

Fire regimes and regional biodiversity declines in north-west Australian tropical savannas? : review of knowledge and recommendations for future research

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ABSTRACT

A key conservation issue in north-western Australia is recent declines in biodiversity, especially among the nationally threatened critical weight range (35g–5kg) mammals. Changed fire regimes are implicated as a cause of these declines, but it is unclear whether declines are related to fire, or to other key threatening processes. In this review, historical and scientific evidence for fire driven declines are examined and critically evaluated. Data suggest we cannot confidently attribute biodiversity declines to fire based on available evidence. This is because historical evidence is circumstantial only, and because scientific evidence showing changes in abundance relating to fire regime may not relate to regional scale declines and range contractions. A way forward in understanding factors driving declines is investigation of key mechanisms underlying fire effects. The importance of correct diagnosis of mechanisms is emphasised as incorrect assumptions can lead to inappropriate management of declining species. Three hypotheses about key mechanisms are raised based on general conservation biology approaches for threatened species, and also on evidence gained from northern Australia ecological studies. These are 1) that declines are driven by increased predation mortality through repeated removal and simplification of vegetation cover by severe fire regimes; 2) that declines are driven by resource limitations caused by too frequent fires; and 3) that declines are driven by failure to retain sufficient source breeding populations in optimal habitats (e.g. unburnt patches) within savanna landscapes for the continued persistence of fire-sensitive species. I suggest prescribed burning operations should aim to explicitly retain long unburnt vegetation patches (>3 years, >1 ha) frequently within the landscape. Our lack of knowledge of key mechanisms driving declines, and evidence that threatened species are fire-sensitive, suggests that indiscriminate application of fire mosaics may be harmful to some threatened species.

Keywords: critical weight range mammals, Kimberley, fire intensity, mechanisms, fire response

INTRODUCTION

Considerable attention has been given to the idea that fire regimes in northern Australia are associated with recent declines in biodiversity. Fire has been invoked, particularly as a threatening agent for the critical weight range (CWR) mammals (35g–5kg) (Andersen *et al.* 2005; Woinarski *et al.* 2001), granivorous birds (Crowley & Garnett 1999; Dostine *et al.* 2001; Woinarski & Tidemann 1992), a number of fire sensitive savanna trees/shrubs (Bowman *et al.* 2001; Russell-Smith *et al.* 2002; Russell-Smith *et al.* 1998), rainforests (Bowman & Panton 1993; Bowman *et al.* 1990; Russell-Smith *et al.* 2004; Woinarski *et al.* 2004) and riparian plant species (Douglas *et al.* 2003). Evidence for fire related declines comes from the apparent historical coincidence of increasingly severe fire regimes with declines (Woinarski *et al.* 2001), observational studies

comparing populations and communities in areas with different fire regimes (e.g. Russell-Smith *et al.* 2004a; Vigilante & Bowman 2004a), and from experimental studies showing fire response (e.g. Williams *et al.* 2003; Radford *et al.* 2008).

Despite this body of evidence, considerable uncertainty remains concerning declines in various species, and the role of fire in these declines. Although it is clear that organisms do respond, sometimes negatively, to fire (Andersen *et al.* 2005; Woinarski *et al.* 2001), it is not clear whether these responses are related to regional scale declines. Many other factors, including grazing by cattle (McKenzie 1981; Franklin 1999; Franklin *et al.* 2005) and other introduced herbivores (Werner 2005), predation and other impacts by introduced animals (Burbidge & Manly 2002; Greenlees *et al.* 2007; Johnson 2006), clearing, and plant invasions (Grice 2006; Rossiter *et al.* 2003; Valentine *et al.* 2007), could all be invoked to explain plant and animal declines in northern Australia.

A key area of uncertainty concerning fire (and other threatening processes affecting northern biota) are the fundamental mechanisms underlying biotic fire responses (Williams *et al.* 2003). An understanding of these mechanisms is crucially important because without them we are blind to the real causal problem of declining biodiversity. Our lack of knowledge of mechanisms underlying fire responses is a serious issue within a land management context. This is because we don't know what outcomes we are aiming for within a prescribed burning operations to mitigate the threatening processes. For instance, should we be aiming to reduce the total area burnt annually or biennially (e.g. reducing fire rotation), to increase the diversity of fuel age structure (e.g. increase resource diversity), to maintain unburnt areas annually or perennially (e.g. for habitat refuge), or to simply reduce the overall fire intensity (but not area) by burning earlier in the year (e.g. to reduce impacts on shrubs and trees). Each of these aims may use a different management strategy to implement them, and would have potentially quite different biodiversity outcomes as their ultimate goals. Current fire management in north western Australian savannas does not explicitly frame prescribed burning objectives in relation to detailed knowledge of mechanisms underlying threatened species ecology. In the absence of this information we are applying fire management blindly.

