

Tree cover–fire interactions promote the persistence of a fire-sensitive conifer in a highly flammable savanna

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Summary

1. *Callitris intratropica* is a long-lived, obligate-seeding, fire-sensitive overstorey conifer that typically occurs in small groves (<0.1 ha) of much higher tree densities than the surrounding, eucalypt-dominated tropical savanna in northern Australia. We used *C. intratropica* groves of varying canopy cover to examine the role of feedbacks between fire and tree cover in the persistence of a fire-sensitive tree species and the maintenance of habitat heterogeneity in a highly flammable savanna.

2. We examined the population structure and floristic composition of *C. intratropica* groves and conducted controlled burns with Aboriginal landowners to test the prediction that groves of *C. intratropica* with closed canopies inhibit savanna fires by physically altering the fuel arrays below trees. We measured pre- and post-burn fuel availability, the probability of burning and fire intensity along transects (55–75 m) spanning entire *C. intratropica* groves and extending into the surrounding savanna matrix.

3. We found that closed-canopy groves of *C. intratropica* had higher densities of seedlings and saplings than open-canopy groves and supported a distinct plant community. Closed-canopy groves also had a lower probability of burning and less severe fires due to a lower availability of fine fuels than the surrounding savanna.

4. *Synthesis.* Our results suggest that the observed regeneration within closed-canopy *C. intratropica* groves within frequently burnt savanna reflects a vegetation–fire feedback. A significant, negative relationship between canopy cover and the probability of burning provides strong evidence that closed-canopy *C. intratropica* groves are capable of excluding low-intensity savanna fires, thereby enabling the persistence of patches of fire-sensitive forest or woodland amid open, highly flammable savanna vegetation. We present our findings as evidence that alternative stable state dynamics may play a role in determining savanna diversity and structure.

Key-words: Aboriginal landscape burning, alternative stable states, determinants of plant community diversity and structure, fire ecology, fire-sensitive species, habitat complexity, patch dynamics, pyrodiversity, tropical savanna, vegetation boundaries

Introduction

The diversity in size and age of habitat patches within an ecosystem is closely linked to the heterogeneity of disturbance across the landscape (Denslow 1995; Hobbs 1996; Turner 2005; Collins & Smith 2006; Peterson & Reich 2008). Thus, in flammable ecosystems, the ecological interactions that influ-

ence burning heterogeneity have important implications for understanding broader patterns of biological diversity and composition. While climate-driven factors such as short-term fire weather, rainfall seasonality and fuel productivity shape the general conditions under which fire occurs in ecosystems, positive and negative feedbacks among plants, animals and their environment further modulate patterns of burning. For instance, high herbivore densities can reduce fuel loads, while high graminoid productivity increases fuel availability, consequently affecting ecosystem flammability at different temporal

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and spatial scales (de Knecht *et al.* 2008; Fuhlendorf *et al.* 2009; Setterfield *et al.* 2010; Mayer & Khalyani 2011). Contrasting fire regimes observed across habitat boundaries also suggest that overstorey woody plant composition and abundance play an important role in altering a system's propensity to burn (Peterson & Reich 2008; Hoffmann *et al.* 2009; Warman & Moles 2009; Staver, Archibald & Levin 2011). Trees and shrubs display a wide range of adaptations that have the potential to facilitate or inhibit fire at the individual level (Bond & Midgley 1995; Schwilk 2003; Kane, Varner & Hiers 2008). How woody plant–fire interactions scale up to affect flammability and burning heterogeneity at the patch, community or ecosystem scale is therefore an important aspect of savanna and forest ecology (Mourik *et al.* 2007; Nowacki & Abrams 2008; Beckage, Platt & Gross 2009; Engber *et al.* 2011; Mandle *et al.* 2011; Kitzberger *et al.* 2012).

