Patch Mosaic Burning for Biodiversity Conservation: a Critique of the Pyrodiversity Paradigm

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Abstract: *Fire management is increasingly focusing on introducing heterogeneity in burning patterns under the assumption that "pyrodiversity begets biodiversity." This concept has been formalized as patch mosaic burning (PMB), in which fire is manipulated to create a mosaic of patches representative of a range of fire histories to generate heterogeneity across space and time. Although PMB is an intuitively appealing concept, it has received little critical analysis. Thus we examined ecosystems where PMB has received the most attention and has been the most extensively implemented: tropical and subtropical savannas of Australia and Africa. We identified serious shortcomings of PMB: the ecological significance of different burning patterns remains unknown and details of desired fire mosaics remain unspecified. This has led to fire-management plans based on pyrodiversity rhetoric that lacks substance in terms of operational guidelines and capacity for meaningful evaluation. We also suggest that not all fire patterns are ecologically meaningful: this seems particularly true for the highly fire-prone savannas of Australia and South Africa. We argue that biodiversity-needs-pyrodiversity advocacy needs to be replaced with a more critical consideration of the levels of pyrodiversity needed for biodiversity and greater attention to operational guidelines for its implementation.*

Keywords: adaptive management, conservation management, fire, monitoring

Quema de Mosaico de Parches para la Conservación de Biodiversidad: una Crítica del Paradigma de la Pirodiversidad

Resumen: *La gestión del fuego se enfoca cada vez más en la introducción de heterogeneidad en los patrones de quema bajo la suposición que la "pirodiversidad genera biodiversidad". Este concepto ha sido formalizado como quema de mosaico de parches (QMP), en la que se manipula el fuego para crear un mosaico de parches representativo de una variedad de historias de quema para generar heterogeneidad en el espacio y tiempo. Aunque la QMP es un concepto intuitivamente atractivo, ha recibido poco análisis crítico. Por lo tanto, examinamos ecosistemas en los que la QMP ha recibido la mayor atención y donde han sido implementadas más extensivamente: sabanas tropicales y subtropicales de Australia y África. Identificamos serios defectos en la QMP: se desconoce el significado ecológico de los diferentes patrones de quema y los detalles de los mosaicos de quema deseados no están especificados. Esto ha conducido a planes de gestión del fuego basados en retórica de pirodiversidad que carece de sustancia en términos de directrices operativas y de capacidad para una evaluación significativa. También sugerimos que no todos los patrones de quema son significativos ecológicamente: esto parece ser particularmente cierto para las sabanas de Australia y África que son altamente propensas al fuego. Argumentamos que la defensa de la biodiversidad requiere de la pirodiversidad necesita ser reemplazada con una consideración más crítica de los niveles de pirodiversidad que se requieren para la biodiversidad y una mayor atención a las directrices operativas para su implementación.*

Palabras Clave: fuego, gestión de conservación, manejo adaptativo, monitoreo

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Introduction

Fire is a key ecosystem driver in many biomes, including grasslands, savannas, boreal forests, and heathlands (e.g., Johnson 1992; Bond 1997; Keeley & Fotheringham 2001). Given the important role of fire in these environments, informed fire management is essential for effective biodiversity conservation, and ecologists need to ensure that they are providing fire managers with the best scientific advice available.

The use of fire and its incorporation into conservation management has changed in parallel with shifts in ecological thinking that have taken place over the past 100 years. Up to the 1970s and early 1980s, ecological systems were viewed in terms of a balance-of-nature paradigm, and equilibrium theory was prominent (see Mentis & Bailey 1990, orthodox vs. contemporary view). The Clementsian-Tansleyan succession model (e.g., Clements 1916) is a good example of this: disturbances alter a system's state, but equilibrium is reestablished over time. Based on this paradigm, fire managers in conservation areas tended to view fire as an agent that "upsets the balance of nature" and prescribed fixed fire intervals or even enforced complete fire exclusion (Pyne 1997; Parr & Brockett 1999).

Growing dissatisfaction with the explanatory and predictive powers of equilibrium models forced a reevaluation of the way ecological systems were interpreted. The importance of both equilibrium and nonequilibrium theory are now recognized, and concepts such as flux, patchiness, and heterogeneity are commonly used to understand and explore biological systems (Pickett & White 1985; Westoby et al. 1989; Wiens 1997). Generally, ecologists and conservation managers no longer see fire as an enemy of nature; rather, they see it as a necessary driver of ecosystem dynamics (but see Ramos-Neto & Pivello 2000; Stephens & Ruth 2005). In most places in the world, fire managers moved away from a focus on suppression a long time ago, and the practice of prescribed rotational burning with fixed monotonic intervals is increasingly considered too rigid (Saxon 1984; Bradstock et al. 1995). As a result, the importance of variability and flexibility in burning is increasingly being promoted, and increased patchiness and heterogeneity is now widely held to be the most appropriate way to burn in fire-prone conservation areas (Bradstock et al. 1995; Keith et al. 2002; van Wilgen et al. 2003; Burrows & Wardell-Johnson 2004).

These changes in fire-management paradigms are only just beginning across much of North America, which does not have a very extensive history of using fire for managing biodiversity. The importance of fire in ecosystem restoration and biodiversity conservation has received considerable attention in the southeastern United States (Sparks et al. 2002; Van Lear et al. 2005), where the reintroduction of burning is recognized as essential for fauna and flora (e.g., Red-cockaded Woodpecker [*Picoides borealis*] and Bachman's Sparrow [*Aimophila aestivalis*], James et al. 1997; Tucker et al. 2004; gopher tortoise [*Gopherus polyphemus*], Aresco & Guyer 1999; invertebrates, Izhaki et al. 2003; endangered endemic plants, Quintana-Ascencio et al. 2003; Liu & Menges 2005). Nevertheless, in the western United States, there has only recently been a shift in focus from fire control to fire management (Backer et al. 2004). Even so the emphasis remains on fuel dynamics and fire suppression, with prescribed fire primarily considered in the context of managing fire hazard rather than biodiversity (Kauffman 2004; Stephens & Ruth 2005), which is only just emerging as a major consideration (Smucker et al. 2005).