In this review I will evaluate the evidence that fire has driven declines of biota in north western Australia. The area of focus in this review will mainly be the wetter northern parts of the tropics in the Top End of the Northern Territory and the Kimberley WA (annual rainfall >600 mm), where up until recently many threatened groups were still abundant (Woinarski *et al.* 2001). Many arid parts of northern tropical savannas had lost threatened groups many decades ago (McKenzie 1981, Johnson 2006) and are not further considered in this review. Threatened groups include the critical weight range (CWR) mammals, granivorous birds and fire sensitive plant species, though in this review I focus primarily on fauna. I will also present what I believe is the way forward to achieve a practical understanding of the key factors involved in declines of these groups. This review will first examine the nature of the evidence that fire influences populations, and whether there is sufficient evidence to attribute fire regimes as one of the key drivers. Second, given the complexity of competing threatening processes, including fire, I suggest a conceptual framework within which to view declining populations. This conceptual framework, originally proposed for conservation of endangered species, focuses on fundamental mechanisms that underlie declines (Caughley & Gunn 1996). By looking behind fire, or other threatening phenomena, this approach seeks to correctly diagnose the cause of declines, so that an effective remedy can be designed to prevent further declines and to promote recovery. Third, I present what I see as the key hypotheses relating to underlying mechanisms that enable fire to influence plant and animal populations. Finally, I recommend the use of the precautionary principal in application of prescribed

management programmes in northern Australia given our basic lack of knowledge of the mechanisms underlying fire effects.

EVIDENCE FOR FIRE INDUCED DECLINES IN NORTHERN AUSTRALIA

The causal link often drawn between biodiversity declines in north western Australia and fire regime change is essentially speculative in nature. This is not to say that fire is not an important factor, nor that fire does not influence plant and animal populations, but simply to state that no causal link between fire responses and regional scale historical declines can yet be made.

Relevance of scientific studies to regional scale declines

Studies showing the impacts of fires cannot necessarily be scaled up to regional or national declines. Evidence that fire regimes in northern Australia do affect plant and animal populations is unambiguous (Andersen *et al.* 2005; Bowman & Franklin 2005; Radford *et al.* 2008; Russell-Smith *et al.* 2003a; Vigilante & Bowman 2004a; Woinarski *et al.* 2004). Numerous experimental and post hoc observational studies have clearly shown that high fire frequency or intense fires lead to reduced abundance of small mammals, shrubs, reduced complexity of woody vegetation structure, and selective removal of obligate seeding shrubs and fire sensitive plants. There is evidence of a dichotomy between species preferring long unburnt habitat (fire-sensitive), and those preferring recently burnt habitats (fire-tolerant), with little evidence of intermediate functional groups (Andersen *et al.* 2005; Felderhoff 2006; Woinarski *et al.* 1999). However fire research in northern Australia, by necessity, has been conducted at relatively small scales or over relatively limited time periods in the context of tropical savannas (Woinarski *et al.* 2005). It is therefore unknown how representative these studies are of the greater savanna landscape. In addition, proving that fire regimes influence abundance does not prove that the same processes are involved in causing regional scale declines.

An example of fire influences not necessarily reflecting regional level dynamics was provided by the Kapalga fire experiment conducted in Kakadu National Park during the 1990's. Animal abundance was recorded across all experimental fire treatments in this study. It was found that all CWR mammal species declined across all treatments, including both high intensity late dry season fires, and in unburnt controls (Andersen *et al.* 2005; Corbett *et al.* 2003a). This suggests the possibility of another more general process operating throughout the area, irrespective of fire regime.