In this study, we examine the potential of a fire-sensitive savanna tree species to exclude fires and thereby contribute to habitat heterogeneity and the persistence of other fire-sensitive species in an Australian tropical savanna. *Callitris intratropica* R.T. Baker & H.G. Smith (syn. *Callitris collumellaris* var. *intratropica* Silba) is a long-lived (> 200 years), obligate-seeding conifer of Gondwanan origin that is widespread throughout northern Australia. The persistence of *C. intratropica* in one of the most fire-prone ecosystems on earth (Russell-Smith *et al.* 2007) is a key question concerning the composition of these savannas. Region-wide declines in the species' abundance had been noted by biologists as early as the 1920s and continue into the present across much of northern Australia (Easton 1922; Bowman & Panton 1993). These, as well as recent and dramatic declines in other species assemblages, notably small mammals and granivorous birds, have been attributed to the shift in fire regimes from Aboriginal patch burning to unmanaged, higher intensity wildfires within the past century (Franklin 1999; Bowman *et al.* 2001; Woinarski *et al.* 2010). Aboriginal landowners have long recognized high *C. intratropica* mortality as a sign of poor fire management (Haynes 1985). Thus, adapting this traditional knowledge and using *C. intratropica* as an indicator of ecologically beneficial fire regimes is of great interest to contemporary management and conservation programmes in Aboriginally owned Arnhem Land and World Heritage Kakadu National Park.

In northern Australian savannas, *C. intratropica* can occur as isolated, mature trees but commonly forms small (typically < 0.1 ha), discrete groves with higher tree densities than the scattered eucalypts, which otherwise dominate the savanna overstorey. *Callitris intratropica* groves vary in canopy cover and can be broadly delineated into two types – open- and closed-canopy groves (Fig. 1). Aside from differences in canopy cover, open-canopy groves appear to differ from closed-canopy groves in their lack of seedling and sapling regeneration and the continuity of the grass understorey. Despite these distinct spatial patterns in *C. intratropica* distribution, the mechanisms and temporal dynamics that maintain these groves remain unclear. It is well established that frequent

savanna fires limit the establishment and recruitment of woody plants (Mourik *et al.* 2007; Hoffmann *et al.* 2009) – especially if they are obligate-seeding species (i.e. incapable of resprouting after fire) like *C. intratropica* (Cohn *et al.* 2011; Prior *et al.* 2011). Conversely, high rates of *C. intratropica* recruitment have been observed in savannas where fire has been excluded (Bowman, Wilson & Davis 1988). *Callitris intratropica* is a long-lived species, and larger trees appear capable of surviving decades of high-frequency surface fires typical of Australian savannas (Prior, Bowman & Brook 2007). We therefore suspect that these open-canopy groves represent a state in which the grove structure has been degraded by one or several severe fires; however, demonstrating a longitudinal degradation from closed- to open-canopy groves to individuals is beyond the temporal scope of this study. Rather, we suggest that groves with varying canopy cover (open versus closed) provide important clues to the mechanisms behind both the persistence of *C. intratropica* and broader patterns of heterogeneity and diversity in these savannas. Our objective is therefore to provide a clear ecological description of these two grove types and examine the fine-scale interaction between *C. intratropica* and savanna fires.