Fire-management strategies that aim to introduce increased fire variability into the landscape through the use of dynamic mosaics across space and time are often referred to as patch mosaic burning (PMB) (Brockett et al. 2001). We undertook a critical analysis of PMB, focusing on the tropical and subtropical savannas of South Africa and Australia, which are among the most fire prone of all ecosystems and are where PMB originated and has been promoted and implemented most widely (Brockett et al. 2001; Andersen et al. 2003; du Toit et al. 2003). We sought to (1) provide an overview of PMB theory, (2) explore how the theory is being applied in practice, (3) examine the relationship between pyrodiversity and biodiversity, and (4) discuss the way forward for improved PMB.

Theory of PMB

With PMB fire variables are manipulated to create a mosaic of patches representative of a range of fire histories, so as to generate heterogeneity across space and time (Parr & Brockett 1999). A key assumption is that fire patterns act as surrogates for biodiversity so that fire patchiness in space and time results in a high level of biotic diversity; in other words, "pyrodiversity begets biodiversity" (Martin & Sapsis 1992). Because different taxa exhibit different responses to fires, it is argued that patchy burning will provide a range of habitats through space and time that will enable the persistence of biota in the regional landscape (Bradstock et al. 1995; Edwards et al. 2001; Burrows & Wardell-Johnson 2003; Panzer 2003). It is important to note that PMB does not refer to variation in fire regimes between habitats within a landscape that are due to underlying geomorphological variation (e.g., Mermoz et al. 2005). Rather it is concerned with introducing variation into burning regimes within a particular habitat. Although PMB is strongly linked to biodiversity conservation, its principles may also be applied to reduce the risk of hazardous wildfires that threaten life and property (e.g., in the North American chaparral, Keeley & Fotheringham 2001).

Clearly, a single fire regime will not adequately cater to all species' needs, so the virtues of pyrodiversity have

been widely promoted by fire ecologists (Saxon 1984; Allan & Baker 1990; Russell-Smith et al. 1997) and cover a variety of taxa including birds (Brooker et al. 1990; Garnett & Crowley 1995; Woinarski & Recher 1997;Woinarski et al. 1999), reptiles (Trainor & Woinarski 1994; Woinarski et al. 1999), mammals (Pye 1991; Masters 1993; Letnic 2003), invertebrates (York 1994), and plants (e.g., Keith & Bradstock 1994; Morrison et al. 1995; Williams et al. 2003). The application of patch burning is increasingly being advocated by conservation management agencies, who have adopted PMB principles into several park fire-management policies. These agencies include the Western Australian Department of Conservation and Land Management (Environmental Protection Authority 2004), the Queensland Parks & Wildlife Service (James & Bulley 2004), and the Federal Parks and Wildlife Service (Kakadu Board of Management and Parks Australia 1998) in Australia, and South African National Parks (Biggs 2002) and North-West Parks & Tourism Board (Brockett et al. 2001) in South Africa.

PMB has also been linked to traditional burning by indigenous peoples in a range of ecosystems globally (e.g., Laris 2002; Vale 2002; Bowman et al. 2004; Mistry et al. 2005). For example, in northern Australia fine-scale mosaic burning has been associated with the traditional practices of Aboriginal people (Russell-Smith 1995; Andersen 1996; Burrows et al. 2004), who have occupied the region for more than 40,000 years (Roberts et al. 1990). Landscape fire management is integral to traditional Aboriginal society (Rose 1995) and is claimed to result in significantly enhanced biodiversity where it is still being practiced (Yibarbuk et al. 2001; Whitehead et al. 2003). Such practices have, however, been severely disrupted throughout most of northern Australia following European settlement. This disruption has been implicated in population declines in a range of taxa, including the native cypress *Callitris intratropica* Baker (Bowman & Panton 1993), granivorous birds (Franklin 1999), and small mammals (Bolton & Latz 1993; Woinarski et al. 2001).

Although the concept of PMB appears relatively simple, fire mosaics are actually highly complex and incorporate a range of facets. First, there is the visible mosaic: the obvious patchwork evident in recently burned landscapes, composed of individual burned patches or fire scars (Griffin 1991; Gill et al. 2003; Bradstock et al. 2005). This mosaic consists of two levels of fire patchiness, depending on the scale of observation: intrapatch heterogeneity (variation in fire intensity, including occurrence of unburned areas, within a burned patch) and interpatch heterogeneity (Gill et al. 2003) (Fig. 1).

Second, there is the invisible mosaic, which refers to patches representing different longer term fire history (Gill et al. 2003; Bradstock et al. 2005) (Fig. 2). The invisible mosaic is often interpreted primarily in terms of time-since-fire (or postfire age), and some interpretations

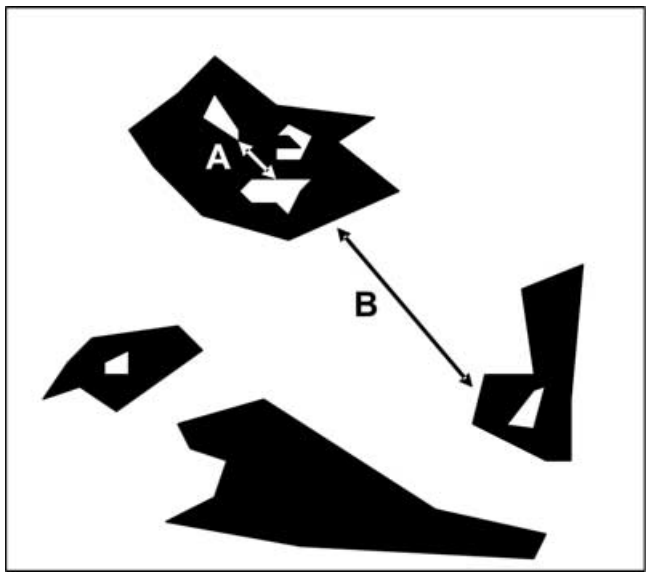


Figure 1. Patches that make up the mosaic viewed at different levels: A, intrapatch (within) patchiness, and B, interpatch (between) patchiness.