More evidence that fire regimes alone are not responsible for mammal declines across northern Australia is provided by high mammal abundance in some areas which continue to have intense, extensive wildfire regimes. At the same time that trap captures at Kapalga/Kakadu

have declined to <1% (Woinarski *et al.* 2001; Woinarski *et al.* 2010), other areas, including the north Kimberley, continue to have trap success equivalent to Kapalga in 1980's (10–30%) up to the present (Start *et al.* 2007; I.J. Radford¹ unpublished data 2009). This is despite the continued occurrence of extensive, high intensity fire regimes in the north Kimberley (Russell-Smith *et al.* 2003c).

Despite the lack of scientifically justifiable linkage between what happens at population and regional levels, it is tempting to believe that population level processes do play a role at larger regional or meta-population levels. Within the broader context, factors that tend to cause declines in population abundance in given areas will obviously have flow-on effects at the larger scale. This might be particularly so in the case of fire, where optimal “source” breeding habitats, for instance in longer unburnt fragments, may be extremely rare in the broader landscape context. Many fires cover thousands of square kilometres and can burn for months in this region (Russell-Smith *et al.* 2003b). This could potentially lead to considerable delay in site recolonisation, particularly for smaller ground based species like the CWR mammals. North Australian biotic declines have not yet been investigated at this landscape scale.

Historical evidence for fire related declines only anecdotal

There is no direct published evidence showing coincidence between historical change in fauna abundance and fire regimes. Fire regimes in northern Australia have been described (Crowley & Garnett 2000; Fensham 1997; Preece 2002; Vigilante 2001), but not systematically quantified, before the 1990s when satellite technology allowing us to measure spatial patterns in fire scars became widely available (though see Bowman *et al.* 2007 for alternative method). Aerial photography has allowed quantification of fire pattern changes prior to removal of Aboriginal occupation in only one published instance in the western desert (Burrows & Christensen 1990; Burrows *et al.* 2006). While fire regimes have been quantified in recent times, there are therefore no continuous records showing the progress of change in fire regimes from that under a traditional Aboriginal management, through Aboriginal depopulation and establishment of pastoralism, through to the periods known for declines of northern species.

There is no evidence that documented declines, such as those of small and medium mammals in Kakadu National Park (Braithwaite & Muller 1997; Woinarski *et al.* 2001), coincide with changes in fire regimes. The earliest quantified fire regime data for Kakadu in the late 1980s, already showed dominance of large scale mid to late dry season fires at that time, though a trend towards increased earlier dry season burning has occurred since

1990 (Russell-Smith *et al.* 1997). This suggests that the period of change to the current regimes, dominated by large scale late dry season fires, had already occurred by the 1990s.

The implication that breakdown of traditional Aboriginal burning practises has led directly to declines in savanna species is not supported by historical evidence. There has been considerable attention given to Aboriginal burning practises, and their role in maintaining threatened species in savanna landscapes. However, while it may be true that traditional Aboriginal burning practises were compatible with maintenance of threatened species, this does not necessarily suggest that they required this traditional burning. Irrespective of the role of Aboriginal burning in plant and animal ecology, breakdown of these regimes in most parts of the northern savannas greatly predates recent declines. While declines of CWR mammals in Kakadu occurred as late as the 1980s and 1990s, movement off country of Aboriginal populations had generally occurred decades previously prior to the 1940s. If there is a link between traditional Aboriginal fire regimes and maintenance of biodiversity, there must be an extensive lag phase. Rather I would argue that patchwork small scale fires generally described within traditional systems (Bird *et al.* 2005; Craig 1997; Haynes 1985; Preece 2002) maintained species by not burning areas or by protecting areas from fire, rather than by providing a diverse range of species specific post-fire successional habitats (see below).

In the absence of direct data linking historical species declines with changes in fire regimes, or linking of site-based fire responses to regional level dynamics, we are left with little certainty as to the causes of species declines in northern Australia. Other factors, particularly cattle grazing (Dawes-Gromadzki 2005; Franklin 1999; Franklin *et al.* 2005; McKenzie 1981; S Legge² unpublished data 2009), have also been convincingly linked with species declines or ecosystem degradation in northern Australia.

