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Patterns of long-term woody vegetation change in a sandstone-plateau savanna woodland, Northern Territory, Australia

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Abstract: Aerial photographs were used to assess changes in woody vegetation cover at 122 locations within a sandstone-plateau savanna woodland in the Victoria River region, Northern Territory, Australia. Despite locally variable vegetation responses, there has been little change in total woody vegetation cover since 1948. Thirty-three locations were also surveyed on the ground. It was found that sites for which vegetation cover had changed over the 50-y period were not significantly different from stable sites in terms of floristic composition, recent fire history, demographic stability among the dominant tree species, or edaphic setting. However, two of the dominant overstorey tree species – *Eucalyptus tetradonta* and *Eucalyptus phoenicea* – showed significantly higher mortality on sites that had experienced vegetation cover decline since 1948. We suggest that observed changes in woody vegetation cover are a consequence of natural cycles of die-back and recovery of at least these two species in response to spatially heterogeneous variables such as dry-season moisture stress. Although the widespread decline of fire-sensitive *Callitris intratropica* populations clearly indicates a historical shift from lower- to higher-intensity burning conditions within the study area, we reject the hypothesis of a landscape-wide process such as changing fire regimes or climatic change as the driving factor behind large-scale vegetation changes detected by aerial photographic analysis.

Key Words: aerial photographs, Australian monsoon tropics, landscape fire, tropical savanna, vegetation dynamics

INTRODUCTION

Savanna landscapes worldwide are noted for their inherent dynamism. The species composition and relative abundances of the mixed trees and grasses that characterize savannas may shift dramatically over time in response to a number of complex ecological factors (Scholes & Archer 1997, Skarpe 1991). It is well known that some Australian savanna environments have undergone significant transformation in the past two centuries (Bowman *et al.* 2001 and references therein). These changes are often attributed to altered land-management conditions accompanying the arrival of Europeans. Specifically, grazing by cattle and other introduced ungulates has caused considerable changes in savanna landscapes both in Australia (Burrows *et al.* 1998, Sharp & Whittaker 2003) and elsewhere (Reid & Ellis 1995, Skarpe 1990), and altered fire regimes

accompanying the shift from Aboriginal to European occupation are thought to have had major and continuing impacts (Bowman 1998, Bowman & Panton 1993, Russell-Smith *et al.* 1998). In addition, it has been predicted on theoretical grounds that increasing concentrations of atmospheric CO₂ may preferentially stimulate woody plant growth in savanna landscapes (Idso 1995, Johnson *et al.* 1993), although Archer *et al.* (1995) de-emphasize the role of CO₂ relative to changing land management. Finally, long-term climatic trends and stochastic weather events such as storms and drought may exert significant influence on savanna landscape dynamics (Fensham & Holman 1999, Williams & Douglas 1995).

Understanding savanna dynamics is difficult, in part because the ecological factors determining savanna distribution and structure are themselves only partly understood (Bowman & Minchin 1987, Williams *et al.* 1996). In north Australian savannas, water drainage and edaphic factors are major determinants of floristic composition (Bowman & Minchin 1987, Sharp & Bowman *in press*). Theoretical models predict that soil texture

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will mediate tree–grass interactions and consequently exert major influence on savanna structure (Knoop & Walker 1985, Walker & Noy-Meir 1982). The effects of fire are contentious: while changing fire regimes are clearly a factor in a number of observed changes, most Australian savanna plants are highly fire-adapted; fire tends to alter Australian savannas structurally rather than floristically (Bowman & Panton 1995, Bowman *et al.* 1988). The most dramatic fire effects have been witnessed for specific fire-sensitive species, generally as a consequence of increased fire intensity following the cessation of traditional Aboriginal burning (Bowman & Panton 1993, Russell-Smith *et al.* 1998).

Vegetation changes in savanna landscapes can affect both ecosystem productivity and conservation value. Additionally, carbon storage in woody savanna plants has major implications for national carbon budgeting in light of global climate-change agreements (IPCC 1997). Finally, understanding the effects of changing land-management practices informs ongoing palaeoecological debates about the consequences of the extraordinarily long period of Aboriginal occupation in Australia (e.g. Bowman 1998).

The present study examines a large area of tall open savanna woodland vegetation on a sandstone plateau in the Northern Territory, Australia, for evidence of landscape-scale woody vegetation change at the 50-y time scale, and seeks to suggest possible causes of observed changes. The study environment provides a suitable model system to investigate these contingencies because some of the variables affecting savanna dynamics are controlled: water drainage is effectively uniform and grazing by domestic and feral stock has been negligible. We predict that if there has been a systematic vegetation response to either the cessation of Aboriginal fire management or to changes in climate, including increased CO₂ concentrations, these changes should occur uniformly across the plateau. If these factors interact with edaphic site characteristics or affect particular vegetation communities preferentially then changes in woody vegetation cover should be systematically related to different edaphic settings or to vegetation community composition. If no systematic relationship exists then observed changes are likely a consequence of site-specific cyclical processes or stochastic events.

STUDY SITE

Environmental setting

The 1400-km² study area is located on the Yambarran Plateau, approximately 350 km south of Darwin and 50 km north-west of Timber Creek (15°40' S, 130°30' E; see Figure 1, inset). The climate of the region is

monsoonal, with highly seasonal rainfall (average rainfall is 938 mm y⁻¹, of which more than 90% falls between November and March) and year-round high temperatures (see http://www.bom.gov.au/climate/averages/tables/cw_014850.shtml). The plateau is bounded on the south by the Victoria River, on the north by the Fitzmaurice River, and on the east by a steep escarpment that isolates it from pastoral lowlands (Figure 1). Soils and landforms have been described by Hollingsworth & Aldrick (1997), vegetation by A. M. Lane & T. M. Orr (unpubl. data), and fire regimes by C. Yates *et al.* (unpubl. data). The parent rock is Protozoic sandstone that has been deeply weathered since the Tertiary to produce sandy skeletal soils associated with rock outcrop and deep sandy soils on lateritized sediments. The plateau is approximately 300–330 m asl and 250–300 m above the surrounding lowlands. It is flat with no well-defined drainage lines. The dominant vegetation on the plateau is tall open eucalypt woodland. Small closed-forest patches occur in fire-protected gorges and clefts along the escarpment edge; these habitats were deliberately excluded from the present study.