The spatial clumping of *C. intratropica* parallels patterns in other fire-prone systems, including congeners elsewhere in Australia (Cohn *et al.* 2011; Prior *et al.* 2011), *Pinus* and *Quercus* species dynamics in North American grasslands (Guerin 1993; Platt 1999; Nowacki & Abrams 2008), shola forests of India (Mohandass & Davidar 2009) and tree groves or bush islands in African and South American savannas (Couteron & Kokou 1997; Furley 2007). It has been argued that the persistence of vegetation boundaries under identical climatic and edaphic conditions is due to alternative stable state dynamics. Alternative stable state theory essentially attributes vegetation with the potential to alter abiotic conditions, thereby deterministically maintaining distinct ecological 'regimes' (Scheffer *et al.* 2001; Folke *et al.* 2004). In the context of fire, for example, the theory has been proposed to explain abrupt ecosystem boundaries between savanna and rain forest (Hoffmann *et al.* 2009; Warman & Moles 2009; Staver, Archibald & Levin 2011) and sclerophyllous shrubland and forest (Perry & Enright 2002; Odion, Moritz & DellaSala 2010). But alternative stable state theory also has conceptual implications for habitat composition at smaller spatial scales, whereby feedbacks between vegetation and disturbance by fire may shape patch-level heterogeneity (Laycock 1991). The classic example of a positive feedback is the grass–fire cycle (D'Antonio, Hughes & Vitousek 2001). Yet fire-impeding species (e.g. Kane, Varner & Hiers 2008) as invaders in flammable systems may alter the probability of disturbance at the patch level, thereby creating a self-promoting negative feedback (Buckley, Bolker & Rees 2007; Stevens & Beckage 2009). Therefore, examining the patterns of burning across the boundary between open- and closed-canopy vegetation within savannas may help elucidate whether and how fire feedbacks affect the persistence of fire-sensitive vegetation at the local scale and habitat heterogeneity at the landscape scale.

