

Fire intensity and the maintenance of habitat heterogeneity in a tropical savanna

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ABSTRACT

Savanna vegetation is associated with a highly seasonal tropical climate which results in high-frequency grass fires. Other studies have shown that there are strong relationships between habitat heterogeneity or patchiness and mammal richness and abundance in the savannas of Kakadu National Park. Fires vary greatly in intensity and impact on vegetation. Both pronounced patchiness and differentiation of ground and canopy strata are fundamental characteristics of savannas. A model to account for what appears to be a dynamic stasis is presented. In this model, low intensity fires create great patchiness in the ground layer. In contrast, both high-intensity fires and absence of fire create patchiness in the tree layer, owing to differential tree mortality and recruitment from the ground layer respectively.

Experimental fires in Kakadu showed different effects on the tree and ground layers, lending some support to the above model. Fire-induced changes in vegetation patchiness, dominant plant species richness and mammal abundance and richness were apparent. It is likely that a fire regime approximating the pattern created by traditional Aboriginal burning is the best management for savanna biodiversity.

INTRODUCTION

The pattern of any vegetation changes with time. The speed at which this happens is determined by the frequency and intensity of disturbance and also the productivity of the system. Huston (1979) has argued that maximum species diversity occurs when the frequency/intensity of disturbance maintains the community in a constant state of disequilibrium. The species never get to a stage where competitive exclusion would occur and thus loss of species is avoided. Denslow (1980) has, in turn, argued that the maximum

species diversity is obtained with disturbances which are of the historically most common size. Frequency and intensity of disturbance, the size of the disturbance patch, and the life history of the species affected are all correlated (Braithwaite and Estbergs 1985).

Regions of greater habitat diversity (for topographic/geological reasons) are often richer in species of animals (i.e. alpha diversity; Woinarski and Braithwaite 1990). Whether habitat diversity can be manipulated with fire to produce increased animal diversity has never, to my knowledge, been tested.

Vegetation patchiness or habitat heterogeneity seems important for a number of reasons.

1. It has become recognized as one of the three main components of biodiversity, the others being genetic diversity and species diversity (e.g. Groombridge 1992).
2. It may be an important predictor of species diversity and animal abundance (e.g. Woinarski and Braithwaite 1990). The scale of the patchiness may be what is most critical.
3. It may represent an appropriate goal for manipulating habitat for maintaining vulnerable mammal species (Braithwaite 1985a).
4. It offers the possibility of identifying areas of high biodiversity using remote sensing.

Savanna ecologists have long identified the four major determinants of tropical savannas as plant available moisture (PAM), available nutrients (AN), fire and herbivory (Frost *et al.* 1986). The first two are regarded as the primary determinants and the latter two are secondary modifiers of savannas. Fire enables eucalypt savanna to push back the boundaries of rainforest or monsoon forest patches (Bowman and Dunlop 1986) and can eliminate them entirely (Bowman and Wightman 1985). Conversely, in the absence of fire, rainforest, monsoon forest and other fire-sensitive species can slowly invade the savanna (Bowman and Fensham 1991) and at least give rise to a more shrubby understorey (Hoare *et al.* 1980).

In the literature on tropical savannas, the tree or canopy layer and the ground vegetation layer have been

seen as semi-independent, competing but co-existing systems (Walter 1971). There have been studies of competition between the root systems of the two strata, with the canopy roots predominating in deeper soil horizons (Knoop and Walker 1985). Braithwaite and Estbergs (1985) have shown that the canopy experiences fires much less than the ground layer. The species of the canopy are long-lived compared with those of the ground layer which is dominated by annuals, short-lived perennials, and the long-persisting juveniles of the canopy species.

In Australia particularly, the savanna seems remarkably stable under what appears to be a wide variety of fire regimes. It is a paradox: how can the savanna be burned and change in so many different ways yet remain savanna? How does the patchiness of the savanna relate to the species diversity of the biota? A simple patch dynamic mechanism for this is proposed and preliminary data from Kakadu National Park examined in its light.

