plant community was subject to a greater diversity modification by grazing, but overall productivity remained higher in the diverse community. Growth of uneaten species in the more diverse stand compensated for grazer consumption: compensation by the community for grazer offtake was 83% in the more diverse community and only 9% in the less diverse community.

McNaughton's study also showed that the ability of a community to maintain its photosynthetic biomass during a period of variable rainfall was significantly associated with its species diversity:

> *"Once again, this greater stability was mediated by fluctuations in species abundance _ some species traded, in the adaptive sense, greater growth rate after a shower for a less rapid drying between showers".*

McNaughton concluded that 'fluctuations in the abundances of species with different adaptive modes may be a mechanism stabilising community function in a varying environment'.

Lavorel and Noble (1992) proposed an 'integrated scheme' to test the hypothesis that stability increased with diversity in an Australian Mediterranean ecosystem. They suggested a nested sampling design that included a ‘pseudo long-term study of succession using different sites of known succession histories’, focussed measurements and focussed experiments. According to the authors, such an approach has been approximated (although not deliberately) by research into garrigue landscapes in France, which are mosaics comprising old fields at different successional stages and *Quercus ilex* (oak) forests. These mosaics are:

> *“… characterised by a high spatial heterogeneity at a variety of scales, a high species diversity, and high frequency and variety of disturbances at all scales …”*

The authors concluded that linking the results from different approaches in the garrigue ecosystems of France provided evidence that stability of the whole system was linked to its diversity: the existence of groups of species able to respond to different disturbances and the existence of several equivalent species within these groups. Further, the approach suggested that:

> *“… the diversity of the landscape itself is important, with a mosaic of patches with different levels of diversity and species compositions”.*

The authors qualified this finding by noting that such an *a posteriori* connection of independent studies could not fully test the initial hypotheses.

Naeem *et al.* (1994) were among the first to experimentally address the relationship between species diversity and general ecosystem processes. Using the ‘Ecotron’, a multi-million dollar closed laboratory facility at Imperial College in Great Britain, they manipulated levels of biodiversity and followed these over time measuring primary productivity, assemblage respiration, decomposition, nutrient retention and water retention. The microcosms constructed by Naeem *et al.* were housed in 16 separate units in which conditions were highly controlled and into which assemblages at three different levels of species richness were placed: a low (nine species), medium (15 species) and high (31 species) treatment. Each assemblage had similar proportions of plants, decomposers, herbivores and parasitoids, and there were at least four replicates for each diversity treatment. The low and medium diversity treatments were subsets of the high diversity treatment. The results of this experiment showed that high diversity communities fixed more carbon and had greater plant cover, and thus more light interception than lower diversity assemblages. However, none of the other parameters measured (nutrient retention, water retention, respiration and decomposition) showed any correlative patterns with species diversity.

Beck (1998) critically assessed the study by Naeem *et al.* (1994). Positive factors associated with the experiment were that:

1) all factors were controlled;
2) it was a manipulative experiment; and
3) multiple trophic levels were manipulated and examined.

However, Beck also identified major flaws with the experimental procedure that limited any conclusions about the effects of biodiversity on ecosystem processes. He noted that:

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> 1) *only three non-random treatments were used. Hence, results could only be applied to the assemblages that were considered in the study and were not applicable more generally;*
> 2) *the study did not and could not differentiate between hypotheses;*
> 3) *given 2), only weak relationships were found between most processes and biodiversity;*
> 4) *species richness was used as the only measure of biodiversity when nearly all definitions note that species richness is a poor measure;*
> 5) *most importantly, there were substantial confounding factors in the experiment such that no unequivocal statements about the role of biodiversity could be made. Species richness was not the only variable altered in the treatments (initial biomass was unintentionally manipulated too); and*
> 6) *as a microcosm experiment it had limited applicability to biodiversity in the field".*

Other recent experiments have renewed attention on the stability-diversity question. Tilman and Downing (1994) described an eleven-year experiment in successional and native grasslands in Minnesota, USA. Plant species richness was altered through the application of seven different rates of nitrogen (increasing fertility led to decreasing diversity in the system studied). The experiment coincided with a severe drought, permitting the testing of resistance to drought of the various treatments. Tilman and Downing reported that the most species-rich plots produced about half their pre-drought biomass during the drought, while the most species-poor plots produced only about one-eighth. Other characteristics such as the rate of nitrogen addition, total aboveground plant biomass, the proportion of total plant biomass from species with the C4 photosynthetic pathway, and differences in these variables among fields, were also correlated with species richness. Species-poor plots also took longer to return to their pre-drought biomass than species-rich plots.

This study was criticised by Givnish (1994). They argued that nitrogen fertilisation – used by Tilman and Downing to reduce diversity, may have selected for species with lower allocation to roots versus leaves, higher stomatal conductance, and greater photosynthetic capacity, thereby confounding results (such species are more likely to have low drought resistance). In response, Tilman *et al.* (1994) performed further analyses of their data, concluding that 'we doubt if other physiological shifts, as suggested by Givnish, would eliminate the effects of biodiversity on ecosystem stability'.

Both Givnish (1994) and Tilman *et al.* (1994) suggested that a cleaner test of the effects of biodiversity on ecosystem functioning would come from direct experimental control of species diversity. Tilman *et al.* (1996) commenced such an experiment in 1993. It involved dividing bare earth into 147 plots located on nitrogen-limited soil planted with 1, 2, 4, 6, 8, 12 or 24 species. The species assigned to each plot were chosen by a separate random draw from a pool of 24 North American prairie species. The impacts of diversity on plant productivity, nutrient capture and nutrient leaching were observed during the second year of growth in the experimental plots, and also in nearby native grassland. The authors concluded that:

> *"... this experiment shows that both plant productivity and resource utilisation were significantly greater at higher plant diversity in these developing grassland ecosystems. The greater nutrient utilisation at higher species diversity resulted in lower leaching loss of soil nitrogen, which should contribute to the sustainability of nutrient cycling and soil fertility in these ecosystems".*

These relationships were also observed in the natural grasslands, 'indicating that the effects of biodiversity observed during ecosystem establishment are maintained in mature ecosystems'. They suggested that their results provide:

> *"... direct evidence that the current rapid loss of species on Earth, and management practices that decrease local biodiversity, threaten ecosystem productivity and the sustainability of nutrient cycling. Observational, laboratory and now field experimental evidence supports the hypotheses that biodiversity influences ecosystem productivity, sustainability and stability".*

However, Tilman *et al.* (1996) may be premature in reaching this conclusion. Other studies have reported quite different results. For example, Robinson *et al.* (1995) tested the susceptibility of plant communities in a California winter annual grassland to invasion by the California poppy. They divided the grassland – which had a generally high abundance of the grass *Bromus diandrus* – into 42 randomly arrayed fenced plots of three sizes: two of 32 m^2, eight of eight m^2 and 32 of two m^2, each plot type replicated to the same total area. The plots were laid out with centres ten metres apart and fenced. The intervening area was grazed by sheep and mowed. All 42 plots were sowed with seeds of the California poppy at a density of 500 seeds/m^2. Invasion success was assessed by three criteria: number of germinated seedlings; number of plants that survived to flower; and total number of fruits produced. The authors reported that plots with fewer resident species, regardless of plot size, were generally not invaded. In general, the number of resident species contributed significantly in all analyses and was the lead variable in tests of germination and persistence rates. A large fraction of the variance in invader success (over 70%) was not explained by general linear modelling, 'indicating a sizeable contribution by unexamined variables'.

Tilman (1997a) later sought to explain what he called 'Robinson *et al.*'s (1995) unexpected relationship between species richness and invasibility' as a possible reflection of '*the unique attributes of Bromus relative to the poppy, and the correlation between Bromus abundance and species richness*' rather than suggestive of a general rule of invasibility.

The experiment reported by Tilman *et al.* (1996) was criticised by Beck (1998), who pointed out that it still only manipulated species richness and manipulated only one trophic level. The results are also only valid for colonising herbs, as these were the only components of biodiversity that were manipulated. Most importantly, Beck (1998) pointed out that weeding effects potentially confounded the seeding treatments. In the diversity treatments used in the experiments, species not part of the pre-defined assemblage were weeded out of the plots if discovered. Hence the potential for greater disturbance in the species-poor plots (which will have a greater proportion of unsuitable invaders) will be higher than in the species-rich plots which will have few, if any, invaders.

Other authors have taken issue with the findings of the experiment by Tilman *et al.* (1996). Aarssen (1997) suggested that plots with higher productivity, which in this case had greater species diversity, had more of the species that are capable of higher biomass production. Less diverse plots had less chance of having the productive species, by chance alone. Hence, he suggested, the finding of the relationship between diversity, productivity and sustainability may be an artefact.

Tilman (1997b) argued that this original finding was not an artefact. Instead, he suggested that this interpretation was a consequence of misinterpreting three related phenomena: the effects of species diversity, the effects of species composition and the reasons these two have effects. He pointed out the logical difficulty of separating the effects of diversity from those of composition in a simple species deletion experiment, pointing out that the approach in the key experiment was the only one likely to measure the effect of diversity. He acknowledged that this 'does not indicate why increased plant diversity caused productivity and nutrient use to increase' (Tilman 1997b, p185). Although several plausible mechanisms have been independently proposed for the observed patterns (e.g. Tilman *et al.* 1997), the reasons why diversity may affect ecosystem processes are still to be unequivocally described.

In other experimental work, Wardle and Nicholson (1996) reported a glasshouse experiment in which they tested the effects of a grass species and nine dicotyledonous grassland species, grown in monocultures and as two-species mixtures, on soil microbial biomass, the respiration:biomass ratio and plant litter decomposition. The microbial respiration:biomass ratio increased when the microbial biomass was operating inefficiently, which is characteristic of a destabilised system. Consequently, they tested the effect of increasing species richness (from one to two species) on this ratio to test the hypothesis that increasing diversity increases ecosystem stability. They found that increasing plant species richness did affect the microbial respiration:biomass ratio, but not in predictable directions.

Huston (1997) describes several "hidden treatments" that generally complicate interpretation of experiments examining the ecosystem function of biodiversity, and in so doing, lists several case studies. As in the examples above, treatment responses that are actually the result of the 'hidden treatment' may be inadvertently attributed to variation in species diversity. The three types of hidden treatments that may occur in "biodiversity" experiments (also alluded to in Aarssen (1997) and Beck (1997)) identified by Huston (1997) are:

- the unintentional alteration of abiotic conditions (e.g. resource levels) or biotic conditions (e.g. predation) in order to create differences in species numbers for 'diversity' treatments;
- non-random selection of species with particular attributes that produce treatment differences that exceed those due to diversity alone; and
- the increased statistical probability of including a species with a dominant negative or positive effect (e.g. dense shade, or nitrogen fixation) in randomly selected groups of species of increasing number or "diversity."

It is obvious that false conclusions about cause-and-effect relationships may be made if an experimental manipulation has multiple components of which only one is identified as the experimental treatment (Underwood 1996). Thus, the general problems described by Huston (1997) must be acknowledged and accounted for in all examinations of the role of biodiversity in ecosystems.

Garnier *et al.* (1997) also criticised the productivity versus species richness experiments of Tilman *et al.* (1996) and Naeem *et al.* (1994). They calculated and compared indices using data from two multi-species experiments one with a substitutive design and one with an additive design. (In a substitutive design, the total densities in monocultures and species mixtures are identical; in an additive design, the density of each species is the same in monocultures and mixtures so that the total density is higher in mixtures). Garnier *et al.* found that in the experiment with a substitutive design, total biomass per pot was always lower in the mixtures than in at least two monocultures. In the experiment with additive design, the biomass per pot was similar for mixtures along a nutrient gradient, but at the highest nutrient level the mixture markedly over-yielded (had a greater biomass) than did the most productive monoculture.

Garnier *et al.* (1997) suggested that the experiments of Naeem *et al.* (1994) and Tilman *et al.* (1996) failed to take into account two points basic to the exploration of the productivity versus species richness question: that monocultures of each species present in the mixture should be grown under the same conditions as the mixtures; and that comparisons between multi-species mixtures and monocultures should be made with *only* the same species. Thus, Garnier *et al.* argued that the correct index for assessing comparative performances of mixtures involving *n* species and monocultures was:

$$I = \frac{{}_{i=1}^{n}P_i}{\sup(M_i)}$$

where P_I = biomass produced by species *i* in the mixture; $\sup(M_i)$ = the biomass produced by the same species in the most productive (or superior) monoculture. If I was >1, then the mixture would be deemed to exploit the environment more completely than a monoculture. They concluded that given confusion in the design of many experiments to test the hypothesis, there is little unambiguous evidence of greater yields in multi-species mixtures compared to those in monocultures of the same species.

Tilman (1997a) conducted another experiment in which he tested, among other things, the effect of species richness on invasibility. He added seeds of up to 54 species to patches of native grassland of varying species richness. He found that the proportion of added species that became established was negatively correlated with initial species richness of plots, ‘suggesting that species-rich sites were more resistant to invasion’. Perhaps more interestingly, he reported results suggesting that native undisturbed grasslands contained many open sites that are invasible without causing ‘detectable displacement of existing species’. He suggested that greater species diversity in such grasslands was possible but was limited by the ability of species to disperse. In addition, ‘establishment differed among functional groups, with legumes being the best invaders in this nitrogen-limited system’.

In a soil litter experiment, Wardle *et al.* (1997) collected litter from 32 plant species, evenly divided between four plant functional groups based on litter quality, habitat and taxonomy. Litter was placed into litterbags so that each bag contained between one and eight species, creating a litter diversity gradient within each functional group and across some functional groups. The litterbags were then placed in the field at a site near Hamilton, New Zealand. According to the authors, the results:

> *“... did not provide any consistent evidence that enriching species diversity of plant litter, particularly between two and eight species, had positive effects on two fundamental components of ecosystem function: i.e. decomposition rate and rate of nitrogen release. We found little evidence to support the ecosystem hypothesis _ or the view that enriched biodiversity is necessarily ‘beneficial’ for ecosystem properties through increasing process rates. Some of our results are supportive of the species redundancy hypothesis _ and the idiosyncratic hypothesis.....”*

Wardle *et al.* (1997) reported that while increasing species diversity from one to two species had clear unidirectional effects, increasing diversity beyond two species did not result in further continuation of these trends. They concluded from this that, within plant functional groups, the species richness needed for maximal rates of the processes examined was ‘likely to be extremely low’.

Three mathematical models were used by Tilman *et al.* (1997) to explore the relationship between biodiversity and ecosystem productivity. They suggested that since ecosystem functioning may depend on both the identity of species and their number, experimental and theoretical studies must distinguish between these two dependencies:

> *“... to attribute effects to species diversity, effects must occur in comparisons of the average responses of two or more levels of diversity. At each level of diversity, there must be numerous replicate ecosystems, each with a random and independent combination of species chosen from the species pool. By having many random species combinations drawn from a large species pool, the mean response among replicate ecosystems at a given level of diversity becomes independent of particular species combinations”.*

The imaginary species pool used in the modelling work was assumed to be identical in all other ways but differed in their ability to utilise specified resources and resource combinations.

The first model considered a homogenous habitat in which all species competed for and were limited by a single resource. Based on resource competition theory, it was assumed that the species with the lowest requirement for a given resource would dominate at equilibrium, displacing all other species. The authors sought to answer the question of how initial species diversity influenced total plant biomass and nutrient use at equilibrium. They found that, on average, total plant biomass increased with diversity:

> *“... because better competitors produce more biomass and because the chance of having better competitors present increases with [original] diversity”.*

The second model examined the effect of biodiversity on ecosystem processes where species differed in their abilities to acquire two or more resources in a heterogeneous habitat. In such a situation, no species would be competitively superior throughout the entire habitat but, rather, would leave sufficient unconsumed resources away from its optimum ratio such that other species could invade and persist. The authors evaluated this model to determine the quantitative relationship between species richness and equilibrial standing crop for species drawn from a pool consisting of all possible species. For numerous random draws of 1–19 species, they found that standing crop increased, variance in standing crop decreased, and concentrations of unconsumed resources decreased with increasing diversity. A similar result was obtained with finite species pools.

