

Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern Territory, Australia

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Abstract This opportunistic study compares the vegetation, fuel loads and vertebrate fauna of part of a 120-ha block of tropical open forest protected from fire for 23 years, and an adjacent block burnt annually over this period. Total fuel loads did not differ significantly between the unburnt and annually burnt sites, but their composition was markedly different, with far less grassy fuel, but far more litter fuel, in the unburnt block. There were major differences between treatments in the composition of trees and shrubs, manifest particularly in the number of stems. There was no overall difference in plant species richness between the two treatments, but richness of woody species was far higher in the unburnt treatment, and of annual and perennial grasses, and perennial herbs in the annually burnt treatment. Change in plant species composition from annually burnt to unburnt treatment was directional, in that there was a far higher representation of rainforest-associated species (with the percentage of woody stems attributable to 'rainforest' species increasing from 24% of all species in the annually burnt treatment to 43% in the unburnt treatment, that of basal area from 9% to 30%, that of species richness from 8% to 17%, and that of cover from 12 to 47%). The vertebrate species composition varied significantly between treatments, but there was relatively little difference in species richness (other than for a slightly richer reptile fauna in the unburnt treatment). Again, there was a tendency for species that were more common in the unburnt treatment to be rainforest-associated species. The results from this study suggest that there is a sizeable and distinct set of species that are associated with relatively long-unburnt environments, and hence that are strongly disadvantaged under contemporary fire regimes. We suggest that such species need to be better accommodated by fire management through strategic reductions in the frequency of burning.

Key words: bird, disturbance, fire regime, mammals, management, rainforest, reptiles, savanna.

INTRODUCTION

Marked seasonality, including a long dry season and high incidence of lightning, dictates that fire is a frequent event in tropical savannas. This high frequency of fires undoubtedly influences vegetation ecology, patterning, structure and floristics, and thereby that of the associated fauna. However, the nature and detail of this response has been debated, with some inconsistent conclusions from the (relatively few) major studies in northern Australia.

The importance of fire to the vegetation patterning of northern Australia has been long recognized. One of the first major ecological descriptions of vegetation in the monsoonal areas of the Northern Territory concluded that the pervasive regime of frequent fire 'caused the most serious deterioration of the forests' (Bateman 1955). An alternative perspective is that the forest environments of northern Australia are remarkably resilient, have evolved considerable adaptations to

frequent fire, and cannot evade fire anyway, except in very limited sites that have some natural or artificial protection from fire. All or parts of this argument are presented in Stocker (1966), Lacey and Whelan (1976), Stocker and Mott (1981), Bowman (1988) and Williams *et al.* (2002), among others. A somewhat intermediate view is now generally prevalent, that there are some fire-sensitive elements (the northern cypress-pine *Callitris intratropica* is the most conspicuous example and the most frequently cited, e.g. Haynes 1985, 1991; Gill *et al.* 1990; Bowman & Panton 1993; Price & Bowman 1994; Bowman *et al.* 2001) within the otherwise generally resilient forests, and that frequent fire preferably in the early dry season is necessary to avoid the more extensive and destructive fires that would otherwise be nearly inevitable (Lonsdale & Braithwaite 1991; Williams *et al.* 1999; Bowman *et al.* 2001). In this world view, frequent fine-scale fire is perceived to be the desired management approach, and this is thought to maintain, or at least resemble, the fire management presumed to have been imposed over many thousands of years by Aboriginal land managers (Haynes 1985, 1991; Price & Bowman 1994; Russell-

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Smith *et al.* 1997a; Bowman 1999; Yibarbuk *et al.* 2001).

Ecological support for frequent (fine-scale, early dry season) burning comes mostly from studies that have documented the destructive effects of more intensive (late dry season) wildfires, which are presumed to be the inexorable consequence of lack of frequent controlled fire. In addition to research on *Callitris*, these studies have included examples of the diminution or damage by wildfire to localized vegetation types embedded within the supposedly fire-prone savanna, most notably patches of monsoon rainforest (Clayton-Greene & Beard 1985; Gill *et al.* 1990; Russell-Smith & Bowman 1992), and studies that have indicated substantial mortality, even within the dominant eucalypts of these open forests, following single relatively high intensity wildfires (Lonsdale & Braithwaite 1991; Williams *et al.* 1999). This argument is supported in part by some evidence that fuel loads build up monotonically with increasing time since fire, such that relatively long unburnt areas become undesirable hazards likely to create or support unusually intense and destructive fire (Gill *et al.* 1990; Lonsdale & Braithwaite 1991; Williams *et al.* 1999).

The ecological argument for frequent burning also rests on some results from experimental plots that have indicated only minor change in floristic composition with long-term exclusion of fire (Bowman *et al.* 1988; Bowman & Panton 1995; Williams *et al.* 2002). This is perhaps the key ecological argument: if there are no or few elements of the environment that are dependent on or even favoured by long-term fire exclusion, then no real management effort should be made to achieve fire suppression or to reduce fire incidence and frequency. This argument is made both for autochthonous ingredients within the eucalypt forest and to suggest that there is little likelihood of invasion of long-unburnt eucalypt forests by immigrant rainforest species. This evidence is based on two main experimental sites (Munmarlary and Kapalga) within Kakadu National Park in the Northern Territory, Australia, with one additional study each on a less crisply designed site in eucalypt forest near Darwin ('Solar Village', Fensham 1990) and on one site near Weipa on western Cape York Peninsula (Bowman & Fensham 1991). These sites and studies are described briefly in the present study. All have design constraints that limit their interpretability, which is largely unavoidable given the logistical impediments (Williams *et al.* in press).

The Munmarlary design comprised two blocks (one in eucalypt open forest and one in eucalypt woodland), each with three replicates of four fire treatments (annual early dry season fire, annual late dry season fire, biennial early dry season fire and fire exclusion). Each plot was only 1 ha in size and was isolated by a graded fire break. Significant structural change in vegetation (most notably to increasing density of saplings

and poles in unburnt plots) was reported briefly after 6 years of treatment (Hoare *et al.* 1980) and more comprehensively after 13 years (Bowman *et al.* 1988). The latter study reported little floristic difference between burnt and unburnt plots and asserted that such change, especially towards invasion by monsoon rainforest species in unburnt plots, was not a likely outcome. This conclusion was further supported after 21 years (Bowman & Panton 1995). However, the final analyses of pattern after 23 years (after which the experiment was abandoned) reported instead substantial floristic differences between treatments, including some invasion of 'rainforest' plant species to unburnt plots, and reduction in the dominance and diversity of annual grasses (Russell-Smith *et al.* in press).

The Kapalga design was more heavily influenced by consideration of the impacts of fire on vertebrate fauna, and hence used far larger (15–20 km²) blocks, with three replicates of four fire regimes (Andersen *et al.* 1998; 2003). The blocks included far more environmental variability than the Munmarlary plots. However, the experiment ran for only 6 years. Riparian vegetation was greatly diminished in the plots subject to late dry season fires and enhanced in the unburnt plots (Douglas 1999); fires substantially affected tree phenology, seed output and recruitment (Setterfield 1997; Williams *et al.* 2002). Deciduous, subdominant plants were more fire sensitive than were the evergreen dominants (Williams *et al.* 2002), and tree mortality was greatest in intense (late dry season) fires, and among the smallest and largest size classes (Williams *et al.* 2002).

Both the Solar Village and Weipa studies were largely opportunistic, in sampling situations that were established not as experimental research sites, but rather as part of a management choice. The Solar Village study (Fensham 1990) was unreplicated, with one moderately large (120-ha) site protected from fire for 10 years adjacent to a site burnt annually and another site burnt at intermediate frequency. Fensham (1990) concluded that although fire exclusion resulted in the development of a dense tall understorey, few facultative monsoon rainforest plant species were favoured. The Weipa study (Bowman & Fensham 1991) considered an open forest of approximately 2 ha that adjoined a monsoon rainforest, and was sampled following 15 years of fire exclusion. This study reported the development, with fire exclusion, of an ecotonal band comprising plant species with rainforest affinities around the rainforest patch, but with little movement of such species into the eucalypt forest beyond this narrow (10–20-m wide) ecotone.

For the impacts of fire on the vertebrate fauna of these tropical forests, the evidence is even less substantial and clear-cut than that for vegetation, and the argument is somewhat more diffuse. Although a limited

amount of response was measured at the Munmarlary experiment (e.g. for birds, Woinarski 1990), the plot size was too small to derive meaningful conclusions. More weight can be given to results from the Kapalga experiment; however, they are equivocal (Andersen *et al.* 2003). This may partly be because of the relatively short duration of the experiment and the spatial uniformity of experimental firing. For mammals, the results are also somewhat confounded by a decline for many species over the course of the experiment, which occurred across all treatments (Woinarski *et al.* 2001; Pardon *et al.* 2003). The results suggest that responses to fire vary markedly between different ecological groupings of animals, with some species showing preference for no or little burning, others for more frequent burning, and yet others with complex responses that depend partly on landscape context and fire patchiness (Trainor & Woinarski 1994; Griffiths & Christian 1996; Williams *et al.* 2002; Andersen *et al.* 2003). A similar array of idiosyncratic responses was described for reptiles by Braithwaite (1987) based on correlative rather than experimental studies.

A number of other studies have suggested that mammals, in particular, are highly responsive to fire regimes, a relationship given added piquancy by recent evidence of decline in elements of the mammal assemblage across northern Australia (Woinarski *et al.* 2001). In a detailed study of the northern brushtail possum, *Trichosurus vulpecula*, Kerle (1985, 1998) found a clear preference for long unburnt forest, and suggested that high fire frequency was detrimental to this species. A study of habitat associations of the black-footed tree-rat, *Mesembriomys gouldii*, (Friend & Taylor 1985; Friend 1987) showed that their abundance was far greater in areas where a dense tall woody understorey occurred, with this characteristically associated with relatively long periods without fire. In a sandstone environment in Kakadu, Begg *et al.* (1981) found significant changes in habitat use, reproduction and/or abundance after a single intense fire for the four mammal species considered (northern quoll, *Dasyurus hallucatus*; sandstone antechinus, *Pseudantechinus bilarni*; Arnhem rock-rat, *Zyzomys maini*; and common rock-rat, *Zyzomys argurus*). Kerle and Burgman (1984) found a similar response in sandstone habitats, with the Arnhem rock-rat disappearing for at least 1 year after fire, and declines for the northern quoll and common rock-rat; and in lowland eucalypt forests they detected marked and sustained (1–2 years at least) declines or absences post-fire for the grassland melomys, *Melomys burtoni*, northern brushtail possum and northern brown bandicoot, *Isodon macrourus*, but increases for the western chestnut mouse, *Pseudomys nanus*.

Across much of the eucalypt forests of northern Australia, approximately 50% (and up to 70% in some regions) is burnt each year (Press 1988; Russell-Smith *et al.* 1997b, 2000, in press; Gill *et al.* 2000; Edwards

et al. 2001, in press; Williams *et al.* 2002). Assuming a relatively random location of these fires (which is not entirely the case, Gill *et al.* 2000), this suggests that the proportion of forests and that unburnt for at least 5 years is approximately $(0.5)^5$, that is 3.1%; and that are unburnt for at least 10 years is $(0.5)^{10}$, that is 0.098%. Gill *et al.* (2000) provide some evidence for such low proportions of long-unburnt forest, with an estimate of 'less than 1%' of lowland forest in Kakadu National Park being unburnt over a 16-year study period. Hence, under prevailing regimes, any species that are dependent on, or favour, relatively long-unburnt forest are being strongly disadvantaged. This may be especially so for those with limited dispersal ability. The distributions of the relatively long-unburnt pockets will be rearranged somewhat each year, depending on the spatial distribution of that year's fires. The management response to this possibility should be threefold: first, are there such species (or at least a substantial number of such species)?; second, even if there are, is it possible to implement a management regime that is more suitable to them?; and third, if this is possible, is it a more desirable one than the present, and what are the risks and costs? This contribution addresses principally the first of these questions, but also considers briefly the others.