A MODEL OF SAVANNA HOMEOSTASIS

While climatic and edaphic factors are the major determinants of the relative dominance of canopy and ground layers in savanna, the balance of dominance can move from one stratum to the other, with fire and herbivores a common agent of change (Belsky 1990). In Australia, fire with some facilitation from wood-eating termites, is the main cause of tree loss (*c.* 70 per cent of total), with windthrow (*c.* 10 per cent) and lightning (*c.* 10 per cent) and termites alone (*c.* 10 per cent) as minor agents (Braithwaite 1985b), and absence of fire the main facilitator of recruitment to the canopy (Hoare *et al.* 1980). The concept of 'clump-interclump' (Hoare *et al.* 1980) or fine scale patchiness of domination by trees or grass, is one of the defining elements of savanna. However, the patchiness within each of the ground and canopy layers is also a typical savanna characteristic which both determines and is determined by fire (Stott 1986).

It is well known, at least in tropical Australia, that early dry season fires are patchy on the ground (Jones 1980). These fires typically burn only part of the ground cover within an area of ignited savanna (Kapalga sub-catchments mean=73.8 per cent, range=30-99 per cent, n=9), leaving many individual small plants untouched by fire (Braithwaite and Estbergs 1985). However, as the young plants are still actively growing at this time of year, they are vulnerable and experience greater mortality during early dry season fires than in the typically more intense late dry season fires (P.A. Werner, personal communication, 1990). Thus I hypothesise that it is these early dry season fires which cause greatest patchiness in ground layer vegetation composition. On the other hand, at very low intensity or no fire, the existing plants grow in size, but little change in patchiness occurs. However,

species may be gradually lost through competitive exclusion (*cf.* Huston 1979), or richness increase due to absence of adversity or increase in favourableness, depending on the type of patch. Similarly, at high intensity, the ground cover receives a much more homogeneous treatment by fire, diminishing patchiness. Patchiness of the ground layer is thus also consistent with the intermediate disturbance hypothesis (Connell 1978).

The situation is different with the canopy. Typically, early dry season fires impact minimally on the canopy (Braithwaite and Estbergs 1985). In fact, the lack of impact on the flowering of fruit trees was a stated reason for the concentration of Aboriginal burning at this time (Haynes 1985). However, high intensity late dry season fires typically scorch high into the canopy (Braithwaite and Estbergs 1985) and this occurs during the period of leaf-flush before the wet season (Braithwaite 1985). Such fires are likely to cause maximum mortality (Lonsdale and Braithwaite 1991) and may create opportunities for subsequent recruitment into the canopy (Fensham and Bowman 1992). With no fires or fires of low intensity, major change in the canopy occurs due to the recruitment of plants out of the ground layer (Hoare *et al.* 1980).

The pattern of change described in the preceding paragraphs is summarized in Figure 1. Change in patchiness can be positive or negative depending on the loss or gain of individuals of fire-sensitive plant species. The degree of change in relation to fire intensity in the canopy layer is opposite to that for the ground layer. If the intensity is low, relative importance shifts towards the canopy and if it is high, it shifts towards the ground layer. At intermediate intensities, transition between the two is minimal. In combination the elements of this model can maintain savanna as a dynamic stasis. While soil moisture and nutrients are the primary determinants of vegetation type, the key to whether savanna changes to grassland or rainforest or remains as savanna is often the ambient fire regime (Frost *et al.* 1986).

In rainforest studies, Denslow (1980) has argued that the most common patch size will support the highest diversity of species. The historic disturbance regime will produce patch sizes which have been most common historically. This is one reason why the documentation of the traditional fire regime of indigenous hunter-gatherers is of significance for contemporary conservation. However, as Braithwaite (1992) has argued, the traditional regime as expressed on the landscape as a whole, is an emergent property of the activities of many quasi-independent individuals and groups. It was not the result of a brilliant ecological master-plan which we can simply take down from the historical shelf and naively apply in a contemporary context (Redford 1991) of roads, tourists, exotic species problems, contemporary technology, and changed Aboriginal culture. It is necessary to

reconstruct the historic pattern of burning and adapt it as best we can using knowledge from any source.