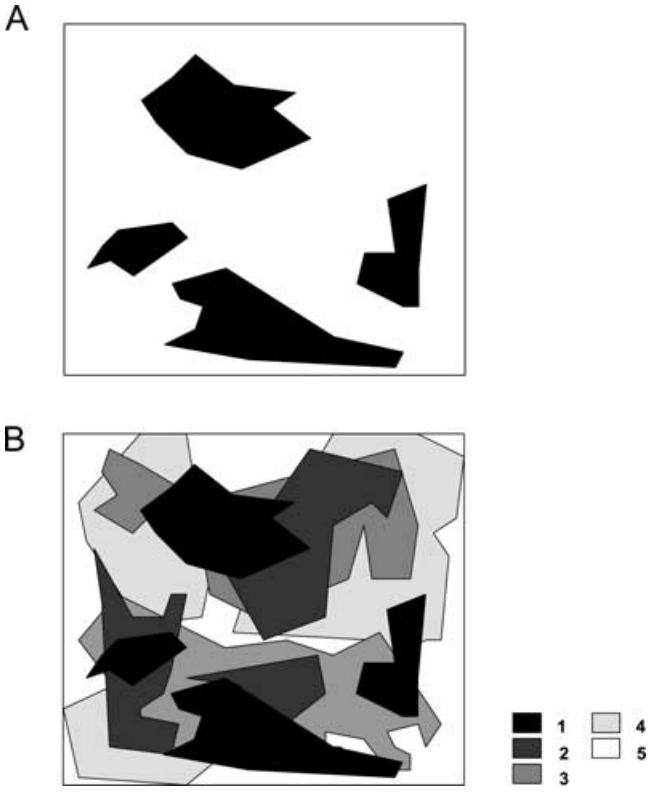


Figure 2. Patch mosaics interpreted in terms of (a) the visible mosaic and (b) the invisible mosaic. The legend in this example refers to postfire fuel age (in years). These patches are not visible like the recently burned patches that comprise the visible mosaic.

of PMB focus solely on this aspect (e.g., Bond & Archibald 2004). Patches are highly dynamic; for example, they decline in size as age increases and subsequent fires impinge on the patch (i.e., there is an inverse relationship between patch age and size) (Gill et al. 2003). Visible and invisible patches in the landscape have a range of attributes including size, shape, position in the landscape, persistence over time, and season of burn, all of which contribute to the uniqueness and diversity of the fire regime.

The interplay between the visible and invisible mosaic is poorly understood, difficult to study, and seldom appreciated. For example, responses to any particular fire may be determined to a large degree by the invisible mosaic, but this has been poorly researched (Andersen et al. 1998). The challenge of dealing with the invisible mosaic is compounded by its highly dynamic nature and its scale-dependent perception by different taxa. Furthermore, it is important to understand how biotic and abiotic factors (e.g., vegetation type, fuel loads, topography, weather, drainage lines, and geomorphology) that influence variation in fire regimes can assist the development of both the visible and invisible mosaic (see Wardell-Johnson et al. 2004; Mermoz et al. 2005). Indeed, it is only relatively recently that practical ways of assessing the invisible mosaic have been developed; these include the use of Geographic Information Systems (GIS), remote sensing, and methods for quantifying patchiness (e.g., Russell-Smith et al. 1997; Brockett et al. 2001; Price et al. 2005).

PMB in Practice

In Australia PMB is increasingly being institutionalized in conservation-management plans. For example, the fire-management strategy for biodiversity outcomes in Tarawi Nature Reserve, New South Wales, includes the promotion of patchiness during wildfire by implementing a patch-burning program with "strategic prescribed fires" (Willson 1999). Similarly, fire management in conservation areas on Bribie Island aim to "burn in a highly variable mosaic pattern" so that a range of ages since fire or seral stages are produced (James & Bulley 2004). Recently, western Australia's Department of Conservation and Land Management established the Fire Mosaic Project, a long-term, landscape-scale experiment in southwestern Australia that aims to apply patch burning over 4000 ha to create a fine-scaled habitat mosaic with a range of seral stages that will promote biodiversity and reduce wildfire hazard (Burrows & Wardell-Johnson 2004).

Despite widespread support for PMB as a strategic goal for biodiversity conservation, conservation managers in Australia have struggled to operationalize it effectively. For example, management plans typically lack details on the scale and distribution of patchiness that is considered desirable and on how fire managers intend to achieve this patchiness. Without such detail it is unlikely that management aims will be achieved or that outcomes of management can even be effectively assessed (Andersen 1999).

Although the concept of PMB originated in Australia (see Saxon 1984), the most sophisticated implementation of it has occurred in South Africa. In South Africa there seems to be a more effective flow of shared ideas and practices between researchers and managers, such as in the development of methods for quantifying heterogeneity (Brockett et al. 2001; Price et al. 2005). There is a higher degree of sophistication of PMB embodied in South African management plans, which embrace a robust system of adaptive management that incorporates detailed monitoring of fire patterns (Brockett et al. 2001; Biggs 2002). In Kruger National Park, for example, rangers apply a clearly articulated PMB system, in which targets for the total area to be burned and details of when to burn, how many ignition points, and where to burn are all specified (Biggs 2002; see also http://www.sanparks.org/parks/kruger/conservation/scientific/key_issues/fire_policy.php). Monitoring systems have also been established to track fire-management progress throughout the year in achieving burn targets and to document changes in fire heterogeneity over the long term.

One of the keys to the success of monitoring and adaptive management in Kruger National Park are "thresholds of potential concern" (TPCs) set for specific indicators of the effects of management interventions (Biggs & Rogers 2003). The TPCs are defined as "those upper and lower levels along a continuum of change in a selected environmental indicator, which when reached, prompts an assessment of the causes, and results in (a) management action to moderate the cause, or (b) re-calibration of the threshold to a more realistic level" (South African National Parks 1997). Fire-management TPCs include targets for the seasonal distribution of fires (the ratio of area burned in late winter and early spring to that burned in late spring/summer should be between 2.25:1 and 1.75:1) and proportion of area burned in each month as the fire season progresses, which is linked to an overall target for the year that is determined by the preceding year's rainfall (van Wilgen et al. 1998; Brockett et al. 2001).

In some instances the establishment of TPCs requires a degree of caution, and it may not always be possible to rely on historical data to set thresholds. Nevertheless, the setting of these limits is a positive start, and potential uncertainties (and consequences) may be overcome by frequently reassessing thresholds and by combining real-world data with modeling.

Monitoring in Kruger also incorporates TPCs relating to desired ecological outcomes (cf. Andersen 1999). Monitoring data on plant and animal populations should be linked directly to fire records to assist with interpretation of the relationship between fire pattern and biodiversity. Adaptive management with mapping and monitoring of fires combined with links to biota is thus critical to the success of this system (Biggs & Rogers 2003; van Wilgen

et al. 2003). Although there have been some attempts to link biodiversity objectives and fire pattern in Kruger and Pilanesberg National Parks (e.g., linking fire heterogeneity and sable antelope [*Hippotragus niger*] movements [Brockett et al. 2001]), the link remains weak. Challenges include choosing which taxa to focus on, the response variable to be measured (e.g. population size, population growth rates, species presence or absence, movements in landscape), and setting the bounds for acceptable variation in time and space.