In the present report, we re-examine the Solar Village 'experiment', now following 23 years of fire exclusion. We consider the response of vegetation, fuel loads and vertebrate fauna, examining in particular whether there is a set of species that are associated with a relatively long post-fire period. We recognize that the lack of replication at this site limits the confidence with which we can draw conclusions from the results. Ideally, this case should be but one of a set of studies at similar fire-protected sites. However, it is an unfortunate reality that such meta-analysis is not yet possible, as there are few, if any, comparable sites in the landscape that would allow us to sample more representatively.

METHODS

Study site

The present study was based at Solar Village, a communally managed property of 120 ha, located approximately 35 km south-east of Darwin (12°37'S, 131°06'E). Fensham (1990) provided a detailed description of the site, on which the present account is based. Annual rainfall is 1695 mm (Myers *et al.* 1997), approximately 90% of which falls in the wet season (November to April).

The southern part of the property (in which our sampling occurred) is dominated by a gentle slope to a low (20 m above the property's drainage lines) ridge of

sedimentary rocks. Soils are grey–brown sandy loams. A small watercourse runs through the property, but was at least 500 m distant from any of our sampling sites.

The landowners preserve the natural vegetation in undisturbed condition. There is little clearing on the property, and cats and dogs are not kept. Since 1978, the goal of fire exclusion has largely been achieved, but fire reached some areas on the property in about 1985, in 1989 and in 1992 (C. Colton & G. Beresford, pers. comm.). These burnt areas were not included in the present study, which sampled only those areas inside Solar Village that had been unburnt for at least 23 years.

The perimeter of Solar Village is marked by a 5-m-wide fire-break. To the immediate south, lies a 386-ha block of unused land that has had a history of annual burning, typically in the early dry season, for fuel reduction purposes. This regime has been consistently

applied since at least around 1978, except that it was not burnt in 2001 (G. Beresford, pers. comm.). The topography and geomorphology of this block is indistinguishable from Solar Village. Subsequently, we use the terms *unburnt* to describe the Solar Village site, and *annually burnt* to describe the site to the immediate south (Fig. 1). Neither the unburnt Solar Village block nor the annually burnt block is grazed by livestock or feral stock.

Sampling design

Between 25 February and 15 March 2002, we sampled two broad environments (ridge top and slope) replicated in both the unburnt and the annually burnt areas. We sampled five 50 m × 50 m quadrats in each of these four categories: unburnt ridge, annually burnt ridge, unburnt slope, annually burnt slope. Quadrats were arranged in two or three parallel lines following the contour line, with the midpoint of adjacent quadrats separated by at least 50 m (Fig. 2).

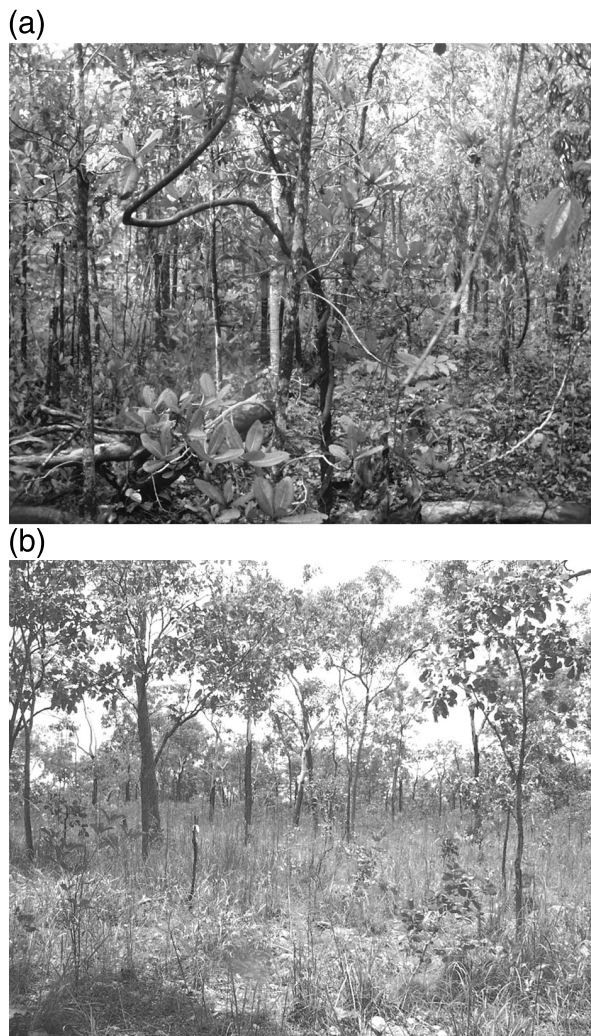


Fig. 1. Photographs of the study area, showing unburnt (top) and annually burnt (bottom) environments.

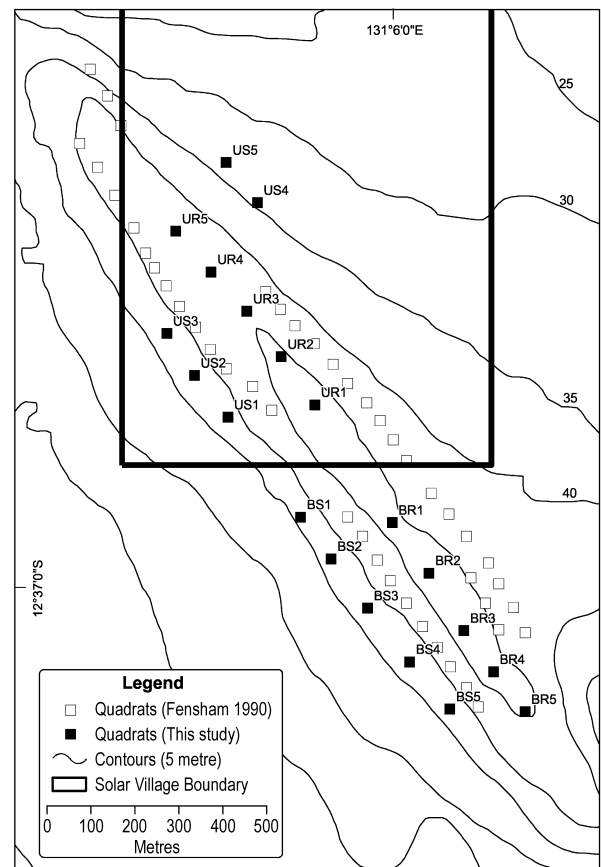


Fig. 2. Arrangement of sampling quadrats. (■), Quadrats sampled during the present study; (□), plots at which vegetation was sampled by Fensham (1990). Contour levels are also shown at 5-m intervals. B, annually burnt; R, ridge; S, slope; U, unburnt.

This arrangement of quadrats in one burnt locale and one unburnt locale weakens the interpretability of, and ability to extrapolate from, our results, because of pseudo-replication. The limited size of the unburnt area prevented any less clumped sampling design.

Fuel load was sampled at five randomly located 1 m × 1 m subplots within every quadrat. At each of these all grass and litter (fallen leaves and unattached twigs less than 1-cm diameter) was harvested at ground level and weighed separately (wet weights). Three of the five grass and litter samples per quadrat were then subsampled, to be oven-dried for 24 h at 70°C. They were then re-weighed to determine dry weight. Total standing dry matter (fuel load, expressed in tonnes ha⁻¹) per quadrat was calculated from the averaged proportion of dry weight to wet weight multiplied by the average wet weight per subplot.

We recorded the occurrence of all woody plants >1.5-m tall within a belt transect (1.5 m × 100 m) placed around two sides of the perimeter of every quadrat. For each stem in this transect, we recorded species identity and measured diameter at breast height. Dead stems were included as a distinct category. In analyses, we tallied frequency distributions for stem diameter classes for each species (and all species combined) and converted these frequency-diameter data to a basal area for each species (and all species combined) in each quadrat.

Plant species composition was also sampled at eight randomly sited 2 m × 2 m subplots in each quadrat. Within each of these subplots we recorded all species present (rooted in the quadrat) and estimated percentage cover for every species. Plant species names follow Dunlop *et al.* (1995). Where these differ from those given by Fensham (1990) we note that difference. For each species, we calculated a mean cover score across all eight subplots. We also tallied the number of different species recorded across the subplots per quadrat, and the number of species in each life form (perennial native grass, annual native grass, perennial sedge, creeper, fern, perennial herb, other herb and tree/shrub). We also categorized each species into a binary class of whether or not it was classified as a monsoon rainforest species by Liddle *et al.* (1994), and defined there as species that are 'either exclusive to, or typically components of, perennially or seasonally closed canopy

vine-forest or vine-thicket vegetation'. We also tallied species richness and cover for exotic plant species. This subplot sampling was designed to sample particularly the understorey, to complement the assessment of trees and shrubs sampled primarily with the belt transects. The subplot assessment included trees and shrubs that were rooted within the subplots, and so provided another measure of the occurrence of these species. This sampling procedure differed in many ways from that adopted by Fensham (1990) following 10 years of fire exclusion at this site, which constrains comparisons.

Vertebrates were sampled using procedures now standard for this region (Woinarski & Ash 2002). For each quadrat, we sampled mammals over a three-night period, using 20 Elliott traps and four possum-sized cage traps (placed around the perimeter of the quadrat, and baited with a mixture of peanut butter, honey and oats), and four pitfall traps (two 20-L and two 10-L plastic buckets, each with 8 m of 30-cm-high driftline fence). We also actively searched for mammals in two spotlight searches each of 10 min. Abundance for each species in each quadrat was calculated as the sum of all captures and the number reported during searches. Any species recorded from signs (tracks, faeces etc.) but not otherwise captured or observed was assigned an abundance value of 1. Reptiles and frogs were sampled using the pitfall traps, spotlight searches and three diurnal searches (each of 10 min). Birds were sampled in eight instantaneous diurnal censuses and two nocturnal censuses per quadrat.

As with plants, we categorized each vertebrate species as preferring rainforest or not, based on indices derived previously from sampling across a large set of rainforest sites and adjacent open-forest/savanna vegetation across monsoonal areas of the Northern Territory (Menkhorst & Woinarski 1992; Gambold & Woinarski 1993; Woinarski 1993).

Analysis

Following the analytical pathway used by Fensham (1990), we used two-way ANOVA to examine the variation between a range of dependent variables (fuel loads, the abundance and richness of plant and animal

Table 1. Variation in fuel loads between quadrats of different fire histories and landscape positions

Fuel	Fire history	<i>F</i> -ratio [†]		Mean dry weight (tonnes ha ⁻¹)			
		Landscape position	Interaction	UR	US	BR	BS
Grass	66.8***	2.9	6.0*	0.67	0.46	2.31	3.50
Litter	12.9**	1.3	0.1	6.84	7.66	4.68	5.30
Total	0.1	3.6	0.9	7.52	8.11	6.99	8.80

P* < 0.05; *P* < 0.01; ****P* < 0.001; [†]two-way ANOVA. Quadrat types: BR, annually burnt ridge; BS, annually burnt slope; UR, unburnt ridge; US, unburnt slope.