Braithwaite (1991) described the seasonal pattern of Aboriginal burning using the historical record from the nineteenth century and found it corresponded well with the results of independent ethnographic studies. The traditional Aboriginal regime had a peak of burning in the early dry season. However, some fires did occur at any time during the 9.5 month fire season (Braithwaite 1991). It has been found by National Park managers that the more country that is burnt during the early dry season the less that is burnt during the late dry season (Press 1988). This is partly due to the fragmentation of the savanna fuel induced by the early fires. The late fires do not carry as far because of the lack of continuity of fuel. For the same reason, parcels of land remain unburnt in an area which had received heavy early burning. Thus the three important elements necessary for the model of savanna homeostasis to work were integral to the traditional Aboriginal burning regime, early fires with some late fires and some areas unburnt.

It follows from Denslow (1980) that the traditional regime described above would maximize species diversity. Thus the proposed model would predict the persistence of the diversity of savanna vegetation. The savannas of north-western Australia have a distinctive and diverse mammal fauna richer than the local rainforest (Braithwaite *et al.* 1985). Thus it might be expected that at least the mammal fauna of the Australian savanna would also operate in synchrony with the patch dynamics of the savanna vegetation.

The direction of changes resulting from the fires of different intensity is likely to be both positive and negative. Because all community change is the result of natality, survival, migration and mortality of individuals of different species, the direction of change is often not predictable. The increase (or decrease) in abundance of a given species may increase or decrease patchiness and may increase or decrease the attractiveness of a piece of land for mammals and other animals.

In this paper, the above model is tested with experimental data on vegetation patchiness, plant and mammal species richness.

METHODS

Within Kapalga Research Station in Kakadu National Park (12° 43' S, 132° 26' E), pairs of 8-ha trapping grids (totalling 128 ha) were established, one located in riparian/woodland vegetation and the other about 0.5 km upslope in open forest. Thus the grids spanned an elevational (20 m) and moisture gradient from riparian vegetation through woodland and into the locally dominant *Eucalyptus miniata*-*Eucalyptus tetrodonta* open forest association. *Sorghum* spp. was the dominant grass understorey (see also Andersen and Braithwaite 1994). Pairs of grids were located in eight different 15-20 km² sub-catchments in the southern

half of Kapalga Research Station. All sites occurred within a 300 km² area. Each of the 16 grids was arranged as 4 rows at 50 m spacing with 20 trapsites at 20 m spacing. They were trapped with 1:4 (wire:Elliott) trap type ratio for two nights every two months. The trapping study went from July 1989 to July 1992.

Twelve species of mammals (Appendix 1), ranging in size from *Pseudomys delicatulus* (10 g) to *Trichosurus vulpecula* (2 kg), were trapped for a total of 46 080 trap nights during the study. The species were classified (Appendix 1) into arboreal (spends some time in trees) and terrestrial (spends no time in trees).

Following pre-fire trapping from July 1989 to May 1990, experimental fires were set in 1990 and 1991 as part of the landscape-scale Kapalga Fire Experiment (Braithwaite 1990; Williams 1994). Two catchments (four grids) were burned in June of both years (Early), two in both Septembers (Late), and two in June in 1991 and 1992 with some remaining unburnt areas also burnt in July and September in 1992 (Progressive). The Progressive regime was an attempt to simulate the Traditional Aboriginal habit of progressively burning later-drying parts of the landscape. At this early stage in the experiment, Progressive as a treatment was not substantially different from Early and has been treated as single annual fire. Another two catchments (four grids) were unburnt throughout. This regime was called Natural as it was initially unclear whether they would be burnt by lightning-ignited fires.

The division of the vegetation into canopy and ground strata at 3 m was based on previous analyses of vegetation structure (Braithwaite and Estbergs 1985). Three measures of patchiness were used. Measures of the patchiness of the fires, of the ground cover composition (<3 m) and the canopy composition (>3 m) were derived.

The patchiness of the fires was measured using the coefficient of variation of scorch height/total height. After each fire the height of scorching (maximum height at which most leaves were dead) and total canopy height were estimated at each trap site. Any scorch height measure is partly confounded by variation in canopy height between sites but the ratio was thought to give more reliable estimates in the present context of minor canopy height variation.