History

At the time of European occupation, the study area had been inhabited and most likely actively managed by Aboriginal people for 40 000 y or more (Mulvaney & Kamminga 1999). Little is known of the pre-European fire regime, but it is likely that the plateau was burnt in a mosaic fashion in the first half of each dry season by numerous small fires associated with the hunting and gathering practices of Aboriginal inhabitants (Bowman 1998, Haynes 1985, Yibarbuk *et al.* 2001). Major disruption of Aboriginal activities occurred approximately 100 y ago when Bradshaw pastoral station was established. However, there has never been any controlled pastoralism on the plateau itself, and steep escarpments isolate the study area from the effects of grazing by feral ungulates. Traditional Aboriginal management of the study area likely continued in a greatly reduced capacity until the 1950s when resident Aboriginal stockmen on Bradshaw Station moved permanently to other properties. Since that time the study area has been completely unmanaged, and has been regularly burnt by uncontrolled wildfires which spread into the area from adjacent lowlands. It is widely acknowledged that in sandstone environments where grazing is negligible, the cessation of active fire management leads to significant increases in fire size, frequency and intensity relative to conditions where traditional management is ongoing (Russell-Smith *et al.* 1998, Yibarbuk *et al.* 2001). A location-specific fire history established by C. Yates *et al.* (unpubl. data) reveals

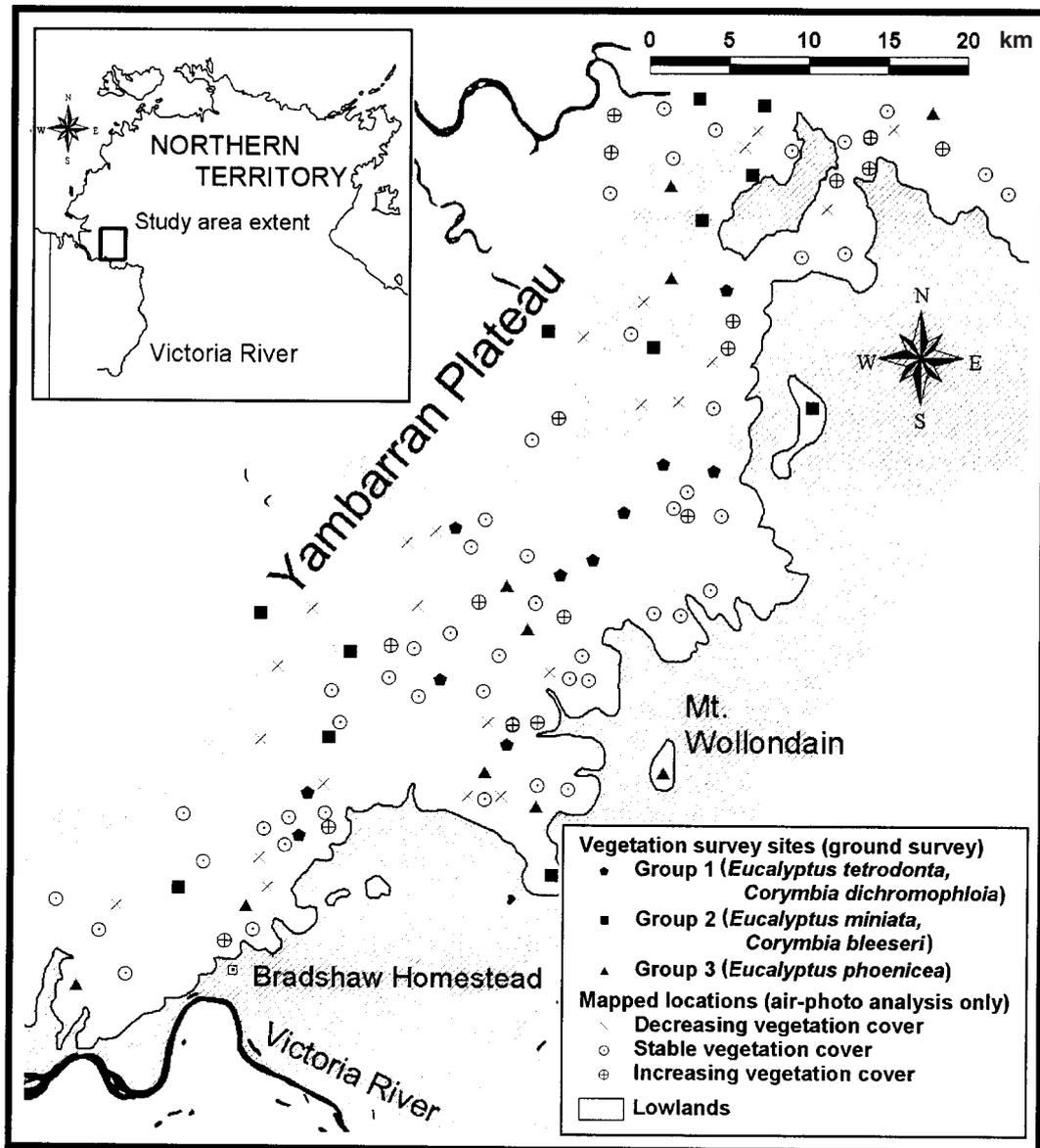


Figure 1. RCI (Relative Change Index) category assignments for 122 locations at which vegetation cover was assessed by air-photo analysis. Symbols at each site represent the direction of woody vegetation canopy cover change, 1948–1993/7. Note that adjacent sites often have opposite change histories even on similar habitats and in the absence of topographic barriers between them. Symbols for the 33 sites that were surveyed from the ground represent TWINSpan-derived vegetation group designations.

that approximately 50% of the study area was burnt each year between 1990 and 1999. We use this 10-y fire history as a proxy for the relative exposure of different environments to fire in a setting where fire is not actively managed.