Table 2. Variation in stem density and basal area for woody plant species and groups of species[†]

Species	RF	<i>n</i>	Stems							Basal area						
			<i>F</i> (UB)	Variation <i>F</i> (RS)	<i>F</i> (UB × RS)	UR	Mean (no. ha ⁻¹)			<i>F</i> (UB)	Variation <i>F</i> (RS)	<i>F</i> (UB × RS)	UR	Mean (m ² ha ⁻¹)		
							US	BR	BS					US	BR	BS
Dead		19	87.8***	2.9 NS	10.3**	1190	756	78	211	0.4 NS	0.2 NS	0.2 NS	1.0	1.0	1.0	1.4
<i>Acacia auriculiformis</i>	Yes	10	138.0***	1.2 NS	1.2 NS	756	912	0	0	17.7***	0.1 NS	0.1 NS	0.6	0.6	0.0	0.0
<i>Acacia holosericea</i>	No	7	8.2*	3.4 NS	3.4 NS	356	78	0	0	2.5 NS	1.5 NS	1.5 NS	0.1	0.1	0.0	0.0
<i>Acacia lamprocarpa</i>	Yes	17	6.2*	5.7*	0.9 NS	645	256	245	78	4.8*	9.4**	0.0 NS	0.2	0.1	0.1	0.1
<i>Acacia latescens</i>	No	7	0.5 NS	1.4 NS	0.9 NS	45	89	0	400	0.0 NS	2.3 NS	0.1 NS	0.1	0.1	0.0	0.1
<i>Alphitonia excelsa</i>	Yes	5	5.4*	0.3 NS	0.3 NS	56	89	0	0	3.9 NS	0.0 NS	0.0 NS	0.1	0.1	0.0	0.0
<i>Alstonia actinophylla</i>	Yes	7	10.2**	0.2 NS	0.2 NS	78	100	0	0	3.7 NS	1.1 NS	1.1 NS	0.4	0.1	0.0	0.0
<i>Brachychiton diversifolius</i>	No	10	7.4*	0.8 NS	0.8 NS	67	67	0	28	10.1**	0.3 NS	0.3 NS	0.1	0.1	0.0	0.1
<i>Brachychiton megaphyllus</i>	Yes	8	3.1 NS	1.1 NS	0.1 NS	56	89	0	44	2.4 NS	0.0 NS	1.5 NS	0.1	0.1	0.0	0.1
<i>Breynia cernua</i>	Yes	8	13.8**	0.9 NS	0.9 NS	133	222	0	0	4.5 *	0.4 NS	0.4 NS	0.1	0.1	0.0	0.0
<i>Buchanania obovata</i>	No	13	7.7*	0.4 NS	0.6 NS	222	145	33	11	2.9 NS	0.3 NS	0.3 NS	0.2	0.1	0.1	0.1
<i>Canarium australianum</i>	Yes	6	11.5**	5.3*	5.3*	44	234	0	0	6.5*	1.2 NS	1.2 NS	0.1	0.3	0.0	0.0
<i>Cochlospermum fraseri</i>	No	5	0.3 NS	0.9 NS	0.3 NS	44	33	44	0	1.1 NS	4.0 NS	0.9 NS	0.1	0.0	0.1	0.0
<i>Corymbia bleeseri</i>	No	4	0.2 NS	4.5*	0.2 NS	33	0	22	0	0.8 NS	1.8 NS	0.8 NS	0.1	0.0	0.1	0.0
<i>Corymbia porrecta</i>	No	6	2.6 NS	1.7 NS	0.1 NS	33	0	100	44	0.4 NS	0.8 NS	0.2 NS	0.3	0.0	0.4	0.3
<i>Croton arnhemicus</i>	Yes	6	22.6***	24.0***	22.6***	745	0	11	0	57.0***	59.2***	57.0***	0.3	0.0	0.1	0.0
<i>Cycas armstrongii</i>	No	16	2.1 NS	9.0**	1.1 NS	67	467	22	222	2.8 NS	9.8**	1.1 NS	0.2	1.3	0.1	0.6
<i>Denhamia obscura</i>	Yes	5	6.0*	0.2 NS	0.2 NS	122	89	0	0	2.8 NS	0.7 NS	0.7 NS	0.6	0.2	0.0	0.0
<i>Erythrophleum chlorostachys</i>	Yes	17	4.6*	4.9*	0.0 NS	445	790	122	456	0.5 NS	0.5 NS	2.1 NS	1.2	1.7	1.7	0.2
<i>Eucalyptus miniata</i>	No	20	3.1 NS	3.1 NS	1.5 NS	245	300	300	623	0.3 NS	0.2 NS	0.1 NS	3.5	3.0	4.4	3.6
<i>Eucalyptus tetradonta</i>	No	19	1.6 NS	0.5 NS	1.7 NS	156	122	156	278	0.4 NS	1.1 NS	0.0 NS	1.3	2.3	1.9	2.9
<i>Ficus opposita</i>	Yes	9	8.4*	0.5 NS	0.5 NS	122	200	0	0	8.9**	1.1 NS	1.1 NS	0.1	0.1	0.0	0.0
<i>Opilia amentacea</i>	Yes	4	3.5 NS	0.0 NS	0.0 NS	89	89	0	0	1.5 NS	1.2 NS	1.2 NS	0.1	0.2	0.0	0.0
<i>Persoonia falcata</i>	No	8	13.7**	2.4 NS	2.4 NS	245	100	0	0	9.7**	0.1 NS	0.1 NS	0.1	0.1	0.0	0.0
<i>Planchonia careya</i>	No	20	16.8***	0.5 NS	2.9 NS	745	512	178	278	9.8**	0.7 NS	0.1 NS	0.6	0.5	0.3	0.2
<i>Terminalia ferdinandiana</i>	No	20	14.7**	6.1*	1.5 NS	1045	589	423	267	8.4*	3.3 NS	0.9 NS	0.9	0.8	0.6	0.1
<i>Xanthostemon paradoxus</i>	No	12	54.6***	19.8***	18.4***	434	1624	11	33	18.3***	6.0*	7.5*	0.5	1.9	0.1	0.1
Total live stems			150.7***	0.0 NS	4.8*	8907	7784	1780	2813	4.0 NS	0.1 NS	0.9 NS	12.7	13.9	9.8	8.0
Total eucalypt			4.9*	1.1 NS	1.9 NS	478	434	600	945	0.5 NS	0.1 NS	0.1 NS	5.2	5.6	6.8	6.7
Total <i>Acacia</i>			25.1***	0.4 NS	2.6 NS	1902	1334	245	489	24.4***	0.0 NS	0.1 NS	0.8	0.8	0.1	0.1
Total rainforest spp.			207.0***	0.4 NS	0.2 NS	3570	3614	389	612	12.1**	1.6 NS	0.8 NS	3.6	3.3	1.7	0.2

P* < 0.05; *P* < 0.01; ****P* < 0.001; [†]values shown are *F*-values from two-way ANOVA for the main effects (fire regime (UB) and topographic position (RS)), their interaction (UB × RS) and means for each of the four treatment classes: BR, annually burnt ridge; BS, annually burnt slope; UR, unburnt ridge; US, unburnt slope. *n*, no. quadrats from which the species was recorded (maximum 20); NS, not significant; RF, whether listed as a monsoon rainforest species by Liddle *et al.* (1994).

species and species-groups) and the two factors of fire history and topographic position. Where appropriate, we transformed non-normal distributions, using $\ln(x + 1)$. Given the three degrees of freedom associated with the two-way ANOVA, only those species recorded from four or more quadrats were considered in analyses. Parametric ANOVA may be invalid for species for which zero values were prevalent. We analysed trends for many species, giving rise to the risk of Type I ('false-change') error, but followed Elzinga *et al.* (2001) in eschewing any 'adjustment' (such as Bonferroni correction) to the probability threshold for significance because this is overly conservative when more than 10 tests are made, and because our tests were not repeated measures of the same data. We compared our results for plants with those of Fensham (1990) following 10 years of fire exclusion at this site.

Patterns in understorey plant, woody plant and vertebrate species composition were examined with

Table 3. Variation in density of stems of differing diameter at breast height (d.b.h.) classes among quadrats of different fire regime and topographic position

d.b.h. class (cm)	UB	<i>F</i> -value [†] RS	UB × RS
All stems			
<1	14.8**	0.2	11.3**
1–5	203.5***	8.5*	5.3*
5–10	40.1***	5.0*	5.2*
10–20	14.6**	0.2	2.2
20–40	0.1	0.5	1.1
>40	0.1	0.1	0.1
Eucalypt stems			
<1	33.6***	19.1***	21.3***
1–5	0.0	0.8	3.2
5–10	0.1	0.2	0.4
10–20	1.1	1.1	1.8
20–40	0.1	0.1	1.2
>40	0.0	0.5	0.5
Acacia stems			
<1	6.4*	0.0	3.5
1–5	18.5***	2.4	0.6
5–10	7.9**	2.9	1.3
10–20	4.3	0.8	0.8
20–40	0.0	0.0	0.0
>40	0.0	0.0	0.0
Rainforest plant stems			
<1	42.2***	1.7	1.0
1–5	83.6***	0.8	0.1
5–10	31.6***	1.1	1.1
10–20	29.0***	0.0	0.0
20–40	2.6	2.6	0.3
>40	1.0	1.0	1.0

[†]*F*-ratios are from a two-way ANOVA for the main effects (fire regime (UB) and topographic position (RS)) and their interaction (UB × RS).

ordination, using multidimensional scaling, within the program PRIMER (Clarke & Gorley 2001). All species were included in the ordination, with abundances untransformed, with compositional similarity of pairs of quadrats assessed using the Bray-Curtis similarity index, and with 100 random starts. The relationship of fire history and topographic position to the resulting ordination patterns was examined using ANOSIM (Clarke 1993), with the significance of the resultant Global R statistic tested by comparison with 1000 random configurations.

RESULTS

Fuel loads

Grassy fuel loads were significantly greater in annually burnt quadrats than in unburnt quadrats (Table 1). The opposite was true for litter fuel loads, such that there was no difference in the sum of these fuel loads between quadrats of contrasting fire history.

There was a weakly significant interaction of fire history and landscape position for grassy fuel (with grass loads lowest in unburnt slope and highest in annually burnt slope quadrats). Overall fuel loads tended to be greater in slope quadrats than in ridge quadrats, but this difference was not quite significant ($P = 0.06$).

Woody plants, sampled in belt transects

There was a marked difference in vegetation structure between the unburnt and the annually burnt quadrats (Tables 2,3; Fig. 3). The total density of stems was nearly fourfold greater in the unburnt than in the annually burnt quadrats (means of 8346 and 2297 stems ha⁻¹, respectively). This disparity was particularly pronounced in the 1–5- and 5–10-cm diameter at breast height (d.b.h.) classes, but was also significant in the <1-cm and 10–20-cm classes. The difference was mostly a result of 'rainforest' species and *Acacia* species. In contrast, there was a weakly significant trend for increased number of eucalypt stems in the annually burnt quadrats, mostly as a result of a high density of eucalypt stems in the <1-cm d.b.h. class in some annually burnt slope quadrats. The proportional contribution of eucalypt stems to total stems was far greater in annually burnt quadrats (33.7 and 33.6% in ridge and slope quadrats, respectively) than in unburnt quadrats (5.4 and 5.6% in ridge and slope quadrats, respectively). The percentage of total stems that were 'rainforest' species increased substantially from annually burnt (means of 25.9 and 21.9% for ridge and slope quadrats, respectively) to unburnt quadrats

(means of 40.6 and 46.2% for ridge and slope quadrats, respectively).

Basal area showed less pronounced variation than stem density. There was no significant overall difference in basal area between the burning regimes (albeit there was a trend for increased total basal area in the unburnt quadrats); however, there was an increase in basal area of 'rainforest' plants and *Acacia* species in the unburnt quadrats. The basal area of eucalypts did not differ significantly between fire regimes or topographic positions; however, their contribution to total basal area was markedly higher in the annually burnt quadrats (70.3 and 84.4% in ridge and slope quadrats, respectively) than in unburnt quadrats (44.3% and 40.1% in ridge and slope quadrats, respectively). Conversely, the percentage of total basal area contributed by 'rainforest' species increased substantially from annually burnt

(means of 14.3 and 3.7% for ridge and slope quadrats, respectively) to unburnt quadrats (means of 35.8 and 24.2% for ridge and slope quadrats, respectively).

Average woody species richness per quadrat was substantially greater in unburnt than in annually burnt quadrats (Table 4). This difference was especially evident for 'rainforest' species. The total number of woody species recorded in the belt transects was 53 for the unburnt quadrats and 23 for the annually burnt quadrats.