For each of the 16 trapping grids, a total of 80 estimates was made. The means and coefficients of variation were used. Estimates of intensity in kW.m⁻¹ (see Williams 1994) from the vicinity of the grids can be derived from the mean scorch height/height ratios (per cent) for 1991 and 1992 fires ($y=3.301+ 87.86x$, $r=0.674$, $p=0.02$). The fire intensities ranged from about 3000 to 12 000 kW.m⁻¹.

The patchiness of the ground and canopy vegetation was estimated separately. The dominant vegetation on each of the 1280 trapping sites was measured in February of each year. The five species with the highest cover/abundance for above 3 m and for

below 3 m were recorded with the Braun-Blanquet estimate. For vegetation <3 m, a 1 m quadrat was used, while for >3 m a 10 x 10 m quadrat was used. The sampling was first done in February 1990 before the first fires in May 1990. The sites were previously burnt by intense late fires in 1985 and 1986, low intensity early fires in 1987 and no fires in 1988 and 1989. Subsequent sampling was done in February 1992 for >3 m and in February 1991 and 1992 for <3 m.

The 1280 sites from different years were classified in <3 m and >3 m data sets using the non-hierarchical, agglomerative clustering program ALOC (Belbin 1987). The >3 m data were for two years (1990 and 1992, 2560 sites) and yielded 25 vegetation groups at the 0.99 heterogeneity level. The <3 m data were analysed in two ways. First, the three years (1990-1992; 3840 sites) were clustered into 15 groups at 0.99 heterogeneity level. Second, the 1991 and 1992, the first two post-fire years were clustered into 27 groups at 0.99 heterogeneity level. Measures of patchiness were derived by calculating a Shannon-Weiner diversity statistic using the numbers of sites of each vegetation group on a trapping grid.

RESULTS

Change in Vegetation Patchiness

Vegetation diversity or patchiness in vegetation composition changed little between 1990 and 1992 for the >3 m fraction but changed greatly between years for the <3 m fraction. For example, the correlation coefficients between years were high when there was little change as in >3 m ($r=0.935$, $p<0.001$) but low for <3 m (1990-1 $r=0.601$, $p<0.05$; 1991-2 $r=0.681$, $p<0.01$; 1990-2 $r=0.705$, $p<0.01$), when change was much greater.

Measures of change have been plotted against mean scorch height/total height percentage (scorch/height, Figs 2-4). It should be remembered, however, that the coefficient of variation of scorch/height, a measure of the patchiness of the fires themselves, increases from zero for no fires to reach highest values between 20 and 60 per cent and decreases steeply as maximum scorch height is approached.

Change in vegetation patchiness from pre-fire to post-fire is plotted against mean scorch height/total height for the 16 trapping grids (Fig. 2). As an aid to interpretation, lines have been drawn in by eye indicating the possible shape of the envelope containing the cloud of data points. The precise shape of these lines is not important for the model presented. The important thing for testing the model is consistent difference between the ground and canopy layers (see Fig.1).

Substantial change in vegetation patchiness took place for vegetation <3 m from 1991 to 1992 (first to

second post-fire year) (Fig. 2a). The change is both positive and negative but most is negative (decreasing patchiness). The most strongly positive changes are the Progressive sites on compartment A (see Williams 1994). The Natural sites with no fires are of course at zero scorch/height. They form a tight group with a slight decrease in patchiness. The Late treatment sites at the other end of the intensity scale show tighter grouping than the other two remaining groupings. The Early and Progressive sites show greatest change but also greatest variability between sites. The overall pattern is one of larger change at the intermediate levels of fire intensity (scorch/height) and less change at high and low intensity.

When the same approach is taken for the canopy (>3 m) vegetation, a different result is obtained (Fig. 2b). The degree of change is much less than for the ground layer. The change in canopy patchiness is greatest at high and low mean fire intensities. The intermediate level of intensity results in least change in canopy patchiness. The no or low intensity situation results in change in patchiness consistent with recruitment from the ground layer (i.e. some of the small individuals are able to grow sufficiently to get into the canopy). The effect of fire protection on the canopy patchiness of the Natural sites was still being played out after five years fire protection. At the other extreme, the very intense fires increase patchiness consistent with substantial mortality of some species of trees and shrubs.