HYPOTHESIS DRIVEN RESEARCH: CAUSAL MECHANISMS UNDERLYING FIRE RESPONSES AND SPECIES DECLINES

Research into fire ecology in northern Australia has mainly focused on patterns of response in different organisms to different fire regimes (Williams *et al.* 2003). This has either been through experimental imposition of fire, or by *post hoc* comparison of biodiversity patterns in areas with different natural fire regimes. The problem with this approach is that we don't know why particular species respond to fire in the way they do. What are the fundamental mechanisms relating to fire that might be driving species declines? Are individuals killed by

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frequent, intense fires, do they starve because food resources are removed, or are they subjected to increased predation or disease due to open stressful environments? These are important questions if we hope to address the cause of reported species declines in northern Australia. Addressing the key mechanism/s causing species declines is a crucial part of any programme to promote recovery of threatened species (Caughley & Gunn 1996). Without direct knowledge of cause, prescribed management treatments, whether prescribed burning or other treatments (e.g. cattle removal, predator culls), may be completely ineffective in halting or reversing declines. Such cases are common through conservation history (Caughley & Gunn 1996).

Despite the need to investigate mechanisms underlying fire responses, few studies have yet attempted this in northern Australia (Williams *et al.* 2003). The exception is that mortality of trees and shrubs due to the effects of fire intensity and season is relatively well understood (Russell-Smith *et al.* 2003a; Williams *et al.* 1999; Williams *et al.* 1998). However, the relative importance of other mechanisms associated with fire responses and declines are poorly known.

The only effective way to address the causes of species declines in conservation biology is correct diagnosis of cause through hypothesis driven experimental testing (Caughley & Gunn 1996). Without these features of the experiment, it is impossible to attribute the effects of mechanisms measured on populations to the mechanism itself, and there will be uncertainty about what results mean (Caughley & Gunn 1996). It is crucial within this approach that experimental treatments are designed with appropriate controls and replication. It is also important, if possible, that treatments replicate practical management treatments that could be imposed to ameliorate key mechanisms causing declines. This is because for effective recovery to be achieved, it must be pragmatic. However, there is no substitute for careful, basic species level research incorporating manipulative management treatments to achieve an understanding of the dominant drivers of population fluctuations in the field.

The effects of fire (or cattle, invasive plants, invasive predators) in northern Australian landscapes are complex. Fire consumes material, changes chemical composition of soils and above ground material, removes living and structural habitat attributes and selectively removes fire sensitive species (Andersen *et al.* 2005; Bowman & Prior 2004; Edwards *et al.* 2003; Russell-Smith *et al.* 2004b; Russell-Smith *et al.* 2003a; Vigilante & Bowman 2004a; Woinarski *et al.* 2004). For this reason, to say that fire as a phenomenon causes a particular response is not very informative about the mechanisms affecting particular threatened species. There could be multiple reasons for a particular response. Evidence from a number of studies suggests that few of the impacts of fire are directly related to mortality due to the heat of the fire itself (Sutherland & Dickman 1999). The exception to this is obviously fire sensitive shrubs and trees, for which fire intensity directly affects their survivorship (Williams *et al.* 1999; Williams *et al.* 1998).

Based on previous research I would like to raise what I see as three key competing, but not mutually exclusive, hypotheses concerning mechanisms underlying fire effects on north western savanna species. These are loosely based on generalised mechanisms used in conservation of endangered species as outlined in Caughley & Gunn (1996), but also use documented literature from northern Australian fire research and elsewhere to derive specific hypotheses. Obviously mechanisms may differ among species and taxonomic groups. However classification of species into functional response groups will allow us greater potential to design management treatments (e.g. prescribed fire or feral animal control) specifically for the benefit of particular threatened species. Such information will be crucial for maintaining critically threatened species.

1) Declines caused by increased predation rates with fire-related loss of ground cover

This hypothesis relates primarily to threatened fauna in northern Australia. Threatened flora declines can be more directly related to fire patchiness and intensity due to relatively simple relationships between fire intensity and plant mortality. However this may not be the case for fauna including the CWR mammals (Clarke 2008). While fauna are subject to direct fire mortality, evidence from southern Australia suggests that abundance post-fire is little related to initial fire mortality (Sutherland & Dickman 1999). The rest of this section will address predation as a process related to post-fire abundance only for fauna.

A number of recent syntheses (Burbidge & Manly 2002; Dickman 1996; Johnson 2006) have identified impacts by the introduced predators (cats and foxes) as possibly the primary drivers of CWR mammal extinctions since European settlement. Extinctions have been most numerous in the arid zone, though they have been a national phenomenon (McKenzie *et al.* 2007). Evidence for the pivotal role of introduced predators in extinctions is provided by patterns of extinction relative to the arrival of these species compared to other influences (Johnson 2006). A number of extinctions, mostly rodents under 1 kg, that occurred in remote northern arid areas predate clearing, arrival of domestic stock or feral herbivores (e.g. rabbits, goats, horses, donkeys) and can only be attributed to the early arrival of cats or foxes (Johnson 2006). There is a significant positive correlation between mammal extinctions on offshore islands and introduction of cats or foxes (Burbidge & Manly 2002).