METHODS

Callitris intratropica aerial survey

Cypress pines (*Callitris intratropica* R.T. Baker & H.G. Smith) are a known persistent indicator of changing

fire regimes (Bowman & Panton 1993). Consequently an extensive aerial survey of *C. intratropica* was carried out along predetermined transects totalling 219 km in length throughout the study area. A helicopter was flown at constant height and speed (150 m and 180 knots) and individual *C. intratropica* trees and/or stumps were counted by a single operator familiar with the species (Bowman) looking through a narrow window in the floor of the helicopter. The helicopter position was recorded by GPS at 30-s intervals and the numbers of living and dead *C. intratropica* trees and stumps were recorded for each transect segment. Special conditions (e.g. dense

C. intratropica clusters in fire-protected gullies) were noted in each transect segment.

Woody vegetation-cover mapping

Aerial photographs from 1948 and 1993/7 were obtained from CSIRO Land and Water (Canberra) and from the Australian Defence Force, respectively, and digitally processed to yield estimates of net woody-vegetation-cover change at 122 locations throughout the study area. Vegetation cover was assessed independently for old and recent photo-mosaics at selected locations measuring 650 × 650 m (i.e. 42 ha) using a semi-automated greyscale-threshold classification methodology (below). A pre-existing land-unit survey (Hollingsworth & Aldrick 1997; see Stewart *et al.* 1970 for an explanation of land-unit categories) was used to ensure that mapped sites captured the full range of existing variation within the study area.

The 122 mapped locations were selected on the basis of the following criteria: (1) woody vegetation within the 650 × 650-m area was homogeneous open woodland, uninterrupted by topographic discontinuities such as escarpments or drainages; (2) vegetation in both 1948 and 1993/7 was not obstructed by recent fire scars or imperfections in the hardcopy photograph; (3) the mapped location was no closer than 2 km to any other mapped location. Vegetation cover at all sandstone-plateau locations meeting these criteria within the study area was assessed by the following sequential methodology, using ERMapper v. 6.1 image analysis software:

- (1) Hard-copy photographs were scanned in 8-bit greyscale and combined to produce georectified mosaics of the entire study area with a resolution of 1 pixel = 2 m.
- (2) Geographically identical 650 × 650-m sections were excised from both the 1948 and 1993/7 parent mosaics at selected locations.
- (3) The excised images were blur-filtered to remove graininess effects caused by the paper texture of the hardcopy photographs.
- (4) The images were contrast-stretched to emphasize the boundaries of individual tree canopies.
- (5) A numerical greyscale threshold (0–255) was chosen to yield a binary classification of tree cover vs. background. The threshold was chosen visually by on-screen comparison of the binary image with the original parent image and continually adjusted until the boundaries of individual tree canopies matched most closely.

Of the 122 mapped locations, 33 were selected for sampling from the ground. These sites were selected so

as to sample the full range of historical and topographic variation, with special efforts made to include sites with contrasting fire histories. Two sites were located on relict escarpment outliers that are known to burn infrequently as a consequence of their isolation from the main plateau (Figure 1).

Vegetation survey

Sampling was conducted in early August 2000. At each site all woody plants were measured within a belt transect measuring 400 × 10 m. Diameter (of each stem at base), and life status (living/dead/partially dead) was recorded for each woody individual. Individual trees were scored 'partially dead' if more than one third of the total basal area was dead. Long-dead individuals without bark were assigned to a separate 'unidentifiable dead' category and were excluded from subsequent ordination analyses.

Ground cover was characterized by recording the presence/absence of the following characteristics within 1-m² plots at 40 equally spaced locations (every 10 m) along the centre line of the transect: annual grasses, perennial grasses, tussock grasses, forbs and exposed rock. Tree cover was estimated by recording the height and living/dead status of the tree canopy directly overhead at 200 equally spaced locations (every 2 m) along the centre line of the transect (tree canopies were assumed to be solid polygons with no concave edges; dead canopy hits were excluded from estimates of total woody cover). Line transects of this form have been shown to produce reliable estimates of cover (Hanley 1978).

The following data were recorded at representative locations on each site: (1) Slope, measured to the nearest 0.5°. (2) Soil texture (clay content) of the surface soil horizon. (3) Soil colour of the surface soil horizon. (See McDonald *et al.* 1994.) A brief description of each site was also recorded, including dominant species, conspicuous evidence of fire and/or grazing, and a general soil description.

Numerical analysis

Community data were entered into the classification programme TWINSpan (Hill 1979) in order to define vegetation community groups according to which subsequent analyses could be performed. The TWINSpan programme successively splits the survey sites into groups on the basis of a DCA ordination and summarizes the compositional differences between the groups. Five pseudo-species abundance 'cut-levels' were defined so as to assign each species at each site into one of five approximately equal abundance classes. As the aim was to examine changes in overall woody plant abundance, the abundance measure (basal area) was not standardized (cut-level minima: 0, 0.05, 0.25, 1.0, and 2.5 m² ha⁻¹)

and the pseudospecies cut-levels representing higher abundances (i.e. dominant overstorey tree species) were given higher weight in the analysis (cut-level weight factors: 3, 4, 5, 6, 6). The three vegetation community groups defined in this way were compared using non-parametric ANOVA tests assessing site edaphic characteristics, a number of woody vegetation indices (including tree death), and vegetation cover change indices.

Stand demographics

Size-class histograms for each overstorey tree species at each site were examined for evidence of episodic recruitment or species non-replacement. A demographic skewness coefficient (Hutchings 1975) and stem density indices for different size classes were used in subsequent ANOVA analyses to look for more subtle demographic differences between sites with different histories of vegetation change.