Change in Plant Richness

Because only the dominant five plant species for each of <3 m and >3 m categories were recorded, a complete vascular plant inventory is not available for the sites. The dominant species richness value is the total number of species recorded on an 80-site trapping grid. Change in species richness is plotted against scorch/height for <3 m in Figure 3a. The patterns are for 1991-92 and show an increase in Natural sites and a decrease in the more intensely burnt Late and Early sites. This produces a negative relationship between mean scorch/height and change in plant richness ($r=-0.523$, $p=0.037$). The pattern is also similar to that obtained for vegetation patchiness in that greatest variation in change in plant richness occurs at intermediate fire intensities (around 60 per cent scorch/height).

Above 3 m, the pattern obtained (Fig.3b) is also similar to that with vegetation patchiness. That is, the intermediate fire intensities (30 per cent) show least variation in degree of change. The increase in richness on the unburnt sites and the decrease in plant richness on the high scorch/height sites confirms the interpretation of the change in vegetation patchiness described above ($r=-0.578$, $p=0.019$). That is, above 3 m, the change is consistent with recruitment of new species at the low intensity end and by loss of species through mortality at the high intensity end.

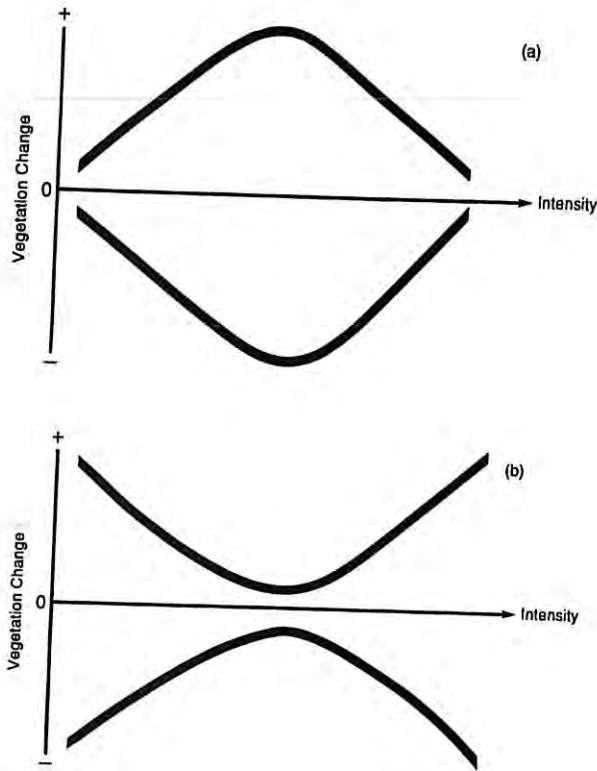


Figure 1. A model of change in habitat characteristics (habitat diversity and plant and animal species richness) in relationship to fire intensity for ground (a) and canopy (b) storey savanna vegetation.

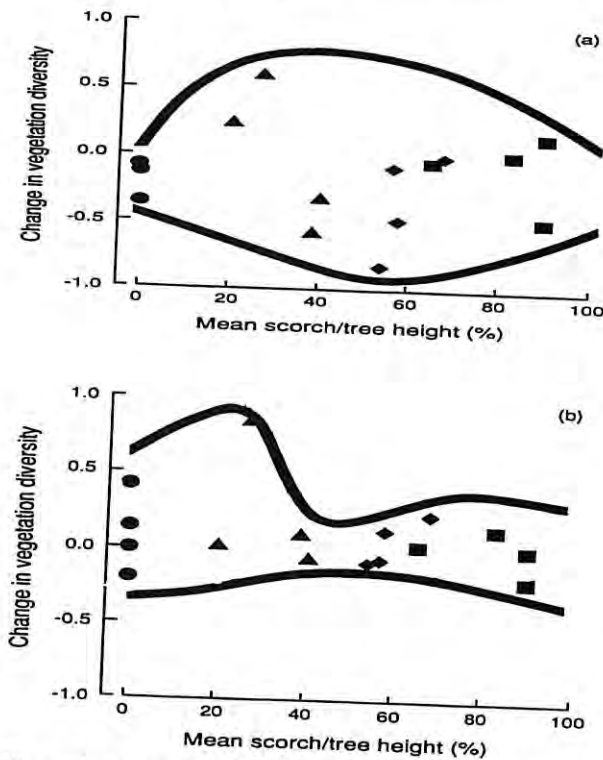


Figure 2. Change in vegetation diversity in relation to mean scorch height / total height ratio for 1990 and 1991 for (a) ground and (b) canopy layer savanna vegetation. The fire regimes were Natural (circles), Early (diamonds), Late (squares), and Progressive (triangles).