Relationship between Pyrodiversity and Biodiversity

Given that species vary considerably in their responses to fire, it is clear that some amount of pyrodiversity is needed for biodiversity conservation. Nevertheless, the question yet to be addressed is how much? The effectiveness of fire patterns as surrogates of biodiversity seems to have been accepted without critical analysis of the *levels* of pyrodiversity actually required for biodiversity. It makes little sense to expend scarce management resources to create fire patterns that have little or no ecological significance. This is of particular relevance in ecosystems that show a high degree of resilience in relation to fire.

Experimental results emerging from South Africa and northern Australia suggest that many elements of the biota in tropical savannas are resistant or resilient to burning across a wide range of fire regimes. This is illustrated by results from a long-term fire experiment in Kruger National Park, where more than 12 different combinations of fire timing and frequency have been maintained on experimental plots located throughout the park for more than 50 years. The experimental fire regimes range from annual fires in the dry season, to fires with different season and frequency combinations, to fire exclusion. An analysis of ant assemblages on the plots shows remarkably little differentiation between experimental regimes (Parr et al. 2004). In Mopane, where annual rainfall is low (mean 450 mm), there was no statistically significant differentiation in assemblage composition between the seven different burning treatments studied (Fig. 3a, analysis of similarity (ANOSIM) $R = 0.210$, $p>0.05$). There was some differentiation in the Satara area (higher rainfall, 550 mm), but the difference was only between unburned sites and all others (Fig. 3b, ANOSIM $R = 0.493$, $p=0.006$) rather than between the different burning treatments. In other words, 50 years of extreme pyrodiversity had either no effect on ants or only resulted in differentiation between burned and unburned sites. Thus extensive pyrodiversity is not required for the conservation of ant biodiversity in Kruger National Park.

Similar responses to fire have been reported for other taxa in Kruger. For example, results of a study of bird responses to a large fire in the park showed that species

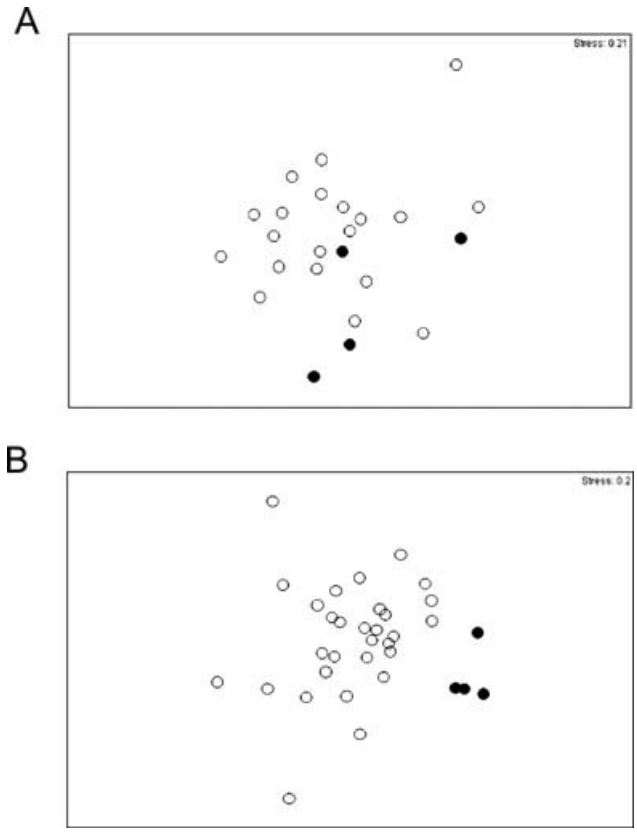


Figure 3. Nonmetric multidimensional scaling ordinations based on ant species composition of sites subject to diverse fire regimes over a 50-year period in the (a) Mopane and (b) Satara areas of the Kruger National Park. Sites remaining unburned over the 50-year period are indicated by filled symbols; open symbols represent five different burning regimes. Analysis of similarity R *values = 0.210 (*p*, not significant) and 0.493 (*p *= 0.006) for Mopane and Satara, respectively. Data from Parr et al. (2004).*

richness and composition do not vary with fire intensity (Mills 2004). It was concluded that bird communities are likely to be robust to all but the most extreme fire policy, and it was therefore suggested that fire managers could take a more cost-effective, hands-off approach without compromising biodiversity (Mills 2004). The same may also be true for woody plants, whose richness and composition appear to be extremely resistant to variation in fire regimes (although vegetation structure does change markedly; S. Higgins & A. Mills, personal communication 2005).

In northern Australia too, several studies have demonstrated that many faunal groups are highly resistant to fires in tropical savannas. For example, most terrestrial vertebrates and invertebrates studied at Kapalga in Kakadu National Park were unaffected by experimental fire regimes ranging from annual high-intensity fire-to-fire exclusion over 5 years (Andersen et al. 2003). As in South Africa,

when taxa were affected, often the only difference was between unburned and burned areas, rather than fine differentiation between different burning patterns. Likewise, plant composition is generally highly resilient, and the major vegetation response is structural (Bowman et al. 1988; Andersen et al. 2003).

Examples of resilience in relation to fire are not confined to tropical savannas. For example, results of recent work have challenged the importance of fire mosaics in arid Australia, where the large number of mammalian extinctions following European settlement has been commonly attributed to the breakdown in fire patchiness arising from traditional Aboriginal fire management (Burbidge et al. 1988; Masters 1993; Letnic 2000). Letnic and Dickman (2005) conclude that patch burning in the Simpson Desert does not benefit small mammals directly; whereas fire-sensitive species (e.g., the desert mouse [*Pseudomys desertor*]) need patches that have remained unburned for several years. Overall small mammals do not require a range of different postfire habitats in the landscape.

Importantly, there is likely to be a positive relationship between fire proneness and ecosystem resilience to fire, with tropical savannas at the extreme of high fire frequency and resilience. As fire frequency and resilience decline, the ecological consequences of different fire histories, and therefore importance of pyrodiversity in maintaining biodiversity, are likely to increase. For example, it has been well documented that different postfire successional stages are important for small mammal diversity in heathlands and eucalypt forests in southeastern Australia, where fire-return intervals are of the order of 10–20 years (Fox 1982; Catling et al. 2001). Similarly, different bird species are favored by different levels of fire severity in North American pine-Douglas-fir forests (Smucker et al. 2005). Rainforests occur at the low fire frequency-resilience extreme; such habitats are so fire sensitive that virtually any fire reduces their conservation values.