RESULTS

Callitris intratropica aerial survey

A total of 494 *Callitris intratropica* trees/stumps were counted, of which 122 were living and 372 were dead. While dead trees were distributed roughly uniformly, living trees were completely absent over much of the study area (see Table 1). Note that the helicopter survey transects were continuous, and therefore included fire-protected gorges and riparian areas that were excluded from this study. Many of the living trees occurred in dense clusters within these sheltered habitats, and not in the open woodlands of the plateau itself; significantly, 52 (43%) of the living trees counted were concentrated in just two such clusters. Thus the helicopter survey provides an overview of *C. intratropica* population dynamics throughout the whole of the study area, but the ground

Table 1. Results of *Callitris intratropica* aerial survey. Living and dead *C. intratropica* trees and stumps were counted by helicopter along aerial transects totalling 219 km in length. Living trees outnumbered dead trees in fewer than 10% of transect segments. Note that these results include trees existing in fire-protected gorges that were not included in the actual study.

	Number of transect segments	%
No <i>Callitris intratropica</i> trees/stumps	38	29.2
Dead trees/stumps only	65	50.0
More dead than living	15	11.5
Equal numbers, or more living than dead	6	4.6
Living trees only	6	4.6
Total	130	100.0

survey provides a better representation of *C. intratropica* persistence within the plateau open-woodland habitats specifically targeted in this study. Of the 33 ground survey transects, 11 contained *C. intratropica* trees or stumps, only three of which included trees that were living. In total 94 *C. intratropica* trees were measured on the ground, of which 11 were living and 83 were dead.

Vegetation cover estimation and historical change

A linear relationship was established between air-photo estimates and field estimates of woody vegetation cover, with $r^2 = 0.59$. A number of factors may have contributed to the imperfect correlation. Ground surveys were conducted 3–7 y after the dates on which aerial photographs were taken. Furthermore, due to vegetation heterogeneity and the limitations of a 400-m linear-sampling transect on the ground (relative to the 42-ha area in which cover was assessed by aerial photography at each site) it is likely that the aerial methodology actually yielded a more accurate estimate of woody vegetation cover than did the ground survey. The same methodology applied on lowland environments with homogeneous vegetation and longer linear transects yielded r^2 values approaching 0.80 (Sharp & Whittaker 2003); this level of accuracy is consistent with the best results obtained by other air-photo classification methodologies (Fensham *et al.* 2002, Kadmon & Harari-Kremer 1999).

The Relative Change Index (RCI) is defined as: $RCI = (\text{vegetation cover } 1993/7) / (\text{vegetation cover } 1948)$. Sites at which $RCI > 1.2$ are classed as 'increasing cover'; sites at which $RCI < 0.8$ are classed as 'decreasing cover'; sites with intermediate RCI values are classed as 'stable'. Sample photo pairs for sites in each category are shown in Figure 2. The spatial distributions of locations with different change histories are shown in Figure 1. Note that adjacent sites on similar habitats often exhibit opposite vegetation responses even in the absence of topographic barriers between them. Cover-change results are displayed graphically in Figure 3. The fact that the fitted line for the 122 points (slope = 1.008; SE = 0.024) is statistically identical to the line of no change (i.e. slope = 1) when anchored at the origin, indicates that there has been no significant net increase or decrease in total woody vegetation cover since 1948. The same is true of the fitted lines for each individual vegetation group, indicating that no group shows a consistent tendency for either vegetation cover increase or decline. That the unanchored line for all 122 points (slope = 0.656; SE = 0.087; intercept = 8.57) has a slope less than 1 indicates that sites with very low cover in 1948 tend to have increased in cover by 1993/7, and vice versa, perhaps indicative of natural cycling.