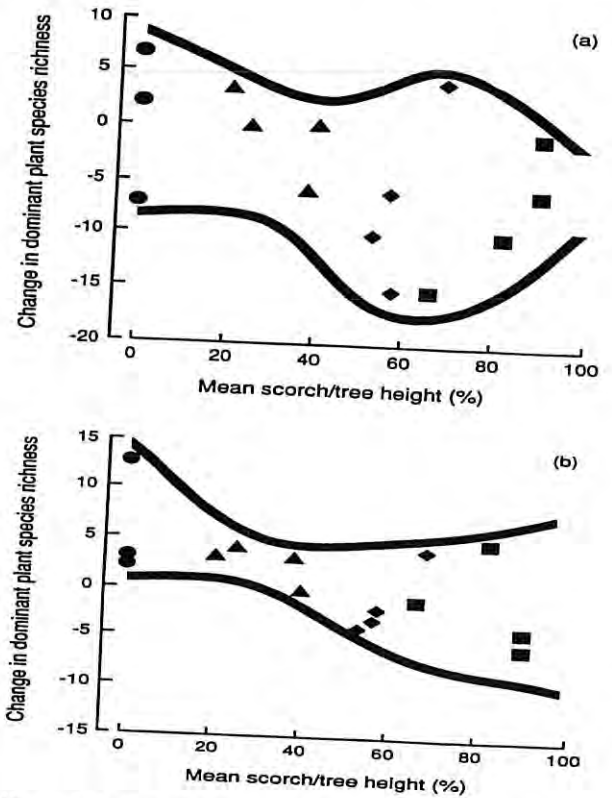


Figure 3. Change in dominant plant species richness in relation to mean scorch height / tree height ratio for (a) ground and (b) canopy layer savanna vegetation. Symbols as in Fig. 2.

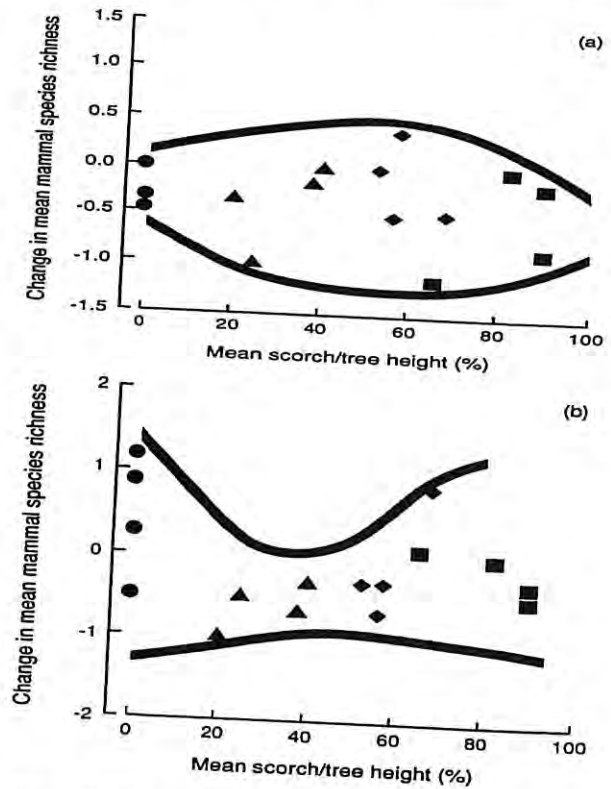


Figure 4. Change in (a) terrestrial and (b) arboreal mammal species richness in relation to mean scorch height / tree height ratio for savanna vegetation for (a) ground and (b) canopy layer vegetation. Symbols as in Fig. 2.