The third model assumed that any given species ‘covered’ that portion of a habitat (in this case defined by two niche axes) where it performed best, but no single species was fully able to exploit the entire range of environmental conditions. Assuming that species are chosen at random from the species pool, the model predicted that total community biomass increased asymptotically with diversity depending on the amount of spatial heterogeneity in the two niche axes relative to niche size, and on niche shape. Variance in coverage increased at low diversity and then asymptotically approached zero as diversity approached infinity.

The authors claimed that their models showed that:

> *“... the effects of diversity come from variation among species. Greater original species diversity incorporates, on average, greater variation in species traits”.*

The models predicted variance among replicate ecosystems that had the same number – but different combinations – of species. According to the authors, this:

> *“... may explain the seemingly ‘idiosyncratic’ dependence of ecosystem functioning on diversity. _ This variance would make it difficult to detect the effects of diversity either if there were only a few replicate plots at each level of diversity or if there had been a biased draw of species”.*

The authors concluded that, based on the results of their modelling work, current rapid rates of species extinctions and of species loss from managed ecosystems may have significant effects on their productivity and sustainability.

Fjeldsa and Lovett (1997) suggested that environmental stability begets biological diversity and that different ecosystem histories may cause functional variation in the response of communities to habitat disturbance. Thus, high species richness may be caused by:

1) heterogeneity in time and space creating shifting opportunities, on a local scale, for large numbers of species;
2) accumulation of species over a long time in places where environmental conditions remained predictable; and
3) overlap of habitat on gradients.

An overall ecosystem framework regarding long-term sustainability was attempted by Chapin *et al.* (1996) and they suggested that:

> *"Negative feedbacks are the key to ecosystem sustainability because strong negative feedbacks provide resistance to natural or anthropogenic changes in interactive controls and maintain the potential for regeneration after perturbation. By contrast, strengthened positive feedbacks amplify an initial change in conditions and push the ecosystem toward some new state".*

and further:

> *"A diversity of species that compete for the same limiting resource generates negative feedbacks at the ecosystem level".*

For example, the overhunting of sea otters on the Pacific Coast of North America led to a significant decline in their abundance. Because the sea otters are the only major predator of sea urchins, overhunting of the sea otters caused an outbreak of urchins: this eliminated the kelp forest which in turn was the habitat for hundreds of fish and invertebrates. Thus, greater diversity within a functional group (in this case urchin predators) that are limited by the same resource would provide insurance against radical ecosystem change.

A number of experiments examining the relationship between diversity and stability or productivity have been presented here. Many have arrived at apparently contradictory conclusions. Pimm (1991) offered an explanation for this:

> *"Surely, goes the criticism, there is some group of organisms in which we will find the result predicted by the theories, if only because there are so many different groups of organisms that the assumptions of the theories must surely match at least one of them! Only when we find predicted relationships in most of the groups for which we have reasonable data will we conclude that the theories are compelling. So, selected examples may support the theories, but they certainly do not provide adequate tests of them. Only many new studies or compilations of existing studies will do that".*

Johnson *et al.* (1996) had a similar perspective. In their view, the empirical evidence so far suggests that intrinsic characteristics of particular ecosystems influence the functional roles of their resident species and, therefore, of species diversity. The nature of the perturbation and the selection of species for study can affect the outcome of diversity-stability experiments. Similarly, a lack of definition of functional groups and phenotypic plasticity all muddy distinctions between species for any experiment looking at functional redundancy. They suggested that reliable information on the functional role of species diversity in ecosystems could only come through meaningful hypothesis testing in controlled experiments, leading to the resolution of cause and effect. Most studies so far have only provided correlative evidence about biodiversity and ecosystem function, with the exceptions of the work of Naeem *et al.* (1994) and Tilman *et al.* (1994, 1996 and 1997), and even these have been criticised.

Naeem (1998) discussed species redundancy and ecosystem reliability in relation to reliability engineering. Ecosystem functioning as used by Naeem refers to '... *the biogeochemical activities of an ecosystem or the flow of materials (nutrients, water,* *atmospheric gases) and processing of energy*'. However, the term 'ecosystem services' has also been used to refer to these processes as they affect human welfare and hence 'ecosystem goods' refer to those products derived from these systems which are used by humans, such as fish or timber. Naeem argues that although local extinctions of species within functional groups occur frequently, it is global extinction that reduces functional group diversity and hence leads to potential ecosystem 'failure' - loss of function. Habitat fragmentation also reduces the ability of species to re-colonise after local extinction. Naeem feels that it is '*almost inescapable*' to conclude that '*... species richness within functional groups provides redundancy in ecosystem functioning, a potentially critical feature affecting ecosystem reliability*'. This parallels engineering design of such structures as bridges and buildings, although Naeem points out that in the case of ecosystems, function does not imply purpose or design, only activity. Hence, redundancy in this sense has positive connotations associated with engineering design rather than negative connotations associated with economic rationalist concepts of 'downsizing'.

3.4 Chapter Summary

There remains considerable scientific uncertainty about the role of biological diversity in the functioning of ecosystems. Species may be assigned to groups on the basis of the ecological role they play. There has been much debate about the degree of redundancy that may be built into such groups: lose a species from a functional group and other species within that group will replace its function in the ecosystem. Empirical evidence to support such conjecture is scarce and experiments designed to test the idea have often not been rigorous.

In theory, redundancy may vary between functional groups – there may be relatively high levels in some and low levels in others. There may also be key species for which there is no functional replacement. The implication of the keystone argument is that some species are critical to ecosystem functioning (their loss may lead to the loss of ecosystem function and, conceivably, to the loss of other species), while others are of lesser importance and will be replaced readily in the system by other species.

Others have argued that the division of species into functional groups is too arbitrary. Some species may perform more than one function; taken together, the suite of functions performed by a given species may not be redundant. It has been suggested – and there is some experimental evidence to support the idea – that the apparent redundancy of species at a given moment in time may simply be an expression of the system's buffering capacity: in changed environmental circumstances, apparently redundant organisms may become extremely useful in maintaining ecosystem function.

It has been suggested that the assignation of species to functional groups often requires more knowledge about species characteristics than is currently available and indeed, that to know what functional group a species belongs to requires as much information as is required to study each species in the first instance. There may also be relationships between apparently 'keystone' species and 'redundant' species that are important to ecosystem functioning but are not currently known.

The scientific debate about the role of biological diversity in ecosystem stability is also largely about the redundancy of species. This too is notable for its lack of hard data. Mathematical models have been used to show that more diverse systems are both more or less stable than simpler systems. Experimental data have also supported both arguments. As Pimm (1991) pointed out, this may be because there is no one answer to the question. Or it may be, as Johnson *et al.* (1996) asserted, that we simply have not yet conducted experiments sufficiently rigorous to test the hypotheses. It is also possible that many of these concepts are so ill defined, or indeed undefinable, that they are 'non-concepts' (*sensu* Peters 1991) and are inherently untestable in their current form.

Of central importance to the debate is clearly the degree to which a species is irreplaceable in terms of its effect on ecosystem function. However, it is also clear that no studies have yet been able to unequivocally show the absolute importance or unimportance of a species in relation to either ecosystem function or to other species. The concept that has slowly been gaining more widespread interest has been that biodiversity within functional groups imparts a greater degree of 'insurance' against major change in ecosystem function. It is apparent that the term ecosystem function is a relative term. Measures of its change can best be made in relation to a specific end that will ultimately be some measure related to the maintenance of 'ecosystem services'. Hence the sustainable delivery of 'ecosystem goods' for some human end.

4 The relationship between diversity and habitat complexity

4.1 The Species/Area Relationship

The species-area relationship (Arrhenius 1921) holds that there will be an increase in the number of species as the size of the sampling area increases (McGuinness 1984), and as such that larger areas contain more species. The species-area relationship has been used to:

- determine the area required to adequately sample species in a particular community (Connor and McCoy 1979);
- characterise community structure and estimate species richness (Connor and McCoy 1979) and;
- find the most appropriate size for reserves in conservation biology (He and Legendre 1996).

The species-area relationship is simply described by a plot of the number of species against the sampling area, resulting in a monotonically increasing curve which is at first steep, but gradually flattens (He and Legendre 1996). Different assemblages produce different species-area curves, with the relationship being exponential for small areas, power for intermediate areas, and logistic for large areas (He and Legendre 1996). The relationship is most commonly described using the power relationship summarised by $S=cA^z$ (or alternatively by $\log S=z\log(cA)$ where S is the number of species, A is the remnant area, c is the number of species per unit area, and z is a constant related to the degree of isolation of communities and the taxa being considered. Although the species-area relationship is usually statistically significant, there is generally a large amount of unexplained variance around the line describing it (Boecklin and Gotelli 1984).

McGuinness (1984) called the species-area phenomenon 'one of community ecology's few genuine laws', yet its cause and significance is still debated. Several explanations have been proposed, and these may operate with different force in different systems and on different scales (Lawton 1996). These hypotheses are described below.

The **passive sampling or random placement hypothesis** (Arrhenius 1921, Coleman 1981) is the simplest explanation for the species-area relationship. It points out that if individuals are randomly distributed, larger samples will contain more species (McGuinness 1984). This hypothesis is often considered a null hypothesis (Connor and McCoy 1979) and can be tested by using the same sampling effort in islands of different area. The passive sampling hypothesis is different from the habitat diversity and area *per se* hypotheses. It views the correlation between number of species and area purely as a sampling phenomenon, rather than as the result of biological processes (Connor and McCoy 1979) or the intrinsic quality of an area.

The **area *per se* or equilibrium hypothesis** (Preston 1960, 1962; MacArthur and Wilson 1963, 1967) states that the species-area relationship is a result of a dynamic equilibrium between immigration and extinction rates which are determined by area and island isolation. The remnant size represents the target area for colonising organisms and limits the total population size. Larger remnants or islands should support larger populations and large populations are less likely to go extinct than small populations. Extinction rates are negatively related to population size (Toft and Schoener 1983, Burkey 1995) because small populations are more vulnerable to demographic, genetic, and environmental stochasticity (Harrison 1991). Demographic stochasticity involves randomness in the order of births and deaths, which only affects the extinction rate significantly if populations are below a certain species-dependent size threshold (MacArthur and Wilson 1967, Ebenhard 1991). Genetic stochasticity can affect the long-term viability of a population as a loss of heterozygosity through drift and a loss of fitness through inbreeding (Harrison 1991) and would also be most important in small populations. Environmental stochasticity and catastrophes involve temporal variation in factors such as weather and the food supply and can affect populations of all sizes, although small populations are particularly vulnerable (Harrison 1991).

The **habitat heterogeneity (or habitat diversity) hypothesis** (Williams 1964, Connor and McCoy 1979) states that the increased species richness of larger areas is due to the greater number of different habitats available. This hypothesis suggests that islands of the same size may contain different numbers of species, depending on the heterogeneity of the habitat (McGuinness 1984). As different habitats support different species, more heterogeneous areas containing more habitats should support more species, most likely due to new conditions that are encountered as climate, soil, topography and many other factors change as area increases (Williams 1943). Even continuous habitat, such as forest, may contain several discrete habitat patches for a particular species (Addicott *et al.* 1987). Species diversity has been found to be positively associated with habitat heterogeneity in several assemblages, both terrestrial (MacArthur and MacArthur 1961, Pianka 1967) and aquatic (Abele 1974, Bronmark 1985).

The **"intermediate disturbance" hypothesis**, McGuinness (1984) extending the hypothesis of Connell (1978, 1979), holds that small areas are disturbed frequently and can thus only support species favoured by disturbance. Large areas, in contrast, are disturbed very infrequently and are thus dominated by a few species able to most efficiently exploit the resources and out-compete other species. Intermediate-sized areas achieve a balance between the two and thus support more species, leading to a 'humped' distribution

(McGuinness 1984, Andersen 1997a).

There are some data to support this last hypothesis. Ant colonies share many characteristics with many marine invertebrates, plants and other sessile taxa – they are modular organisms occupying fixed positions, and have similar resource requirements to co-occurring species; thus, competition is a prominent factor in community dynamics (Andersen 1991a). Humped diversity patterns in ant communities have been found along gradients of stress (Andersen 1992) and disturbance (Majer 1985). Species richness of butterflies has also been found to peak at moderately disturbed sites although the relative abundance of the species decreased from natural to urban areas (Blair and Launer 1997).

Sampling designs used in studies attempting to resolve causal factors underlying the species-area relationship on islands usually confound the three first-mentioned hypotheses (MacNally and Watson 1997). The use of standardised transect areas within one vegetation type in remnants of different sizes (e.g. Kelly *et al.* 1989) reduces bias due to habitat heterogeneity and passive sampling. The close correlation between area and habitat number, however, makes it virtually impossible to disentangle the effect of habitat number from that of area on species-richness (Kohn and Walsh 1994). It has been suggested that the most likely explanation of the species-area relationship for terrestrial systems is a combination of the area *per se* and habitat heterogeneity hypotheses (Rafe *et al.* 1985, Kelly *et al.* 1989, Kohn and Walsh 1994). It is also possible that species-area curves may be different for different subsets of an assemblage (McGuinness 1984). Most studies of the species-area relationship assume there is no temporal variation in species-richness although there is turnover in species composition (Gilbert 1980).

Hart and Horwitz (1991) presented a range of models that could be used for explaining the relationship between species number and area, including one set that proposed habitat diversity as a causal agent. They used data on the occurrence of invertebrates on individual stones within a shallow, riffle habitat in Finland to explore the issue. They found that habitat differences could account for some of the deviations between the observed number of species in a combined sample and those expected by passive sampling: this arose because:

> *"... dissimilar habitats tend to contain dissimilar species, so that the union of these habitats yields a greater number of species than the union of two similar habitats... In spite of this demonstrated habitat effect, the generally poor fit of the passive sampling model suggests that the assumptions of the particular sampling model used here need to be altered ... or that habitat diversity on finer scales than measured here ... may contribute to the observed patterns".*

Irrespective of which hypothesis best explains species number and area, a critical assessment of both habitat complexity and environmental variation is needed to gain an insight into the distribution and abundance of species. The application of the species-area relationship and island biogeographic theory to reserve design and conservation biology, particularly the 'equilibrium' assumption behind the theory, has come in for strong criticism because of its reliance on area alone and lack of consideration of other habitat and environmental factors (Margules *et al.* 1982, Boecklen and Gotelli 1984).

4.2 Habitat Complexity and Environmental Variation

Although the species-area relationship has been well studied, there has generally been a lack of detailed investigation within such studies of how the environment influences both habitat complexity and habitat heterogeneity, and how these habitat attributes determine, in turn, the distribution and abundance of species. The following examples highlight studies, particularly from Australia, that have endeavoured to study causative and predictive links between organisms and their environment.

Abbott (1976) compared habitat structure and plant, arthropod and bird diversity between mainland and island sites near Perth, Western Australia. He attempted to address two questions:

1) is the number of resident or breeding passerine species at a site related to the diversity of arthropods collected at that site by sweeping? and
2) is the impoverishment of passerine species on island sites related to islands having less density or diversity of arthropods?

He found significant positive correlations between arthropod Order diversity and bird diversity and between vertical foliage diversity and bird diversity. While the island sites had more individual arthropods than the mainland sites, they belonged to fewer Orders. Hence, this study implicates both habitat diversity and prey species diversity at the Order level as being linked to overall passerine diversity.

Braithwaite *et al.* (1983) studied the relationship between forest habitat and densities, species richness and diversity of eight species of arboreal marsupials at Eden, New South Wales. They found that high densities and diversity of arboreal marsupials were correlated with forests with foliage containing high nutrient concentration, large basal area of gums and peppermints, a longer time since fire and higher floristic diversity. This was not the case with forests composed of low foliage nutrient species such as *Angophora floribunda*, *Eucalyptus bosistoana* and *E. sideroxylon*. The response of arboreal marsupials to low foliage nutrient species may also be complicated by the presence of secondary (perhaps toxic) compounds and tougher waxier foliage which may be related to nutrient levels. They cautioned that no measure was made of the understorey flora, such as species of *Acacia,* which are known to be important for the sugar glider. Additionally, the sugar glider and to some extent the feathertail glider seemed to be favoured by post-fire successional regeneration of *Acacia* species and reached peak densities up to 30 years post fire. Other arboreal species were still increasing in abundance beyond 30 years.