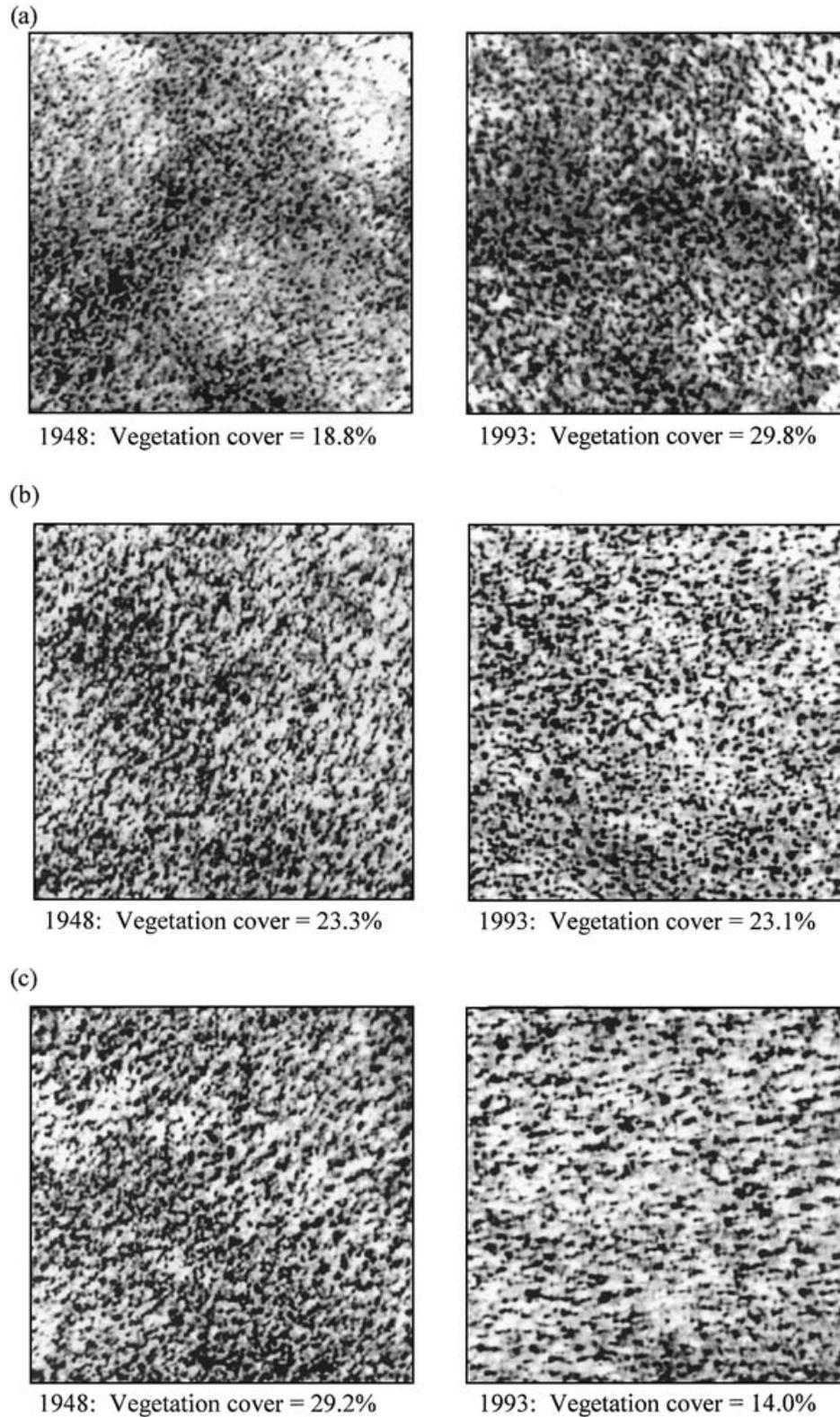


Figure 2. Sample aerial photograph pairs and estimates of woody vegetation cover change (1948–1993) for selected survey sites, as determined by semi-automated digital photomosaic classification. (a) Increasing woody vegetation cover (RCI = 1.59); (b) Stable woody vegetation cover (RCI = 0.99); (c) Decreasing woody vegetation cover (RCI = 0.48). All photomosaic segments measure 650 × 650 m. Spatial resolution of the parent mosaics is 1 pixel = 2 m.

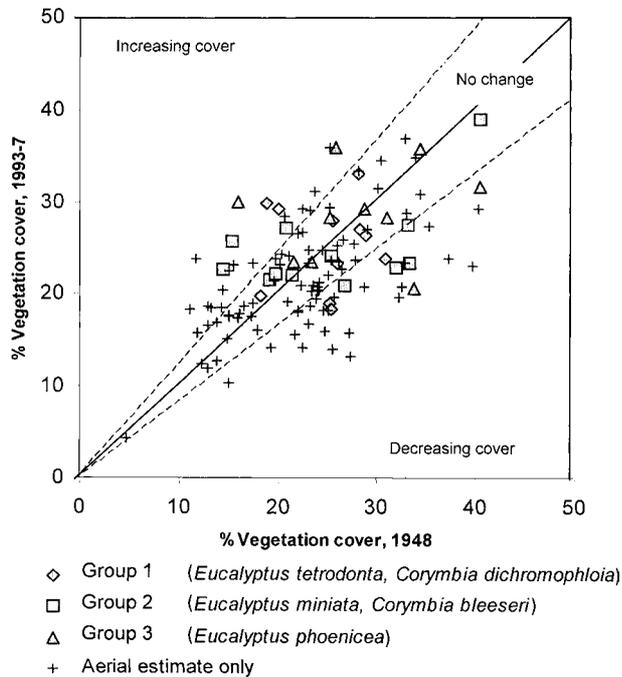


Figure 3. Estimates of woody vegetation cover change, 1948–1993/7, at 122 mapped locations, as determined by aerial photograph analysis. TWINSpan vegetation group designations are shown for the 33 locations that were also surveyed on the ground. The line with slope = 1 represents no change in vegetation cover. Dashed lines represent arbitrary boundaries between RCI categories (i.e. 'decreasing', 'stable' and 'increasing' cover).

Vegetation survey and definition of vegetation groups

Thirty-nine woody species were recorded on 33 survey sites. This floristic database formed the basis for the subsequent TWINSpan categorization by which each site was assigned to one of three vegetation groups, each characterized by distinct overstorey dominant tree species. The abundances and vegetation group affinities of 20 major woody species are shown in Table 2. Non-parametric one-way ANOVAs were used to assess patterns of variation in edaphic and vegetation characteristics (variables identified in Methods above) as they relate to vegetation group. Results for those variables for which the three groups were significantly distinct ($P < 0.05$) are shown in Table 3.

Vegetation group 1 is characterized by a mixture of *Eucalyptus tetradonta* and *Corymbia dichromophloia* on flat, rock-free, lateritic soils with continuous perennial grass cover. Vegetation groups 2 and 3 exist on locations that are rockier, more topographically discontinuous, and more dominated by annual grasses than are group 1 sites, perhaps as a consequence of shallower soils. Groups 2 and 3 are edaphically indistinct but floristically distinct from one another: group 2 is dominated by mixed *Eucalyptus miniata* and *Corymbia bleeseri*, while

group 3 is dominated by *Eucalyptus phoenicea*. All three vegetation groups are similar with respect to average soil characteristics (mean clay content = 0.15 ± 0.02), total woody vegetation abundance (mean basal area = $7.12 \text{ m}^2 \text{ ha}^{-1} \pm 0.30$), patterns of tree death (mean dead basal area = $0.70 \text{ m}^2 \text{ ha}^{-1} \pm 0.08$), the demographic structure of the woody community (mean skewness = 8.94 ± 1.78), and historical woody vegetation change (mean RCI = 1.05 ± 0.05). Note also that all three groups have a high average burning frequency and no site is completely fire-protected.

