THE ECOLOGY OF FIRE –
DEVELOPMENTS SINCE 1995 AND OUTSTANDING QUESTIONS

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A great deal is already known about fire ecology in Australia, because careful observation of fire effects have been informing fire management for many thousands of years and scientific study of fire ecology has been going on for over a century, especially in the fields of forestry, evolutionary ecology, and land management. In this paper, I review some of the key questions of fire ecology identified in *The Ecology of Fire* (1995) for which I perceive there is a need for an expanded research effort and for better communication to politicians, policy makers, land managers, and the public at large. These include (i) better knowledge of fire history in particular areas, (ii) a more sophisticated understanding of what is meant by 'fire mosaic' and how different spatial patterns of fire might affect ecological processes, (iii) developing tools for predicting ecological responses to particular fire regimes, and (iv) the more comprehensive use of experimental and adaptive management at a landscape scale, given that environmental conditions will always be changing and ecological knowledge will never be complete.

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Bushfire is on the agenda more than ever… internationally. The attention of the public and politicians has been captured by extensive media coverage on big fires in the last 5 years: Portugal, France, California, Colorado, South Africa, Indonesia, the Amazon – and 2001-02 and 2002-03 in south-eastern Australia. The various enquiries that have followed these fire events, at least in Australia (e.g. the NSW Joint Select Committee on Bushfires 2002, the Victorian Government's Inquiry into the 2002-2003 Victorian Bushfires (Esplin *et al.*, 2003), the House of Representatives Select Committee Inquiry into the Recent Australian Bushfires (Nairn, 2003), and the Council of Australian Governments National Inquiry into Bushfire Mitigation and Management (Ellis *et al.*, 2004), have revealed many misconceptions about fire characteristics and about the ecological impacts of bushfires. For example, the Hansard record of submissions to the House of Representatives Select Committee Inquiry includes the following:

> *Wouldn't that mosaic type burning allow animals to move into another area and not be burned out, whereas a feral fire would burn out the whole area and, as we saw in many parts of Australia last summer, there would be gullies full of dead native animals? ... I call them 'feral' because of their impact – the intense feral fires that burn asphalt.*

Ms S. Panopoulos, House of Representatives Select Committee on the Recent Australian Bushfires. Hansard 8th July 2003, p. 40.

> *…a lightning strike in there would destroy an enormous amount of biodiversity, which has now happened. It has destroyed the biodiversity to the point, as I said earlier, where it has vapourised any known seed stock that may have been below the ground, because it sterilised the earth to 40 feet below the surface in some areas.*

Mr A. Schultz, House of Representatives Select Committee on the Recent Australian Bushfires. Hansard 8th July 2003, p. 41-42.

It would be well worth assessing the issues raised in these public airings of people's perceptions, because the nature of the misunderstandings may point to ways of better educating the Australian community about ecological effects of fire. The various inquiries have also highlighted the demands that the development of policy in relation to fire management and mitigation will increasingly make on ecology, and have revealed significant gaps in our knowledge. For the purposes of this paper, I focus especially on the challenge of achieving life and property protection without compromising biodiversity conservation. These dual responsibilities of many land managers are often in conflict and in some situations there may not be satisfactory compromises – the situation highlighted in a My Fair Lady song: "…make a plan and you will find, that she has something else in mind, and so rather than do either you do something else that neither likes at all!"

We already know a great deal about fire ecology, because careful observation and experimentation have been informing indigenous management of fire, to achieve specific management objectives, for many thousands of years (e.g. Hill, 2003; Liddle, 2003). Scientific study of fire ecology in Australia has been going on for many years too, especially in the fields of forestry, evolutionary ecology, and land management for conservation. For this paper, I was asked to review developments in fire ecology since *The Ecology of Fire* (Whelan, 1995), a task that is too large for this article. Much of the recent published work is summarised in a number of excellent recent monographs and the references therein (Table 1), especially *Flammable Australia* (Bradstock *et al.,* 2002), which reviews the state of knowledge on fire and biodiversity for a range of different ecosystems. I focus here on some key areas in Australian fire ecology in which I perceive a need for a renewed or broadened research effort, particularly in relation to land management

In writing *The Ecology of Fire,* I identified a set of questions, in each of these main topic areas, which I saw to be particularly important yet had been ignored or poorly studied. These are summarised in Table 2. The studies presented at the Bushfire 2006 conference, some of which are presented in this volume, present an interesting test of the development of fire ecology in recent years, especially in relation to their coverage of ecological processes, taxa and approaches used. In the following sections, I have selected some important areas in which land management for ecologically sustainable bushfire mitigation and management make demands on ecological knowledge, and I explore the limits to our current ability to satisfy these demands.