A total of 58 woody plant species was recorded in the belt transects. Of 26 individual species recorded from at least four quadrats, 17 species showed a significant difference in stem density between quadrats of different fire histories (Table 2). This high proportion of significant results suggests that the influence of Type I errors is minor. In all cases, this difference was for a

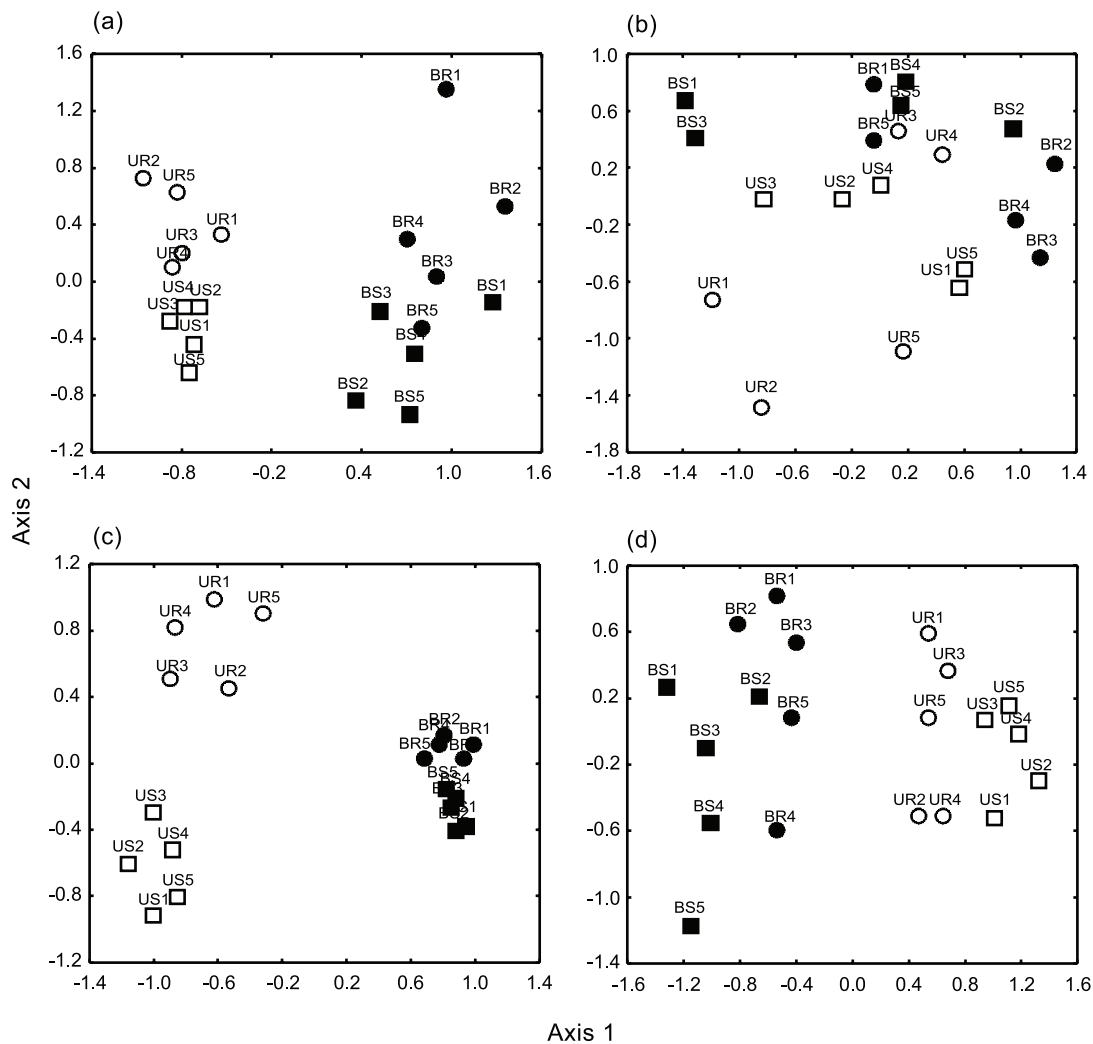


Fig. 3. Ordinations of quadrats by their (a) woody plant species composition, as measured by stem frequency in belt transects (stress = 0.12); (b) woody plant species composition, as measured by basal area derived from belt transects (stress = 0.15); (c) plant species composition, as measured by cover scores in subplots (stress = 0.10); and (d) vertebrate species composition (stress = 0.15). B, annually burnt; R, ridge; S, slope; U, unburnt. Quadrat types: (●), annually burnt ridge; (■), annually burnt slope; (○), unburnt ridge; (□), unburnt slope.

higher value in unburnt quadrats: 10 of these species were not recorded at all in any annually burnt quadrat. Significant increases were observed for all 12 of the

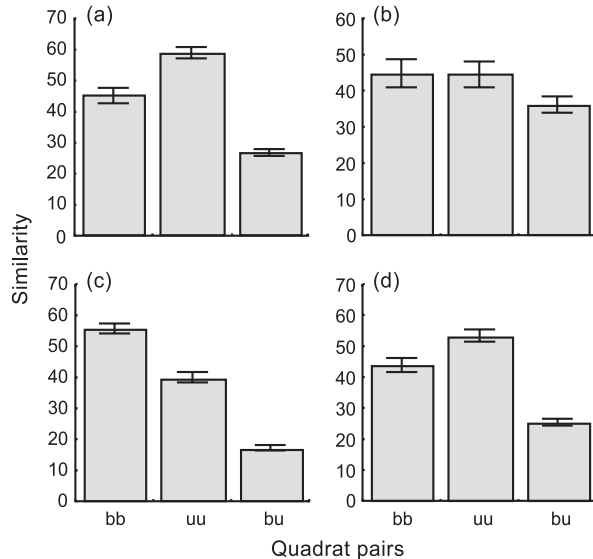


Fig. 4. Similarity in species composition between pairs of quadrats. (a) stem frequency; (b) basal area; (c) understorey cover; (d) vertebrates. Only pairs of quadrats of like topographic position are considered: bb, pairs of annually burnt quadrats; bu, pairs of quadrats, one of which is burnt and one of which is unburnt; uu, pairs of unburnt quadrats. Histogram bars show means, with whiskers equal to one standard error.

‘rainforest’ species and for seven of the 14 non-rainforest species (Table 5). Dead stems were far more abundant in the unburnt than the annually burnt quadrats.

For eight of the 26 species, stem density varied significantly with landscape position. For five of these species, this significance was weak ($0.01 < P < 0.05$). *Cycas armstrongii* showed a more significant ($P < 0.01$) association with slope rather than ridge, and two species (*Croton arnhemicus* and *Xanthostemon paradoxus*) showed a highly significant variation in stem density associated with an interaction of fire regime and landscape position (the former being particularly abundant in unburnt ridge quadrats and the latter on unburnt slope quadrats). Only two other taxa showed significant interaction terms: *Canarium australianum* (weakly) and dead stems.

The pattern for variation in basal area for individual species largely recapitulated that for stem density, but was more subdued, given the relatively minor contribution to basal area from the smaller diameter stem classes. Rainforest-associated plants contributed 9% of the total basal area in annually burnt quadrats, rising to 30% in unburnt quadrats.

Ordination of the quadrats by their woody plant species composition (based on stem density) showed clear segregation along axis 1 of all annually burnt quadrats from all unburnt quadrats (Fig. 3a). There was less striking segregation of ridge quadrats from slope quadrats along axis 2. The positioning of

Table 4. Variation in the richness of woody plant species in quadrats

Variable	UB	<i>F</i> -value	UB × RS	UR	Mean		
		RS			US	BR	BS
No. woody plant species	166.6***	3.2	2.1	25.2	21.6	9.2	8.8
No. woody rainforest spp.	170.7***	0.0	0.3	11.2	11.6	2.0	1.6

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; †*F*-values are from a two-way ANOVA for the main effects (fire regime (UB) and topographic position (RS)), their interaction (UB × RS) and means for each of the four treatment classes: BR, annually burnt ridge; BS, annually burnt slope; UR, unburnt ridge; US, unburnt slope.

Table 5. Cross-tabulation of frequencies of species by their relative abundance in unburnt versus annually burnt quadrats and association with rainforest

Plant/animal group considered	Association with rainforest (no. species)	Significantly more abundant in unburnt quadrats (no. species)	No difference in abundance between unburnt and annually burnt quadrats (no. species)		Significantly less abundant in unburnt quadrats (no. species)
Shrub and tree species (no. stems)	Yes	12	0		0
	No	7	7		0
Plant species in ground-layer subplots (cover) [†]	Yes	12 (5)	13 (4)		1 (1)
	No	6 (4)	19 (10)		16 (14)
Vertebrates (abundance)	Yes	7	1		2
	No	2	13		8

†Values in parentheses exclude tree and shrub species.

quadrats in the ordination space was very tightly associated with burning history ($R = 0.92$, $P < 0.001$) and less tightly, but still highly significantly, with landscape position ($R = 0.46$, $P < 0.001$). The ordination suggested no tendency for the quadrats nearest the property boundary (annually burnt ridge (BR)1, annually burnt slope (BS)1, unburnt ridge (UR)1 and unburnt slope (US)1) to be transitional in species composition, although quadrat BR1 was slightly aberrant in species composition compared with the other annually burnt ridge quadrats. Ordination patterns based on basal area rather than number of stems were substantially less clear-cut (Fig. 3b), but still were significantly related to fire regimes ($R = 0.29$, $P = 0.04$), although not to topographic position ($R = 0.06$, $P > 0.1$). Pairs of unburnt plots tended to have more similarity in their species composition of woody stems than did those of pairs of annually burnt quadrats (Fig. 4).

All plant species, sampled in 2 m × 2 m subplots

A total of 145 plant species were recorded in the 160 sampled subplots, of which 67 species were recorded in at least four quadrats (Table 6). These 67 species included 29 shrub and tree species, and two exotic species.

For saplings and trees, analysis of the relationship with fire regime and topographic position for the tree and shrub species in this subplot dataset were generally consistent with that derived from the belt transect (Table 2).

For other plant life forms, the distributional pattern was strikingly different, with a higher proportion of species showing increased abundance (frequency and/or cover) in annually burnt quadrats, and a relatively high proportion of species responding significantly to topographic position and to interactions of topographic position and fire regime. For perennial grasses, five of the seven species were significantly more abundant in the annually burnt quadrats, and only one (*Eriachne trisetata*) was less abundant in them. Four of the seven perennial herb species were significantly more abundant in the annually burnt quadrats, and none was more abundant in the unburnt quadrats. Three of the 11 creeper species were more abundant in the annually burnt quadrats, and two were more abundant in the unburnt quadrats. Four of the 12 'other herb' species were more abundant in the annually burnt quadrats, and three were more abundant in the unburnt quadrats. The sole perennial sedge was more abundant in the unburnt quadrats. Of the 38 species listed in Table 6 (other than trees and shrubs), 16 were recorded in quadrats in only one of the two fire regimes, with seven reported only from unburnt quadrats and nine reported only from annually burnt quadrats.

At the quadrat level, there was no significant overall difference in richness between the unburnt and annually burnt sites (Table 7); however, there were significant differences in quadrat-level richness for many life forms. Trees and shrubs, and exotic species had significantly higher quadrat-level richness in the unburnt site, and perennial grasses, annual grasses, perennial herbs and annual herbs had significantly greater species richness in the annually burnt sites. The pattern was generally similar for total cover, except that there was no significant difference for cover of trees and shrubs (a somewhat perplexing result, perhaps a result of the plot size being too small for the effective measure of cover in this group of species), and that the cover of 'other herbs' was greatest in unburnt quadrats. The total number of plant species recorded was similar between the total set of unburnt and annually burnt quadrats (99 and 103 species, respectively), but there were pronounced differences in the species richness summed over all quadrats for annual grasses (one and nine species, respectively), 'other herbs' (15 and 23 species, respectively), perennial grasses (five and eight species, respectively) and trees and shrubs (50 and 24 species, respectively), but not for creepers (12 and 13 species, respectively), perennial herbs (13 and 14 species, respectively), perennial sedges (one and two species, respectively), and ferns (two and zero species, respectively). Notably, the understorey in the annually burnt quadrats was dominated by perennial grasses, with little cover of annual grasses and no exotic plant species.