In a further investigation, Braithwaite *et al.* (1984) studied the above relationship with regard to soil parent materials. They demonstrated that vegetation communities with high concentrations of nutrients in the foliage occur on soils of high fertility, thus providing a predictor of the suitability of an area for arboreal marsupials based on geology. Pausas *et al.* (1995) concluded that the main factor predicting the occurrence of arboreal marsupials was the availability of food. When this was not a limiting factor, forest structure (as it affected the number of potential nest trees) was the most important determinant of habitat quality.

Generalising on a global basis, Strong *et al.* (1984) commented that the total number of insect species associated with plants is strongly influenced by how common and widespread or local and rare the plants are, this being an example of the species-area relationship:

> *"Very simply, geographically widespread species of plants have more sorts of insects feeding on them than similar but less widespread species".*

Tree architecture is also a determinant of insect diversity. Nevertheless, these two factors (architecture and geographic range) do not account for all variation in diversity (Strong *et al.* 1984).

New (1988) suggested that much of the interpretation of Australian insect-plant communities draws heavily on principles from examples studied elsewhere in the world. In general, insect diversity is greater on trees than on other plants, partly because their structure or 'architecture' is more complex, and partly because trees are the last plants to appear in the succession from bare ground to forest and are long-lived compared to earlier successional plants. According to New, plant feeding insects and the green plants on which they feed together constitute about 70% of all known living species: one might expect that an understanding of the organisation and complexity of these associations would assist in the monitoring of changes in biodiversity. Of an estimated 108,000 species of insects in Australia, 60,000 (or more than 50%) are plant feeders.

The effect of a loss of forest structure on insect diversity was shown by Holt and Coventry (1988), who studied the effect of tree clearing and pasture establishment on a population of mound-building termites in north Queensland. They found that only two of the six mound-building species found in undisturbed woodland recolonised the pasture. Both were detritus feeders and were able to utilise available leaf material and cattle dung.

Torgersen *et al.* (1995) investigated the spatial heterogeneity of soil invertebrates and edaphic properties in old growth forest in western Oregon, USA. They sampled two 50 m radius circular plots in adjacent high density and low density forest stands at the end of June in two consecutive years – the nature of the experiment meant that results may have been confounded by within-treatment effects. The first plot, a mixture of old and regrowth conifers with a high density of remnant trees, was centred on one living old-growth Douglas fir. The second was centred in the first sampling year around an old growth stump burned 70+ years before and, in the next year, at the base of a young Douglas fir.

The study showed that spatial pattern in soil O-horizon depth, soil moisture, temperature, pH and soil invertebrate numbers and biomass changed between years and differed between the old growth and regrowth stands. For example, a total of 16,747 and 16,683 microarthropods [per 20 litres of soil] were counted in the old and regrowth plots in 1992 and 2,976 and 5,149 in 1993.

Basset (1996) studied the insect-plant relationships between leaf-chewing insects on ten species of trees in regrowth lower and mid-montane forest on Mt Kaindi, Papua New Guinea over one year. Leaf chewing insects were measured and an assessment of the abundance of herbivores and of their potential enemies was made. The host specificity of insects in captivity was also measured. A large number of regional and local variables were measured in order to investigate potential predictors of species richness, percentage of specialist species and abundance and biomass of leaf-chewing insects. He found that local species richness varied by more than four fold between the poorest and richest tree species and that the proportion of specialist species was also significantly different among tree species. Most of the variation in insect species richness was accounted for by five properties of the tree species: number of young leaves available, ant (enemy) abundance, leaf palatability, leaf water content and altitudinal range. He suggested that in complex environments such as tropical rain forests, local processes may be more important in maintaining species richness of local herbivores than in less complex systems such as temperate woodlands.

Blanche and Westoby (1996) investigated the diversity of gall-forming insects on eucalypts in Australia. They found that between-site differentiation was the main mechanism behind the species-area effect:

> *"The patchy distribution of most eucalypt species within their geographic ranges _ , and possibly the low dispersal ability of many gall-forming insect species _ , are likely to inhibit immigration between sites. The size of the individual patches, rather than the total geographic range size of a host eucalypt species, would then influence local extinction rates of insect species and could result in these rates being similar on large and small geographic range host species".*

Bird species were the subject of study by Braithwaite *et al.* (1989) who surveyed at 39 sites within 500,000 hectares of eucalypt forest on the south coast of New South Wales. The area was divided into 31 eucalypt communities and altitude, temperature, rainfall, landform profile, basal area of dead trees, basal area of all trees, basal area of acacias and indices of foliage nutrient concentrations (nitrogen, phosphorus, potassium and magnesium) were used as predictors. Bird species richness over all surveys and in summer was not correlated with the same environmental variables as the arboreal marsupial fauna in the Eden Region and was correlated with foliar magnesium and tree basal area. Bird species richness in winter was negatively correlated with altitude and temperature but was positively correlated with tree basal area.

Austin *et al.* (1996) generated regression models of tree species richness for a 40,000 km^2 area of forest in southeastern New South Wales. Using a dataset consisting of 7208 plots in which the presence or absence of tree species was recorded, they used four continuous variables (annual rainfall, mean annual temperature, mean daily radiation and plot size) and four categorical factors (soil nutrient index, rock type, topography and seasonality of rainfall) to define the environmental space. All were significant predictors of species richness when tested separately. The final model contained, in order of entry, the following: temperature, plot size, radiation, topography, nutrients, rainfall and rock type.

The maximum number of tree species was found in warm, mesic environments on protected sites with low radiation: these were usually protected south-facing gullies and lower slopes with moderate to high nutrient levels. Maximum eucalypt species richness, in contrast, was found at high temperatures, in intermediate rainfall and radiation conditions on ridges with aseasonal rainfall and high nutrient levels. Most, but not all, predictors were associated with water balance. Austin *et al.* concluded that their models were consistent with an available energy hypothesis based on actual evapotranspiration, and that studies of patterns in species richness should include local and regional environmental variables.

Information on trees as nesting and foraging sites for twelve species of small native ground-dwelling mammals were summarised by Dickman (1991) using data from 13 study areas between 1978 and 1990 in the forests of southeastern and southwestern Australia. He found that trees used for foraging were generally large, mature and with a complex system of branches and that over half of all nest/shelter sites were in trees, logs or litter.

Catling and Burt (1995) presented the results of studies undertaken in 13 areas on the mid south coast of NSW between 1989 and 1992. They measured ground-dwelling mammal distribution and abundance in relation to basal area of trees, foliage nutrient levels and habitat complexity score. Previous work indicated that on a local scale where there is relative homogeneity in floristic composition, structural components of the forest are important. However Catling and Burt found that at the regional scale, composition of the ground-dwelling mammal fauna in southeastern forests is determined more by the complexity of the understorey than by nutrient status. Previous work also suggested that forest associations with high site productivity generally act as population sources and associations with low productivity act as sinks. For arboreal fauna a threshold in nutrient status exists below which some species cannot persist regardless of vegetation structure. On the other hand, for small ground-dwelling mammals, a threshold exists in forest structure below which they cannot persist, regardless of nutrient status. They concluded that a significant reduction in understorey complexity would result in a decrease in diversity and abundance of small and medium-sized mammals and an increase in large grazing mammals.

Cork and Catling (1996) reviewed, synthesised and drew together general trends from studies investigating the relationships between the distributions of arboreal and ground-dwelling mammals and environmental, structural and leaf compositional variables in the eucalypt forests of north and south eastern New South Wales. Studies on arboreal marsupials comprised two broad categories in terms of the explanatory variables that appeared to be important:

1) studies suggesting nutrient status was the prime determinant of habitat quality; and
2) studies suggesting that structural variables might be equally or more important.

These two explanatory themes can be seen as consistent with a hierarchical model whereby structural and climatic variables – above a nutritional or phytotoxicological threshold – become more important in explaining the distribution and abundance of arboreal marsupials. Structural variables (i.e. habitat complexity) alone have been found to be the most important predictor of ground-dwelling mammals. Hence, climatic or regional level measurements will not be an adequate predictor of species distribution and abundance at the local level, in those regions where structure is demonstrably the most important factor. Thus, factors related to forest structure such as disturbance (from fire or logging) become important determinants of species distribution and abundance in such regions.

Coops and Catling (1997) summarised Australian papers that demonstrated the relationships between forest structure and the abundance of different mammalian fauna:

> *"For example, a dense understorey has been shown to be important for many ground-dwelling mammals (Fox and Fox 198; Catling et al. 1982; Bennett 1990a; Catling 1991; Claridge et al. 1991; Catling and Burt 1995a), arboreal mammals (Davey 1989, Lindenmeyer 1989; Lindenmeyer et al. 1991) and birds (Braithwaite et al. 1989), particularly along water bodies such as creeks or drainage lines (Lunney and O'Connell 1988). Also relationships have been shown between forests with little understorey and particular ground-dwelling mammals. The white-footed dunnart,* Sminthopsis leucopus*, prefers forests with a sparse understorey and little ground vegetation (Lunney and Ashby 1987) and the eastern grey kangaroo,* Macropus giganteus*, prefers forests with a grassy ground cover and few shrubs in the understorey (Catling and Burt 1995a)".*

They suggested that airborne videography could be used to predict habitat complexity and that maps could be produced showing the mosaic of forest complexity which, in turn:

> *"... should enable managers to predict the composition and, to some extent, the abundance of some faunal groups across the landscape".*

Coops and Catling (1997) expanded this idea to arboreal mammals. Since airborne videography can be used for individual tree recognition, it may be possible to use it to identify trees suitable for certain species of arboreal mammals (e.g. those with a large number of cavities not surrounded by dense vegetation, considered to be preferred habitat for the mountain brushtail possum, *Trichosurus caninus* [Lindenmeyer *et al.* 1996]). Thus, the technique may be valuable in predicting habitat suitable for some arboreal and some ground-dwelling mammals.

4.3 Chapter Summary

Species diversity increases as the size of the sampling area increases: thus, larger areas contain more species. Although this relationship has been known for decades, the reasons explaining it have not yet been confirmed. It may simply be an artefact of sampling (if individuals are randomly distributed, larger samples will contain more species), but three other plausible hypotheses exist. It seems likely that the true explanation for the relationship is a combination of two hypotheses: the area *per se* hypothesis, which suggests that the relationship is a result of a dynamic equilibrium between immigration and extinction rates which are determined by area and isolation; and the habitat heterogeneity hypothesis, which states that the increased species richness of larger areas is due to the greater number of different habitats available compared with smaller areas.

The relationship between habitat complexity and species diversity is still unclear. There are good data showing that the diversity of ground dwelling small-to-medium sized mammals in the southeastern forests of New South Wales increases as the understorey increases in complexity. Other data suggest that foliar nutrient content is correlated to the distribution and diversity of arboreal marsupials in similar forests. Since this appears to be closely related to soil parent material, geological variables may predict the suitability of an area for such species.

Some patterns in the abundance of tree-dwelling, leaf-eating insects have emerged in the literature: the geographic distribution of host species, patch size of host species and tree architecture account for much of the diversity amongst this group of insects.

There is increasing evidence of the fine-scale heterogeneity of landscapes, both spatially and over time. The distribution of some species – particularly arthropods – may be similarly heterogeneous.

All of the studies reviewed have investigated links between certain components of biodiversity and their environment and encouraging predictive links have been found. However, none of the studies have attempted to study biodiversity *per se* and its relationship to environment. It is apparent that the study of biodiversity *per se* and ecosystem function, and the search for predictive links between biota and environment are at different scales and may not be easily brought together. Diversity *per se* and ecosystem function can essentially only be studied at ecosystem scale, whereas biota and their environment must necessarily be studied at a finer scale.

5 The effects of disturbance on diversity

5.1 Background

One of the major themes running through the ecological literature over many years is the critical role of disturbance in ecosystems and its influence on diversity. The intermediate disturbance hypothesis (Connell 1978, 1979) has been influential in studies of this nature, stating that an 'intermediate' level of disturbance leads to the greatest species diversity. Both lack of disturbance and too frequent disturbance are thought to lead to a decrease in species diversity. However, many studies examining the issue of disturbance simply investigate the effects of disturbance *per se*. Other major aspects of the study of disturbance regimes are successional processes (used in the broad sense) that occur after a disturbance. Since the literature in this area is large, the following appraisal of the literature will primarily deal with anthropogenic rather than non-anthropogenic disturbances and how they may affect diversity, focussing particularly on Australian studies. This allows a closer focus on those issues that may be relevant for SoE reporting.

5.2 Successional Studies

Peet (1992) summarised work done on the predictable changes in community structure and ecosystem function that occur during succession and examined mechanisms that might be responsible for those patterns. He cited critical review papers that called for a reformulation of succession theory using a mechanistic approach. He suggested that successional change at the community or ecosystem level could be understood to some degree as a consequence of population processes of the component species that are themselves a consequence of species attributes. These population processes include establishment, growth, reproduction, loss to predation and death. His synthesis of the literature identified four phases of forest development for southeastern North America:

1) establishment phase;
2) thinning phase;
3) transition phase; and
4) steady-state phase.

These phases may apply to old field succession or to post-logging (for example, see Bormann and Likens 1979) or fire disturbances, and also may apply to other forest types such as boreal and montane. They did not seem to apply, however, to extreme high elevation sites where growth rates were very slow and where low levels of recruitment resulted in the thinning phase being skipped. Low elevation semi-arid woodlands in Arizona also showed the episodic and low level of recruitment of the extreme high elevation sites. Major successional trends in forest biomass, production, nutrient cycles and species diversity could be interpreted as reflecting underlying population processes during the four phases or similar phases of secondary succession. However, other successional trends were more a product of climatic change. For example, establishment may have occurred at cooler or wetter periods in the past and hence, disturbance may have lead to dominance by another suite of species than that predicted by considering population processes alone. After a discussion on primary and secondary succession and different usages of the terms, Peet (1992) proposed his own definitions:

1) primary succession: successions where the dominant mechanisms involve long-term environmental change; and
2) secondary succession: succession where the dominant mechanisms are population processes.

He suggested that it was not possible to fully separate disturbance from succession, as the distinction depends on the scale of investigation.

At a fine scale, Brown and Nelson (1993) studied the influence of successional stage on habitat use by three species of skink in the central highlands of Victoria. A variety of habitat variables were measured, but important predictors were different between the species. They concluded that a number of factors determined reptile occurrence or abundance but that there was no single predictor variable.

At a broader scale, Fastie (1995) studied primary succession following glacial retreat at Glacier Bay Alaska via the use of tree ring counts. He found multiple pathways of succession that could not be accounted for by site differences in texture and lithology of soil parent material. Initial conditions were found to be important and three distinct successional pathways were evident. Multiple successional pathways could arise because of spatial or temporal variability in site environmental characteristics. Seed sources for newly de-glaciated surfaces would be dominated by production from recent recruitment in surrounding stands of vegetation, forming a positive feedback. Fastie suggested that no single sequence of species replacements and no single mechanistic model of plant community change was mandatory. Species interactions were assumed to influence only the rate of community change, not the sequence of dominance. The important point raised is that despite the three pathways being distinguished by single species replacements and additions, the resulting communities have the potential to differ substantially in ecosystem properties, particularly in the case of nitrogen-fixing alder shrubs. This would have substantial consequences for successional pathways and ecosystem function for many centuries.