Relative Change Index (RCI) ANOVAs

Site-level comparisons. The Relative Change Index (RCI) was calculated as above for all 33 survey sites. Eight sites were classed as 'decreasing', 18 as 'stable', and seven as 'increasing' in woody vegetation cover. Two-way ANOVAs were performed (using the same edaphic and vegetation indices defined above) to assess patterns of variation between sites with different vegetation-change histories (i.e. RCI categories) and to look for interactive effects between RCI categories and vegetation groups. No edaphic or vegetation variables showed significant patterns of variation among the RCI categories, and no significant interactions were detected. Observed historical vegetation change is therefore unrelated to edaphic setting, total woody vegetation abundance, demographic structure, and patterns of total tree death.

Species-level comparisons. Indices of tree death and stand demographic structure were generated for each species at each site in order to identify individual tree species likely to be responsible for observed vegetation cover changes. Two-way ANOVAs were performed to assess patterns of variation simultaneously across RCI categories and TWINSpan vegetation groups, and to look for interactive effects. Sites where the species in question was absent or present in low abundance (density $< 25 \text{ trees ha}^{-1}$ and basal area $< 1.0 \text{ m}^2 \text{ ha}^{-1}$) were excluded so that sites with a low sampling intensity for the species in question would not skew the average index values for sites at which substantial stands of the species were present. It was found that there were no significant RCI/vegetation-group interactions for any species. Where significant variations occurred among RCI categories the results are shown in Table 4.

DISCUSSION

Decline of *Callitris intratropica* stands

The widespread decline of *C. intratropica* populations indicated by both aerial and ground surveys suggests

Table 2. Average abundance values (basal area) and significant vegetation group affinities for 20 species recorded on 33 survey sites. Vegetation group designations derive from subsequent TWINSpan analysis. Groups bearing the same letter are not significantly ($P < 0.05$) different from one another with respect to the abundance of the species in question.

Species	Average basal area ($m^2 ha^{-1}$) and % frequency (in parentheses)									
		Group 1 (n = 11)			Group 2 (n = 12)			Group 3 (n = 10)		
Overstorey dominants										
+ <i>Eucalyptus phoenicea</i> F. Muell.	A	0.066	(45)	B	1.144	(67)	*C	2.755	(90)	
+ <i>Eucalyptus tetradonta</i> F. Muell.	*A	2.209	(100)	B	0.715	(83)	B	0.569	(80)	
+ <i>Corymbia dichromophloia</i> (F. Muell.) K. D. Hill & L. A. S. Johnson	*A	2.501	(100)	B	0.034	(33)	B	0.438	(70)	
+ <i>Eucalyptus miniata</i> A. Cunn. ex Schauer	A	0.732	(100)	*B	1.533	(100)	A	0.314	(50)	
+ <i>Corymbia bleeseri</i> (Blakely) K. D. Hill & L. A. S. Johnson	A	0.032	(36)	*B	1.427	(100)	C	0.547	(80)	
Sub-dominants										
+ <i>Erythrophleum chlorostachys</i> (F. Muell.) Baill.		0.521	(64)		0.425	(75)		0.447	(100)	
+ <i>Corymbia ferruginea</i> (Schauer) K. D. Hill & L. A. S. Johnson	A	0.113	(18)	A	0.090	(33)	B	0.608	(90)	
<i>Petalostigma quadriloculare</i> F. Muell.	A	0.106	(73)	AB	0.278	(92)	B	0.386	(100)	
<i>Grevillea</i> sp.	A	0.381	(100)	B	0.096	(83)	B	0.144	(100)	
+ <i>Callitris intratropica</i> R. T. Baker & H. G. Sm.		0.052	(9)		0.179	(33)		0.231	(60)	
+ <i>Terminalia latipes</i> Benth.	A	0.015	(73)	A	0.073	(92)	B	0.197	(100)	
+ <i>Buchanania obovata</i> Engl.		0.065	(91)		0.065	(100)		0.055	(100)	
<i>Calytrix extipulata</i> DC.		0.019	(36)		0.018	(25)		0.135	(70)	
+ <i>Owenia vernicosa</i> F. Muell.		0.011	(18)		0.029	(58)		0.121	(70)	
<i>Grevillea decurrens</i> Ewart & O. B. Davies		0.021	(73)		0.063	(75)		0.017	(70)	
<i>Gardenia</i> sp.		0.023	(82)		0.016	(75)		0.021	(60)	
<i>Persoonia falcata</i> R. Br.		0.024	(100)		0.013	(100)		0.024	(100)	
<i>Planchonia careya</i> (F. Muell.) Kunth		0.010	(64)		0.018	(75)		0.014	(60)	
<i>Stenocarpus acacioides</i> F. Muell.		0.003	(36)		0.002	(25)		0.010	(60)	
<i>Acacia dimidiata</i> Benth.		0.003	(36)		0.001	(25)		0.006	(50)	
Average total basal area ($m^2 ha^{-1}$)		7.230			6.794			7.375		

+ denotes species capable of reaching the overstorey canopy.

* denotes a dominant overstorey species for a particular vegetation group. Overstorey dominants are defined as any species comprising at least 20% of the total woody basal area of the group. Only species with 50% or greater occurrence in any single group are shown here. An additional 19 species were recorded for which data are not shown.

Table 3. Significant results of non-parametric two-way ANOVAs assessing variation of edaphic site variables across TWINSpan-derived vegetation groups and Relative Change Index (RCI) categories. Groups bearing the same letter are not significantly ($P < 0.05$) different from one another with respect to the variable in question. No variable showed significant patterns of variation relative to RCI categories, and no significant interactions occurred, so results are as from one-way ANOVA across TWINSpan categories alone.