If historical extinctions of CWR mammals in the arid zone are related to predator pressure from introduced cats and foxes, it is plausible that recent declines in northern Australia are also related to this factor. In this region, decreased ground cover and structural simplification in recent years due to frequent large scale fires would contribute to the predator effect. Fire regime directly affects the amount of ground cover available for small and medium mammals. So even though Australian CWR mammals are adapted to a range of fire regimes which pre-date human occupation of Australia, they are not

adapted to predation by cats and foxes. Small mammal species in Australia are known to respond positively to increasing vegetation structural complexity and cover (Law & Dickman 1998; Spencer *et al.* 2005; Sutherland & Dickman 1999). It has been shown that small mammal abundance can be influenced by structural habitat attributes protecting them from predators (Arthur *et al.* 2005). It is clear that fire can affect ground vegetation cover and vegetation structure (Andersen *et al.* 2005; Edwards *et al.* 2003; Russell-Smith *et al.* 2003a; Vigilante & Bowman 2004a; Woinarski *et al.* 2004). Fire regimes of high frequency, extensive coverage, lack of habitat refuge and extended periods before vegetation recovery would be most likely to cause declines in species requiring cover from predators.

Evidence of the primary importance of introduced predators relative to fire per se was provided by Short & Turner (1994). They documented no effect of vegetation seral stage on CWR mammals of Barrow Island where there are no feral cats. None of these CWR mammals are found on mainland sites where cats are present. Similarly, extinctions of CWR mammals on many north western offshore islands are most directly related to presence of introduced predators, particularly cats.

Although few studies have explicitly compared causes of fauna mortality (predation, starvation) or factors affecting mortality (predator populations, structural shelter from predators provided by vegetation), between burnt and unburnt habitats in north west Australia, increases in many predator species are well documented in recently burnt habitats. It is known that many predator species increase in recently burnt, or actively burning habitats (Corbett *et al.* 2003b). Increase in predatory bird species such as black kites, or insectivorous species such as magpie larks, has been documented in recently burnt habitats in several northern Australia studies (Braithwaite & Estbergs 1987–88; Corbett *et al.* 2003b; Woinarski *et al.* 1999; Woinarski *et al.* 2004), though this has not been directly tested in northern Australia in relation to fire. There is a varied fire response among reptile predators, with some species including the frilled neck lizard preferring recently burnt country, while others do not (Andersen *et al.* 2005; Corbett *et al.* 2003b). It is not known how feral cats and foxes respond to fire in northern Australia.

It is currently unknown whether the mechanism of cat predation and removal of vegetation cover (through frequent fires or by cattle) is an important mechanism driving declines in north western tropical savannas. Cats are known to be present throughout the Kimberley and to have been present as naturalised populations since as early as 1890 (Abbott 2002). Foxes periodically invade this region from the south in favourable seasons. Nothing is published of population dynamics of introduced predators in relation to the fire cycle in tropical Australia, nor the impacts they have on associated mammal populations. This should be an important area of future research into declines in northern CWR mammals, either through use of predator shelter, or more directly through cat baiting/culling treatments. Given the weight of

evidence for a strong predator effect this would be a priority for future research.

An obvious objective of fire management for savanna species susceptible to predation (e.g. CWR mammals), would be to provide sufficient vegetation cover for them to avoid predators. Unlike many other groups, CWR mammal species require relatively large areas of habitat in order to persist (>1ha). It will therefore be critical within fire management treatments, to provide for this explicitly. Random ignitions are unlikely to provide this habitat structure due to the deterministic nature of fuel removal by fire (van Wilgen *et al.* 2004). Systematic and targeted effort may be required to provide significant late seral stage, high biomass/ground cover vegetation within burnt areas, particularly if optimal habitat for mammals have >2 years growth. There may be a need to include some suppression activities in northern land management agency repertoires in order to protect such patches against wildfire.