Burning for Biodiversity Conservation

Given the importance of informed and effective fire management for conservation areas, a more structured and systematic approach to PMB is needed. This is relevant both to conservation reserves that are already using fire to manage biodiversity and to regions such as western North America, where issues relating to "burning for biodiversity" are just emerging. The following guidelines should assist in formalizing PMB policy.

Establish the Relationship between Pyrodiversity and Biodiversity

The question of how much pyrodiversity is required for biodiversity is fundamental to effective PMB. Its resolution requires a greater understanding of the importance of the invisible mosaic to the persistence of species, rather than simply basing management approaches solely on the visible (e.g., time-since-fire) mosaic (Bradstock et al. 2005). The issue is particularly relevant to highly mobile fauna, such as some granivorous birds, whose food resources undergo complex spatiotemporal dynamics that may be significantly influenced by fire (Woinarski et al. 2005).

Spatial scale is critical when considering the relationship between pyrodiversity and biodiversity, so it is important to identify the appropriate sizes for habitat mosaics generated by fire. In particular, to what extent do species require patchy burning within a habitat that is burned, as opposed to mosaic burning per se? The latter is a particularly important question for the tropical savannas of northern Australia, where population declines in small mammals have been attributed to broadscale reductions in fine-scale patchiness (Braithwaite 1995; Price et al. 2005). Nevertheless, fine-scale patchiness may not necessarily have positive biodiversity outcomes; some animals perceive it as fragmentation rather than (positive) heterogeneity (Sullivan & Sullivan 2001). It is therefore important to identify keystone structures in the habitat that drive animal distribution and abundance (Tews et al. 2004). This requires an improved understanding of habitat availability, dispersal, and resource needs for the target biota (Gill & Bradstock 1995; Bradstock et al. 2005; Woinarski et al. 2005).

Key to answering these questions is on-going monitoring as part of adaptive management combined with spatial modeling and computer simulations. The latter can be particularly useful given the challenges posed by very large spatial scales, very long time periods, confounding factors in the field, and the need for replication.

Where evidence suggests that much of the biota does not require a high degree of pyrodiversity, attention can be directed at those species with special fire-management requirements: regimes for these species are unlikely to adversely influence species that are more fire resistant (Andersen et al. 2003; Parr et al. 2004). In many cases fire-sensitive species simply require relatively infrequently burned habitat (e.g., *Callitris intratropica*, Bowman & Panton 1993; obligate seeders, Russell-Smith et al. 2002; northern brown bandicoot [*Isoodon macrourus*], Pardon et al. 2003); therefore, a combination of frequently and less frequently burned habitat may adequately cater to the great majority of species in the landscape (Andersen et al. 2005). Increasing the extent of relatively infrequently burned habitat can be achieved either by reducing the proportion of the landscape burned each year or by setting prescribed fires more strategically (Andersen et al. 2005).

Identify the Management Interventions Required

At some given scale, fire is inherently heterogeneous—landscapes are seldom burned entirely, and fire behavior varies markedly within burned areas. The use of low-intensity fire is often promoted because of its small-scale

patchiness (Russell-Smith 1995; Bowman et al. 2004). Nevertheless, higher intensity fires are also characteristically patchy, but at larger spatial scales, with fire severity varying markedly between areas, including some remaining unburned (Turner et al. 2003). Thus, there will always be some level of pyrodiversity regardless of management intervention. Once the extent of pyrodiversity that is required to maintain biodiversity has been identified, management needs to determine to what extent this is achieved regardless of active intervention and when explicit management intervention is required. In northwestern Australia, for example, the need to increase the area of relatively long-unburned habitat has been identified as a management priority (Woinarski et al. 2004; Andersen et al. 2005).

Establish Clear Operational Guidelines and Targets

A sound understanding of the extent of pyrodiversity required for biodiversity, the interventions required to achieve it, and methods of evaluation can only be translated into effective management through the provision of clear targets and operational guidelines. Targets should include total percentage of area burned, desired patch-size frequency distribution, and seasonal distribution of fires (Biggs 2002), and operational guidelines should cover the number and timing of fires and ignition locations (which may be random).

Implement Effective Monitoring and Feedback

Any PMB procedure should incorporate an effective feedback process involving systematic monitoring (see Andersen 1999; Schreider et al. 2004). Effective feedback requires timely and accurate mapping of burned areas, combined with monitoring both of fire heterogeneity and effects on biota. In South Africa and northern Australia, much work has been done in terms of fire mapping, quantifying changes in fire heterogeneity, and linking these to management interventions following concerns about the increasing prevalence of large-scale, late-season fires (Brockett et al. 2001; Edwards et al. 2001; Woinarski et al. 2004; Price et al. 2005). Nevertheless, much work remains to be done in linking fire patterns to biodiversity outcomes. To this end, the use of TPCs based on ranges or frequency distributions needs to be encouraged (see also Bradstock et al. 1995; van Wilgen et al. 1998; Keith et al. 2002).

Conclusion

Scientists have an obligation to critically test rather than uncritically promote popular ideas and theories. This has not always been apparent with PMB, which has been widely promoted as *the* solution in many protected areas on the basis of untested assumptions and limited supporting evidence. In most cases the ecological significance of different burning patterns remains unknown, and details of desired fire mosaics remain unspecified. This inevitably leads to fire-management plans based on pyrodiversity rhetoric but lacking substance in terms of operational guidelines and capacity for meaningful evaluation.

As a first step, biodiversity-needs-pyrodiversity advocacy needs to be replaced by a more critical consideration of the levels of pyrodiversity needed for biodiversity. It is possible that much pyrodiversity is ecologically superfluous (Turner 2005). Moreover, not all ecologically significant fire patterns will be of equal conservation importance—the identification of critical patterns deserves priority attention.

Without a more analytical and systematic approach to PMB, leading to formalized fire policy that managers can effectively implement, it is unlikely that management aims will be met because the process of adaptive management cannot be fulfilled: actions to achieve strategic aims will remain unarticulated, and feedback for their continual refinement will be ineffective (Andersen 1999).