Edaphic site variable	Mean (\pm SE) by TWINSpan vegetation group					
		Group 1: <i>E. tetradonta</i> , <i>C. dichromophloia</i> (n = 11)		Group 2: <i>E. miniata</i> , <i>C. bleeseri</i> (n = 12)		Group 3: <i>E. phoenicea</i> (n = 10)
% slope**	A	0.09 \pm 0.09	B	1.33 \pm 0.41	B	1.95 \pm 0.43
% rock prevalence**	A	0.7 \pm 0.7	B	44 \pm 10	B	43 \pm 11
% annual grass prevalence**	A	27 \pm 7	B	55 \pm 10	B	76 \pm 9
% perennial grass prevalence**	A	80 \pm 6	B	33 \pm 10	B	38 \pm 12
10-y fire frequency*	A	5.6 \pm 0.3	AB	4.7 \pm 1.4	B	4.0 \pm 0.6

* = $P < 0.05$ ** = $P < 0.01$.

a historical shift from low-intensity to high-intensity burning regimes, most likely due to the cessation of traditional Aboriginal fire management. *Callitris intratropica* occurs across a wide range of edaphic habitat settings (Bowman *et al.* 1988); its distribution is limited primarily by fire (Bowman & Panton 1993, Bowman &

Wightman 1985, Bowman *et al.* 1990). Healthy *Callitris intratropica* stands require a fire regime characterized by frequent low-intensity early-season burning; fires at this time of year are small and patchy, and the resulting mosaic of burnt and unburnt grass serves to block the spread of later high-intensity fires. Traditional Aboriginal fire

Table 4. Significant ($P < 0.05$) results of non-parametric ANOVAs assessing demographic and mortality indices for each dominant species individually, on the basis of RCI categories. Groups bearing the same letter are not significantly different from one another with respect to the index in question.

Species	Mean (\pm SE) by vegetation change (RCI) category					
		Decreasing cover		Stable cover		Increasing cover
<i>Eucalyptus tetradonta</i>		(n = 7)		(n = 15)		(n = 5)
Proportion of basal area dead**	A	0.200 \pm 0.045	B	0.067 \pm 0.021	B	0.050 \pm 0.031
<i>Eucalyptus phoenicea</i>		(n = 3)		(n = 10)		(n = 3)
Proportion of basal area partially dead*	A	0.858 \pm 0.071	AB	0.643 \pm 0.047	B	0.462 \pm 0.101

* = $P < 0.05$ ** = $P < 0.01$.

Note: n varies for each species because sites with a low sampling intensity (basal area $< 1.0 \text{ m}^2 \text{ ha}^{-1}$ or density $< 25 \text{ trees ha}^{-1}$) for the species in question are excluded in the calculation of demographic and mortality indices.

management has been shown to produce precisely this sort of mosaic (Haynes 1985). Where fire regimes have changed, dead *C. intratropica* stumps are termite-resistant and thus highly persistent. *Callitris intratropica* is therefore recognized as a valuable long-term indicator of changing fire regimes by both researchers (Bowman & Panton 1993, Bowman *et al.* 2001, Price & Bowman 1994) and traditional Aboriginal managers (Haynes 1985) alike. The dramatic decline in *C. intratropica* populations within the study area is most likely a direct consequence of the depopulation of the area by Aboriginal people in the last 100 y, and is consistent with similar declines elsewhere in the Northern Territory (Bowman & Panton 1993).

Aerial analysis of vegetation change

While some locations within the study area have experienced woody vegetation increase and others have experienced vegetation loss, average net change across the entire study area has been approximately zero since 1948 (Figure 3). The spatially patchy nature of observed changes does not support the controversial hypothesis (Archer *et al.* 1995, Idso 1992, Johnson *et al.* 1993) that rising atmospheric CO_2 concentrations as a consequence of global deforestation and industrial emissions will drive savanna systems toward a condition of generally increased woodiness. Note however that the effects of CO_2 enrichment are generally thought to be negligible in settings where plant growth is nutrient-limited (as is likely in the present study) rather than light- or water-limited (Polley 1997). It is also clear that no other landscape-wide process such as climate change or changing fire regimes is uniformly affecting savanna vegetation dynamics within the study area. The popular perception of widespread vegetation thickening in the region, based primarily on comparisons of historical and contemporary photographs (as in Jacklyn 2000), does not accurately reflect vegetation dynamics on the Yambarran Plateau (see also Sharp & Whittaker 2003).

ANOVA analyses

That tree death and historical change in vegetation cover do not vary significantly among the three vegetation groups, and that associated edaphic factors do not vary significantly among RCI categories, suggests that woody vegetation change (and tree death) within plateau woodlands is not a product of interactions between landscape-scale processes and site-specific edaphic or habitat characteristics. Obviously this conclusion does not apply to fire-protected gorges and other sheltered habitats on the margins of the plateau, which may contain pockets of monsoon rain forest, *Callitris intratropica* and other fire-sensitive flora (Russell-Smith & Bowman 1992).

Examining patterns of stand structure and tree death for each species individually provides additional insight into the nature and causes of observed changes. That the demographic skewness index for every overstorey species shows no significant pattern of variation relative to change history indicates that observed vegetation changes are not a consequence of processes that would be expected to alter the demographic stand structure of the species. Thus observed increases are not a consequence of episodic recruitment events, and observed declines are not a consequence of inhibited germination or juvenile non-recruitment. Significant patterns of tree death and/or partial death are evident for two dominant *Eucalyptus* species (Table 4). This result strongly suggests that die-back by *E. tetradonta* and/or *E. phoenicea* may account for observed patterns of woody vegetation decline on sites where these species are dominant.

It is clear, due to the particular environmental history of the Yambarran Plateau, that observed change patterns are not a direct consequence of spatially variable historical management (i.e. fire and grazing) treatments. Grazing has always been negligible, and there has been no active fire management on the plateau for 50–100 y. Furthermore, because vegetation changes were shown to be unrelated to 10-y fire frequency, it is unlikely that observed patterns reflect spatial differences in average 'natural' burning conditions. It is similarly unlikely that

observed changes are a consequence of individual catastrophic fire events occurring before the fire history became available; most fires burn late in the season and therefore with high intensity, so it is not possible for the area to burn any 'hotter' than it did in the 10-y period for which the fire history is known. In addition, patterns of change appear spatially random: adjacent sites in similar habitats exhibit opposite change responses despite the absence of topographic barriers between them (see Figure 1). Finally, stand demographics indicate that all dominant overstorey species are reproductively viable and demographically stable regardless of fire regime.