Compared with the annually burnt quadrats, the unburnt quadrats had significantly and substantially greater richness and more extensive cover of rainforest-associated plant species, even when trees and shrubs were excluded (Table 7). A far higher proportion of rainforest-associated species was more abundant in the unburnt quadrats than in the annually burnt quadrats, whereas the opposite was true for species not associated with rainforest (Table 7). The proportion that rainforest-associated plant species contributed to total plant species richness increased from 8% in annually burnt to 17% in unburnt plots, and the proportion that these species contributed to total cover increased from 12 to 47%, respectively.

Table 8 summarizes the categorization of plant species by response to fire regime, with information collated and condensed from both the belt transects and subplots, and compares this categorization with that reported by Fensham (1990) after 10 years of fire exclusion. Of 49 species for which results were reported in both of the studies, 22 (45%) showed no significant difference in cover between fire regimes after 10 years, but this had fallen to 16 (33%) after 23 years. Twenty-one of the 49 species showed no change in categorization from 10 to 23 years of treatment. Of the remaining species, changes from 10 to

Table 6. Variation in the incidence and cover of plant species recorded in eight 2 m × 2 m subplots per quadrat[†]

Species	RF	n	Incidence							Cover						
			F (UB)	Variation F (RS)	F (UB × RS)	UR	Mean US	BR	BS	F (UB)	Variation F (RS)	F (UB × RS)	UR	Mean US	BR	BS
Creepers																
<i>Ampelocissus acetosa</i>	No	10	12.5**	2.0 NS	0.0 NS	1.0	1.4	0.0	0.4	2.7 NS	0.7 NS	0.5 NS	2.4	6.2	0.0	0.4
<i>Ampelocissus frutescens</i>	No	18	0.0 NS	2.0 NS	1.1 NS	3.0	1.6	2.4	2.2	2.3 NS	0.0 NS	2.5 NS	6.0	1.6	5.8	10.8
<i>Austrodolichos errabundus</i>	No	6	13.8**	10.6**	10.6**	0.0	0.0	0.2	3.0	13.8**	10.6**	10.6**	0.0	0.0	0.2	0.3
<i>Dioscorea transversa</i>	Yes	5	12.1**	6.8*	6.8*	0.6	4.2	0.0	0.0	3.6 NS	2.7 NS	2.7 NS	0.6	8.2	0.0	0.0
<i>Dunbaria singuliflora</i>	No	5	6.6*	0.0 NS	0.0 NS	0.0	0.0	1.2	1.2	6.6*	0.0 NS	0.0 NS	0.0	0.0	1.2	1.2
<i>Galactia tenuiflora</i>	Yes	4	4.8*	6.2*	4.8*	0.2	0.0	3.0	0.0	4.5*	5.0*	4.5*	0.2	0.0	8.4	0.0
<i>Ipomoea triloba</i>	Yes	4	0.7 NS	0.7 NS	0.0 NS	0.8	0.4	0.4	0.0	0.4 NS	1.0 NS	0.0 NS	0.8	0.4	0.6	0.0
<i>Parsonsia velutina</i>	Yes	5	7.4*	2.7 NS	2.7 NS	0.6	2.4	0.0	0.0	7.2*	3.0 NS	3.0 NS	0.6	2.8	0.0	0.0
<i>Rhynchosia minima</i>	No	6	6.6*	6.6*	2.9 NS	0.2	0.0	1.2	0.2	3.5 NS	5.4*	2.0 NS	0.4	0.0	1.8	0.2
<i>Smilax australis</i>	Yes	8	46.6***	18.2***	18.2***	0.6	2.6	0.0	0.0	16.9***	8.6**	8.6**	1.0	6.0	0.0	0.0
<i>Vigna lanceolata</i>	No	4	0.5 NS	4.8*	0.5 NS	0.4	0.0	0.8	0.0	0.5 NS	4.8*	0.5 NS	0.4	0.0	0.8	0.0
Perennial herbs																
<i>Flemingia parviflora</i>	No	20	0.2 NS	0.8 NS	1.8 NS	4.6	4.2	3.8	5.8	0.2 NS	1.2 NS	1.2 NS	33.2	15.2	20.6	20.8
<i>Flemingia trifoliastrium</i>	No	16	13.6**	13.6**	6.8*	1.0	1.8	1.8	6.4	14.3**	5.7*	6.6*	5.0	2.6	21.2	87.0
<i>Helicteres A78389</i>	No	5	14.7**	14.7**	14.7**	0.0	0.0	2.6	0.0	6.5*	6.5*	6.5*	0.0	0.0	7.0	0.0
<i>Darwiniensis</i>																
<i>Hibbertia lepidota</i>	No	19	0.2 NS	13.6**	0.2 NS	5.0	2.2	4.4	2.2	0.6 NS	10.3**	0.3 NS	5.4	2.6	4.4	2.4
<i>Knoxia stricta</i>	No	13	21.5***	8.7**	30.1***	1.4	0.2	1.0	5.0	40.0***	17.8***	45.5***	1.4	0.2	1.2	6.4
<i>Phyllanthus flagellaris</i>	No	13	15.1**	6.1*	2.0 NS	0.6	0.0	3.6	1.4	15.1**	6.1*	2.0 NS	0.6	0.0	3.6	1.4
<i>Tacca leontopetaloides</i>	Yes	16	0.6 NS	0.6 NS	0.6 NS	2.4	2.4	1.2	2.4	0.6 NS	0.6 NS	1.0 NS	2.6	2.4	1.2	2.6
Other herbs																
<i>Chlorophytum laxum</i>	No	4	16.0**	16.0**	16.0**	0.8	0.0	0.0	0.0	16.0***	16.0***	16.0***	0.8	0.0	0.0	0.0
<i>Commelina ensifolia</i>	Yes	5	5.8*	3.9 NS	3.9 NS	0.0	0.0	2.0	0.2	5.8*	3.9 NS	3.9 NS	0.0	0.0	2.0	0.2
<i>Crotalaria medicaginea</i>	No	4	1.1 NS	1.1 NS	0.0 NS	0.0	0.2	0.2	0.4	1.1 NS	1.1 NS	0.0 NS	0.0	0.2	0.2	0.4
<i>Crotalaria montana</i>	No	6	4.0 NS	1.0 NS	0.0 NS	0.2	0.0	0.6	0.4	4.0 NS	1.0 NS	0.0 NS	0.2	0.0	0.6	0.4
<i>Desmodium pulleni</i>	No	4	5.3*	0.0 NS	0.0 NS	0.0	0.0	0.4	0.4	5.3*	0.0 NS	0.0 NS	0.0	0.0	0.4	0.4
<i>Elephantopus scaber</i>	Yes	15	18.3***	0.0 NS	0.0 NS	3.6	3.4	0.6	0.6	18.4***	1.6 NS	2.0 NS	14.2	7.8	0.6	1.0
<i>Euphorbia schultzei</i>	No	5	3.3 NS	3.3 NS	5.1*	0.0	0.2	1.8	0.0	3.3 NS	3.3 NS	5.1*	0.0	0.2	1.8	0.0
<i>Hibiscus meraukensis</i>	Yes	6	1.0 NS	4.0 NS	0.0 NS	0.4	0.0	0.6	0.2	1.3 NS	1.3 NS	0.1 NS	0.4	0.0	0.6	0.4
<i>Hyptis suaveolens</i> #	No	8	19.5***	1.5 NS	1.5 NS	3.2	1.8	0.0	0.0	8.1*	1.7 NS	1.7 NS	12.6	4.6	0.0	0.0
<i>Polygala D25064</i>	No	4	1.1 NS	1.1 NS	0.0 NS	0.2	0.0	0.4	0.2	1.1 NS	1.1 NS	0.0 NS	0.2	0.0	0.4	0.2
<i>Mudginberri</i>																
<i>Polygala eriocephala</i>	No	4	5.6*	2.0 NS	2.0 NS	0.0	0.0	0.2	0.8	5.6*	2.0 NS	2.0 NS	0.0	0.0	0.2	0.8
<i>Spermacoce leptoloba</i>	No	6	7.0*	7.0*	5.3*	0.2	0.0	3.0	0.2	7.0*	7.0*	5.3*	0.2	0.0	3.0	0.2
Perennial grasses																
<i>Alloterpopsis semialata</i>	No	16	23.7***	2.6 NS	0.5 NS	2.0	0.4	4.8	4.2	17.2***	0.4 NS	1.6 NS	2.0	0.4	9.4	14.4
<i>Chrysopogon fallax</i>	No	10	158.9***	6.9*	6.9*	0.0	0.0	3.8	5.8	21.7***	5.2*	5.2*	0.0	0.0	26.6	77.6
<i>Eriachne avenacea</i>	No	8	0.1 NS	16.0***	0.1 NS	2.6	0.0	3.0	0.0	0.8 NS	6.5*	0.8 NS	62.0	0.0	30.2	0.0
<i>Eriachne trisetata</i>	No	10	112.1***	6.5*	6.5*	2.2	3.6	0.0	0.0	14.0**	0.1 NS	0.1 NS	44.2	39.0	0.0	0.0

Table 6. (continued)