Holt *et al.* (1995) described an experiment conducted in Kansas, USA into the effects of fragmentation on vegetation succession. Principally, the experiment tested the effect of patch size on vegetation dynamics. Holt *et al.* subdivided a newly abandoned agricultural field into an array of experimental patches that were left undisturbed but were separated from each other by a continuously mowed inter-patch matrix. They found that species richness did increase with patch size, but the mean number of species per unit area did not vary among patches of different sizes. Clonal species were more prone to local extinction in smaller patches. Spatial heterogeneity in vegetation, measured as local community dissimilarity, increased over time in all patches but to a lesser extent in the largest patches. The authors concluded that:

> *"... patch size does not markedly affect the rate or pattern of early secondary succession, at the scales imposed in our experiment".*

The major disturbances affecting Australian ecosystems and successional processes can be categorised into five types: fire, grazing, logging and vegetation clearance, mining and fragmentation. Although weeds can be invasive in the absence of disturbance, they are generally a response to a disturbance regime and should not generally be seen as a disturbance in their own right. They are discussed where relevant under the other five disturbance types, below.

5.3 Fire

While fire is a major component of many Australian ecosystems, it is changes in fire regime and their effect on biodiversity that are focussed upon below.

Christensen and Kimber (1975) reviewed the short term effects (over four years) of prescribed burning on vegetation, some small mammals, macropods and birds in wet (Karri) and dry (Jarrah) sclerophyll forests in southwest Western Australia. They concluded that prescribed burning should be undertaken such that it results in a mosaic pattern in order to maximise biodiversity and reduce the risk of species loss. They suggested that factors unlikely to favour this mosaic were high intensity fires and very frequent fires. The limited data on mammals suggested that no one burning regime would encourage maximum population levels of all mammal species, but that birds appeared far less sensitive to the transitory changes brought about by fire.

Fox and McKay (1981) studied small mammal succession following fire in southeastern eucalypt forest with two types of understorey in Myall Lakes National Park in New South Wales. The forest with the heath elements contained a significantly more diverse small mammal community. They suggested that for some small mammals, understorey vegetation might be a better predictor of distribution than canopy vegetation. A replacement sequence in time was observed for species reaching their maximum abundance post fire, which ranged from one year for *Pseudomys novaehollandiae* to eight years for *Rattus fuscipes*. Maintenance of suitable habitat to preserve the range of species in the landscape would therefore require a mosaic of adequately sized patches at different seral stages to be maintained.

In the same area, Fox and Fox (1986) studied the effect of fire frequency on the structure and floristic composition of a woodland understorey. They had one study site, part of which was burnt once in twelve years (at year six), and the other part twice in twelve years, but in the same season and with the same intensity. Twelve transects were used. Two years after the second fire, the authors found that that part of the site burnt twice in twelve years had significantly more plant species, higher shrub density and greater cover than that part of the site burnt once. However, this larger number consisted mainly of vegetative regenerators and those species found only on the part of the site burnt once were all obligate seedling regenerators. They suggested that the implications were that too frequent burning (less than six years) may lead to loss of obligate seedling regenerators while areas not burnt often enough (greater than twelve years) may lose some vegetatively regenerating species and short-lived obligate seedling regenerators.

In the Sydney area, Clark (1988) carried out simulated control burns to examine the effect on populations of understorey plant species on Hawkesbury sandstone on the Woronora Plateau. A total of 37 plant species on twelve plots were assigned to spring burn and autumn burn treatments and a control and were monitored for six years until a second fire treatment, after which they were followed for one year. Most pre-fire species returned by twelve months after fire. However, eight species had numbers consistently below pre-fire levels regardless of treatment, seven showed better recovery on the autumn burn plots and eight showed better recovery on the spring burn plots. The overall pattern was that recovery was better in autumn after the first burn but it was better in spring after the second burn, in terms of both species richness and abundance.

Christensen and Abbott (1989) reviewed literature on the effects of fire on soils, nutrient cycling, micro-organisms, vascular flora, soil and litter and other invertebrates, reptiles, amphibians, birds, mammals and exotic plants in the Karri and Jarrah forests in Western Australia. They noted that there had been few studies on burning regimes (as opposed to single fire events). They found no evidence for dramatic or permanent change in soil properties and nutrient cycles following low intensity fire. However, their summary of the effects of fire on biota was more equivocal, dealing primarily with the response to a single fire event, which they regarded as only producing transient effects. They proposed some principles as a guide to devising fire regimes that maintained conservation values and were compatible with fire protection objectives. These were:

- institute a high diversity fire regime including unburnt controls, minimising fires at the intense end of the spectrum;
- monitor a) special indicator species and b) core (keystone) species (they suggested that in forests and woodlands of southern Western Australia such species would include the eucalypts Jarrah, Marri, Karri and Wandoo);
- monitor direction of change in the community;
- determine the nature of past fire regimes; and
- use relevant information from other places.

In south-eastern Australia, Catling (1991) reviewed the effects of prescribed burning on the mammals using 97 sites from four case studies (Nadgee Nature Reserve, Kosciusko National Park, Jervis Bay and Chaelundi State Forest), with particular reference to the long term relationships between two extreme fire regimes and forest structure. These regimes were: a long term regime (fire regime 1) of autumn burns at low intensity (<500 kw/m) and high frequency (<8 years); and a long term regime (fire regime 2) of spring burns at high intensity (>3500 kw/m) and low frequency (>20 years). He concluded that fire regime 2 would enhance the complexity of forest structure and that fire regime 1 would reduce it.

These findings have implications for the habitat suitability of the forests for mammal species, since species richness and abundances decrease for many small and medium sized mammal species as habitat complexity is lost (Catling and Burt 1995), while the abundance of species favoured by open environments increases. On the other hand, intense fires may reduce populations, in the short term at least, but habitat suitability for some arboreal mammal species is increased by the creation of habitat resources such as hollows.

In Victoria, Collett and Neuman (1995) studied the effects of two spring fires within three years on epigeal Coleoptera at family and species level in dry sclerophyll forest over a 6-year period. They found that the diversity and richness of most Coleopteran families had not changed following the two fires, either on their own or cumulatively. However, activity of Staphilinid beetles (Staphylinidae), the most abundant of all taxa trapped, declined significantly after the second fire relative to pre-first fire levels, which reduced the activity (i.e. abundance) of total Coleoptera and that of total predators.

Collett and Neuman suggested that as only activity was affected and not diversity and taxon richness, pre-fire levels should be regained in the absence of further fires. However, their conclusion that two short-rotation low-intensity spring fires could be applied in this forest type without causing significantly adverse impacts on litter-inhabiting Coleoptera seems premature: both control and impact sites had not been burnt for 35 years prior to the experiment and hence the impact of a third fire may well have an impact on already depressed Coleoptera populations.

Braithwaite (1996) summarised experimental data on the relationship between biodiversity and fire in the savannas of northern Australia. The effects of fire on various components of biodiversity were many and varied, for example, the author suggested that:

> *"The impact of fire intensity on the phenology of a single species appears relatively simple, but when the range of life history responses from the savanna species is considered, the collective outcome of the interaction with fire becomes complex".*

The author speculated that a traditional Aboriginal burning regime would maximise species diversity since the most common patch size will support the highest diversity of species, and:

> *"The historical disturbance regime will produce patch sizes which have been most common historically"*

Thus, the author concluded that a traditional burning regime – whatever that was – in the savannas of northern Australia would maximise biodiversity through maintaining habitat diversity, savanna patchiness, and species diversity, and by protecting endemic species.

More broadly, Gill (1996) reviewed fire effects on the Australian biota, using several floral and one faunal species as focal examples. He concluded that the relationships between fires, fuels, plants and animals have various levels of dependency, but that knowledge of the interactions of fire and most organisms was limited. Wilson (1996) reached a similar conclusion in her review of the effects of fire on Australian vertebrates.

Ants have been used as target taxa to assess the impact of fire as a land management tool on biodiversity in Australia by a number of authors (Andersen 1991b; Neumann 1992; Vanderwoude *et al*. 1997, York 1994, 1996). These studies examined forests in north-coastal New South Wales, southeast Queensland, the Northern Territory and southern Western Australia. All studies identified significant effects of fire on the ant assemblages with respect to species diversity and community structure although the response of ants to fire were variable across the coarser scales (e.g. continental, as suggested by Andersen 1997a). This led one author (Friend 1996) to suggest that there was doubt that "sound management decisions can be made from the invertebrate fire ecology data collected to date". He justified this comment by highlighting the broad taxonomic resolution that many others had previously used, the brevity of the studies and the shortcomings of experimental design in previous work. Although these comments may apply to many earlier studies examining the effects of fire on invertebrates, the studies listed above suggest that ants should be a target taxon in studies of this type. The use of ant species diversity and functional groups in particular was found to be effective in identifying taxa of importance in some studies (e.g. Vanderwoude *et al.* 1997, York 1996).

Mushinsky and Gibson (1991) reviewed the role of fire in the maintenance of terrestrial habitat structure, including work conducted in Australia. They found that despite the plethora of published papers on this issue, few definitive statements could be made regarding general patterns or trends. While most researchers recognised the mosaic pattern characteristic of fire-dependent systems as beneficial to most resident species, a 'lack of understanding prevents *a priori* predictions on the outcome of a fire'. They concluded that:

> *"To bring fire ecology into the realm of the predictive sciences, greater attention needs to be paid to the details of habitat structure. The question of how fire characteristics, fire behaviour, and fire intensity _ affect habitat structure, and in turn, its influence on faunal assemblages, is rarely completely addressed".*

5.4 Grazing

Although a widespread land use, grazing and its interaction with the maintenance or loss of diversity has only been examined in a few studies in Australia.

Wimbush and Costin (1979) reported results from a 14-year study of the effects of grazing on subalpine vegetation on Mt Kosciusko. The basis of the experiment was two pairs of initially similar plots, of which one plot in each pair was subjected to grazing by sheep, while the other was not. The two plots of each pair were located close to each other but apparently were not identical in character (introducing the possibility of confounding effects). Fire was excluded from all plots. They found that grazing had a pronounced negative effect on the production of seed heads of a number of native herbs. They also found that the number of 'intermediate and major' herb species found on one of the grazed plots fluctuated between 5 and 11, with no clear trend, while the corresponding number on the paired ungrazed plot increased from 6 to 16. The number of 'minor' herbs on the grazed plot remained fairly constant at 6 or 7 while the corresponding number on the ungrazed plot decreased from 5 to 2.

Also in the subalpine zone, Williams and Ashton (1987) tested the effects of disturbance and grazing by cattle on the dynamics of heathland and grassland communities on the Bogong high plains in Victoria. Graziers claimed that continued grazing by cattle helped maintain grasslands that otherwise were being invaded by heathland species. Williams and Ashton (1987) conducted replicated experiments using grazed and ungrazed plots, and concluded that the establishment of heath species in grasslands was primarily due to disturbances which caused bare ground. Cattle's grazing was one such disturbance; however, the continued presence of cattle inhibited the growth of palatable heath species to maturity. Thus, the authors predicted that the removal of cattle from the Bogong high plains would likely result in 'an expansion of heath in those sites where shrub seedlings have established'. Paradoxically, however:

> *"It is primarily a delayed response to disturbances that have allowed shrub seedlings to establish in the first place, and undoubtedly the frequency of such disturbances is increased vastly by cattle activities".*

The authors therefore concluded that continued cattle grazing as a means of inhibiting the expansion of heathlands could not be recommended.

In Tasmania, Gibson and Kirkpatrick (1989) studied the effect of cessation of grazing on grassland and grassy woodland at four sites on the Central Plateau. They found that vegetation response to cessation of grazing was strongly correlated with site productivity with the greatest changes in structure and composition occurring at the most productive sites. The higher altitude less productive sites took longer to recover from grazing and were impacted more in terms of bare ground and dominance of shrubs over grass than the lower more productive sites where grazing reduced competition from grasses and shrubs and increased herb species richness.

In a study of the distribution and abundance of ground-dwelling mammals in south-eastern New South Wales, Catling and Burt (1995) predicted that a significant reduction in understorey complexity would result in a decrease in diversity and abundance of small and medium sized mammals and an increase in large grazing animals. They provide an example from an area that had been grazed by cattle for about 40 years:

> *"Habitat complexity scores for sites were clumped and mostly below score 7, indicating a uniform forest with poor structure compared with those from a forest reserve where scores were spread across the range indicating a forest of diverse habitat complexity. In the grazed area few small mammals were captured and most were introduced pests (i.e. house mouse and black rat)".*

As an overseas example of areas with a much longer history of grazing land use, Dennis *et al.* (1997) studied the response of epigeal beetles to varied grazing regimes (sheep, and sheep plus cattle with different summer grazing intensities) on upland grasslands in the Scottish Borders area. Vegetation composition and structure was also measured. They found that 27 of the 32 Coleoptera species did not respond significantly to the experimental treatments. However there were correlations between the abundances of ten species and heavier grazing (particularly sheep plus cattle); between six species and the taller mean vegetation height of plots grazed at lower intensities; and between eight species and low grazing intensity or ungrazed areas in which a higher mean vegetation height was accompanied by a wider plant species diversity. They concluded that a wider diversity of Coleoptera would be maintained by creating a mosaic of structurally varied grassland patches, with each associated assemblage of beetle species accumulating a larger overall species total.

5.5 Logging and Vegetation Clearance

Although not fully similar in effect, both logging and vegetation clearance provide an insight into the effects of the removal of structural and or floristic complexity and its effects on diversity, over a range of spatial and temporal scales.

Curry *et al.* (1985) studied the change in arachnid communities in the short term resulting from forestry operations by comparing logged and unlogged upper slopes and creeklines in karri forest in southwest Western Australia. They found no prolonged reduction in species richness, but did find considerable changes to the composition and structure of the arachnid community. There were also considerable fine-scale differences in the response to management practices with creeks having a longer-term reduction in species richness than adjacent ridge sites.

Taylor and Haseler (1995) investigated the effect of different logging regimes (clearfell and a number of partial logging systems) on bird species richness and abundance. They concluded that less drastic habitat modification through partial logging was less detrimental to bird populations than clearfelling. The authors also noted that the logged areas surveyed were all surrounded by mature forest:

> *"In an extensive area of partially logged forest where mature forest is absent the impact of logging may be greater".*

Kavanagh *et al.* (1995a) studied the distribution of seven species of nocturnal forest birds and eight species of mammals as well as bats in two groups (microchiropterans and megachiropterans) in relation to the logged/unlogged mosaic in southeastern New

South Wales. They stratified the survey area by geology (parent material) and logging history and sampled 200 sites. They found that at the compartment scale, geology or its analogue was a more important factor affecting the abundance of most species of nocturnal forest birds and mammals than logging. At a broader scale, geology became less important than elevation and predominant vegetation community and some confounding effects between geology; elevation and vegetation community were evident. Little evidence was found to suggest that logging had caused any major changes to the distribution of nocturnal forest birds and mammals. However, little insight is given by the data as to the effects of several cutting cycles on this fauna.

Kavanagh *et al.* (1995b) duplicated their study from southeastern New South Wales in northeastern New South Wales and looked at eight species of nocturnal forest birds and nine species of arboreal marsupials from 291 sites. They used a larger number of environmental variables to determine patterns of species distributions and found that the dominant gradient contrasted higher-elevation forests with lower-elevation forests. A second major gradient contrasted wet forest types with a dense mesic understorey with dry forest types having an open or sparse understorey. A third major gradient represented logging intensity. The most species-rich environments were the disturbed coastal environments while greatest numbers of animals were recorded in the higher-altitude forests. Most species occurred with similar frequency in logged and unlogged forests. The interaction between disturbance and other environmental variables complicated the general patterns found, as the study reflected broader land-use patterns only.