FIRE HISTORIES

The ecological and evolutionary forces moulding the characteristics and distributions of species in fire-prone landscapes could be more thoroughly explored if we had information about fire histories at a range of scales. I came to the conclusion in 1995 that better fire histories are needed, with more techniques in more communities (Table 2). This is still the case, though there have been significant developments. The

TABLE 1. Recent monographs addressing current knowledge in fire ecology

Abbott, I. & Burrows, N. (eds) (2003) "Fire in the Ecosystems of South-west Western Australia: Impacts and Management", Backhuys, Leiden.
Andersen, A.N., Cook, G.D. & Williams, R.J. (eds) (2003) "Fire in Tropical Savannas: The Kapalga Experiment. Springer, N.Y.
Bradstock, R.A., Williams, J. & Gill, A.M. (eds) (2002) "Flammable Australia: The Fire Regimes and Biodiversity of a Continent", Cambridge University Press, Cambridge.
Bowman, D.M.J.S. (2000) "Australian Rainforests: Islands of Green in a Land of Fire", Cambridge University Press, Cambridge
Cary, G., Lindenmayer, D. & Dovers, S. (eds) (2003) "Australia Burning: Fire Ecology, Policy and Management issues", CSIRO Publishing, Melbourne.
Esplin, B., Gill, A.M. & Enright, N. (2003) "Report of the Inquiry into the 2002–2003 Victorian Bushfires", State Government of Victoria, Melbourne.
Ellis, S., Kanowski, P. & Whelan, R.J. (2004) "Council of Australian Governments – National Inquiry into Bushfire Mitigation and Management", Australian Government, Canberra.
Mackey, B., Lindenmayer, D., Gill, A.M., McCarthy, M. & Lindesay, J. (2002) "Wildlife, Fire and Future Climate", CSIRO Publishing, Melbourne.
NSW Nature Conservation Council Conference Proceedings 1998, 2000, 2002, 2004 (http://www.nccnsw.org.au)

Table 2. 'Outstanding questions' identified in Whelan (1995)

Chapter	Issues and Questions
Fire the Phenomenon	Better fire histories needed, with more techniques in more communities. How much do extremes in inter-fire intervals vary from the average fire period? What are the effects of topography and local climate on fire patchiness? To what extent are unburned patches consistent in successive fires? Simple, repeatable estimation of fire characteristics, of ecological relevance, are needed. We need more information on post-fire physical conditions.
Survival of Individual Organisms	We are lacking knowledge of the effects of season and frequency of fires on mortality of resprouting woody plants. More research is needed on the dynamics of soil- and canopy-stored seed banks. What conditions of fire and environment favour the evolution of bradyspory (serotiny)? Why is there growth-stimulation in woody plants after some fires but not others? What are seed dispersal distances in relation to spatial patterns of fires? How does life-history influence survival of fire by animals? How does this interact with the season of burning and fire characteristics? What are the responses to fire in historically fire-free environments?
Approaches to Fire Studies	"No one would now dream of testing the response to a treatment by comparing two plots, one treated and the other untreated" (Fisher and Wishart, 1930 – in Underwood, 1986). The design of a study must be related to the question – which defines the inference(s) that will be made from the results.
Plant Populations	How does fire patchiness affect the proportion of plants that survive? How does patchiness or extent influence post-fire herbivore-plant interactions? How does pre-fire seed dispersal affect survival of the seed bank? How does post-fire seed dispersal determine seed survival to germination? Do causes of seedling mortality vary among seasons? How do plant populations respond to a sequence of fires? Do the chance elements of post-fire climate have an over-riding effect on plant population dynamics?
Animal Populations	How do different sorts of fires affect mortality, emigration and survival? What is the importance of recolonisation *vs.* survival within a burned area? Are animals found in refuges after fire those that happened to be there prior to the fire or did they actively seek out refuges? What is the relative importance of food, cover and predation in post-fire population dynamics? What explains highly variable results of post-fire populations of soil and litter invertebrates?
Communities	We badly need experimental studies of changes in community parameters with replication of fires. We particularly need experiments manipulating fire frequency and season over long time spans. More than a single trophic level needs to be included in experimental studies. More focus on the role of below-ground interactions (e.g. mycorrhizae). A critical review of plant succession theory as it relates to fire ecology in different ecosystems is overdue. How important are specific conditions in community changes after fire (e.g. post-fire climate, pre-fire community composition)?
Management	"It is obvious that there is unlikely to be sufficient ecological information to be certain of the ecological effects of *any* prescribed fire regime. Hence, management will have to be experimental." "It is unlikely that all objectives for land in multiple use will be able to be achieved under one fire regime"

summary by Gill (2002) of the range of sources of evidence for past fire regimes in SW Australian forests is applicable to the inference of fire history in general. The techniques he reviewed include:

- interpretation of burning practices of indigenous people;
- monitoring and historic records;
- 'annual' rings and fire scars;
- banding in leaf-bases of *Xanthorrhoea*;
- demographic structure of plant populations;
- inference or modelling based on plant life histories;
- palynological and charcoal data.

Some of these techniques are contentious (see Enright *et al.*, 2005) and some are applicable in only a limited number of situations. Some provide point-based and others area-based estimates of between-fire intervals; a distinction that is very important.

While the research challenges of inferring past fire regimes are important and fascinating, high-quality monitoring is needed today to inform the decision-makers of the future. Satellite-based mapping of fire–affected areas exists at different scales for various parts of Australia and is widely available, from a range of sources, via the internet. The COAG Bushfire Inquiry (Ellis *et al.*, 2004) considered that this is such an important development that it recommended: *That the Australian Government and the state and territory governments jointly provide additional resources and work in partnership to establish and refine a national program of fire regime mapping.* In this conference, the paper by Barrett (2006) on the use of satellite imagery to model bushfire severity in the 2003 NSW/ACT fires shows that we have come a long way since 1995, and approaches like this will allow future assessment of how factors such as tree mortality, recruitment, erosion, and community composition vary in relation to fire intensity after a particular fire event. A particular challenge for satellite mapping is improving the detection of fires under cloudy conditions and of fire severity in areas with dense forest canopies. Barrett (2006) also reminds us of an important feature of bushfires in heterogeneous landscapes – namely, that they are not uniform within the fire boundaries.

What has changed since 1995? Although we do not have precise fire histories for ecosystems in most parts of the continent, and some results are still contentious, it is now clear and generally accepted that pre-Aboriginal and pre-European fire regimes varied from one place to another, at various scales, strongly influenced by climate and ignition interacting with landscape and vegetation (see Kershaw *et al.*, 2002). We recognise that these differences in fire history among regions will have shaped the evolution of organisms. It is also clear that European settlement has resulted in a marked change in fire regime in many areas, although once again there are few empirical data that would allow precise quantification of the change. Nevertheless, as ecologists we recognise that the changes in fire regime that have accompanied European settlement, population growth, forestry and urban expansion are certain to have different effects on organisms, depending on their evolutionary histories. Additional effects will certainly accompany the future changes in fire regime caused by climate change, ever increasing landscape fragmentation, and alteration to plant communities by weed invasion. We have not yet communicated this level of understanding to the general public.

MOSAICS OF FIRE AGES VS FIRE REGIMES

Scientific studies in many regions suggest that the continuous application of a single fire regime over a landscape may be detrimental to biodiversity (see, for example, a range of studies presented in Abbott & Burrows, 2003 and Andersen *et al.*, 2003). The corollary, that biodiversity would best be protected with a fire "mosaic" in the landscape, has been seized on as a solution to the trade-off between biodiversity conservation and protection of lives and property, and has been presented as such to recent bushfire inquiries, as a fuel-reduction prescription. It is important to define the term "mosaic" here, because it is being used undefined, both in the scientific literature and in policy statements, in two different ways. One is to describe a landscape that has patches of vegetation of different ages after fire, even though each patch might be being burnt with the same return time. This is not a mosaic of fire regimes; it is a mosaic of fire ages. Such a prescription may protect adjacent properties if the return-time were short enough, but it would not sustain a species of animal, for example, that is fire-sensitive and dependent on dense cover in the ground and mid-storey layers. On the other hand, a landscape with a mosaic of fire regimes would have some patches that are rarely burned, some more frequently, some in each season, some small, some large, some high intensity, and some cooler.