Species	RF	<i>n</i>	Incidence							Cover						
			<i>F</i> (UB)	Variation <i>F</i> (RS)	<i>F</i> (UB × RS)	UR	Mean		BS	<i>F</i> (UB)	Variation <i>F</i> (RS)	<i>F</i> (UB × RS)	UR	Mean		BS
<i>Heteropogon triticeus</i>	No	10	248.9***	3.7 NS	3.7 NS	0.0	0.0	7.4	5.8	78.0***	1.9 NS	1.9 NS	0.0	0.0	80.2	110.0
<i>Mnesithea rotboelliioides</i>	No	12	73.0***	0.7 NS	1.3 NS	0.4	0.2	5.0	6.2	17.8***	4.8*	4.9*	0.4	0.2	19.0	60.2
<i>Sorghum plumosum</i>	No	7	72.1***	38.4***	38.4***	0.0	0.0	6.4	1.0	36.3***	18.1***	18.1***	0.0	0.0	38.4	6.6
Perennial sedges																
<i>Scleria brownii</i>	Yes	6	10.5**	0.4 NS	0.4 NS	0.8	1.2	0.0	0.0	10.5**	0.4 NS	0.4 NS	0.8	1.2	0.0	0.0
Trees and shrubs																
<i>Acacia auriculiformis</i>	Yes	7	14.5**	0.1 NS	0.1 NS	1.6	1.8	0.0	0.0	3.8 NS	0.3 NS	0.3 NS	6.2	3.4	0.0	0.0
<i>Acacia lamprocarpa</i>	Yes	11	4.8*	3.5 NS	2.3 NS	2.8	0.8	0.6	0.4	5.5*	2.0 NS	0.9 NS	3.6	1.6	0.8	0.4
<i>Acacia latescens</i>	No	9	1.7 NS	1.7 NS	0.6 NS	0.8	0.0	1.0	0.8	4.0 NS	0.4 NS	0.4 NS	0.8	0.0	1.6	1.6
<i>Alphitonia excelsa</i>	Yes	4	5.3*	0.0 NS	0.0 NS	0.4	0.4	0.0	0.0	4.9*	0.1 NS	0.1 NS	0.6	0.8	0.0	0.0
<i>Alstonia actinophylla</i>	Yes	5	2.5 NS	0.6 NS	0.0 NS	0.4	0.6	0.0	0.2	1.9 NS	0.1 NS	0.2 NS	10.4	6.4	0.0	1.0
<i>Brachychiton diversifolius</i>	No	4	0.4 NS	3.6 NS	0.4 NS	0.0	0.8	0.0	0.4	0.4 NS	3.6 NS	0.4 NS	0.0	0.8	0.0	0.4
<i>Brachychiton megaphyllus</i>	Yes	14	0.2 NS	0.2 NS	0.2 NS	1.4	1.0	1.0	1.0	0.6 NS	0.4 NS	3.9 NS	6.4	1.2	1.8	11.8
<i>Breynia cernua</i>	Yes	12	10.0**	1.1 NS	0.1 NS	2.0	2.4	0.0	0.8	4.4 NS	2.2 NS	0.2 NS	2.8	6.0	0.0	1.8
<i>Buchanania obovata</i>	No	14	0.7 NS	0.7 NS	0.0 NS	1.2	0.8	1.6	1.2	0.7 NS	1.2 NS	0.7 NS	3.0	1.8	9.8	1.8
<i>Calytrix exstipulata</i>	No	4	5.3*	0.0 NS	0.0 NS	0.4	0.4	0.0	0.0	3.9 NS	0.1 NS	0.1 NS	0.8	0.6	0.0	0.0
<i>Canarium australianum</i>	Yes	7	0.1 NS	2.0 NS	2.0 NS	0.4	1.4	0.2	0.2	5.0*	5.8*	4.3 NS	0.6	11.0	0.2	1.0
<i>Croton arnhemicus</i>	Yes	6	38.5***	48.1***	38.5***	3.6	0.0	0.2	0.0	3.7 NS	7.8*	3.7 NS	22.0	0.0	4.0	0.0
<i>Cycas armstrongii</i>	No	15	0.8 NS	3.2 NS	0.1 NS	1.0	2.0	1.4	2.8	3.5 NS	3.3 NS	6.3*	10.2	5.2	5.6	36.4
<i>Denhamia obscura</i>	Yes	4	5.1*	1.3 NS	1.3 NS	1.2	0.4	0.0	0.0	3.4 NS	0.5 NS	0.5 NS	2.6	1.2	0.0	0.0
<i>Distichostemon hispidulus</i>	Yes	6	5.6*	3.1 NS	1.4 NS	0.2	0.0	1.4	0.4	3.8 NS	2.4 NS	0.6 NS	0.4	0.0	1.8	0.6
<i>Erythrophleum chlorostachys</i>	Yes	15	3.3 NS	18.9***	1.2 NS	0.6	2.4	1.0	4.0	1.7 NS	0.7 NS	0.1 NS	1.6	15.6	21.8	29.4
<i>Eucalyptus miniata</i>	No	19	6.5*	16.5***	1.0 NS	1.4	2.6	2.0	4.0	6.1*	6.4*	0.2 NS	2.6	9.4	9.2	19.2
<i>Eucalyptus tetrodonta</i>	No	9	0.7 NS	3.5 NS	0.0 NS	1.2	0.2	1.8	0.6	0.7 NS	3.5 NS	0.1 NS	3.0	0.2	3.8	1.6
<i>Exocarpos latifolius</i>	Yes	4	6.4*	1.6 NS	1.6 NS	0.2	0.6	0.0	0.0	2.7 NS	2.3 NS	2.3 NS	0.2	6.2	0.0	0.0
<i>Ficus opposita</i>	Yes	4	1.5 NS	1.6 NS	0.4 NS	0.2	0.8	0.0	0.2	1.0 NS	1.4 NS	0.7 NS	0.2	2.6	0.0	0.4
<i>Livistona humilis</i>	No	9	0.5 NS	0 NS	0.0 NS	0.6	0.6	0.4	0.4	1.8 NS	0.0 NS	1.3 NS	7.6	0.6	9.0	19.0
<i>Opilia amentacea</i>	Yes	5	1.3 NS	0.3 NS	0.3 NS	0.4	0.8	0.2	0.2	1.3 NS	0.1 NS	0.2 NS	4.4	4.2	0.0	2.2
<i>Persoonia falcata</i>	No	10	11.8**	0.5 NS	0.5 NS	1.0	1.4	0.2	0.2	11.0**	0.8 NS	0.8 NS	1.0	1.6	0.2	0.2
<i>Petalostigma quadriloculare</i>	No	19	1.0 NS	38.1***	4.2 NS	5.6	0.8	5.0	2.6	0.1 NS	7.8*	0.8 NS	16.2	0.8	13.0	5.0
<i>Planchonia careya</i>	No	19	0.7 NS	1.3 NS	0.0 NS	2.2	2.8	2.6	3.4	0.0 NS	0.2 NS	1.7 NS	8.8	4.8	5.8	7.8
<i>Sida cordifolia</i> #	Yes	6	9.7**	3.9 NS	3.9 NS	1.8	0.4	0.0	0.0	6.8*	2.9 NS	2.9 NS	2.8	0.6	0.0	0.0
<i>Terminalia ferdinandiana</i>	No	20	5.4*	5.4*	2.4 NS	4.0	2.0	2.0	1.6	0.3 NS	2.6 NS	1.2 NS	21.4	5.0	11.4	8.2
<i>Urena lobata</i>	Yes	10	70.1***	0.9 NS	0.9 NS	3.2	4.0	0.0	0.0	25.4***	1.4 NS	1.4 NS	3.2	5.2	0.0	0.0
<i>Xanthostemon paradoxus</i>	No	11	5.4*	12.2**	2.4 NS	0.4	3.0	0.0	1.0	33.6***	39.8***	30.9***	1.2	61.0	0.0	3.8

P* < 0.05; *P* < 0.01; ****P* < 0.001; †values shown are *F*-values from two-way ANOVA for the main effects (fire regime (UB) and topographic position (RS)), their interaction (UB × RS) and means for each of the four treatment classes: BR, annually burnt ridge; BS, annually burnt slope; UR, unburnt ridge; US, unburnt slope. *n*, no. quadrats from which the species was recorded (maximum 20); NS, not significant; RF, whether listed as a monsoon rainforest species by Liddle *et al.* (1994); #, exotic species.

23 years were not always consistent in trend, nor did they tend towards more extreme responses; for example, *Eucalyptus miniata* saplings were significantly more abundant in the unburnt sites after 10 years, but the incidence and cover of this species was greater in annually burnt sites after 23 years; and *Eriachne avenacea* was significantly more abundant in annually burnt sites after 10 years, but showed no significant difference after 23 years. Including species that were inadequately sampled in one or other of the studies, a smaller proportion of species showed no significant difference between fire regimes after 23 years than after 10 years (30% compared with 49%, respectively), with a correspondingly far higher proportion of species showing significant association with the unburnt regime (44% after 23 years and 23% after 10 years).

Ordination of all quadrats by their understorey composition (Fig. 3c) showed a clear segregation by fire regime and by topographic position

(R (fire regime) = 0.98, $P < 0.001$; R (topographic position) = 0.84, $P < 0.01$). For understorey cover, there was less clear segregation of annually burnt ridge and slope quadrats than that between ridge and slope quadrats in the unburnt treatment. Similarity between pairs of quadrats was appreciably highest when that pair comprised two annually burnt quadrats; in contrast, pairs of unburnt quadrats tended to have more dissimilar composition for the plants recorded in the 2 m × 2 m subplots (Fig. 4).

Vertebrates

A total of 72 vertebrate species (comprising four frog, 14 reptile, 41 bird and 13 mammal species) was recorded from the 20 sampled quadrats (Table 9). There was no significant difference between fire regimes in the richness of mammals, birds and frogs, or in the total abundance of mammals and frogs. The

Table 7. Variation in the species richness and cover of plant life-form groups recorded in eight 2 m × 2 m subplots per quadrat†

Plant groups	Variation			Mean			
	F (UB)	F (RS)	F (UB × RS)	UR	US	BR	BS
Species richness							
Creepers	0.0	0.4	0.9	3.8	4.8	4.4	4.2
Perennial herbs	10.1**	12.3**	0.0	6.0	3.8	8.0	5.8
Ferns	2.9	0.0	0.0	0.4	0.4	0.0	0.0
Other herbs	6.9*	14.4**	1.2	5.0	2.2	8.8	3.8
Annual grasses	10.7**	7.4*	4.7*	0.2	0.0	2.2	0.4
Perennial grasses	70.0***	12.9**	0.5	2.8	1.6	6.6	4.8
Perennial sedges	2.3	0.3	6.3*	0.4	0.8	0.6	0.0
Trees and shrubs	18.8***	0.9	0.0	19.2	20.8	13.0	14.2
Rainforest species	59.6***	3.6	4.2	14.8	19.4	8.2	8.0
Non-rainforest species	34.4***	26.6***	0.5	22.6	15.0	33.8	23.8
Rainforest species‡	16.1***	0.6	2.6	6.0	7.8	4.2	3.6
Non-rainforest species‡	38.2***	26.1***	1.7	12.2	5.8	24.8	14.0
Exotic species	40.9***	0.2	0.2	1.6	1.4	0.0	0.0
All species	4.1	13.0**	3.6	36.2	33.0	43.6	33.2
Cover							
Creepers	0.0	2.9	2.3	1.5	3.2	2.4	2.5
Perennial herbs	13.3**	1.3	8.2*	6.2	3.0	7.7	15.1
Ferns	1.9	0.3	0.3	0.1	0.1	0.0	0.0
Other herbs	15.0**	18.6***	1.5	3.8	1.6	1.8	0.6
Annual grasses	5.9*	1.3	0.9	0.0	0.0	0.6	0.2
Perennial grasses	45.8***	0.1	7.0*	13.7	5.0	26.3	33.7
Perennial sedges	4.5	0.1	2.3	0.1	0.2	0.1	0.0
Trees and shrubs	1.9	2.3	0.1	19.1	25.6	14.6	20.7
Rainforest species	16.1***	0.9	0.2	17.1	21.6	6.3	7.7
Non-rainforest species	56.7***	0.0	9.7**	28.0	17.5	43.7	55.3
Rainforest species‡	19.5***	0.0	0.2	8.5	9.4	1.7	1.1
Non-rainforest species‡	69.5***	0.8	10.4**	17.0	3.5	33.7	41.3
Exotic species	9.4**	0.6	0.6	1.9	1.2	0.0	0.0

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; †values shown are H -values from Kruskal–Wallis ANOVA for differences between fire regimes, F -values from two-way ANOVA for the main effects (fire regime (UB) and topographic position (RS)), their interaction (UB × RS) and means for each of the four treatment classes: BR, annually burnt ridge; BS, annually burnt slope; UR, unburnt ridge; US, unburnt slope; ‡excluding trees and shrubs.

richness and abundance of reptiles was greater in the unburnt quadrats. The total abundance of birds was greater in the unburnt quadrats, although in this case, there was a far stronger interaction effect, with abundance especially highest in the unburnt slope quadrats.

Of 39 species recorded from at least four quadrats, 23 species varied significantly in abundance between quadrats of contrasting fire regimes, with nine of these species reported from quadrats in only one of the two treatments. Eleven individual species (the skinks *Glaphyromorphus darwiniensis* and *Glaphyromorphus douglasi*; bar-shouldered dove, *Geopelia humeralis*; dusky honeyeater, *Myzomela obscura*; green-backed gerygone, *Gerygone chloronotus*; northern fantail, *Rhipidura rufiventris*; white-gaped honeyeater, *Lichenostomus unicolor*; white-throated honeyeater, *Melithreptus albogularis*; yellow oriole, *Oriolus flavo-cinctus*; black-footed tree-rat; and common brushtail possum) were significantly more abundant in unburnt quadrats (although this was complicated by significant interaction terms with topographic position for dusky honeyeater and white-throated honeyeater). Twelve individual species (forest kingfisher, *Todiramphus macleayii*; grey butcherbird, *Cracticus torquatus*; little friarbird, *Philemon citreogularis*; mistletoebird, *Dicaeum hirundinaceum*; long-tailed finch, *Poephila acuticauda*; northern rosella, *Platycercus venustus*; red-backed fairy-wren, *Malurus melanocephalus*; rainbow lorikeet, *Trichoglossus haematodus*; yellow-throated miner, *Manorina flavigula*; northern quoll; northern brown bandicoot; and pale field-rat, *Rattus tunneyi*) were significantly more abundant in the annually burnt quadrats, including two species (forest kingfisher and mistletoebird) for which there was a significant interaction term with topographic position.