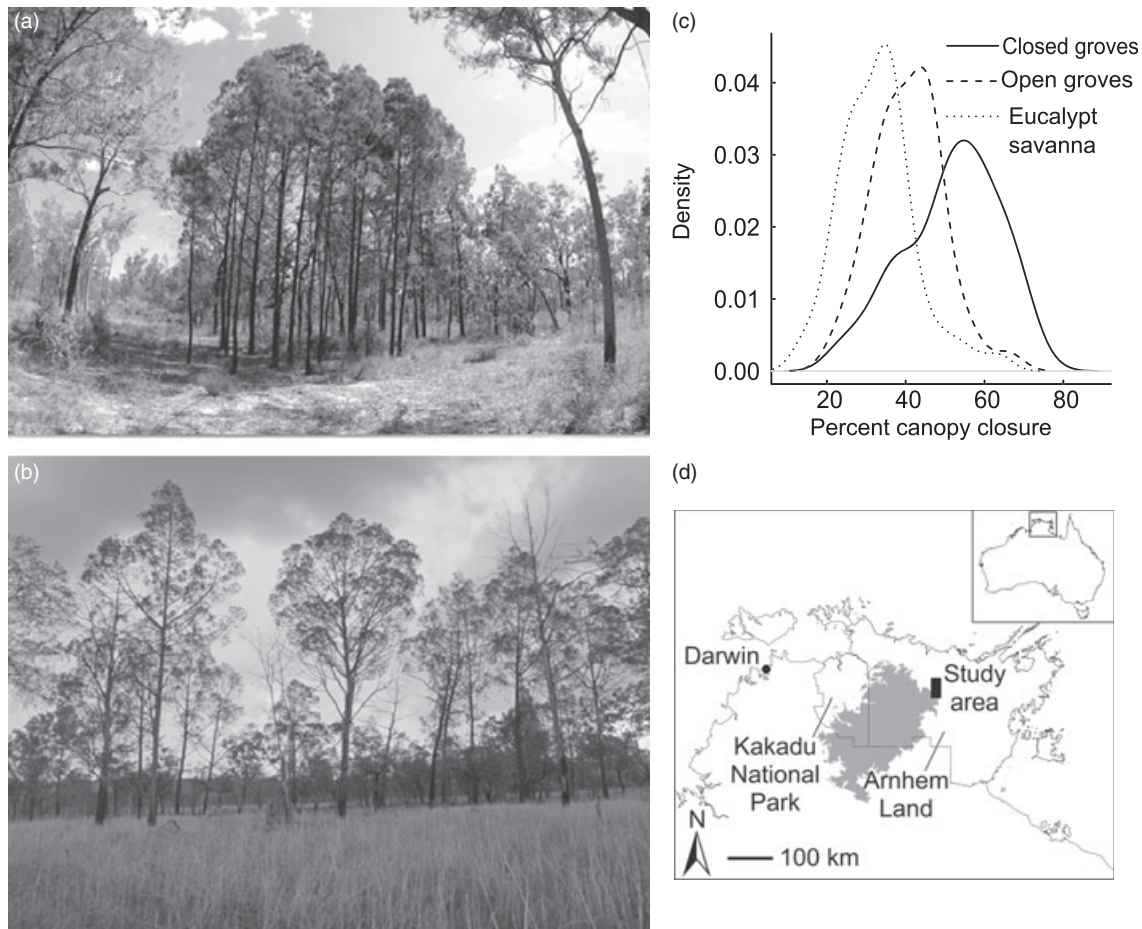


Fig. 1. The context of the study system. (a) Closed-canopy groves of *Callitris intratropica* form clearly defined habitat boundaries with the matrix of open savanna dominated by *Eucalyptus tetradonta* and *Eucalyptus miniata* and are clearly distinguishable from (b) open-canopy *C. intratropica* groves. (c) Canopy cover distributions (derived from hemispherical photographs) illustrate differences among plots in closed-canopy groves, open-canopy groves and open eucalypt savanna. (d) A map of Arnhem Land shows the study site in relation to Kakadu National Park and the Arnhem Plateau (shaded grey).

Here, we first describe the floristic composition and community and population structure of open- and closed-canopy groves of *C. intratropica* in relation to the surrounding matrix of eucalypt savanna. Using controlled burns conducted with Aboriginal landowners, we then empirically test the prediction that closed-canopy groves of *C. intratropica* inhibit savanna burning by physically altering the habitat below trees. We specifically address the following hypotheses:

- 1 The composition and structure of woody understorey vegetation in closed-canopy groves of *C. intratropica* differ from that of open-canopy *C. intratropica* groves and savanna.
- 2 *Callitris intratropica* regeneration is greater in closed- than in open-canopy groves.
- 3 Fine fuel cover and biomass are lower within closed-canopy groves of *C. intratropica* than in the surrounding savanna.
- 4 The probability of burning and fire intensity are lower within closed-canopy groves of *C. intratropica*.

Materials and Methods

STUDY SITE

Surveys of *C. intratropica* groves and experimental savanna fires were conducted at Dukladjarranj along the Cadell River on the northern rim of the Arnhem Plateau, within the Djelk Indigenous Protected Area of north-central Arnhem Land, Northern Territory (Fig. 1d). The Arnhem Plateau is a low massif (<400 m) of deeply dissected Middle Proterozoic quartzose sandstone and is a regional centre of species endemism (Woinarski *et al.* 2006). The region is characterized by very short fire return times (1–3 years), and 40–60% of the landscape may burn annually (Gill *et al.* 2000; Edwards & Russell-Smith 2009). A general trend within the past century towards unmanaged, higher intensity wildfires occurring in the late dry season is widely attributed to the decline of Aboriginal patch burning across most of the region (Bowman *et al.* 2001; Yibarbuk *et al.* 2001; Russell-Smith *et al.* 2007). Our study site Dukladjarranj is a Gunei language group Aboriginal clan estate comprising an area of *c.* 90 km² and has been under nearly continuous management since before European colonization. Detailed descriptions of the study area are provided by Yibarbuk *et al.* (2001) and Murphy & Bowman (2007).

SURVEY OF CALLITRIS GROVES

In the mid-dry season (July–August) 2010, a total of 21 discrete *C. intratropica* groves were randomly selected at Dukladjarranj ranging in size from 100 to 650 m². Ten closed-canopy (>50% canopy cover) and five open-canopy groves were situated east of the Cadell River in an area of open savanna, which had last burned in 2008. In addition, three groves of each type were located to the west of the Cadell River among more rocky country, which had experienced a late dry season, intense burn in October 2009. LANDSAT-derived fire history for the study site is currently available only as far back as 2006. Vegetation surrounding groves in both areas consisted of open savanna-woodland dominated by *Eucalyptus tetradonta* and *Eucalyptus miniata* [mean basal area = 7.5 m² ha⁻¹ ± 0.7 (SE); mean density = 168 stems ha⁻¹ ± 18 (SE)].