The hypothesis that threatened savanna species have undergone declines due to removal of ground vegetation cover is consistent not only with increased fire activity, but also with cattle impacts. The intensity of grazing enterprises has been positively correlated with declines in small mammals and a number of bird groups (Franklin 1999; Franklin *et al.* 2005; McKenzie 1981). Although environmental impacts by cattle presumably differ from fire impacts in some respects (e.g. species specific selective pressures, differing effects on woody plant species), both processes remove and alter herbaceous vegetation structure and thereby alter habitat cover attributes relevant to prey species. In this respect both processes might contribute to declines of CWR mammals and some bird species through removal of cover. Although removal of herbaceous cover has not been postulated as a mechanism underlying declines in birds (e.g. threatened finch species), widespread removal of shrub layer vegetation under severe fire regimes, may have a similar impact on birds through increased predation (e.g. by raptor species), to those postulated for mammal species by cat and fox predation.

Other mortality factors related to fire regime

I have focused here primarily on the hypothesis that loss of protection from predators is a key mechanism underlying possible increases in mortality rates in burnt landscapes. There could be other sources of increased mortality in burnt landscapes. Parasitism and disease, along with predation, is a major mortality factor in ecological communities. The role of an increasingly stressful environment due to extensive fire may have effects on plant and animal fitness in burnt (or long unburnt) landscapes. This mechanism has been little investigated in northern Australian biota in relation to fire, though some research into the role of parasitism in threatened finch species has been undertaken (Tidemann *et al.* 1999). In this case parasitism was thought to be secondary to other factors driving declines in these threatened finch species (Dostine *et al.* 2001; Franklin *et al.* 2005).

Tests of the predation (herbivory)/ground cover hypothesis

There are a number of ways of testing the predation-ground cover hypothesis. An initial step is to gather evidence that there are increased numbers of predators, or predator activity in areas with lower vegetation cover and structural complexity (i.e. due to recent fires). The next step is to document the relative impact of predation on prey populations at sites with differing vegetation cover. This will involve detailed demographic study and analysis of the fate of individuals from prey populations (predation or not, which species of predator). Finally, to fully demonstrate the importance of predation and habitat cover on populations, we need to design studies which experimentally manipulate habitat cover and predation levels (preferably within a factorial experiment) in order to test for their relative importance. For the latter to be successful such experimentation should include appropriate experimental controls where no habitat or predator manipulations are imposed, and also should be done at sites where data on pre-treatment population dynamics is available. Only in this way can responses be confidently attributed to experimental treatments within spatially and temporally variable savanna ecosystems.

2) Declines caused by fire-related change in resource availability

The resource limitation hypothesis is perhaps the key alternative hypothesis to the predation-fire hypothesis for declines among northern savanna species. This hypothesis has been raised to explain declines in tropical granivorous birds, including a number of finch species. The hypothesis is that a shortage of grass seeds, particularly during the wet season, is a major factor leading to declines (Dostine *et al.* 2001; Garnett & Crowley 1994). Frequent fires are thought to reduce or stop perennial grasses, including *Triodia* spp. and *Alloteropsis* spp., from producing seeds for a year or more. This hypothesis is currently being tested in a major study across northern Australia (S. Garnett³ & S. Legge⁴ pers. comm. 2007). A similar mechanism may operate to reduce the extent and abundance of many granivorous native rodent species in northern savannas (Start *et al.* 2007).

Fruiting and flowering of a number of tree species has been shown to be affected by fire (Vigilante & Bowman 2004b). This could have impacts not only on recruitment of the trees themselves, but also on populations of organisms that depend on these resources. Species known to feed on fruits and flowers and also thought to be threatened, include possums (e.g. *Petropseudes dahlia* and *Wyulda squamicaudata*) and arboreal rodent species (e.g. *Conilurus penicillatus* and *Mesembriomys macrurus*)

(Thompson 1996). The importance of this factor in causing declines populations has not been investigated.

Frequent high intensity fire regimes may reduce total ecosystem productivity and therefore the levels of multiple savanna resources. Frequent fire has been shown to have important effects on soil nutrient levels, including nitrogen reserves in tropical Australian savannas (Cook 1994; Cook 2003). Fire is also known to influence soil microbial communities, which in turn can influence resources available to and survival of tropical plant species, including a number of rainforest species (Bowman & Panton 1993). The influence of these key resources, not only for particular species, but for overall ecosystem functioning and productivity, is a key area of future research in regard to fire regime impacts in savannas.