Clearly there is much work to be done to elucidate the intricacies of effective PMB. Overcoming knowledge deficiencies and uncertainty, particularly surrounding the invisible mosaic and the autecology of vulnerable species, is a necessary challenge to both ecological researchers and to fire managers. Only then will good science and informed decisions ensure effective fire management and sustainable biodiversity conservation.

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Literature Cited

Allan, G., and L. Baker. 1990. Uluru (Ayers Rock-Mt Olga) National Park: an assessment of a fire management programme. Proceedings of the Ecological Society of Australia **16:**215–220.

Andersen, A. N. 1996. Fire ecology and management. Pages 179–195 in C. M. Finlayson and I. van Oertzen, editors. Landscape and vegetation ecology of the Kakadu region, Northern Australia. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Andersen, A. N. 1999. Fire management in northern Australia: beyond command-and-control. Australian Biologist **12:**63–70.

Andersen, A. N., R. W. Braithwaite, G. D. Cook, L. C. Corbett, R. J. Williams, M. Douglas, A. M. Gill, S. Setterfield, and W. J. Muller. 1998. Fire research for conservation management in tropical savannas: introducing the Kapalga fire experiment. Australian Journal of Ecology **23:**95–110.

Andersen, A. N., G. D. Cook, and R. J. Williams, editors. 2003. Fire in tropical savannas: the Kapalga experiment. Springer, New York.

Andersen, A. N., G. D. Cook, L. K. Corbett, M. M. Douglas, R. W. Eager, J. Russell-Smith, S. A. Setterfield, R. J. Williams, and J.C.Z. Woinarski. 2005. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. Austral Ecology **30:**155–167.

Aresco, M. J., and C. Guyer. 1999. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management **63:**26–35.

Backer, D. M., S. E. Jensen, and G. R. McPherson. 2004. Impacts of fire-suppression activities on natural communities. Conservation Biology **18:**937–946.

Biggs, H. C. 2002. Proposed policy for the ecosystem management of fire in the Kruger National Park. South African National Parks, Skukuza.

Biggs, H. C., and K. H. Rogers. 2003. An adaptive system to link science, monitoring, and management practice. Pages 59–82 in J.T. du Toit, K. H. Rogers, and H. C. Biggs, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C.

Bolton, B. L., and P. K. Latz. 1993. The Western Hare-wallaby *Lagorchestes hirsutus* (Gould) (Macropidae) in the Tanamai Desert. Australian Wildlife Research **5:**285–293.

Bond, W. J. 1997. Fire. Pages 421–446 in R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. Vegetation of southern Africa. Cambridge University Press, Cambridge, United Kingdom.

Bond, W. J., and S. Archibald. 2004. Confronting complexity: fire policy choices in South African savanna parks. International Journal of Wildland Fire **12:**381–389.

Bowman, D. M. J. S., and W. J. Panton. 1993. Decline of *Callitris intratropica* R. T. Baker and H. G. Smith in the Northern Territory: implication for pre- and post-European colonisation fire regimes. Journal of Biogeography **20:**373–381.

Bowman, D. M. J. S., B. A. Wilson, and R. J. Hooper. 1988. Response of *Eucalyptus* forest and woodland to four fire regimes at Munmarlary, Northern Territory, Australia. Journal of Ecology **76:**215–232.

Bowman, D. M. J. S., A. Walsh, and L. D. Prior. 2004. Landscape analysis of Aboriginal fire management in Central Arnhem Land, north Australia. Journal of Biogeography **31:**207–223.

Bradstock, R. A., D. A. Keith, and T. D. Auld. 1995. Fire and conservation: imperatives and constraints on managing for diversity. Pages 323–333 in R. A. Bradstock, T. D. Auld, D. A. Keith, R. T. Kingsford, D. Lunney, and D. P. Silvertsen, editors. Conserving biodiversity: threats and solutions. Surrey Beatty and Sons, Sydney.

Bradstock, R. A., M. Beward, A. M. Gill, and J. S. Cohn. 2005. Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitats and animals. Wildlife Research **32:**409–423.

Braithwaite, R. W. 1995. Fire intensity and the maintenance of habitat heterogeneity in a tropical savanna. CALMScience Suppl **4:**189–196.

Brockett, B. H., H. C. Biggs, and B.W. van Wilgen. 2001. A patch mosaic burning system for conservation areas in southern African savannas. International Journal of Wildland Fire **10:**169–183.

Brooker, M. G., R. W. Braithwaite, and J. A. Estbergs. 1990. Foraging ecology of some insectivorous birds in forest and woodlands of the wet-dry tropics of Australia. Emu **90:**215–230.

Burbidge, A. A., K. A. Johnson, P. J. Fuller, and Southgate, R. I. 1988. Aboriginal knowledge of the mammals of the central deserts of Australia. Australian Wildlife Research **15:**9–39.

Burrows, N. D., and G. Wardell-Johnson. 2003. Fire and plant interactions in forested ecosystems of south-western Australia. Pages 225–268 in I. Abbott and N. Burrows, editors. Fire in ecosystems of south-western Australia: impacts and management. Backhuys Publishers, Leiden, The Netherlands.

Burrows, N. D., and G. Wardell-Johnson. 2004. Implementing fire mosaics to promote biodiversity and reduce the severity of wildfires in south-western Australian ecosystems. Proceedings of the 11th Annual AFAC conference and inaugural Bushfire CRC conference. Bushfire CRC, Melbourne, Australia.

Burrows, N. D., A. A. Burbidge, and P. J. Fuller. 2004. Integrating indigenous knowledge of wildland fire and western technology to conserve biodiversity in an Australian desert. Proceedings of Millennium Assessment, bridging scales and epistemologies conference. Millennium ecosystem assessment. Available from http://www.millenniumassessment.org/en/About.Meetings.Bridging.Proceedings.aspx (accessed February 2006).

Catling, P. C., N. C. Koops, and R. J. Burt. 2001. The distribution and abundance of ground-dwelling animals in relation to time since wildfire and vegetation structure in southeastern Australia. Wildlife Research **28:**555–564.

Clements, F. E. 1916. Plant succession: analysis of the development of vegetation. Publication 242. Carnegie Institute, Washington, D.C.

du Toit, J. T., K. H. Rogers, and H. C. Biggs. 2003. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C.