Pausas *et al.* (1997) used a forest simulation model of eucalypt dynamics to predict habitat quality, and the effects of logging on this, for arboreal marsupials in the southeast forests of New South Wales. According to the authors, arboreal marsupials in these forests are relatively homogenous, both taxonomically and functionally, and their occurrence is strongly dependent on the availability of food and availability of nesting sites. The main effects of logging on habitat quality were considered to be the removal of den trees, and variations in the abundance of tree species with different values for arboreal marsupials. Pausas *et al.* predicted a differential reduction in habitat quality for arboreal mammals under timber harvesting regimes, depending on whether the harvesting took place in a gully or on a ridge and whether the soils had high or low nutrient levels. For example, in gullies with high nutrient soils, an intense timber harvest periodically over 1,000 years would result in a habitat quality reduction of 47 per cent; if the gullies had soils with very low nutrient levels, the decline would be 42 per cent. Ridges would suffer greater declines. The authors concluded that their model was useful for investigating alternative hypotheses and could be improved as more detailed data become available.

Hamer *et al.* (1997) compared butterfly assemblages at four sites on Sumba, Indonesia that differed in level of human disturbance and hence forest structure. They found that species diversity of butterflies was highest in unprotected secondary forest but that the species occurring at highest density in these areas had wide geographical distributions. Those species occurring at highest density in undisturbed primary forest had restricted ranges of distribution. A derived index of biogeographical distinctiveness decreased with increasing disturbance, supporting the hypothesis that the most characteristic species of undisturbed climax forest have the smallest geographical ranges of distribution. They concluded that human disturbance may result in the presence of butterfly assemblages of higher species diversity but of lower biogeographical distinctiveness and hence of lower value in terms of global biodiversity conservation.

Danielson (1997) reviewed literature on the resilience of avian communities of tropical rainforest to habitat degradation (selective logging and fragmentation). He raised the question as to whether communities in areas of unstable ecoclimatic histories may be more robust to change than those that evolved in places which were palaeoclimatically stable. Implicit in this question is the assumption that stable communities are more complex but also more fragile than unstable communities and hence more prone to human impact. Of the studies examined, he found that those from Asia and Latin America did not confidently demonstrate differences in the resilience of bird communities between stable and unstable areas. However, studies from Africa gave some stronger evidence for differences in fragility of local avifaunas. However, all of the studies suffered from a lack of suitable controls, differing census methods, inadequate description of disturbance regimes and differences in the intensity of disturbance.

Also working in a tropical rainforest, Turner *et al.* (1997) surveyed tree species with girth >30 cm in primary and 100-year-old secondary forest (formerly cleared for agriculture) in Singapore. They recorded more species from the primary forest (340 species in 16 plots) than in the secondary forest (281 species in 43 plots).

This contrasted with other studies of secondary tropical forest, where the species-richness of primary forest had been reached within 80 years. The authors offered two highly speculative explanations for this: 1) the often large-seeded primary forest trees may require larger frugivores to disperse their seed – such species are now extinct or rare in Singapore; and 2) degraded sites in Singapore have thin, highly acidic and infertile soils ‘which may result in a very slow rate of forest development at those locations’.

5.6 Mining

Fox and Fox (1984) studied small mammal recolonisation (two rodents: the introduced house mouse and the native New Holland mouse, *P. novaehollandiae*) during the first ten years following mineral sand mining at Myall Lakes National Park in New South Wales. The house mouse reached its maximum three years after mining and was associated with bare sand, soil hardness and vegetation structure. The New Holland mouse reached its maximum abundance 8–9 years after mining, after appearing at the 4–5 year mark and was associated with proportion of heath plants present, vegetation structure, amount of dead plant cover and topsoil depth. They found that this species replacement series was stretched in time such that the post-mining environment more closely approximated primary rather than secondary succession.

The Australian mining industry has used ant species diversity (richness and composition) as a major indicator of rehabilitation success for more than 20 years (Andersen 1997b). In doing so, a broad level of general principles have emerged, notably that ant diversity at mine sites being rehabilitated may reflect recolonisation by other invertebrates (Andersen 1997b) and soil microbial biomass (Andersen and Sparling 1997). More broadly, Andersen (1991b) noted evidence that the relative abundances of ant species were strongly influenced by habitat disturbance. In mesic southern Australia, for example, opportunistic ant species will increase in abundance following fire, grazing, mining and intensive recreation.

Majer (1992) presented data on the recolonisation of ant species on rehabilitated mined areas from various regions in Australia, South America and South Africa. These showed that the number of ant species recolonising such sites three years after rehabilitation increased along a climatic gradient: Fewest species were recorded in Mediterranean climates, and most species were recorded in tropical monsoonal climate. The author equated the number of colonising species with the resilience of the animal community. He also noted that this finding conflicted with previous work, and he suggested that only standardised surveys of community resilience carried out in different climatic zones would answer the question of the relative resilience of different communities.

Andersen (1995, see also Andersen 1990 and Andersen 1993) reviewed the use of ant functional groups as indicators of ecosystem restoration following mining. Despite ant species showing clear successional patterns at minesites undergoing restoration, the link between these patterns and more general changes in ecosystems had been inadequately studied. However, Andersen (1995) gave examples of positive correlations between ant species richness and total invertebrate richness for areas mined for bauxite in Western Australia. There were also positive correlations between the composition of plant species, ordinal composition of invertebrates (on the ground and on ground vegetation) and species composition of beetles and grasshoppers in disturbed and pristine sites in and around Ranger uranium mine in the Northern Territory, and between ant species richness and soil microbial biomass at disturbed sites.

A number of studies have evaluated the effectiveness of rehabilitation of bauxite mines (Majer *et al.* 1984), sand mines (Majer and de Kock, 1992) and uranium mines (Andersen 1993). They have shown that ant community structure and composition are related to the state of revegetated areas in a number of ways, following the succession of ant species through time and the build-up of species richness. These characteristics are also related to other biotic and abiotic variables.

Rehabilitation is also related to the differential succession of different functional groups, from which information about the ecology of the succession can be derived. Key findings from studies assessing the rehabilitation of minesites are that ant species diversity and richness can be related to the state of areas that have been mined (Majer *et al.* 1984) and that the succession process for ants may follow that of the plants used in the revegetation programs. The process may 'stall' on occasions, however. This may arise as a possible consequence of a rehabilitated area becoming dominated by opportunistic vegetation, such as fast growing *Acacia* species at Ranger uranium mine: Andersen 1993. The recolonisation by different functional groups of ants was also a key element of describing the state of the revegetation with respect to target control areas.

Ants have been used to monitor the effects of fluoride pollution from sand mining (Madden and Fox, 1997) and aeolian contaminants from ventilation shafts, which aerate mines (Read 1996). Read (1996) examined habitat preferences and seasonal activity cycles of ant assemblages and found that habitat type affected the efficacy of ant monitoring. In these sites, dominant ant genera were suppressed by environmental stresses caused by salt spray from an underground mine. Remediation of the salt spray resulted in recolonisation of dominant ants at the expense of opportunistic ants, as would be predicted by the functional group classification scheme (Andersen 1990). However, Read (1996) stated that these results were inconsistent owing to limitations in the sampling regime and that further work considering the ecology of key ant species was required before unequivocal assessments of the usefulness of ants as environmental monitors could be made.

Madden and Fox (1997) examined the effect of fluoride pollution on arthropod recolonisation after sand mining at Tomago in New South Wales. In this study, fluoride was found to have a number of direct effects on arthropods through its toxicity as well as substantial indirect effects through the modification of vegetation structure. With respect to the need to choose target taxa when designing experiments to assess the effect of disturbance, it is interesting to note that Madden and Fox (1997) state that:

> *"… arthropods exhibit a variety of responses to fluoride pollution, including a decrease in diversity. Domestic honeybee colonies have traditionally been used as indicators of ecosystem health in fluoride-polluted areas, despite considerable evidence that they are tolerant to its toxic events. Ants, which appear to be particularly sensitive, may be far better as a measure of the degree of fluoride stress on an ecosystem".*

In a study of other invertebrates, Holl (1995) quantified the nectar resources provided by reclaimed coal surface mines and examined the role that nectar resources might play in determining butterfly composition on a variety of sites in Virginia, USA. She found that while reclaimed areas provide much more abundant and diverse nectar resources than did the surrounding hardwood forests, most of the 52 butterfly species commonly found in the reclaimed sites were widespread, generalist species. Results suggested that the timing of the flight season in most butterfly species was constrained by factors other than nectar resources; hence it was unclear whether these sites provided a resource that might otherwise limit butterfly populations in the region.

5.7 Fragmentation

Habitat fragmentation involves the division of continuous habitat into smaller, more isolated areas (Saunders *et al.* 1991, Andren 1994). Although it occurs naturally through fire (Wright 1974) and windfall (Foster 1980), the most important cause is human land use for agriculture, forestry and the development of housing (Burgess and Sharpe 1981). Fragmentation results in a loss of original habitat area, a decrease in habitat patch size, and an increase in isolation of the remaining fragments (Andren 1994). These effects make some species (particularly those unable to persist in the new environment created by clearing) more vulnerable to local extinction (and, in the longer term, to global extinction) through stochastic events such as fire and drought.

Habitat fragmentation also leads to an increased vulnerability of fragments to invasion by non-native species and results in an increase in new habitat (e.g. monocultures of crops, urban environments) which may cause continual disturbance to habitat at the edge of the fragment (Andren 1994, Paton 1994). This leads to a decrease in core habitat along the ecotones well beyond the actual loss of area (Yahner 1988).

In North America, Askins *et al.* (1987) surveyed bird populations in 46 forest tracts in Connecticut in relation to forest area, isolation and vegetation structure. They found that patch area is a significant indicator (positive correlation) of both the number of individuals and the number of species of forest-interior birds. They also found that more individuals were detected at sites with a high density of herbs and that more individuals and species were found at sites with a greater diversity of trees. For interior-edge birds, the number of individuals and the number of species were predicted best by vegetation rather than forest area variables. Patch size was not a strong predictor for this group of species. Overall, they found that the number of species and the density of forest birds was similar in forests of different sizes, but the composition of the bird community showed consistent differences once birds are grouped into forest-interior and interior-edge species.

In an Australian example, Bennett (1987) (see also Bennett 1990a 1990b 1993) conducted a study of mammals in a fragmented environment at Naringal in SouthWest Victoria. He found that species richness of remaining mammal assemblages was determined to a significant extent by patch size, habitat richness within patches, grazing by cattle within patches and time since isolation of each patch. Large, diverse, ungrazed, recently formed patches would form one extreme whereas small, homogeneous, grazed, long-time fragmented patches would form the other. Hence any single variable on its own will not be an adequate predictor of mammalian species richness in fragments. Similarly, alteration of any one of the variables individually would be predicted to still have a significant effect on mammalian species richness.

Fragmentation experiments have also been undertaken. Robinson *et al.* (1992) described a habitat fragmentation experiment conducted in successional grassland in Kansas. They reported that the degree of habitat fragmentation had no effect on ecosystem and community measures such as soil properties, rates of plant succession and local community diversity at several trophic levels. However, there were significant differences at the level of individual species and populations. For example, of the 206 vascular plant species found, 40 occurred in only one patch type. The cumulative proportion of these unique species varied significantly with the level of fragmentation. A more pronounced effect was recorded for foliar arthropods: in general, cumulative species counts, as well as proportions unique to each patch size, were higher in the least fragmented treatment. There was also a strong effect of patch size on the population densities of vertebrate species.

The authors separated vascular plants into two broad functional groups: clonal species that propagated largely by vegetative means, and non-clonal species which reproduced by seeds. Over a period of five years, persistence of nonclonal plants did not vary systematically with patch size, whereas clonal plant populations were much less likely to persist in the smallest patch size. The authors reasoned that clonal plants were less able to disperse between fragments, thus reducing the opportunity for re-invasion. They concluded that:

> *"... our results show that different components of an ecosystem can respond in different ways to habitat fragmentation and that the effects seen among populations can be hidden at the level of aggregated community variables. _ Our experimental results highlight the need for detailed population analyses to interpret observational data from fragmented habitats".*

More broadly, Hobbs (1993) reviewed the scant literature dealing with the changes in ecosystem processes which have occurred as a result of rapid land clearance for agriculture in the wheatbelt of Western Australia, particularly changes occurring in physical and chemical fluxes across the landscape including radiation, wind, water and nutrients. He speculated that the long term viability of ecosystem processes and hence the maintenance of their biodiversity within remnants will be largely determined by the 'leakiness' of the outside agricultural system in terms of its influence on the remnants via the above-mentioned fluxes.

In one of only a few studies that consider habitat condition at the same time as fragmentation, Dunstan and Fox (1996) studied the effects of fragmentation (island size, isolation and microhabitat) and disturbance on the abundance and species richness of ground-dwelling small mammals in 24 rainforest remnants on the Robertson Plateau, New South Wales. Small mammal species richness was low, but the two native species (*Rattus fuscipes* and *Antechinus stuartii*) were abundant. Overall species richness and abundance decreased significantly with decreasing remnant size and increasing disturbance, and native species richness on its own decreased even more significantly.

Turner (1996) reviewed the evidence of species loss in fragments of tropical rainforest. He found that enough studies had been conducted to conclude that fragmentation was 'a major threat to local biodiversity', although it was not yet possible to quantify the relative importance of different mechanisms such as restriction of population size, forest edge effects or the invasion of exotic species.

Differences in the persistence of species in remnants is related to their life history strategies and the flexibility of these strategies in the face of disturbance (Abensperg-Traun *et al.* 1996), thus explaining why arthropods display an extraordinarily complex range of responses to fragmentation (Ingham and Samways 1996).

While different species of insects may respond very differently to habitat fragmentation, it is generally the case that specialised species, which are more closely linked to their host, prey, or habitat type being more susceptible to fragmentation than generalist species (Didham *et al.* 1996). In general terms, habitat fragmentation has been found to alter the guild structure of termites (de Souza and Brown 1994), proportions of insect predators and parasites to herbivores (Kruess and Tscharntke 1994) and proportions of arachnid habitat specialists to generalists (Webb and Hopkins 1984). It has also changed insect-mediated processes such as pollination, seed predation and dispersal and nutrient recycling (Janzen 1987), and rates of herbivory on native trees (Nuckols and Connor 1995).

Land clearance and the associated fragmentation of habitats is 'the single largest threat to biodiversity' in Australia (Commonwealth of Australia 1996). Habitat fragmentation leads to the disappearance of species, either by their exclusion from the remaining area or by demoting species from 'abundant' to 'rare' and from 'rare' to 'extinct' (de Souza and Brown 1994).

Biological diversity, measured by species richness as it most commonly is, is greatly determined and dominated by arthropods, particularly insects (Kruess and Tscharntke 1994). Habitat fragmentation has been found not only to affect insect abundance and diversity, but also may potentially alter interactions between insects and other organisms (Didham *et al.* 1996). More specialised insect species are, by definition, more closely linked to their host, prey, or habitat type and are thus more susceptible to fragmentation than generalist species (Didham *et al.* 1996). Area, degree of isolation, edge effects and fragment shape, and habitat connectivity are thought to be the main processes affecting biotic communities in habitat fragments (Didham *et al.* 1996).

Habitat fragments have often been regarded as 'islands' in a sea of urbanisation or agriculture (Andren 1994). Predictions taken from the study of island biogeography have been extrapolated to predict how numbers of species within habitat fragments or nature reserves will decrease with increasing isolation and decreasing fragment size (Diamond 1975, Higgs and Usher 1980, Coleman 1981). However, many studies have pointed out that the theory of island biogeography has low explanatory power when applied to habitat fragmentation. The differences in the habitat surrounding true islands and habitat islands result in important differences in rates of extinction and colonisation (Gilbert 1980, Margules *et al.* 1994, McCoy 1982, Boecklin and Gotelli 1984).

Remnant habitat areas are different from true islands in several ways. As well as the loss of original habitat area, decrease in habitat patch size, and increase in isolation of the remaining fragments, habitat fragmentation also leads to an increase in new habitat which causes changes to the old, particularly on the boundary between the two habitats (Andren 1994). A decrease in core habitat beyond the actual loss of area is thus only one result of habitat fragmentation (Yahner 1988). Habitat islands smaller than 0.5 hectares may be composed entirely of 'edge' with no 'core' area (Mader 1984), although the effects of edges are specific to each organism (Ingham and Samways 1996). The boundary or edge in a habitat fragment is windier, sunnier and drier than the interior, and has a greater variety of microhabitats (Bierregard *et al.* 1992). Due to their high levels of heterogeneity, edges contain species from both adjoining landscapes, as well as species which thrive best at the edge itself and may thus contain more species than either adjoining habitat (Ingham and Samways 1996).