A higher proportion of rainforest-associated species was more abundant in the unburnt quadrats than in the annually burnt quadrats, whereas the opposite was true for species not associated with rainforest (Table 5). In addition to the species on which Table 5 is based, other rainforest-associated species that were recorded from fewer than four quadrats and that were recorded only in unburnt quadrats included the orange-footed scrub-fowl, *Megapodius reinwardt*, and varied triller, *Lalage leucomela*.

Ordination of the quadrats by their vertebrate species composition showed a very strong segregation of all unburnt quadrats from all annually burnt quadrats on the first axis (Fig. 3). Quadrats were further segregated by topographic position along this same axis, with a progression in species composition from annually burnt slope to annually burnt ridge to unburnt ridge to unburnt slope quadrats. The positioning of quadrats was very significantly related to fire history ($R = 0.93$, $P < 0.001$) and to landscape position ($R = 0.53$, $P < 0.001$).

Table 8. Frequency of species categorized according to preferred fire regime after 10 years (Fensham 1990) and after 23 years (the present study)

	Species inadequately recorded in Fensham (1990) (n)	Total after 23 years (n)	Preference after 10 years†				Total (n)
			Unburnt (n)	[Unburnt (n)]	No difference (n)	[Annually burnt (n)]	
Preference after 23 years†							
Unburnt (n)	3	0	4	0	0	7	16
[Unburnt (n)]	2	4	3	0	0	9	15
No difference (n)	1	2	9	0	4	16	21
[Annually burnt (n)]	0	1	2	1	3	7	9
Annually burnt (n)	0	0	4	2	4	10	10
Total (n)	6	7	22	3	11	49	71
Species inadequately recorded in the present study (n)	2	0	10	2	2	16	
Total after 10 years (n)	8	7	32	5	13	65	

†Bracketed preferences indicate that the significant difference is possibly confounded by a significant interaction effect with topographic position and/or that the effect is not consistent across different measures of abundance (e.g. stem count and cover).

Table 9. Variation in the abundance of individual vertebrate species recorded from at least four quadrats, and of species richness and total abundance of vertebrate groups

Species	RF	<i>n</i>	<i>F</i> (UB)	Variation		UR	Mean abundance		
				<i>F</i> (RS)	<i>F</i> (UB × RS)		US	BR	BS
Reptiles									
<i>Carlia amax</i>	No	12	0.6 NS	46.6***	0.6 NS	2.4	0.2	3.4	0.2
<i>Carlia munda</i>	No	13	0.3 NS	12.4**	1.4 NS	1.2	2.2	0.2	2.6
<i>Glaphyromorphus darwiniensis</i>	No	4	6.1*	1.9 NS	1.9 NS	0.2	0.8	0.0	0.0
<i>Glaphyromorphus douglasi</i>	Yes	20	16.5***	0.8 NS	1.6 NS	4.6	3.2	1.4	1.6
<i>Menetia maini</i>	NA	4	1.1 NS	1.1 NS	0.0 NS	0.4	0.2	0.2	0.0
Birds									
<i>Geopelia striata</i> (peaceful dove)	No	10	0.1 NS	0.6 NS	0.5 NS	1.4	1.6	0.4	1.2
<i>Geopelia humeralis</i> (bar-shouldered dove)	Yes	14	107.1***	9.6**	0.7 NS	6.4	12.8	0.2	1.0
<i>Trichoglossus haematodus</i> (rainbow lorikeet)	No	7	7.8*	2.9 NS	0.7 NS	0.0	0.4	1.0	2.8
<i>Aprosmictus erythropterus</i> (red-winged parrot)	No	7	1.5 NS	2.8 NS	1.5 NS	1.0	0.2	0.4	0.2
<i>Platycercus venustus</i> (northern rosella)	No	7	6.8*	1.3 NS	0.1 NS	0.4	0.0	2.0	1.4
<i>Cacomantis variolosus</i> (brush cuckoo)	Yes	6	1.9 NS	0.7 NS	0.7 NS	0.2	0.2	0.4	1.8
<i>Dacelo leachii</i> (blue-winged kookaburra)	No	5	0.2 NS	0.2 NS	0.2 NS	0.4	0.2	0.2	0.2
<i>Todiramphus macleayii</i> (forest kingfisher)	No	8	6.1*	0.6 NS	6.1*	0.0	0.4	1.4	0.4
<i>Merops ornatus</i> (rainbow bee-eater)	No	4	0.1 NS	1.3 NS	0.4 NS	0.4	0.2	0.4	0.0
<i>Malurus melanocephalus</i> (red-backed fairy-wren)	No	7	15.9***	0.1 NS	0.1 NS	0.0	0.0	5.6	6.0
<i>Pardalotus striatus</i> (striated pardalote)	No	9	0.9 NS	0.2 NS	0.1 NS	0.4	0.6	1.2	1.0
<i>Smicrornis brevirostris</i> (weebill)	No	14	1.2 NS	14.6**	4.1 NS	5.2	3.8	7.6	0.4
<i>Gerygone chloronotus</i> (green-backed gerygone)	Yes	4	5.4*	0.8 NS	0.8 NS	0.4	0.8	0.0	0.0
<i>Philemon argenticeps</i> (silver-crowned friarbird)	No	12	0.1 NS	0.6 NS	0.1 NS	1.4	0.6	1.6	1.0
<i>Philemon citreogularis</i> (little friarbird)	No	7	4.4*	0.2 NS	3.1 NS	0.0	0.4	1.0	0.4
<i>Manorina flavigula</i> (yellow-throated miner)	NA	9	6.7*	0.1 NS	0.1 NS	0.4	0.2	3.0	3.2
<i>Lichenostomus unicolor</i> (white-gaped honeyeater)	Yes	9	46.8***	0.5 NS	0.5 NS	2.4	3.2	0.0	0.0
<i>Melithreptus albogularis</i> (white-throated honeyeater)	No	15	19.2***	3.6 NS	5.3*	4.2	13.2	1.6	1.2
<i>Lichmera indistincta</i> (brown honeyeater)	No	7	4.0 NS	9.0**	2.2 NS	0.2	4.6	0.0	0.8
<i>Myzomela obscura</i> (dusky honeyeater)	Yes	5	19.7***	19.7***	19.7***	0.0	7.0	0.0	0.0
<i>Rhipidura rufiventris</i> (northern fantail)	Yes	6	9.2**	0.7 NS	0.7 NS	1.2	1.8	0.0	0.0
<i>Coracina papuensis</i> (white-bellied cuckoo-shrike)	No	15	0.0 NS	1.4 NS	1.2 NS	3.0	2.2	3.4	1.2
<i>Oriolus flavocinctus</i> (yellow oriole)	Yes	6	4.4*	6.1*	2.1 NS	0.2	2.4	0.0	0.4
<i>Cracticus torquatus</i> (grey butcherbird)	No	16	9.8**	2.2 NS	0.2 NS	0.6	1.2	1.8	3.6
<i>Cracticus nigrogularis</i> (pied butcherbird)	No	10	2.2 NS	1.4 NS	3.7 NS	0.4	0.6	1.4	0.4
<i>Poephila acuticauda</i> (long-tailed finch)	No	4	4.9*	0.0 NS	0.0 NS	0.0	0.0	0.6	0.6
<i>Dicaeum hirundinaceum</i> (mistletoebird)	No	10	35.3***	1.6 NS	5.9*	0.0	0.2	1.8	0.8
Mammals									
<i>Antechinus bellus</i> (fawn antechinus)	NA	9	0.6 NS	0.9 NS	0.3 NS	0.2	0.8	1.0	1.0
<i>Dasyurus hallucatus</i> (northern quoll)	Yes	4	6.4*	1.6 NS	1.6 NS	0.0	0.0	0.6	0.2
<i>Isoodon macrourus</i> (northern brown bandicoot)	Yes	11	10.0**	0.4 NS	0 NS	0.4	0.2	2.0	1.6
<i>Trichosurus vulpecula</i> (common brushtail possum)	NA	13	29.4***	0.3 NS	0.5 NS	2.6	2.6	0.6	0.2
<i>Macropus agilis</i> (agile wallaby)	No	14	3.5 NS	0.3 NS	0.1 NS	2.6	2.8	0.8	1.0

Table 9. (continued)

Species	RF	<i>n</i>	<i>F</i> (UB)	Variation <i>F</i> (RS)	<i>F</i> (UB × RS)	UR	Mean abundance US	BR	BS
<i>Mesembryomys gouldii</i> (black-footed tree-rat)	NA	10	6.8*	2.7 NS	1.0 NS	2.6	0.8	0.4	0.2
<i>Rattus tunneyi</i> (pale field-rat)	NA	7	19.1***	1.8 NS	1.8 NS	0.0	0.0	1.2	2.8
Total abundance									
Frogs			0.0 NS	0.8 NS	0.0 NS	0.2	0.4	0.2	0.4
Reptiles			7.9*	1.0 NS	0.1 NS	9.4	8.0	5.8	4.8
Birds			5.5*	6.4*	15.6**	30.8	60.6	38.2	31.6
Mammals			0.1 NS	0.2 NS	0.1 NS	8.8	7.4	7.6	7.2
Species richness									
Frogs			0.0 NS	0.8 NS	0.0 NS	0.2	0.4	0.2	0.4
Reptiles			9.9**	0.3 NS	2.5 NS	3.6	4.4	3.0	2.6
Birds			1.2 NS	3.6 NS	7.3*	9.8	14.4	13.6	12.8
Mammals			1.0 NS	0.5 NS	1.0 NS	3.4	3.6	4.8	3.6

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ⁱvalues shown are *F*-values from two-way ANOVA for the main effects (fire regime (UB) and topographic position (RS)), their interaction (UB × RS) and means for each of the four treatment classes: BR, annually burnt ridge; BS, annually burnt slope; UR, unburnt ridge; US, unburnt slope. *n*, no. quadrats from which the species was recorded (maximum 20); NA, insufficient information available from given references to code for monsoon rainforest affiliation; NS, not significant; RF, whether the species is associated preferentially with monsoon rainforest, based on references given in text.

Edge effects and independence of quadrats

There was no tendency for the quadrats nearest the property boundary (BR1, BS1, UR1 and US1) to be transitional or exceptionally placed in any of the ordinations (Fig. 3d). There was no tendency for the quadrat closest to the property edge to be more dissimilar in species composition from its nearest neighbour of like fire regime than for other pairs of similarly spaced quadrats of like fire regime (Table 10). That is, the 'edge' quadrats were typical of those of the set sampled with similar fire regime and topographic position. Likewise, there was no tendency for the similarity in species composition of quadrats to be ordered along the length of the sampling extent (Fig. 3), implying that differences between quadrats reflect fire histories rather than any underlying environmental gradation.

There was no significant relationship between the separation distance and similarity in species composition of quadrats of like fire regime and topographic position for any of the variables considered: understorey cover ($r_s = -0.23$), understorey frequency ($r_s = -0.24$), understorey cover with trees and shrubs excluded ($r_s = -0.22$), basal area ($r_s = 0.21$), stem frequency ($r_s = 0.05$), and vertebrates ($r_s = -0.04$), with $P > 0.05$ and $n = 40$ throughout.

DISCUSSION

The study design imposed constraints on the interpretation of, and ability to extrapolate from, the results. This is one site only, and so sampled plots are pseudo-replicated. However, our results (ordinations and regression of similarity against distance between pairs of like plots) suggest no significant tendency for proximate plots to be any more similar in species composition than those more distantly separated, over the range of separation distances sampled. If plots 100 m apart are non-independent then so too are plots 400 m apart. There is also a high level of consistency in the results for those elements (trees and shrubs) that were sampled by two different procedures (belt transects and subplots), thus improving confidence in the analyses and their interpretation.