Edwards, A., P. Hauser, M. Anderson, J. McCartney, M. Armstrong, R. Thackway, G. Allan, C. Hempel, and J. Russell-Smith. 2001. A tale of two parks: contemporary fire regimes of Litchfield and Nitmiluk National Parks, monsoonal northern Australia. International Journal of Wildland Fire **10:**79–89.

Environmental Protection Authority. 2004. Review of the fire policies and management practices of the Department of Conservation and Land Management. Bulletin 1151. Environmental Protection Authority, Perth.

Franklin, D. C. 1999. Evidence of disarray amongst granivorous bird assemblages in the savannas or northern Australia, a region of sparse human settlement. Biological Conservation **90:**53–68.

Fox, B. J. 1982. Fire and mammalian succession in an Australian coastal heath. Ecology **63:**1332–1341.

Garnett, S., and G. Crowley. 1995. The decline of the Black Treecreeper *Climacteris picumnus melanota* on Cape York Peninsula. Emu **95:**54–61.

Gill, A. M., and R. A. Bradstock. 1995. Extinctions of biota by fires. Pages 309–322 in R. A. Bradstock, T. D. Auld, D. A. Keith, R. Kingsford, D. Lunney, and D. Silvertsen, editors. Conserving biodiversity: threats and solutions. Surrey Beatty and Sons, Sydney.

Gill, A. M., G. Allan, and C. Yates. 2003. Fire-created patchiness in Australian savannas. International Journal of Wildland Fire **12:**323–331.

Griffin, G. F. 1991. Will it burn—should it burn? Management of the spinifex grasslands of inland Australia. Pages 63–76 in G. P. Chapman, editor. Desertified grasslands: their biology and management. Academic Press, London.

Izhaki, I., D. J. Levey, and W. R. Silva. 2003. Effects of prescribed fire on an ant community in Florida pine savanna. Ecological Entomology **28:**439–448.

James, F. C., C. A. Hess, and D. Kufrin. 1997. Species-centered environmental analysis: indirect effects of fire history on Red-cockaded Woodpeckers. Ecological Applications **7:**118–129.

James, R., and G. Bulley. 2004. Fire management system: Bribie Island. Queensland Parks and Wildlife Service, Brisbane.

Johnson, E. A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge, United Kingdom.

Kakadu Board of Management and Parks Australia. 1998. Kakadu National Park Plan of Management 1999–2004. Commonwealth of Australia, Jabiru.

Kauffman, J. B. 2004. Death rides the forest: perceptions of fire, land use, and ecological restoration of western forests. Conservation Biology **18:**878–882.

Keeley, J. E., and C. J. Fotheringham. 2001. Historic fire regime in southern California shrublands. Conservation Biology **15:**1536–1548.

Keith, D. A., and R. A. Bradstock. 1994. Fire and competition in Australian heath: a conceptual model and field investigations. Journal of Vegetation Science **5:**347–354.

Keith, D. A., J. E. Williams, and J.C.Z. Woinarski. 2002. Fire management and biodiversity conservation: key approaches and principles. Pages

401–428 in R. A. Bradstock, J. E. Williams, and M. A. Gill, editors. Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge, United Kingdom.

Laris, P. 2002. Burning the seasonal mosaic: preventative burning strategies in the wooded savanna of southern Mali. Human Ecology **30:**155–184.

Letnic, M. 2000. Dispossession, degradation and extinction: environmental history in arid Australia. Biodiversity and Conservation **9:**295–308.

Letnic, M. 2003. The effects of experimental patch burning and rainfall on small mammals in the Simpson Desert, Queensland. Wildlife Research **30:**547–563.

Letnic, M., and C. R. Dickman. 2005. The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. Austral Ecology **30:**24–39.

Liu, H., and E. S. Menges. 2005. Winter fires promote greater vital rates in the Florida Keys than summer fires. Ecology **86:**1483–1495.

Martin, R. E., and D. B. Sapsis. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. Pages 150–157 in H. M. Kerner, editor. Proceedings of the symposium on biodiversity in northwestern California, 1991. Wildland Resources Centre, University of California, Berkeley.

Masters, P. 1993. The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern Territory. Wildlife Research **20:**803–813.

Mentis, M. T., and A. W. Bailey. 1990. Changing perceptions of fire management in savanna parks. Journal of the Grassland Society of Southern Africa **7:**81–84.

Mermoz, M., T. Kitzberger, and T. T. Veblen, 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. Ecology **86:**2705–2715.

Mills, M.S.L. 2004. Bird community responses to savanna fires: should managers be concerned. South African Journal of Wildlife Research **34:**1–11.

Mistry, J., A. Berardi, V. Andrade, T. Krahô, P. Krahô, and O. Leonardos. 2005. Indigenous fire management in the cerrado of Brazil: the case of the Krahô of Tocantíns. Human Ecology **33:**365–386.

Morrison, D. A., G. J. Cary, S. M. Penjelly, D. G. Ross, B. G. Mullins, C. R. Thomas, and T. S. Anderson. 1995. Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and time-since-fire. Australian Journal of Ecology **20:**239–247.

Panzer, R. 2003. Importance of in-situ survival, recolonization, and habitat gaps in the postfire recovery of fire-sensitive prairie insect species. Natural Areas Journal **23:**14–21.

Pardon, L. G., B. W. Brook, A. D. Griffiths, and R. W. Braithwaite. 2003. Determinants of survival for the northern brown bandicoot under a landscape-scale fire experiment. Journal of Animal Ecology **72:**106–115.

Parr, C. L., and B. H. Brockett. 1999. Patch-mosaic burning: a new paradigm for savanna fire management in protected areas? Koedoe **42:**117–130.

Parr, C. L., H. G. Robertson, H. C. Biggs, and S. L. Chown. 2004. Response of African savanna ants to long-term fire regimes. Journal of Applied Ecology **41:**630–642.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Price, O., A. Edwards, G. Connors, J. Woinarski, G. Ryan, A. Turner, and J. Russell-Smith. 2005. Fire heterogeneity in Kakadu National Park, 1980–2000. Wildlife Research **32:**425–433.

Pye, T. 1991. The New Holland Mouse (*Pseudomys novaehollandiae*) (Rodentia: Muridae) in Tasmania: a field study. Wildlife Research **18:**521–531.

Pyne, S. J. 1997. World fire: the culture of fire on earth. University of Washington Press, Seattle.

Quintana-Ascencio, P. F., E. S. Menges, and C. W. Weekley. 2003. A fire-explicit population viability analysis of *Hypercum cumulicola* in Florida rosemary scrub. Conservation Biology **17:**433–449.