Some lepidopteran larvae may grow faster on habitat edges because they are warmer, host plant quality is higher, and mortality from pathogens and parasites is lower (Cappucino and Martin 1997). Disturbance due to humans is greater at the edge of a habitat remnant so species favoured by disturbance are more abundant at edges than in the core habitat (Yahner 1988). Studies suggest that edge effects for many vertebrate species usually occur within 50m of an edge (Paton 1994), but edge effects are different for different species (Yahner 1988, Neville and Black 1997). Species that thrive on edges and disperse well at the scale of fragmentation may become excessively abundant at the expense of other species in a fragmented landscape (Cappucino and Martin 1997). The size of the edge relative to the interior may thus have a large effect on the species richness of a habitat fragment (Andren and Angelstam 1988).

The new anthropogenically created habitat is not devoid of species adapted to its conditions and many species, such as some soil and litter arthropods thrive in the artificial habitats created in gardens (Davis 1980). Other species living in the new habitat, including potential predators and competitors, are not necessarily restricted to this habitat and may invade the remnant (Andren 1994). As habitat fragment size decreases, the effects of interactions from adjacent habitats should increase (Andren and Angelstam 1988). The rate of such invasions probably depends on the difference between the new and old habitats with very different habitats having a low species overlap (Bauer 1989). Invading species may not only increase the species-richness of a habitat fragment, but will also change the species composition. Thus the original species will not necessarily be preserved and species richness on the regional level may decrease as new species out-compete or prey on the original species (Gaston 1996c).

Bauer (1989) demonstrated that the species-richness of isolated habitat areas conforms to that predicted by the theory of island biogeography, but that this relationship is often masked by the invasion of fragments by vagrant species from surrounding habitats. This leads to a substantial change in the species composition and richness of the area. Different species respond differently to a landscape's pattern and these do not necessarily coincide with human perception of the landscape (Ingham and Samways 1996). Although some taxa have general patterns of tolerance and intolerance to changing conditions, all orders have species of both habits, therefore patterns should be examined at the species level, as well as the assemblage level (Ingham and Samways 1996).

The presence of a species in a habitat remnant may be a function not only of patch size and isolation, but also of the neighbouring habitat (Andren 1994). Whilst animals living on 'true' islands are unable to inhabit the surrounding areas, some species living in habitat remnants are able to utilise resources in the intervening areas such that the remnant does not behave as an island for these species (Andren 1994). Such habitat generalists are thus able to survive in very small patches (Andren 1994). Changes in the disturbance regime or in the quality of habitat resulting from habitat fragmentation may also lead to altered abundances of organisms (Harrison 1991).

A variety of effects due to habitat fragmentation have been observed. It has altered the abundance of understorey insectivorous birds (Stouffer and Bierregaard 1995), caused a decrease in amphipod abundance whilst increasing scorpion abundance in the same sites (Margules *et al.* 1994), and decreased susceptibility of trees to attack by herbivorous insects (Nuckols and Connor 1995). The habitat destruction accompanying fragmentation may lead to an increase in the absolute abundance of previously inferior competitors as the negative effects of habitat fragmentation on this species are more than compensated for by the reduced competition from the dominant species (Moilanen and Hanski 1995). Patchiness, which is a similar but finer scale phenomenon than that of habitat fragmentation, has been found to affect aggregation of ladybird predators, resulting in population explosions of their aphid prey (Karieva 1987).

The mobility of species may also determine their ability to persist in habitat fragments. Margules (*pers. comm.* in Sarre 1997), for example, reported results from his habitat fragmentation experiment at Wog Wog in southeastern New South Wales. The only two species of beetle that had never been found in the pine forest 'sea' outside the remnant 'islands' of original forest had both declined in both range and abundance 12 years after the fragmentation event took place.

Smaller fragments have a greater proportion of edge habitat than larger fragments of the same shape. This implies that finer habitat fragments should contain a greater proportion of disturbance-related, non-native, generalised and opportunist species than larger fragments and that larger fragments should contain a higher proportion of species specialised to the original habitat. This is supported by findings that small or isolated heathlands tend to be invaded by species from surrounding areas (Webb and Hopkins 1984). The impact of habitat fragmentation is thus best measured using species characteristic of the core habitat of that fragment (MacNally and Watson 1997).

5.8 Interactions and Other Disturbances

Although disturbance effects are synergistic, few studies investigated multiple types of disturbance and their interactions. Some of these are discussed below.

In a study investigating disturbance effects on regrowth communities, Allen and Forman (1976) undertook a plant species removal experiment in three six-year-old fields in New Jersey over a single growing season. They found that community recovery correlated inversely with cover of species removed and that the most abundant and tallest species exerted the strongest influence. However, other species were actually less important than their abundance would suggest and others may be more important than their abundance suggests. A species' importance was also dependent on whether it was the removed or the remaining species. The study indicated that both community structure (vertical layering and horizontal patchiness) and species composition (reproductive patterns and interspecific interactions) were important in predicting community recovery from a stress but that changes in vegetation composition showed few consistent patterns (were relatively unpredictable) and were dependent on many interacting factors.

Friend (1979) looked at the response of small mammals to clearing and burning of eucalypt forest for pine plantations in Gippsland Victoria. Small mammals were trapped before, during and after a clearing operation for pine establishment on ridges and in adjacent gullies. There was little survival or movement from the ridge areas, but *Rattus fuscipes* and *Antechinus stuartii* began recolonising the cleared areas (windrows) from retained gully habitat.

Further work was undertaken by Friend (1982) who studied mammal populations in pine plantations and eucalypt forests in the same area as Friend (1979). Not surprisingly, he found that species richness was lower and the proportion of exotic species was higher in plantations and that most arboreal marsupials, insectivores, nectarivores and tree hollow users were uncommon in plantations and were restricted to suitable habitat in retained native forest. Mammal species richness was greatest adjacent to native forest and near edges.

Wilson *et al.* (1990) surveyed the distribution of small mammals on predominantly public land in the Otway Ranges of Victoria, particularly in relation to plant species richness and the incidence of the plant fungal disease *Phytophthora cinnamomi* and fire. They found that the most species-rich small mammal communities were recorded in the two most plant-species-rich sclerophyllous communities.

However, two plant-species-rich sclerophyllous communities contained no native animals. The authors conjectured that this was due to past disturbance: sites in one such community had been logged and another had been cleared (it had since regenerated but was isolated from other native bush by farmland). The greatest abundance of native small mammals was recorded in non-sclerophyllous communities with a high proportion of grasses and sedges in their understorey and which occurred in wet areas and had comparatively richer soils. The authors noted that a previous study of heathlands in Australia, California and South Africa had found that the abundance of small mammals was lower in the Australian communities due, perhaps, to lower soil nutrient levels that resulted in lower plant biomass. Wilson *et al.* concluded that the abundance of small mammals in their study similarly appeared to be related to the productivity of plant communities.

Using ordination analysis, Wilson *et al.* (1990) found that both a previous wildfire and *P. cinnamomi* infection were associated with low diversity of small mammal species (both types of disturbance reduce habitat complexity, at least in the short term). A wildfire had passed through the study area in 1983; few small mammals appeared to have survived the fire or the immediate post-fire period. Burnt areas were colonised first by the introduced small mammal *Mus musculus*, but later by native species as the vegetation underwent successional changes. Similarly, in a rehabilitated mining area, *M. musculus* was the only small mammal resident at some sites for up to five years after revegetation, while native mammals were trapped only rarely and were assumed to be transients. Vegetation communities on the rehabilitated mined areas had a higher proportion of graminoids and introduced species, lower species numbers and lower percentage ground cover than unmined areas. In general, the regeneration of mined areas was 'considerably retarded' compared with that following wildfire. Overall, the authors concluded that their studies confirmed:

> *"… the importance of floristically diverse vegetation communities for small mammal species richness and for particular species such as (the locally rare)* Pseudomys novaehollandiae. *… The studies show that wildfire and mining have major effects on small mammal communities and highlight the differences in regeneration and recolonisation that follow these disturbances".*

Jenkins and Kitching (1990) manipulated water-filled treeholes in a subtropical rainforest in Lamington National Park, Queensland by emptying them of their water and biota and then re-filling them with water in order to study food web reassembly after a major disturbance. They found that the original community was gradually restored as the food web reassembled and that the increasing number of trophic links (i.e. habitat complexity) in the food web provided a good overall measure of community recovery. The largest proportion of the increased links during food web reassembly could be attributed to trophic interactions between predators and their prey.

Majer (1992) discussed the resilience and inertia of Mediterranean ecosystems in the face of disturbance. He defined inertia as the ability of the ecosystem to resist external stress (perhaps comparable to Pimm's [1991] 'persistence' – see earlier in this report), and resilience as the degree, manner and pace of recovery of the ecosystem to the pre-disturbance level. Majer hypothesised that the combination of drought and high temperatures in summer, along with certain types of disturbance, presented particular problems in Mediterranean Australia. For example, if a disturbance occurred in spring, the buffering capacity of the vegetation and leaf litter would be reduced, 'at precisely the time of greatest adversity'. By contrast, a disturbance occurring in autumn 'should have a lesser impact on the biota than one in spring'. He noted that there were few data to test this hypothesis.

Busch and Smith (1995) studied the ecology of *Populus fremontii* and *Salix goodingii* in relation to invasion by the weed species *Tamarix ramosissima* and *Tessaria sericea* as a result of anthropogenic hydrological perturbations in two riparian ecosystems (the lower Colorado River floodplain and the Bill Williams River) in southwestern USA. The aim of the study was to assess the effects on community structure and function of interspecific competition between the two native species and the weed species. They measured hydrology, soil moisture, soil, plants, plant water relations and community structure. Experimental removal of *Tamarix* where *Salix* was co-dominant led to greater growth, less negative water potentials and higher leaf conductance in the remaining *Salix*. Distinct adaptations for dealing with salinity and water stress seemed to be responsible for shifts in riparian community structure, which accompany ecosystem change.

The functional consequences of pollution on microarthropod assemblages (Acari and Collembola) were evaluated by Henegan and Bolger (1996) in a Norway spruce plantation forest soil in Kilkenny, Ireland. They used potential components of polluted or 'acid' rain (nitric acid, sulphuric acid, ammonium nitrate, ammonium sulphate and ammonium chloride) which was sprayed on field plots over a four-year period. Assemblages of microarthropods from these plots were then introduced into laboratory microcosms where leaching of ammonium-N, nitrate-N, sulphate-S, chloride, calcium, magnesium, potassium and sodium components were measured over a ten week period.

They found that the biomass of microarthropod assemblages from ammonium nitrate, urea and sulphuric acid plots were greater than that from nitric acid, water, ammonium sulphate and ammonium nitrate plots. Many but not all of the differences between elemental losses were elevated or diminished losses from those soils containing animals originating in ammonium chloride or ammonium sulphate field plots. Significant differences were found for all parameters (except sodium) when losses from soils containing animals from all sprayed plots were compared with losses from soils with undisturbed assemblages. They observed that there was a role for fauna in elemental fluxing from decomposing material and that assemblages that had developed in a forest soil in response to the spraying of different simulated acid rain components had variable effects upon the leaching of nutrients and on respiration. Their experiment suggested that mineralisation of nitrogen was enhanced when microbial populations were least active, which might indicate that mineralisation rates are highest when the microarthropods are grazing most intensely, since the predominant microarthropod/microbial community interaction was via consumption of microbial biomass production.

Jackson and Fox (1996) used chronosequence analysis on 72 ant species from 44 sites at Tomago, New South Wales to examine whether ant community structure varied with the type of disturbance and time since disturbance. They collected 25 habitat variables at each site covering vegetation structure, floristics, ground cover and soil variables with the key variables being percentage canopy cover of the site, percentage of bare ground and a vegetation index. Their results suggested that fire had a minor effect on the community over time while the impact of clearing and mining was much more severe. Species composition at cleared or mined sites, after 18 years, approached but did not match controls. The ant species succession seemed to closely follow the vegetation succession; hence, they suggested that vegetation could be used as a bio-indicator for evaluating the extent of habitat damage and recovery after disturbance.

5.9 Chapter Summary

The volume of Australian literature on the role of fire in determining diversity is relatively large. Nevertheless, there is a paucity of studies that examine the effects of multiple fires occurring in the same area over time, as well as a paucity of studies that are well designed, due in part to the often opportunistic nature of fire ecology research. Some authors have noted the need for more long-term studies on the impact of fire on biodiversity and habitat structure.

Australian studies on the role of pastoral grazing on biodiversity consistently find that the presence of grazing reduces biological diversity, but there is greater ambiguity about the relationship between logging and biodiversity.

The relationship between habitat fragmentation and biodiversity has been the subject of study since MacArthur and Wilson's theory of island biogeography was first promulgated in the late 1960s. Much of the study to date has been observational: well-designed, controlled field experiments on the effects of fragmentation are relatively scarce. Nevertheless, there is consensus among scientists that habitat fragmentation is a major threat to biodiversity through such mechanisms as gross habitat loss, increased isolation of populations and thus reduced opportunities for recolonisation, and increased vulnerability to stochastic events, edge effects, and increased disturbances.

Vegetation succession following disturbance has also been the subject of numerous studies. One issue raised is the possibility of multiple pathways of succession, dependent at least partly on initial floristic composition and environmental conditions.

Other causes of disturbance, notably mining, have created opportunities for the study of restoration ecology and the development of ecosystems on previously degraded land. Such studies have indicated the importance of the nature of disturbance in determining its impact on biodiversity.

Ants in particular have been well studied in association with mining rehabilitation, and they have been proposed as bioindicators of disturbance and the diversity of recolonising biota. At fine scales, there appears to be some evidence supporting this notion; however, several authors have cautioned that the use of any particular taxon or limited group of taxa as indicators of overall diversity patterns at a broad scale may give misleading results.

6 Towards developing surrogate indicators of biodiversity

6.1 What is a Surrogate Indicator?

The Resource Assessment Commission (1993) defines a surrogate indicator as:

> *"... a quantity or combination of quantities used to obtain information about the target in lieu of measuring the target more directly".*

RAC refers to the 'target' as an entity about which information is desired, such as a particular species, a community, or a measure of biodiversity. However, in the opinion of the RAC, the use of surrogates is questionable unless the following assumptions hold:

> *"... that there is a model linking the surrogate and the target, that this link is constant or varies in a known way in space and time, and that the surrogate can be measured more readily, easily or cheaply than the target".*

Therefore, fundamental to the use of any surrogate indicator of biodiversity is the assumption that a correlation exists between the surrogate and biological diversity (Ferrier and Watson 1996). This link, or correlation, can range from a very simple qualitative model based on biological 'common sense', to a mathematical or statistical model requiring extensive data collection and analysis (RAC 1993).

The need for such a link probably explains the poor results obtained by Ferrier and Watson (1996) when using ground-dwelling invertebrates to evaluate broad surrogates such as vegetation mapping, environmental classification, environmental ordination, raw environmental distance, canonical ordination and species distribution modelling. These authors did not attempt to establish a correlation between ground dwelling invertebrates and the broad surrogates that were used (i.e. vegetation mapping, abiotic environmental classification, abiotic environmental ordination, canonical ordination, and modelling of species distributions). It is therefore not surprising that generally poor results were obtained. Had they chosen phytophagous (plant feeding) insects as taxa to evaluate broad surrogates such as vegetation mapping, then the results may have been different. (Note though that canopy tree models developed by Ferrier and Watson 1996 performed well as surrogates for both canopy and understorey flora, and vertebrates.) They concluded that modelling performs better when using species that exhibit a strong environmental relationship.