Relationship between Vegetation Diversity and Mammal Abundance and Richness

Before the experimental fires in 1990, the relationship between total mammal abundance and vegetation patchiness and between mean species richness of mammals and vegetation patchiness was positive and was significant in five out of twelve cases, mainly with the tree layer (Table 1). However, after the commencement of the experimental fires the simple relationships disappeared. The fire regimes appear to have much less impact on the relationships with the slower variable of the canopy heterogeneity (>3 m, Table 1).

Change in Mammal Richness

The patterns of change in mammal species richness are similar to those obtained with plant richness and vegetation heterogeneity (Fig.4). Change in terrestrial mammal richness is relatively minor at low and high intensities and greatest around 60 per cent scorch/height. Change in arboreal mammal richness again shows similarity with earlier canopy patterns, with greatest change at low and high intensities and least change at intermediate intensities.

DISCUSSION

The strong positive relationship between mammal richness (diversity) and vegetation patchiness was lost for terrestrial mammals immediately the fire regimes were imposed. The effects of fire on the ground vegetation were immediate and the impact on terrestrial mammals was similar. It is suggested that in the absence of fire the mammal numbers on the burnt sites would not quickly respond as they appear to have on the Natural sites. It must be remembered that for two years before the fires started in 1990, all sites were unburnt. Thus it would appear that longer-term spelling (more than a couple of years) for some places may be required to see such an impact.

These preliminary data provide some support for the idea that a complex regime consisting of patches burned by a range of different fire types ultimately drives habitat heterogeneity which is, in turn, important for the mammals. The canopy and ground layers certainly behave differently. They represent slow and fast variables. The ground layer responds most strongly to the intermediate fire intensities which are also the most spatially variable. This part fits the conventional wisdom. The patchy early dry season fires are

TABLE 1

Correlation coefficients between mammal abundance and richness and ground and tree layer heterogeneity before and after experimental fires on Kapalga. * p<0.05 ** p<0.01 *** p<0.001.

MAMMALS	HETEROGENEITY			
	GROUND LAYER ABUNDANCE	GROUND LAYER RICHNESS	TREE LAYER ABUNDANCE	TREE LAYER RICHNESS
PRE-FIRES (1990)				
All	0.430	0.304	0.802***	0.739***
Terrestrial	0.103	0.678**	0.416	0.568*
Arboreal	0.356	0.440	0.562	0.771***
POST-FIRES (1991)				
All	0.212	0.245	-	-
Terrestrial	0.232	0.221	-	-
Arboreal	0.224	0.068	-	-
POST-FIRES (1992)				
All	0.105	0.304	0.239	0.592*
Terrestrial	0.064	0.197	0.161	0.584*
Arboreal	0.127	0.142	0.250	0.094

pragmatically convenient for breaking up the country in order to prevent the spread of later, more intense fires. This enhances property protection and is intuitively appealing as a conservation measure. It increases habitat heterogeneity and limits the largely presumed destructive effects of late fires. Most importantly, some areas are also protected from burning. These patches not only contribute to habitat heterogeneity but allow recruitment into the canopy from the ground layer.

In northern Australia, the present biodiversity of the savanna landscape appears to be maintained by an historic anthropogenic fire regime. It is probable that an approximation of the landscape pattern produced by the traditional Aboriginal burning regime maximizes biodiversity through maintaining habitat diversity, savanna patchiness and species diversity and protecting endemic species. The research task is to determine and optimize that fire mosaic.

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APPENDIX 1

List of mammal species caught during study classified into arboreal and terrestrial, and marsupial and native rodent categories.

STRATUM HABIT	MARSUPIAL	RODENT
Arboreal	<i>Dasyurus hallucatus</i> <i>Antechinus bellus</i> <i>Phascogale tapoatafa</i> <i>Trichosurus vulpecula</i>	<i>Melomys burtoni</i> <i>Mesembriomys gouldii</i>
Terrestrial	<i>Sminthopsis virginiae</i> <i>Isodon macrourus</i>	<i>Pseudomys delicatulus</i> <i>Pseudomys nanus</i> <i>Rattus colletti</i> <i>Rattus tunneyi</i>