Ramos-Neto, M. B., and V. R. Pivello. 2000. Lighting fires in a Brazilian savanna national park: rethinking management strategies. Environmental Management **26:**675–684.

Roberts, R. G., R. Jones, and M. A. Smith. 1990. Thermoluminescence dating of a 50,000 year-old human occupation site in northern Australia. Nature **345:**153–156.

Rose, D. B. 1995. Country in flames. Proceedings of the 1994 symposium on biodiversity and fire in North Australia. Biodiversity series, paper 3. Department of the Environment, Sport and Territories and Australian National University, Canberra.

Russell-Smith, J. 1995. Fire management. Pages 216–237 in T. Press, D. Lea, A. Webb, and A. Graham, editors. Kakadu—natural and cultural heritage and management. Australian National University, Canberra.

Russell-Smith, J., P. J. Ryan, and R. Durieu. 1997. A LANDSAT MSS-derived fire history of Kakadu National Park, monsoonal northern Australia, 1980–1994: seasonal extent, frequency and patchiness. Journal of Applied Ecology **34:**748–766.

Russell-Smith, J., P. G. Ryan, and D. C. Cheal. 2002. Fire regimes and the conservation of sandstone heath in monsoonal northern Australia: frequency, interval and patchiness. Biological Conservation **104:**91–106.

Saxon, E. C. 1984. Anticipating the inevitable: a patch-burn strategy for fire management at Uluru (Ayers Rock-Mt Olga) National Park. CSIRO Division of Wildlife and Rangelands Research, Alice Springs, Northern Territory, Australia.

Schreider, E. S., A. R. Bearlin, S. J. Nicol, and C. R. Todd. 2004. Adaptive management: a synthesis of current understanding and effective application. Ecological Management and Restoration **5:**177–182.

Smucker, K. M., R. L. Hutto, and B. M. Steele. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications **15:**1535–1549.

South African National Parks. 1997. Revised management plan for the Kruger National Park. South African National Parks, Skukuza.

Sparks, J. C., R. E. Masters, D. M. Engle, and G. A. Bunkenhofer. 2002. Season of burn influences fire behavior and fuel consumption in restored shortleaf pine-grassland communities. Restoration Ecology **10:**714–722.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications **15:**532–542.

Sullivan, T. P., and D. S. Sullivan. 2001. Influence of variable retention forests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology **38:**1234–1252.

Tews, J., U. Brose, V. Grimm, K. Tielborger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography **31:**79–92.

Trainor, C. R., and J.C.Z. Woinarski. 1994. Responses of lizards to three experimental fires in the savanna forests of Kakadu National Park. Wildlife Research **21:**131–148.

Tucker, J. W., W. D. Robinson, and J. B. Grand. 2004. Influence of fire on Bachman's Sparrow, an endemic North American songbird. Journal of Wildlife Management **68:**1114–1123.

Turner, M. G. 2005. Landscape ecology in North America: past, present and future. Ecology **86:**1967–1974.

Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and the Environment **1:**351–358.

Vale, T. R., editor 2002. Fire, native peoples and the natural landscape. Island Press, Washington, D.C.

Van Lear, D.H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implication for species at risk. Forest Ecology and Management **211:**150–165.

van Wilgen, B.W., H. C. Biggs, and A.L.F. Potgieter. 1998. Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. Koedoe **41:**69–87.

van Wilgen, B.W., W.S. W. Trollope, H. C. Biggs, A.L.F. Potgieter, and B. Brockett. 2003. Fire as a driver of ecosystem variability. Pages 149–170 in J. T. Du Toit, K. H. Rogers, and H. C. Biggs, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C.

Wardell-Johnson, G., M. Calver, D. Saunders, S. Conroy, and B. Jones. 2004. Why the integration of demographic and site-based studies of disturbance is essential for the conservation of jarrah forest fauna. Pages 394–417 in D. Lunney, editor. Conservation of Australia's forest fauna. Royal Zoological Society of New South Wales, Mosman, Australia.

Westoby, M., B. H. Walker, and I. Noy-Meir. 1989. Opportunist management for rangelands not at equilibrium. Journal of Range Management **42:**266–274.

Whitehead, P. J., D.M.J.S. Bowman, N. Preece, F. Fraser, and P. Cooke. 2003. Customary use of fire by indigenous peoples in northern Australia: its contemporary role in savanna management. International Journal of Wildland Fire **12:**415–425.

Wiens, J. A. 1997. The emerging role of patchiness in Conservation Biology. Pages 93–107 in S.T.A. Pickett, R. O. Ostfeld, M. Shachak, and G. E. Likens, editors. The ecological basis of conservation. Chapman and Hall, London.

Williams, P. R., R. A. Congdon, A. C. Grice, and P. J. Clarke. 2003. Effect of fire regime on plant abundance in a tropical eucalypt savanna of northeastern Australia. Austral Ecology **28:**327–338.

Willson, A. 1999. Fire management plan Tarawi Nature Reserve July 1999–July 2004. New South Wales National Parks and Wildlife Service, Lower Darling District, Buronga.

Woinarski, J.C.Z., and H. F. Recher. 1997. Impact and response: a review of the effects of fire on the Australian avifauna. Pacific Conservation Biology **3:**183–205.

Woinarski, J.C.Z., C. Brock, A. Fisher, D. Milne, and B. Oliver. 1999. Response of birds and reptiles to fire regimes on pastoral land in the Victoria River District, Northern Territory. Rangeland Journal **21:**24–38.

Woinarski, J.C.Z., D. J. Milne, and G. Wanganeen. 2001. Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. Austral Ecology **26:**360–370.

Woinarski, J.C.Z., J. Risler, and L. Kean. 2004. Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern Territory, Australia. Austral Ecology **29:**156–176.

Woinarski, J.C.Z., R. J. Williams, O. Price, and B. Rankmore. 2005. Landscapes without boundaries: wildlife and their environments in northern Australia. Wildlife Research **25:**377–388.

Yibarbuk, D., P. J. Whitehead, J. Russell-Smith, D. Jackson, C. Godjuwa, G. P. Cooke, D. Choquenot, and D.M.J.S. Bowman. 2001. Fire ecology and Aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. Journal of Biogeography **28:**325–344.

York, A. 1994. The long-term effects of fire on forest ant communities: management implications for the conservation of biodiversity. Memoirs of the Queensland Museum **36:**191–199.