Sampling at *C. intratropica* groves consisted of between two and five adjacent 5-m-wide transects, depending on the size of the grove. Transects ran from 25 m outside the grove, completely through the grove, and extended 25 m beyond the far side of the grove into the eucalypt savanna matrix. Hence, transect length varied from 55 to 75 m, and all transects ran parallel to the prevailing south-easterly trade winds, which spread dry season fires. In each transect, we recorded the diameter at breast height (d.b.h.) and *x*- and *y*-coordinates of all trees ≥130 cm tall.

A line was marked down the centre of each transect at 5-m intervals beginning at 2.5 m, effectively defining a plot centre for adjacent 5 × 5 m plots along the length of each transect. In alternating 5 × 5 m plots, we recorded the species and counted all shrubs and small trees (<5 cm d.b.h.) in each of two size classes (50–200 cm and ≥200 cm). Vouchers were collected and identified at the Northern Territory Herbarium in Darwin. At each 5 × 5 m plot centre, hemispherical canopy photographs were taken 1 m above ground level using a fish-eye lens (Pentax DA 10–17 mm; Pentax Ricoh Imaging, Ltd, Denver, CO, USA) mounted on a tripod. For sites consisting of only two parallel transects, photographs were taken every 5 m along the centre line joining the two transects due to the time constraints of taking canopy photographs at dawn and dusk to prevent sun flares. Canopy cover was measured from each photograph as the percentage of closed-canopy pixels using the Gap Light Analyzer software (Frazer, Canham & Lertzman 1999). Tree coordinates were plotted in a GIS database to derive tree counts for each 5 × 5 m plot and the distance of the *C. intratropica* individual nearest to each plot centre.

BURNING HETEROGENEITY AND EXPERIMENTAL FIRES

The heterogeneity of habitat burning was measured at all 21 *C. intratropica* groves by recording the centre of each 5 × 5 m plot as burnt or unburnt after fires had passed around and/or through the grove. We also recorded scorch heights (maximum height of damaged, browned foliage) on 12 trees in the savanna matrix around each *C. intratropica* grove, a metric that has been shown to be correlated with fire intensity in this region (Williams, Gill & Moore 1998; Setterfield *et al.* 2010). However, it is important to note that scorch height may better reflect the effect of fire on vegetation (i.e. fire damage) than the actual behaviour of the fire (Hood 2010). Burn measurements at the 15 groves east of the Cadell River were recorded within several days of fires, which occurred during the course of the study, whereas measurements at the six groves west of the river were recorded approximately 8 months after a late fire in the previous dry season.

Variation in fuels and fire behaviour across the boundary between savanna and closed-canopy *C. intratropica* groves was examined in greater detail by intentionally setting fires under the supervision of Aboriginal landowners at seven of the 21 *C. intratropica* groves. One additional grove was accidentally burned from helicopter by local rangers in our absence, and we were therefore able to record fuel data but not aspects of fire behaviour and fire intensity. The area of savanna surrounding all eight of these groves last burned in 2008.

At each of the eight groves, per cent cover was estimated and mean height measured for available fuels within 1 × 1 m quadrats at each 5 × 5 m plot centre before burning and immediately after fires had passed the transects. Fuel categories included tree litter (the leaf litter layer above humus and soil horizons), live graminoids, dead graminoids, shrubs <50 cm tall and coarse fuels (woody debris >0.64 cm diameter). Three 10-g samples of litter and grass fuels were also collected and sealed in plastic bags inside and outside each *C. intratropica* grove. Samples were weighed before and after oven-drying to determine fuel moisture. In addition, before burning at each grove, the standing biomass of litter, dead graminoids and live graminoids was cut and weighed from three, randomly placed 1 × 1 m quadrats inside the *C. intratropica* grove and three quadrats outside the grove.