6.2 Landscapes or Species?

Whether individual species can serve as indicators of the state of biodiversity or whether greater focus should be applied to the level of ecosystems and landscapes is a subject of debate in the scientific literature, and is an important focal point for future efforts to conserve biodiversity. For example, what do remotely-sensed images of the loss of particular vegetation types indicate about the potential loss of above and below ground species in those landscapes?

Franklin (1993) argued that the need for a broad level approach became vividly apparent once we looked beyond the vertebrates and vascular plants to the far more numerous 'smaller' organisms. He contended that:

> *"... it is not just the soil that supports the vascular plants but, at least equally, the plants that function as the life support system for the soil. Maintenance of the below ground elements of diversity requires an ecosystem approach that provides for a healthy and diverse above ground energy source".*

Furthermore, the vast majority of invertebrates, which may comprise 90% of total biodiversity, are currently unknown and, in a practical sense, are unknowable. These organisms will only be conserved as ecosystems are conserved. This is not to say that there is no need for direct measurement of species, as these measurements will be critical to establishing links between surrogates and biological diversity. However, definitional problems still arise as to the boundaries of any given ecosystem.

6.3 Issues Arising from this Review

Surrogate indicators will not tell us about the loss of particular species: only a system to monitor the presence or absence of all species could do so, and this would not involve the use of surrogate indicators. What we seek here are indicators that can give us general trends in the state of the biodiversity. They should be capable of addressing the questions:

- are conditions becoming more or less suitable for the maintenance of our biodiversity?
- is diversity being lost from the environment and,
- if so, is the rate of loss changing over time?

It appears from this review that three (not mutually exclusive) avenues might be explored in the development of surrogate indicators of trends in biodiversity:

- the use of organisms or groups of organisms
- ecosystem function, and
- habitat complexity.

Organisms as indicators. The use of species, suites of species or functional groups as indicators of environmental change is a widely discussed topic (Saunders *et al.* 1998, Yen and Butcher 1997, Simberloff 1998). The emphasis on quick, reliable, goal-driven biotic indicators of everything from 'biodiversity' to various disturbances (natural and anthropogenic, biotic and abiotic) has led to the development of a broad-based literature examining the application of this approach and its effectiveness.

Indicators have been used to predict biodiversity over wider scales than that at which they have been studied and also to assess environmental change due to human impact. The approach of using invertebrates for this purpose has been promoted by some because of the diversity of invertebrates in all systems, their habitat specificity, their ecological importance and the complexity of their responses to environmental change (New 1995; Yen and Butcher 1997).

There is an abundance of literature suggesting that non-marine invertebrates can be used to assess environmental change. Yen and Butcher (1997), in a wide-ranging overview evaluating non-marine invertebrates and their conservation (for Environment Australia), identified 'the definition and application of 'indicator' taxa' as an area in need of immediate clarification for the effective conservation of invertebrates.

They also identified 'the selection and use of priority invertebrate taxa to monitor areas for nature conservation' as in urgent need of research. They suggested that no one group would serve as an effective universal priority group and that it would be more effective and practical to select a suite of priority taxa for each relevant habitat.

Despite the large literature base dealing with the use of organisms as indicators, there are clearly costs to the shortcut they offer. These include a lack of generality of any findings, and little chance of addressing landscape-scale management goals with precision and accuracy. Certainly, this review has uncovered little or no evidence that the status of certain species reflect the status of biodiversity more generally.

Simberloff (1998) argued for a more critical interpretation of biotic indicators and their use for the assessment and conservation of biodiversity. He was particularly critical of the indicator species concept as a shortcut to the monitoring and managing of biodiversity, which he defined as including species richness and composition, physical structure and processes. In addressing the concept he argued that managers use indicators for two reasons:

> … first because their presence and fluctuations are believed (or hoped) to reflect those of other species in the community, and second because they are believed to reflect chemical and/or physical changes in the environment (Landres *et al.* 1988).

He discussed only the former, dismissing the latter because:

> *"... there is no reason why a species particularly sensitive to chemical pollution, for example, need necessarily reflect the status of a large number of species".*

Of the former, he argued that the indicator species concept is problematic because there is no consensus on what an indicator is supposed to indicate and because it is difficult to know which is the best indicator species even when agreement is reached on what it should indicate. He also pointed out the logical inconsistency of many advocates of indicators and the confused goals of many of those who use them to assess anything from species richness to ecosystem “health”. In particular he argued that:

> *“...* reductio ad absurdum *of this confusion of goals is the proposition (Noss 1990) that we should monitor virtually everything as indicators – a large group of species, dominance-diversity curves, canopy height diversity, percent cover, nutrient cycling and predation rates etc. The problem with this full set of indicators leaves nothing to be indicated as opposed to measured directly. Of course the absence of resources to do all this measurement was the raison d’être for indicator species in the first place!”*

Simberloff (1998) also identified the fact that there was a dearth of studies supporting the generality of indicators beyond the specific studies in which they were used.

The review of Simberloff (1998, see also that of Murtaugh 1996) identified many problems in (and offered several solutions to) the use of indicators for the assessment of biodiversity and how it is affected by a diverse range of impacts. The concept does not appear to be supported by robust theory or a large body of empirical data. Where data exist, the conclusions that may be drawn from them remain ambiguous.

Nevertheless, the use of such species or groups of species for monitoring change in terrestrial ecosystems should not be ruled out, as long as the purpose is clear and unambiguous and an explicit link has been established between the indicator species and the impact being monitored. For example, ants have shown promise as indicators of minesite disturbance. Furthermore, organisms as indicators may well already be a useful tool in certain situations, provided those using them acknowledge the limitations of their use when designing surveys and drawing conclusions from them.

Ecosystem Function. A simple technique (Tongway and Hindley 1995) exists for ‘ground level’ monitoring of ecosystem function. It is known as Landscape Function Analysis or LFA (Tongway *et al.* 1997), and it may be feasible to extend such monitoring to the remote sensing level through the use of habitat complexity scores (Coops and Catling 1997).

If dysfunctional landscapes are shown to be accompanied by change in the set of species occurring there, then a program to monitor the integrity of ecosystem functioning may be informative about trends in biodiversity. Alternatively, if Australian ecosystems support high levels of species redundancy and remain functional despite the loss of species, such a monitoring program may not be so useful for the purpose of biodiversity indicators.

Some papers cited referred to the role of ‘redundant’ species that may provide the system with a buffering capacity in the face of environmental change. For instance, the co-occurrence of species with similar ‘function’ but differential response to driving forces such as climate, provide buffering to climate variability. These species may often be regarded as redundant. But given the relatively high level of species extinctions (either global or local) that have occurred in Australia in the recent past, it may be that the buffering capacity of Australian ecosystems is currently relatively low. Species replacement experiments are the only real way of addressing this problem.

Habitat Complexity. The close relationship between habitat complexity and the species abundance of small-to-medium ground dwelling mammals in forests, and the promise of remote sensing techniques for monitoring changes in habitat complexity, offers hope that this measure may form the basis of a surrogate indicator. An advantage of this as a surrogate indicator is that it takes into account the role played by disturbance in the abundance of species. However, a similar relationship between ground-dwelling mammals and habitat structure cannot be assumed to apply in habitats other than those in which the relationship has been demonstrated. Nor is it known if the relationship applies to other biota, or whether a given small-to-medium sized mammal assemblage is in turn a surrogate indicator of other components of the biodiversity. The relationship between habitat complexity and the diversity of plant-dwelling insects deserves further investigation.

The effects of various disturbances, and of habitat loss and fragmentation, on trends in biodiversity need careful consideration in the development of surrogate indicators. Some disturbance agents, such as fire and disease, may affect habitat complexity and would therefore be captured by the use of that measure as an indicator. Others, such as the presence or absence of feral animals, may not. In addition, the long term impact of fragmentation on biodiversity is poorly understood: it may be that species may be lost in the future as a result of fragmentation that occurred some decades in the past. Conversely, the effect of efforts to redress fragmentation by providing habitat corridors between fragments on biodiversity is unknown, and may complicate development of reliable surrogate indicators.

6.4 Potential Indicator Species

Of all potential taxonomic groups available, ants have been widely used as bioindicators of rehabilitation success in Australia, particularly in studies investigating the effects of various types of mining disturbance. They are well known taxonomically, abundant and diverse, functionally important in ecosystems and sensitive to environmental change, making them ideal candidates for use as bioindicators (Vanderwoude *et al.* 1997). Importantly, they can also be classified into functional groups (Table 1): this allows for predictions to be made about how different components of ant assemblages will respond to environmental stress and disturbance (Majer 1983, Andersen 1995), allowing the construction of testable *a priori* hypotheses.

As Andersen (1997a) pointed out, this approach is highly scale-dependent, with the notion of dominance at finer scales being based primarily on whichever species is abundant and tending to win competitive interactions. On a global scale, dominant species are defined on the basis of their status when disturbance and environmental stress are low. Despite the need for care when attempting to generalise the ecology of ant functional groups across scales, they provide an effective framework for investigating an array of questions.

As well as using ant functional groups for environmental assessment, ant species diversity (with respect to richness and composition of assemblages) is also an important characteristic to consider in studies evaluating the ecology of disturbance.

Table 1: Greenslade's functional group classification of ants (from Andersen 1990)

Group	Common taxa	Relevant features
1. Dominant Dolichoderinae	*Iridomyrmex*	Highly abundant, active and aggressive; able to monopolise resources
2. Associated subordinate Camponotinae	*Camponotus* *Polyrhachis*	Always co-occurring with *Iridomyrmex*, to which they are competitively subordinate
3. (a) Hot climate specialists	*Melophorus* *Meranoplus*	Behavioural and morphological specialisations which enable coexistence with *Iridomyrmex*
(b) Cold climate specialists	*Prolasius* *Notoncus*	Restricted to cool and wet regions where the influence of *Iridomyrmex* is reduced
4. (a) Cryptic species	Many small ponerines and myrmicines	Foraging exclusively within soil and litter; eyes minute or absent
(b) Sub-cryptic species	Many small formicines and dolichoderines	Foraging mostly within soil and litter; eyes larger
5. Opportunists	*Rhytidoponera* *Paratrechina*	Extremely specialised behaviour; poor competitors
6. Generalised myrmicines	*Monomorium* *Pheidole* *Crematogaster*	Unspecialised behaviour, but successful competitors due to rapid recruitment and effective defences
7. Large, solitary foragers	*Myrmecia* *Leptogenys*	Unlikely to interact much with other ants because of their large body size, low population densities and/or specialised diet

Andersen (1997a) reviewed the uses of ants as bioindicators, considering multiscale issues in ant community ecology. In particular he found that estimating patterns of species richness and composition using surrogates was scale dependent, noting that a majority of workers examined their systems from relatively small plots despite wishing to develop a predictive understanding of community ecology at a range of spatial scales. In so doing, Andersen (1997a) recognised the difficulty in generating broad generalisations derived from biodiversity indicators. He stated that "at a continental scale, it seems absurd even to suggest that diversity patterns in any particular taxon might be representative of all others". This statement echoes that of Lawton *et al.* (1998), who found that the uncritical use of indicators to assess biodiversity was likely to lead to misleading findings.

Despite this, the rationale for using ants as target taxa that may act as surrogates for diversity has been supported by several studies showing that, under specific local conditions and at fine scales, the richness of some ant groups may give a confident prediction of overall ant species diversity. Andersen (1997) examined ant species richness in the seasonal tropics at Kakadu National Park and found that assessment of certain "target" ant genera gave adequate assessments of overall ant species diversity, whilst assessing all ant genera was not as effective. This supported his earlier finding that overall genus richness had limited reliability as a surrogate of species richness (Andersen 1995), a contention derived from the assessment of any assemblages from throughout Australia. In both these studies it was also clear that the scale of observation (local, regional or national) was a strong determinant of the strength with which prediction could be made and that decisions about which target taxa to use would have to be made with respect to these.

Lawton *et al.* (1998) examined the effects of habitat modification in a tropical forest in Cameroon for a number of ecologically diverse animals taxa; birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites and soil nematodes. These groups were sampled in 1992–94 from forests that were considered "near primary" (lightly and selectively logged at least 70 years before they were sampled) along a disturbance gradient to "manually cleared farm fallow" (cleared of tress and other vegetation in 1990, weeded to prevent tree regeneration, in a manner similar to the fields created by local farmers). They found that species richness generally declined with increasing intensity and frequency of disturbance, although no one group acted as an effective indicator taxon for changes in species richness in the others. Furthermore, they also found that species turnover between sites along the gradient also differed between taxonomic groups, indicating that compositional responses to disturbance were also different.

They concluded that:

> *"... attempts to assess the impacts of tropical forest modification and clearance using changes in the species richness of one or a limited number of indicator taxa (including popular groups such as birds or butterflies) to predict changes in the richness of other taxa may be highly misleading".*

6.5 Chapter Summary

This review set out to find and summarise information on the linkages between habitat conditions, ecosystem processes and biodiversity in order to assist with the current search for meaningful surrogate indicators for monitoring biodiversity. In practice, the review had to attempt to synthesise over 50 years of community ecology theory in relation to this issue. Despite the large amount of literature dealing with the issue both specifically and in more tangential fashions, there is effectively scant empirical data to be able to prove more than simple linkages between specific elements. Essentially there is little known about the relationship between habitat conditions, ecosystem processes and biodiversity *per se* at all scales, and what is known at one scale cannot be reliably generalised to different spatial or temporal scales.

It is apparent that the importance of biodiversity cannot be assessed other than in relation to a specified function, and in most if not all cases, this will be some human use – even if it is human appreciation of the natural world. However, science cannot determine the existential value of biodiversity *per se* as there is ultimately no end point in ecosystem development - all ecosystems are unique products of 3.5 billion years of evolution and environmental change and functionality will change over time irrespective of human inputs. Similarly, certain species will become locally and globally extinct over time as part of the ongoing evolution of life on earth.

Therefore in relation to indicators, a cautious implementation is warranted. Given the lack of understanding of linkages between biodiversity and ecosystem function, broad level indicators such as amount of land cleared may serve a more useful purpose in the short term than measurements of genetic or species diversity. That is, an ecosystem level approach rather than a within-ecosystem approach will probably give best results overall for the measurement of the state of biodiversity until more detailed linkages are investigated, if ever.

Although an experimental approach to this issue is crucial if any useful linkages are to be evaluated for SoE reporting, any experiment must be clearly focussed and address specific aspects of ecosystem function which can be measured. The most fruitful areas of scientific investigation in relation to biodiversity may be those of an applied nature dealing with such fields as agriculture, forestry, mining and the field of restoration ecology, where ecosystems are being rehabilitated, recreated or even artificially created. In these instances, the role of disturbance and structural and functional redundancy are crucial issues that must be addressed if a long-term functioning ecosystem is to be achieved.

7 What would be an appropriate experiment?

7.1 Introduction

In light of the outcome of the review, a workshop was held in March 1998 to review the draft of this manuscript and to develop an experimental approach, if feasible, to the development of surrogate indicators for determining the state of Australian biodiversity. It was attended by 22 participants primarily from CSIRO Wildlife and Ecology, the Institute of Wildlife Research at University of Sydney, CSIRO Land and Water, ACT Office of the Commissioner for the Environment and Environment Australia. All participants were asked to review the draft report before attendance. A list of workshop participants is given in Appendix 1.

A number of issues related to the development of surrogate indicators for biodiversity were raised at the workshop. In particular, it was agreed that before a valid group of surrogate indicators could be produced, the relationship – if any – between a suite of environmental variables and biodiversity needs to be established. As pointed out in the body of this review, few such relationships have yet been established.

Workshop participants initially separated this search for indicators into two components, namely:

- do the indicators act as surrogates for biodiversity in the undisturbed state?
- do the indicators act as surrogates for changes to biodiversity in response to disturbances that change biodiversity at the genes, species or ecosystem levels?

Several approaches were considered as possible options for rigorously researching these questions. The Condition-Pressure-Response framework adopted by the State of the Environment Reporting Unit of Environment Australia explicitly requires some explanation of patterns observed so that the causal links between pressures and states can be responded to appropriately. In this sense, the most powerful investigative technique would be experiments manipulating factors such as disturbance, fire regimes or fragmentation.