Tests of fire-resource limitation hypothesis

There are a number of ways of testing the resource limitation-fire hypothesis. Initial work needs to be done documenting the key resources used by the target species. Some of this information can be gained through faecal analysis, field observations and isotope analyses of animal tissue. The dynamics of resources then needs to be documented, particularly with respect to fire succession. The relationship between dynamics of the target species and the resources can then be assessed. Relationships between resources, and the factors that potentially affect their dynamics (rainfall, nutrient flushes, fire) will begin to allow an ecosystem level understanding of regulation of populations. If patterns are similar among different trophic levels in the ecosystem, even with a lag phase, this might be circumstantial evidence that the resource partially determines the dynamics of the target species. If resources do not relate to species dynamics, it may be that resource fluctuations are independent of species numbers and demographic variables. This would indicate that some other feature in the ecosystem is driving populations. The final definitive test for the role of resources in population fluctuations is use of resource supplementation or removal experiments, both in the presence and absence of recent fire.

3) Declines caused by post-fire recolonisation failure in frequently burnt landscapes

Research into landscape scale functioning of species in northern savannas has not been undertaken and is likely to be a major challenge to ecologists. Conceptualisation of population processes within the larger landscape scale context, however, may be beneficial for an understanding of the role of fire and underlying mechanisms in the vast northern savanna landscapes.

One area of theory that may be applicable to fire regimes in northern savannas is metapopulation theory (Hanski 1994; Hanski & Gilpin 1991). Briefly this theory focuses on populations as functioning within a matrix of habitats across a landscape which vary in their quality or benefit to particular species (e.g. due to resource, predator

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or disease distribution). This is a useful concept in terms of fire regime effects in northern savannas because recently burnt and longer unburnt habitat will differ in quality for different species depending on whether they are early or late fire succession species. Fire sensitive species (those responding negatively to recent fire) are likely to require long unburnt habitats as “source” or breeding habitats within the landscape. A “source” habitat is one in which a species can maintain populations and/or increase in numbers to provide excess individuals to allow dispersal and colonisation of other habitats. Source populations will be required for each species within a landscape to provide individuals for establishment of populations in “sink” habitats or newly available suitable source habitats. In a fire context this would include habitats that had temporarily become unsuitable for breeding populations due to some effect of fire (e.g. increased predation or resource limitation). In the context of burnt landscapes “sink” habitats may be areas that are unable to support populations of the species.

Although populations of threatened species in northern savanna landscapes have not been investigated in this way, there are a number of studies which at least support the notion that some species use patches of unburnt habitat within burnt landscapes as refuges. *Pseudomys desertor* and *Pseudomys nanus* at Purnululu National Park (Partridge *et al.* unpublished), and *Rattus tunneyi* and *Pseudomys nanus* at Mornington Station in the Kimberley (Legge *et al.* 2008) are both largely restricted to areas within burnt landscapes of higher vegetation biomass where recent fire had been excluded. While other mammal species are apparently unaffected by fire patchiness (e.g. *Pseudomys delicatulus*) this indicates the possibility that populations of some species will use these patches as source habitats for recolonisation into surrounding areas.

In a metapopulation context, biodiversity declines and extinctions in northern Australia may occur where source populations and recolonisation rates are insufficient to allow for re-establishment of fire sensitive species (e.g. CWR mammals) in frequently burnt landscapes. If CWR mammals require >2 years between fires for habitat to be suitable, there may be insufficient source habitats and dispersal opportunities to allow persistence across much of the savanna landscape.

One approach to testing the effect of differing source sink patterns in allowing persistence of populations would simply be to compare post-fire re-establishment/colonisation rates under differing fire regimes. This would involve gathering baseline data on population dynamics of target species, and then applying management fire regimes to those areas. Such work would best be applied to fire-sensitive species such as CWR mammals or threatened finches. There are three primary fire regime patterns that should be compared based on the above discussion and previous literature. These are (i) fire regimes where patches of long unburnt vegetation (>2 years) are deliberately protected (1ha–1km² scale) as habitat refuges within burnt areas, (ii) landscapes with a diverse but more or less random patch mosaic burning (frequent broad-

scale burning at low fire danger periods) to reduce the intensity and size of wildfires, and (iii) landscapes under ambient fire regimes consisting of extensive and intense dry season fires, typically with few unburnt patches or shelter refuges (few, scattered unburnt patches). It would be expected that recolonisation rates would be greater where there is greater fire patchiness (greater diversity of vegetation structure) and more unburnt patches retained. Given the sparseness of dispersing individuals in extensive savanna landscapes this type of study would require substantial trapping or sampling effort.