This single study site may be unrepresentative of the broader environment. Indeed, the annually burnt treatment appears to us to be in unusually good condition compared with much similar open forest elsewhere in this region. We recorded no exotic species in it, an understorey dominated by perennial grasses rather than the annual grasses that are more typical and mark poor condition, few dead trees, reasonable recruitment of eucalypt saplings, and an abundant mammal fauna. We suspect that this 'health' is partly a result of the absence of livestock or feral stock (elsewhere shown to have substantial impacts on biodiversity in tropical

eucalypt forests and savanna woodlands, Woinarski & Ash 2002), very limited human access and use, and the 'success' of the diligent early burning regime in preventing late dry season fires. Thus, the annually burnt area in this study may mark an unusually successful achievement of the prevailing conservation management goal, and we are comparing an ideal example against the unburnt treatment.

This study showed major differences in plant and animal species composition between the two areas subjected to contrasting fire regimes. In the unburnt quadrats, trees and shrubs were more diverse, and stem density was far greater. The shrub and tree species composition was markedly different, and this difference was directional, towards a greater representation of rainforest-associated elements. Although the canopy in the unburnt quadrats was still dominated by *Eucalyptus miniata* and *Eucalyptus tetradonta*, and these two species still contributed the greatest basal area, this was nowhere near as pre-eminent as in the annually burnt quadrats. Instead, very many other tree and shrub species had developed a dense tall understorey or subcanopy. We would predict that, with another 10–20 years of fire exclusion, the eucalypt overstorey would be likely to further diminish in relative importance, with less likelihood of replacement as increasing shade and greater interspecific competition limited eucalypt recruitment.

There were also major differences between treatments in the composition of plant species other than trees and shrubs. Again, this difference was directional, with greater representation of rainforest-associated plants in the unburnt quadrats. In contrast to the trees and shrubs category, quadrat-level species richness and cover were higher in the annually burnt quadrats for most life forms. However, the similarity in plant species composition was greater within the set of annually burnt than within the set of unburnt quadrats: that is, there was more beta-diversity. Whereas the annually

burnt quadrats converged to one relatively floristically rich composition, the unburnt quadrats were a more heterogeneous set.

Related studies are notably different in plot size, sampling procedure or duration of imposition of fire regimes. Nonetheless, the vegetation responses reported here are broadly similar to but more amplified than those reported in other studies. With some idiosyncratic exceptions, our results are consistent with those reported for the same site after 10 years of fire exclusion (Fensham 1990), but, after a further 13 years of the application of the treatments, exhibit more extreme divergence between annually burnt and unburnt treatments. The unburnt treatment progressed further towards rainforest species composition, although such progression could not be enumerated precisely because of differences in sampling techniques.

This progression towards an increased proportion, or dominance, of 'rainforest' species is not consistent with the conclusions of Bowman *et al.* (1988) and Bowman and Panton (1995), after 13 and 21 years of fire exclusion at Munmarlary, although Russell-Smith *et al.* (in press) recorded an increase in rainforest plant species there after 23 years. We suspect that the differences are for two reasons: plot size/location and semantics. The Munmarlary plots are small (1 ha) and isolated, whereas Solar Village provides a larger arena in which rainforest colonization and expansion can occur. There must be a higher probability of random or other dispersal of rainforest propagules to the 120 ha of unburnt vegetation at Solar Village than to the 1 ha plots at Munmarlary. Once established, there is also far more room to expand. The Solar Village area also includes a riparian strip (that was not sampled in the present study) from which rainforest-associated plants can spread through continuous forest. In contrast, there was no riparian area near the Munmarlary open-forest plots, and the plots were also all isolated, almost

Table 10. Consideration of the similarity of 'edge' quadrats to that of their nearest neighbour of like fire regime[†]

Variable considered	Mean similarity index		<i>z</i>	<i>P</i>
	Edge and closest like neighbour	Closest like neighbours (excluding edge quadrat)		
Understorey cover	50.4	51.4	0.24	NS
Understorey cover (excluding shrubs and trees)	63.7	59.7	0.60	NS
Basal area	47.3	34.6	1.33	NS
Stem frequency	55.5	45.5	1.33	NS
Vertebrates	50.8	51.7	0.49	NS

[†]Values shown are the mean similarity index of this pair (i.e. 'edge' quadrat and that of their nearest neighbour of like fire regime), compared with that of all other pairs of nearest quadrats of like fire regime (e.g. BR1/BR2 cf BR2/BR3, BR3/BR4, BR4/BR5, etc). Also shown in body of table are *z*-scores from Mann-Whitney *U*-tests for this comparison: NS, no significant difference.

hermetically sealed, from the nearest such potential rainforest source areas by perimeter fire breaks. The second reason for different conclusions is in the definition of a rainforest-associated plant. Bowman *et al.* (1988) and Bowman and Panton (1995) provided no definition; however, some of the species that they demonstrated as increasing in unburnt plots at Munmarlary (e.g. *Erythrophleum chlorostachys*, *Antidesma ghaesembilla*, *Alphitonia excelsa*) are listed as rainforest-associated species by Liddle *et al.* (1994). The rainforest species list given in Liddle *et al.* (1994) is generous and contestable (R. Fensham, pers. comm.), but at least it provides a yardstick – there is no other such listing available. There is a gradation from obligate rainforest species to those that occur mostly in rainforest but are present also (in less abundance) in open forest, and it is something of an artifice to cut this continuity, especially so as the very definition of rainforest may be extremely slippery (Bowman 2000, 2001; Hill 2000; Lynch & Neldner 2000; Neldner & Lynch 2001).

Notwithstanding these design and interpretational differences, there is clear consistency in all studies that, with increasing length of time without fire, a suite of generally broad-leaved woody species increases (in abundance, particularly in density of saplings, and over time, in poles and small trees), and that, concomitantly, grass cover and richness decreases. Woody species that increase in these forests typically include *Xanthostemon paradoxus*, *Erythrophleum chlorostachys*, *Alphitonia excelsa*, *Terminalia ferdinandiana*, *Planchonella* (*Pouteria*) *pohlmanniana*, *Canarium australianum* and *Briedelia tomentosa* (Bowman *et al.* 1988; Fensham 1990; Gill *et al.* 1990; Bowman & Fensham 1991; Bowman & Panton 1995; Russell-Smith *et al.* in press).

Likewise, there were major differences in reptile, bird and mammal assemblages between the treatments, with these differences towards greater representation of rainforest-associated species in the unburnt quadrats. However, species richness was generally little different between annually burnt and unburnt quadrats, except for a higher diversity of reptiles in unburnt quadrats. These results are broadly consistent with other studies, for example in corroborating previously observed associations of brushtail possums and black-footed tree-rats with long-unburnt areas and dense tall shrubby understorey (Friend & Taylor 1985; Kerle 1985, 1998; Friend 1987). In this case, the association may be because these environments provide a greater, and a more seasonally equitable, supply of fleshy fruits (notably from plant species such as *Breynia cernua*, *Buchanania obovata*, *Denhamia obscura*, *Ficus opposita*, *Opilia amentacea*, *Persoonia falcata*, *Planchonia careya* and *Terminalia ferdinandiana*, all of which were more abundant in the unburnt quadrats). Frequent fires lead not only to a decrease in the abundance and/or stature of such plant species, but also reduce, or even prevent,

fruit production (Williams 1997), as has been demonstrated also in savannas of other continents (Sanaïotti & Magnusson 1995). In contrast, vertebrates such as the long-tailed finch and pale field-rat that consume mainly grass seeds or their stems, leaves and roots occurred only in the dense grass understorey of the annually burnt quadrats.

The results of the present study show that there is a substantial set of plant and animal species that are disadvantaged by a regime of high fire frequency, and thus that the prevailing management outcome is sub-optimal for them, and that their landscape-wide population is less than their potential. The species most disadvantaged by frequent fire may have long been eliminated from this landscape. Those slightly more tolerant may eke out an existence in the tiny pockets of monsoon rainforest, which comprise <0.5% of the landscape (Russell-Smith *et al.* 1992), but which are nonetheless relatively persistent because they occupy sites that are either too wet to support fire or are protected from fire by topographical features. The results here suggest that many such species may extend more broadly across the landscape if that landscape is managed with substantially reduced frequency of fire. The results also suggest that recent broad-scale decline in many mammals, notably including brushtail possum and black-footed tree-rat, may be a result of, at least in part, an increased fire frequency and concomitant decrease in the extent of relatively long-unburnt areas. Although such species may persist in landscapes with a pervasive high frequency of fire, this occurrence may be as sink populations, maintained largely by ongoing recruitment from pockets of the more suitable longer-unburnt forest. However, we acknowledge that this argument fits only a proportion of the mammal species exhibiting patterns of pervasive decline. Other declining mammals appear to prefer, or at least tolerate, a moderately high frequency of fire (e.g. pale field-rat, northern quoll, northern brown bandicoot). Fire impacts on fauna may be related to the intricacy (heterogeneity or patch size) of fire histories, with more fine-scale patterns providing a broader menu of resources and options for shelter than regimes based on extensive fires, or extensive areas left unburnt (Woinarski *et al.* 2001; Yibarbuk *et al.* 2001). The Solar Village set-up cannot consider this factor, except insofar as there was no tendency for increased mammal richness in the quadrats closest to the treatment boundary, and that there was relatively high abundance and diversity of mammals within both of the uniform burning regimes.

The two locales sampled at this site show a divergence in biodiversity attributes. The biota of both the annually burnt and the unburnt treatments are rich, and may represent desirable states. However, one of these states now occupies almost all of the tropical savannas and open forests, whereas the other is realized

extremely rarely. We would argue that this is not an ideal outcome, and that instead land managers should attempt to provide also for that suite of biota that prefer long-unburnt forests. Such a goal has been recently recognized by some land managers. For example, the current plan of management for Kakadu National Park states that:

A major issue in managing habitats in the lowland woodlands is that a fine-scale mosaic of patches that covers a range of fire histories should be developed. Currently there are few areas that remain unburnt for more than a few years (Kakadu Board of Management and Parks Australia 1999).

The question then becomes, is such management possible? This question has been addressed previously through the lens of risk minimization: that frequent 'fuel-reduction' burning is necessary to prevent destructive fire. That argument has hinged largely on the premise of an accumulation of fuel loads with increased time since fire, such that fires in longer-unburnt forests may become uncontrollable conflagrations (Lonsdale & Braithwaite 1991; Williams *et al.* 1999; but cf. Gill *et al.* 2000). The Solar Village site suggests that this premise has some limitations, as the total ground layer fuel was not significantly different between the unburnt and annually burnt treatments. This does not necessarily mean that fires will behave in the same way in the two treatments, as the drying and burning characteristics of the fuels (largely a thick layer of fallen leaves in the unburnt treatment, and a dense understorey of tall grass in the annually burnt treatment) may differ substantially, with generally higher flammability of the grassy fuels (Gill *et al.* 2000). The argument is also complicated by the uncertainty or unpredictability of the flammability of the relatively dense shrub layer in the unburnt treatment. However, these results suggest that there may be a threshold, beyond which time since fire no longer results in increases in fuel load, and may in fact mark a decline in fuel loads and hence risk of intense fire (Gill *et al.* 2000). Indeed, fires have spread to parts of the Solar Village site over the last 5 years (in areas not sampled in this study), and were suppressed and extinguished without exceptional problems.

The present paper suggests that the existing regime appears to have some substantial, and hitherto largely discounted, biodiversity costs. The fire regime strategy that we recommend involves a balance of minimizing the risk of extensive uncontrolled wildfire through a judicious and not over-zealous use of early dry season burning, with the extent of that early burning driven by continual assessment of the spatial distribution of fire histories in order to ensure that a reasonable proportion of the landscape is maintained in a relatively long unburnt state. We do not have the knowledge yet to parameterize this equation, but suggest that the current proportion of long-unburnt forest should be increased.

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