Creating a mosaic of fire regimes across a landscape, with fire intervals, seasons and intensities in the mosaic that are appropriate for particular ecosystems, appears to be a reasonable goal for ecological burning in a range of ecosystems (e.g. spinifex grasslands in arid Australia; Letnick & Dickman, 2005). In others, such as the seasonal tropical savannas of northern Australia, the majority of species appear resilient to a range of fire regimes (Parr & Andersen, 2006). However, the questions of what is achievable across a particular landscape and what are the appropriate scale of patches and mix of regimes are difficult to answer, as highlighted by Wardell-Johnson *et al.* (2006). They described the intrinsic patchiness of fires that burned in particular landscapes, under particular climatic conditions, with a view to establishing operational guidelines for achieving a defined scale of mosaic.

What scale and pattern should be prescribed? Burrows & Abbott (2003) argued, as one of their "scientific principles to guide fire management" for conservation, that the *scale, or grain size, of the mosaic should (a) enable natal dispersal; (b) optimise boundary habitat (interface between two or more seral states); and (c) optimise connectivity (ability of fauna to cross between seral states)*. Many of the ecological processes I identified in 1995 as needing further study are relevant to the question of how the biota might respond to mosaics of fire ages or to mosaics of fire regimes (Table 2), including seed dispersal distances, patchiness and plant mortality, patchiness and plant-herbivore interactions, refugia and recolonisation of animals. Each species of organism may be unique in its ability to find, survive in and recolonise from refuges, and we cannot study each in turn. We may therefore have to predict responses to various mosaics from a limited set of life-history studies and then test these predictions with landscape-level experiments (see below).

ECOLOGICAL RESPONSES TO FIRE REGIMES

Inappropriate fire regimes have been recognised as potentially threatening to the conservation of biodiversity. Popular perceptions of what is "inappropriate" understandably focus on high-intensity fire, as in the comments by politicians quoted above. High-intensity fire certainly kills plants and animals and changes the 'look' of a landscape for years or decades, even centuries, in some ecological communities. In 1995, I argued that knowledge of the effects of high intensity fire on animal behaviour, mortality and source of re-establishment of populations was very scanty, and a recent review of fires in heathlands (Keith *et al.,* 2002) suggests that this is still the case, although the recent fires in 2001-02 and 2002-03 in south-eastern Australia are providing an opportunity for examining post-fire populations of plants and animals in sites of high fire intensity.

Frequency is another important element of fire regime in assessing inappropriate fire regimes. How frequent is too frequent? This is a difficult question to answer as a generalisation, because there is substantial variation from one region to another. In making predictions about the effects of fire regimes on the biota, Whelan *et al.* (2002) argued that the lack of empirical data made it necessary to infer responses from knowledge of life histories of the organism, other ecological processes, and characteristics of the fires, the landscape and the climate (Fig. 1). Using this approach, it is possible to use information on the time to first reproduction for obligate seeder shrubs to identify an inappropriate fire regime. The time to first reproduction for shrub species in south-western Australian Jarrah forests (Gill, 2002) appears to be as short as 2 years, but from about 1 to >9 years in Hawkesbury Sandstone woodlands (Keith, 1996). If these patterns are general within each region, a fire frequency of every four years might not cause local extinctions in jarrah forest, whereas fire intervals of less than 10 years would be expected to reduce biodiversity in Hawkesbury sandstone woodlands.

The box represents the life cycle of the organism, and the arrows represent attributes of the environment. (1) represents the processes determining survival, (2) represents the processes determining where colonists come from and when, (3) represents processes determining continued survival within the burned area, and (4) represents the processes determining rates of growth of individuals and the potential for

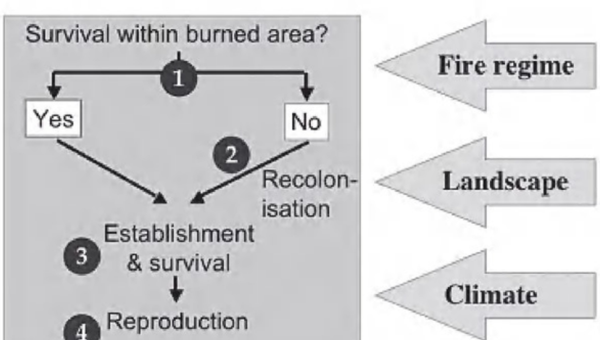

FIG. 1. Diagram of processes contributing to population change after fire (Whelan *et al.,* 2002).

reproduction and population increase.