The scales at which studies are made has been identified as a major factor influencing the generality of any conclusions made in ecology (MacNally and Quinn, 1998); the importance of asking the questions at appropriate temporal and spatial scales was also consistently emphasised at the workshop. The need to examine any of the disturbances of interest at several scales is paramount, owing to the absence of significant evidence allowing the translation of results across scales (Levin 1992). Given the terms of reference of this review to examine appropriate indicators of habitat conditions and ecosystem processes of biodiversity at national scales, there is clearly a need to consider long-term experiments on ecosystems of all types, a view echoed world-wide by ecologists (Carpenter *et al.* 1995). A 'natural' level of species turnover in all ecosystems was also identified as an important measure to estimate. This would again require relatively long studies owing to the inherent variability in most systems and the difficulty in assessing biodiversity for many taxa.

The intention of the research options described below is to:

- *recognise* changes in biodiversity with respect to changes in the indicator; and
- *understand* these changes in biodiversity.

With respect to the goals of the review there were several possible approaches. The fact that large scale management ‘experiments’ are occurring on a daily basis in the National Park, State Forest and mining sectors in relation to fire and other forms of disturbance was raised, as a potential source of useful information. Unfortunately, much potentially useful information from these activities has been rendered un-useable due to a lack of formal experimental design including a lack of controls and replication, changes in techniques and technologies over time and a lack of basic before and after monitoring (see RAC 1992).

Coarse-scale manipulations are the most appropriate and powerful research tool but require enormous financial, logistic and temporal commitments. Given the difficulties stated at the workshop in obtaining such commitments from funding bodies, studies of this type are described to give guidelines as to some of the benefits of this approach. A second, mensurative approach – perhaps more feasible in the current funding climate – was proposed at the workshop and is described in outline below.

7.2 Manipulative Ecosystem Experiments

Manipulative experiments are the most powerful way to assess causal relationships in ecology (Underwood 1997). Mensurative experiments are primarily used to examine changes in patterns whereas manipulation is used to examine process. The merits of the two types of experiments have been discussed at length, although Underwood (1997) also states that ‘the distinction between types of experiments is a distraction’. The key issue is not what type of experiment is performed but how the experiment is designed with respect to its purpose; a logical null hypothesis must also be tested.

Although manipulation is seen as an effective way of determining causal and general relationships in ecology, the scale over which such experiments would be undertaken to examine the key aspects of this review precluded detailed description of them. The logistic difficulties of describing such experiments are amplified by the need to perform them for each of the pressures separately.

Several large-scale manipulative experiments have been undertaken in a variety of habitats (Carpenter *et al.* 1995). Major factors that have been considered include the effects of wide-ranging predators, fire and nutrient input, and habitat fragmentation (Margules *et al.* 1994). In addition, coarse-scale pollution episodes such as oil spills and long term hydrocarbon production have given the opportunity to evaluate some of the broad implications of these perturbations on ecosystems (Peterson *et al.* 1996). Generic problems with these types of experiments in 'outdoor' laboratories include the difficulties in replicating treatments, the uncontrollable environments in which they take place, and dealing with inherent fluctuations in the systems. Furthermore, financial resources tend to constrain experimental design, leading to trade-offs in spatial extent, replication and duration (Carpenter *et al.* 1995). Compounding this problem, reviews of the outcomes of these independent experiments reveal that many of the conclusions reached are limited to local conditions, with few substantial generalities emerging (Reynolds 1994).

Ecosystem experiments have been performed in a range of habitats and consider the range of possible ecosystem responses, from biogeochemical variables and changes in community structure through to interactions between the biota and ecosystem processes. The following comments address some of the general issues central to coarse-scale manipulations.

As Carpenter *et al.* (1998) pointed out, ecosystem experiments are an effective way of making science relevant to management, particularly when the paradigm of ecosystem management (Christensen *et al.* 1996) is adopted. However, they also described how management tends to coarser spatial scales and shorter time frames than most ecological research:

> "*... the mismatch of time scales between managers' expectations and ecosystem change is among the most serious obstacles to effective watershed management*".

The same could easily be said for any proposed experiments to determine surrogate indicators of biodiversity.

In terrestrial systems it has long been recognised that catchments are the most appropriate unit in which to establish experimental replicates (e.g. Likens *et al.* 1970), particularly if coarse-scale ecosystem processes are being monitored. Many previous experiments employed paired catchments to assess responses to landscape modification and disturbance. In such experiments, both catchments are monitored in pre-treatment studies, after which one catchment is manipulated and the other serves as a reference. Although there are significant limitations on the extent to which such experimental designs can detect environmental impacts on natural populations (see Underwood 1991), previous work using these approaches does offer an insight into how they can contribute to understanding the causal links between coarse-scale disturbance and ecosystem responses.

For instance, the experiments by Likens *et al.* (1970) in the Hubbard Brook experimental forest in the USA, in which trees were removed and regrowth inhibited, showed that biogeochemical cycles, hydrological flows and erosion were altered. In demonstrating the linkage between terrestrial systems and downstream aquatic systems, this experiment was also able to provide information leading to management recommendations of tree harvesting practices to improve water quality, wildlife habitat and forest productivity (Likens *et al.* 1978).

A similar experiment examining the effects of acid rain in Norway has also yielded similarly valuable results. In this, the effects of acid deposition on soil and run-off chemistry in a forest were examined using a roof over the catchment to exclude acid rain (Wright *et al.* 1993). Interestingly, as well as showing the mechanisms and rates of change of run-off and streamwater chemistry after the input of acid pollutants, the results of the experiment suggested that the effects of acid rain were reversible. This linking between the understanding to be gained from manipulative experiments and the testing of the worth of management strategies makes them a vital part of future investigations into any environmental pressures (Carpenter *et al.* 1995).

In Australia, ecosystem experiments have examined fragmentation (Margules 1992), predator removal (Newsome *et al.* 1989), and fire (Andersen and Braithwaite 1992, Andersen *et al.* 1998). Results have been slow to emerge from the fragmentation experiment, highlighting the need for a long-term approach to experiments of this type and the inherent difficulties of coarse-scale experiments examining fragmentation (Margules 1992, and subsequent personal communication). While on the other hand, predator removal experiments conducted at Yathong Nature Reserve in semi-arid New South Wales have demonstrated over only several rabbit breeding seasons, that prey (rabbit) limiting predation is possible, only after the intervention of a widespread environmental event, such as drought. Results are also starting to emerge from one of the world's largest fire experiments at Kapalga Research Station in Kakadu National Park. In this experiment, four different types of fire representing a range of those that normally occur in the area were applied over the period 1990–94. The aim of the research was to find the optimal management regime to satisfy a range of often conflicting community concerns. The experimental focus was on six core projects. These were nutrients and atmospheric chemistry, temporary streams, vegetation, insects, small mammals, and vertebrate predators. The experimental design included replication of fire treatments at a landscape scale, making it possible to directly relate responses to the intensity and timing of fire.

7.3 Mensurative Ecosystem Experiments

Despite their enormous relevance to environmental policy and the management of landscapes, manipulative ecosystem experiments are difficult to initiate (Carpenter *et al.* 1995). The need for dedicated sites, sustained funding, and inter-disciplinary teams for each type of disturbance render them logistically difficult. Hence, there is a need for research approaches that will give adequate representation in the short term. The use of carefully designed mensurative experiments is an appropriate and worthwhile approach that will yield substantial insights into how habitat condition and ecosystem processes may affect biodiversity.

Participants at the workshop discussed the possible design of a mensurative experiment to address the question: what is the relationship between changes in landscape/ecosystem function and biodiversity in response to disturbance? The workshop proposed a survey of paired, replicated plots along a transect stratified by major environmental factors. A set of possible indicators of 'ecosystem function' would be devised. Each possible indicator would be assessed on each plot, and correlations between such indicators and the state of biodiversity sought. Given resource constraints, a pilot study could be initiated in a well-studied region where techniques for the measurement of indicators are known to work. If successful, it could be repeated in other regions. For example, a study on the correlation between Landscape Function Analysis (LFA) and biodiversity could be undertaken in disturbed sites or along a disturbance gradient in different local climatic regions. If successful, a link between LFA and/or biodiversity and remote sensing could be investigated and an attempt made to predict LFA and/or biodiversity across the region.

A wide range of issues would need to be addressed in planning such an experiment. Firstly, the hypotheses to be tested must be explicitly formulated and a list of testable indicators would need to be devised. Target taxa would also need to be identified. The perennial problem of disentangling natural variation would need solution, and an appropriate region in which to conduct the pilot study would need to be selected. On this point, several workshop participants suggested that the Australian Capital Region, which extends across 17 local government areas in southeastern NSW and the ACT, would be a suitable region for a pilot study. This region has one of the widest ranges of environmental conditions, for it's area, in Australia. It is relatively well studied and documented with vegetation mapping, fauna data sets and GIS coverage. Other issues pertinent to the design of such a study include the practicality of finding an adequate number of paired sites for which disturbance history was well-known, and the technical and theoretical feasibility of measuring relevant indicators at varying scales.

Workshop participants debated the range of disturbance intensities that should be canvassed by such a mensurative experiment. For example, would it be sufficient to look at 'cleared' versus 'uncleared', or should there be a spectrum of clearance? The consensus that emerged was that a range of disturbance intensities should be included: this would help to define the shape of the biodiversity response and permit more sophisticated predictive modelling.

7.4 Chapter Summary

Ideally, a manipulative experiment or series of experiments would provide the most powerful test of any linkages. However, cost may be prohibitive, conversely, a mensurative experiment would be easier to conduct, but less powerful in its conclusions. The way forward may be the integration of data from existing long-term manipulative experiments and on-going management experiments with new data derived from a series of mensurative experiments within appropriate IBRA regions. In the absence of proven linkages, it is premature to suggest that there are such things as 'indicators' of biodiversity, and it may be the case that certain components of biodiversity can only be assessed using direct measures.

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Appendix 2: Spreadsheet of ALL References

Procedure for Assessment

Assessments were conducted with the aid of an Excel spreadsheet to record the necessary information and "pigeon hole" each reference. As each reference was read, information was recorded into the spreadsheet.

The methodology of pigeon-holing will follow a simple format. Each reference will be categorised according to the following criteria:

- Location — A region, country, or "global".
- Main Interaction — Ecosystem Processes, Habitat Quality and/or Habitat Complexity
- Scale — Site, local or regional.
- Type — *experimental (E), modelling (M), review (R), survey (S), theoretical (T) or observational (O).*
- Parameter measured — One or more of the following parameters:

SO	soil	MA	mammals
SC	soil compaction	AN	terrestrial animals
SE	soil erosion	AA	arboreal mammals
SN	soil nutrients	AS	small ground dwelling mammals
SS	soil salinity/chemistry	AM	medium to large ground dwelling mammals
SB	soil biota	AT	bats
SD	soil disturbance	AB	birds
WA	water	AR	reptiles
WT	stream turbidity	AH	amphibians
WN	stream nutrient levels	AF	fish
WS	stream salinity	AI	terrestrial invertebrates
WD	sedimentation levels	AQ	aquatic invertebrates
WY	water yield/stream flow	DI	disease
WH	general hydrological effects	WE	weeds
WB	water biota	FE	exotic vertebrates, feral animals
PL	terrestrial plants	HB	animal habitat, habitat structure, tree hollows, etc
PT	trees	PP	primary producers
PS	shrubs	CO	consumers
PG	grasses	DE	decomposers
PH	herbs		
PM	mosses and lichens		
PE	epiphytes		
PA	aquatic flora		
PN	plant nutrients		
PS	seed stores		

National State of the Environment Reporting Products

The following products are available from the Community Information Unit 1800 803 772, Facsimile 02 6274 1970, and via the Internet addressed presented below.

Australian State of the Environment Reports

State of the Environment Advisory Council (1996) *Australia: State of the Environment 1996*, Independent report to the Commonwealth Minister for the Environment, Department of the Environment, Sport and Territories (CSIRO Publishing), Melbourne, Vic.

http://www.environment.gov.au/epcg/soe/soe96/full_report/soe_acrobat.html

Commonwealth of Australia (1996) *Australia: State of the Environment 1996 – Executive Summary*, Independent report presented to the Commonwealth Minister for the Environment by the State of the Environment Advisory Council, Department of the Environment, Sport and Territories, Canberra.

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Environment Australia (1997) *Australia: State of the Environment - Key findings from the first independent national report*. Department of the Environment, Canberra. (Available as an 8-page brochure or as a set of 8 posters.)

http://www.environment.gov.au/epcg/soe/soe_env/keyfindings.pdf

Environmental Indicator Reports

Environmental indicators have been developed for each of the seven national state of the environment reporting themes: Human Settlements, Biodiversity, The Atmosphere, The Land, Inland Waters, Estuaries and the Sea, and Natural and Cultural Heritage. A series of indicator reports, one for each theme, has been published and are available at:
http://www.environment.gov.au/epcg/soe/soe_env/env_indicators/indicators.html

Technical Papers For an introduction and access to the following papers, see
http://www.environment.gov.au/epcg/soe/soe_env/tech_papers/tech_papers.html

Australian State of the Environment Technical Papers Series Number 1

- Air Quality and Human Health (by H. Peach)
- Case Study of the Cultural Landscapes of the Central Victorian Goldfields (by J. Lennon)
- Cities in Transition: Changing Economic and Technological Processes and Australia's Settlement System (by P. Newton, J. Botchie, and P. Gipps)
- Culture and Heritage: Historic Environment (by D. Marshall and M. Pearson)
- Culture and Heritage: Indigenous Languages (by J. Henderson and D. Nash)
- Culture and Heritage: Oral History (by L. McCarthy, P. Ashton, and H. Graham)
- Culture and Heritage: Shipwrecks and Associated Objects (by S. Kenderdine)
- Distribution of Petroleum Resources in Australia (by S. Radke, V. Passlow, R. DeNardi, and S. le Poidivin)
- Drinking Water Quality (W. Maher, I. Lawrence and A. Wade)

- The Environment and Food Quality (by P. Rowland, G. Evans, and J. Walcott)

- Evaluation of the Feasibility of Remote Sensing for Monitoring National State of the Environment Indicators (by J. Wallace and N. Campbell)

- From Plesiosaurs to People: 100 Million Years of Environmental History (by M. Archer, I. Burnley, J. Dodson, R. Harding, L. Head and P. Murphy)

- Genetic Indicators for State of the Environment Reporting (by A. Brown, A. Young, J. Burdon, L. Christidis, G. Clarke, D. Coates and W. Sherwin)

- Impacts of Anthropogenic Activities, Water Use and Consumption on Water Resources and Flooding (by P. Crabb)

- Indoor Air Quality (by S. Brown)

- Material Culture and the Cultural Environment: Objects and Places (by M. Anderson)

- Nutrients in Marine and Estuarine Environments (by J. Brodie, A. Kennedy and P. Cosser)

- Potential Sources of Sediments and Nutrients: Sheet and Rill Erosion and Phosphorus Sources (by C. Rosewell)

- The Register of the National Estate: Who, What, Where? (by R. Purdie)

- Review of Impacts of Displaced/Introduced Fauna associated with Inland Waters (by A. Arthington and F. McKenzie)

- Seagrasses of Australia (by H. Kirkman)

- State of Habitat Availability and Quality in Inland Waters (by J. Jackson)

- Subtidal Macroalgal Assemblages in Temperate Australian Coastal Waters (by J. Craig Sanderson)

- Water Quality for Maintenance of Aquatic Ecosystems: Appropriate Indicators and Analysis (by P. Liston and W. Maher)

Australian State of the Environment Technical Papers Series Number 2

- Climate Extremes Indicators for State of the Environment Monitoring (by N. Nicholls, B. Trewin, and M. Haylock)

- The interaction between habitat conditions, ecosystem processes and terrestrial biodiversity - a review (by M. Doherty, A. Kearns, G. Barnett, A. Sarre, D. Hochuli, H. Gibb and C. Dickman)