The most fire-protected site (Mount Wollondain; see Figure 1) is an isolated escarpment outlier that is relatively impermeable to fires originating in surrounding lowlands. In 1990–2000 fires burned completely around the escarpment outlier on five occasions without burning the top, and the site itself actually burnt only once, in 1995. Yet this site is indistinguishable from frequently burnt sites on similar habitats in terms of both floristic composition and 50-y vegetation-change response. It is clear then that observed change patterns cannot be attributed to variations in fire regime in any straightforward way. Note however that fire may interact with other random or stochastic variables to produce observed effects.

Coastal and subcoastal portions of north Australia are subject to both tropical cyclones and intense convective storms that may produce extremely localized winds with velocities as high as 200 km h⁻¹ and 90 km h⁻¹, respectively; large savanna trees may be snapped off at the base or uprooted entirely (Williams & Douglas 1995). Localized damage to tree stands by stochastic strong-wind events, and subsequent recovery, may account in part for the discontinuous and spatially random nature of observed vegetation dynamics on the Yambarran Plateau, but cannot account for significant associations between vegetation cover decline and the abundance of standing dead trees in stands dominated by *E. tetradonta* and *E. phoenicea* (Table 4).

Fensham & Holman (1999) report that tree die-back in response to drought is a major factor affecting savanna vegetation dynamics in subtropical Queensland. Die-back is spatially patchy and is apparently a consequence of complex interactions between local rainfall deficits, soil conditions and competition between trees. While the extreme reliability of the summer (December–April) monsoon rainfall in the present study area makes 'drought' per se impossible, Fensham & Holman emphasize that tree species in areas with reliable summer rainfall may be poorly adapted to water stress and therefore susceptible to die-back in response to even relatively minor rainfall deficits. In the present study area, thunderstorms in the 'buildup' season (September–November) produce substantial rainfall in some years,

but the timing of these storms varies from year to year and the storms themselves are spatially patchy. Stochastic early season rainfall events or their absence may then account for the apparent randomness of observed patterns of vegetation thickening and loss if an especially long dry season predisposes trees to death. Fensham & Holman (1999) suggest that *Eucalyptus* species are more susceptible to drought-related die-back than are *Corymbia* species. This is consistent with the results of the present study, in which two of three dominant *Eucalyptus* species (*E. tetradonta* and *E. phoenicea*), but neither of the dominant *Corymbia* species (*C. dichromophloia* and *C. bleeseri*), exhibited significant relationships between standing-dead basal area and vegetation-change history (Table 4). It is therefore plausible that a natural cycle of die-back and recovery in response to dry-season moisture stress is the primary mechanism responsible for observed patterns of woody vegetation change on the Yambarran Plateau.

Implications for conservation management and palaeoecological theory

The change in fire regime responsible for the decline of *Callitris intratropica* populations is likely to have other, less visible impacts on woody vegetation within the study area. *Callitris intratropica* was the only fire-sensitive obligate-seeding woody species encountered at the 33 survey sites, despite edaphic characteristics providing favourable habitat for a number of obligate-seeding shrubs and the confirmed existence of some of these species at (presumably fire-sheltered) locations near the study area (C. Yates *et al.* unpubl. data). The occurrence of two fires within the maturation period of an obligate-seeding species is often sufficient to eliminate the species; thus obligate-seeders are especially vulnerable to local extinction from fire (Russell-Smith *et al.* 1998). The persistence of scattered living *C. intratropica* trees on the plateau is likely due to their size and longevity; it is likely that shorter-lived obligate-seeding shrubs have disappeared completely from sandstone plateaux in and around the study area in the past 100 y.

A mere reduction in fire frequency is unlikely to be sufficient to avoid these effects. For instance, no obligate-seeding shrubs were recorded at the site on Mount Wollondain (see Figure 1) despite its highly fire-sheltered location, and all of the *C. intratropica* trees encountered there ($n = 23$, basal area = 0.80 m² ha⁻¹) were dead. The longer fire interval was visibly evident in the form of increased grassy fuel loads and understorey shrub accumulation, and it is likely that where burning frequencies are low, fire intensity is correspondingly higher (Williams *et al.* 1999). It seems then that the protection of fire-sensitive taxa on sandstone plateaux,

even on sites that are relatively fire-sheltered, requires active and deliberate fire management in the form of early-season burning.

The presence of declining *C. intratropica* stands throughout the study area is a strong testimony to the regularity and thoroughness with which Aboriginal inhabitants managed fire in the region prior to settlement by Europeans. It is likely that other species will have also declined for which there is no persistent visible indicator of their former presence. For example, frilled lizard (*Chlamydosaurus kingii* Gray) populations decline significantly in response to the same fire regime that is destructive of *C. intratropica* stands (Griffiths & Christian 1996). Changing fire regimes may also be responsible for widespread declines of granivorous bird populations across northern Australia (Franklin 1999) and for the almost complete disappearance of many small mammal species in virtually uninhabited, ecologically intact north Australian landscapes (Woinarski *et al.* 2001).

The results of this study suggest that the dominant tree communities on sandstone-plateau habitats are resilient to changing fire regimes. Total woody vegetation cover is roughly constant in the long term, and small-scale patterns of change are likely the result of natural stochastic die-back and regeneration cycles related to dry-season moisture stress and possibly to wind-kill. However, fire-sensitive flora and perhaps fauna as well are in decline as a consequence of unmanaged fire. Conservation concerns may require the re-implementation of active fire management more closely approximating that historically practiced in the region by traditional Aboriginal inhabitants.

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