A significant advance in the last decade has come in the area of defining the limits of tolerance of many plant species to extremes of fire regime. Because the empirical data are limited, these guidelines for ecological burning (e.g. Kenny *et al.,* 2003) are typically based on prediction from some of the key life-history characteristics, such as fire-sensitivity vs ability to sprout after fire, presence of a dormant vs transient seed bank, time to first reproduction. A similar approach should be possible with animals, and there have been some developments in this direction. For example, Friend & Wayne (2003) described the development of a framework for predicting fire responses of fauna based primarily on shelter, dietary and breeding requirements. Tasker *et al.* (2006) reviewed the published Australian literature on fire and fauna since 1995 and classified the studies according to the robustness of their design in terms of being able to infer cause-and-effect. This project will lead to the development of guidelines for ecological burning for fauna in NSW.

Approaches such as these are badly needed by land managers who have the dual responsibilities of protecting the neighbours outside the boundaries and protecting the biodiversity within. They are, however, sets of predictions – not empirical findings. As generalisations from those life-history characteristics that are considered to be "vital attributes" in the context of fire, they may not apply in all regions nor for all fires. It is critically important that the fragile ecological basis for guidelines such as these be acknowledged and that a process be developed for refining the knowledge for each particular location and learning whether the processes operating at one location for a functional group or individual species differ from those at another location. I consider that the next advance needed in fire ecology is the widespread development of an experimental approach to management, which is explored below.

EXPERIMENTS AND ADAPTIVE MANAGEMENT

In *The Ecology of Fire*, I included a chapter on approaches to fire studies, because I was strongly influenced by arguments of experimental ecologists, such as Tony Underwood (see Underwood, 1997). In the early 1980s, he asked me why fire ecologists concerned with the effects of different fire regimes on plant populations and communities had not manipulated fire regimes in replicated experiments. Many of the approaches used to infer fire effects are indeed flawed – and as scientists we should have known this for a long time: "No one would now dream of testing the response to a treatment by comparing two plots, one treated and the other untreated" (Fisher & Wishart, 1930 – cited in Underwood, 1986).

It is a sobering experience to review the papers on fire responses that have been published in the last 10 years and see how many infer a response to some aspect of fire based on a difference between two sites that experienced different fires. The important point here is not that such studies are worthless, because all ecological studies relating to fire contain important, hard-won observations. The issue is what inference is drawn from the observations. A finding of a statistically significant difference in mean seedling density in two sites, one burned in spring one year and the other burned the following autumn, can tell us only that the sites differ, no matter how much replication of quadrats we add, how well stratified we make them across each site, and how often we sample and for how long.

Parr & Chown (2003) presented an insightful summary of the components of a well designed fire ecology experiment – including appropriate scale, spatial replication, temporal replication, duration, and measurement of fire parameters. In reviewing research into fire and fauna in South Africa, they were unable to draw conclusions about the general effects of fire on the faunas of savanna, grassland or fynbos, because of the dearth of well-designed, well-replicated, comprehensive studies that test hypotheses about the ecological effects of fire. This is difficult for ecologists to accept, when so much effort is required even to gain this limited information. It is also difficult for managers, who are seeking certainty in conclusions about the effects of particular fire regimes in order to guide their fire management plans.

The Kapalga experiment in the Northern Territory was a landscape-scale fire experiment designed to test the effects of season of burning in tropical savannas on a range of elements of biodiversity (Andersen *et al.,* 2003; 2005). Experimental units were catchments 15-20 km^2, and fire treatments (early dry season, late dry season and unburnt) were replicated. The study was expensive to set up and maintain and ran for five years, which was sufficient in the tropical savanna habitat to have repeated fires in the treatment sites. A study of this scale in temperate Australia, designed to test the effects of season and/or frequency of fires would need to continue for considerably longer and would probably be unsupportable in terms of continued resource demands.

There are good reasons for the dearth of well-designed, well-replicated, comprehensive studies at a large scale: they are expensive and difficult to conduct. There are trade-offs between the scale of the study and the amount of spatial replication. For example, a study completed several years ago (see Whelan & York, 1998 for the 1st instalment) was designed to test the effect of season of burning on post-fire recruitment of two bradysporous, obligate-seeder shrubs. We chose three replicate sites in which both species occurred, and in each site we set up four, 1-2 ha plots. We randomly assigned fires in each of two springs and two autumns to the four plots, and conducted (and contained!) the fires, with considerable input of resources by the Sydney Catchment Authority. Within each plot, we set up replicated locations into which we put 50 seeds, and applied two watering treatments – to test whether watering would offset any differences between seasons in recruitment. The reviewers of the manuscript argued that a major flaw in the study was the fact that the burned treatments were only 1-2 ha, and this scale issue was likely to be significant because of herbivory: herbivores were likely to concentrate in small burned plots thus elevating grazing pressure above what would be expected in a 'real' fire. This may be true, but larger experimental plots would have been out of the question unless we had been prepared to sacrifice some of the replication. Instead we included a grazing-exclusion treatment within the plots.