MOSAIC THEORY AND APPLICATION OF PRESCRIBED BURNING AMIDST UNCERTAINTY ABOUT MECHANISMS

Given the level of uncertainty concerning the role of fire in regional declines of fauna, and the lack of a clear understanding of fire-related mechanisms underlying declines, what should fire management and land owners be applying? Anecdotal evidence of increased instances of dry season fires, and the number of uncontrolled ignition sources, suggests that some form of protective burning should be attempted. However, what should this prescribed burning be trying to achieve as a target?

One approach to fire management put forward in northern Australia and elsewhere is the patch mosaic burning approach. In extensive landscapes such mosaics of different post-fire seral stages are designed not so much to provide barriers to fire, as regrowth is rapid enough not to allow fire breaks to be established for long, but to reduce overall fuel loads and therefore reduce fire intensity and increase patchiness of wildfires. In terms of goals relating to threatened fauna, this is a bet-hedging approach that aims to provide a range of post-fire habitats. This approach is argued to provide a range of habitat types, structures and resources in the hope that animals will benefit. Diversity in habitat structure and seral stage is argued generally to be beneficial to both flora and fauna (Law & Dickman 1998).

However, the benefit that flora and fauna will derive from a fire mosaic will vary according to the specific requirements of the species concerned. If, as I argue, many of the CWR mammals require longer term unburnt patches (>2 years), a randomly applied fire mosaic may not provide this. This is because areas of high fuel beneficial to these species will selectively burn under a random ignition approach. Achieving several years without fire in significant patches throughout the landscape may require considerable targeted burning, probably similar to traditional Aboriginal burning. It also may require fires to be put out. This is seldom done in northern landscapes due to lack of personnel, available resources and the remoteness of the country. Land management agencies in northern Australia do not have the resources available which would allow them to apply fine scale mosaic burning to large areas, or to undertake suppression of wildfires.

I believe that a key aim in applying mosaics in north western savannas should be to provide late seral stage or high biomass/cover vegetation patches, or longer unburnt fuels, for maintenance of threatened species. As discussed above there is considerable evidence that many species, including the CWR mammals, will benefit directly through retention of longer unburnt habitat areas (>3 years or >5 years in more arid areas) (Andersen *et al.* 2005; Corbett *et al.* 2003a; Pardon *et al.* 2003). It appears that too much fire, not too little, is the main problem facing most of the threatened species in north western savannas (Andersen 1999). In contrast to north eastern savannas, where intensive management has allowed effective fire suppression and associated environmental problems including exotic plant invasion (Grice 2006; Radford *et al.* 2008) and land degradation due to overgrazing (Ash *et al.* 1997; Cook *et al.* 2004), there appears to be little evidence that threats to ecosystems in north western Australia result from a lack of fire. In this context, and with abundant ignition sources (both natural and anthropogenic), it is difficult to make the argument that land managers need to burn specifically to provide recently burnt habitat for wildlife. Evidence showing that most of the threatened species in northern savannas are, if anything, fire sensitive (need access to long unburnt areas), suggests that burning in this region should be aimed at protecting or promoting retention of patches of long term unburnt vegetation (3–5 years) (Andersen 1999).

It is often implied that milder, patch mosaic burning regimes would benefit biodiversity in northern Australia by buffering the effects of the severe regimes currently underway. Indeed for plants the application of low intensity early season broad-scale fires could be argued to facilitate the survival and recovery of fire sensitive species, as mortality of these species is directly related to fire intensity (Russell-Smith *et al.* 1998). However, the same may not be effective for maintaining other fire sensitive species such as the CWR mammals, within savannas, as these species may need long unburnt areas, not just reduced intensity fires. These fauna species will only benefit from regimes where vegetation cover from grasses and shrubs are retained in significant areas (>1ha) throughout the landscape. Extensive early dry season burning to reduce later wildfire intensities, as advocated in many published papers, may not benefit species like the CWR mammals if dense vegetation patches are removed.

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