Good quality monitoring and comprehensive record-keeping in the past have allowed some researchers to design 'retrospective experiments', comparing aspects of biodiversity in replicated sites with different fire histories. Wittkuhn *et al.* (2008) shows how good CALM fire records in the Walpole region of WA, from 1972 to 2002 are being used to design studies that will test hypotheses about the impact of various between-fire intervals on biodiversity. Reasonable fire records over a >25 year time span enabled Cary & Morrison (1995) to use this approach to examine the impact of short between-fire intervals on the balance between obligate seeder and sprouter species in Sydney sandstone plant communities. Similarly, Burrows & Wardell-Johnson (2003) and Watson & Wardell-Johnson (2004) have used long-term fire records for sites with different fire histories (in the Jarrah forest region of WA and in south-east Queensland, respectively) to identify the plant species for which abundance was associated with frequently burned sites and those that were more abundant in sites burned less often. The Jarrah forest study was based on a long-term set of experimental burns in the "Lindesay Forest Block", in which season and frequency were manipulated. Measurement of fire responses (e.g. seedling density, survival) after a number of unrelated fires and at different times post-fire could be effective in testing the consistency of fire responses without needing complex, large-scale experimental treatments.

There appears to be quite a collection of long-term, manipulative fire experiments in Australia, many with relatively small plots, but nevertheless plots are replicated and fire regimes have been maintained. Given the resources needed to achieve this, it would be sensible to make more use of these experiments. What is needed is an accessible record of them across Australia, perhaps based on the information once collected by the Ecological Society of Australia to catalogue long-term ecological research sites (LTERs). The COAG Bushfire Inquiry (Ellis *et al.,* 2004) argued for the establishment of a national network of long-term ecological research sites to provide a basis for long-term monitoring of the impacts of fire regimes and fire events.

Although it may be unrealistic to expect landscape-level experiments to be set up in all major fire-prone ecosystems of Australia, land managers are conducting fires at a variety of scales, almost every year. How many of these are designed in collaboration with research staff, so that they can answer the very questions that land managers are asking of ecologists? An adaptive management approach to finding what fire regimes are appropriate for biodiversity conservation should have the following steps (Fig. 2): (i) make explicit the biodiversity objectives, (ii) recognise the lack of knowledge and clarify the questions that need to be answered, (iii) design burning prescriptions that can answer these questions, (iv) devise and fund monitoring and other data-collection activities, (v) review and communicate results, and (vi) use the new knowledge to modify the management prescription.

Adaptive management with these elements often meets with resistance from managers, because of the perceived delays, constraints imposed by needing to apply agreed treatments consistently, and costs

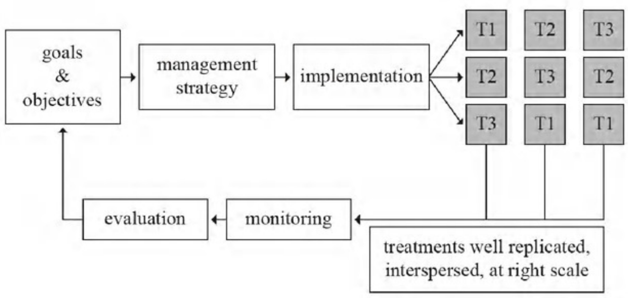

FIG. 2. Schematic diagram illustrating the steps involved in an adaptive management program (Whelan, 2003).

associated with monitoring. However, this seemed to me, in 1995, to be the only way in which fire managers will be able to know whether the burning prescriptions they are setting, based on ecological burning guides (themselves based on limited evidence), are actually maintaining biodiversity. There has been progress in the last decade, with a number of discussions of experimental approaches to management at conferences that include managers and scientists (e.g. the NSW Nature Conservation Council series – Gill, 2003), and a finding in the Report of the COAG Inquiry (Ellis *et al.,* 2004) supporting adaptive management as a way forward. The most recent example is the paper by Burrows *et al.* (2008), illustrating how such a program is being set up to determine the effects of fire management treatments on mainland Quokka populations. There is a good incentive for research ecologists to become involved in adaptive management in relation to fire – it might be the only way to get treatment plots at a sufficiently large-scale to make a reviewer happy!

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