These fires enabled us to measure fire behaviour and fuels before, during and after burning. Fires were lit as an arc of patch fires *c.* 50 m upwind from each *C. intratropica* grove, so that the fires connected into a single front moving parallel with the transects. As fires approached *C. intratropica* groves, rate of spread was measured at three locations and height of the flame front was measured at five locations. Wind speed was measured with a hand-held anemometer, while temperature and humidity were derived from observations at Jabiru and Maningrida airports, the nearest meteorological stations located *c.* 150 and 65 km from the field site, respectively. During the burns, we used the amount of water vaporized from open calorimeters to measure the energy released by the fire as a proxy for fire intensity (Perez & Moreno 1998). Aluminium cans were filled with 50 g of water, weighed to the nearest 0.01 g and placed at ground level at each 5 × 5 m plot centre before burning. Five control cans were placed outside the burn area to account for ambient evaporation. Cans were collected and reweighed immediately after the fire passed, and water loss due to vaporization was determined by subtracting the mean water loss in the control cans from the water loss of the burnt cans.

ANALYSES

All data modelling employed linear and generalized linear models (GLMs) with model selection based on Akaike Information Criterion (AIC_c) as outlined in the information-theoretic framework (Anderson & Burnham 2002). We used mixed models wherever possible, incorporating site (i.e. each *C. intratropica* grove) as a random effect to account for the slight random variation in both environmental conditions and fire events among groves (Bolker *et al.* 2009). For all response variables that produced normal errors, we employed spatially explicit linear mixed models (LMMs), which incorporated the *x*- and *y*-coordinates of all sample points to account for spatial autocorrelation (Crawley 2007) using the 'lme' function in the 'nlme' package in R (Pinheiro *et al.* 2009). For analyses of data with binomial and Poisson distributed errors, we used GLMs or generalized LMMs (GLMMs; 'lmer' package in R), which do not allow for spatial structure to be incorporated into the analyses. For clarification, all model types, data transformations and global parameterizations

are listed for each response variable in Table S1 (See Supporting Information).

The hypothesis that woody plant composition differs among open- and closed-canopy *C. intratropica* groves and the eucalypt savanna matrix was explored using non-metric multidimensional scaling (NMDS) as part of the 'vegan' package in R (Oksanen *et al.* 2011). The ordination used 3-dimensions (based on scree plots of NMDS stress values) and Bray–Curtis dissimilarities to model the differences among all 5 × 5 m plots based on the composition and abundance of 59 plant species (excluding *C. intratropica*). We also tested the strength of this separation as a function of plot location (eucalypt savanna versus open-canopy versus closed-canopy *C. intratropica* groves) with a permutational multivariate analysis of variance (PERMANOVA) also based on Bray–Curtis dissimilarities using the 'vegan' package in R.

We tested for structural differences in the woody plant community among closed-canopy groves, open-canopy groves and savanna by modelling the total count of shrubs and small trees in each plot as a function of grove type (open- versus closed-canopy) and plot location using a GLMM with log-normal Poisson errors for overdispersed data (Elston *et al.* 2001). Plot location was based on the distance of each plot centre to the nearest *C. intratropica* individual to group plots into three categories: (i) inside grove (< 5 m); (ii) grove edge (5–10 m); and (iii) outside grove (> 10 m). We selected a categorical over a continuous distance variable in this and subsequent analyses because we expected our dependent variables to display a threshold rather than a continuous response across the habitat boundary.

We tested the hypothesis that open- and closed-canopy *C. intratropica* groves differ in regeneration patterns by examining population structures based on tree size classes. We calculated the mean and standard error of stem density among *C. intratropica* groves of each type (open- versus closed-canopy groves) for 5 cm d.b.h. classes, beginning with 0–4.9 cm.

To test the hypothesis that closed-canopy groves of *C. intratropica* have lower fine fuel availability, we employed LMMs to examine the importance of plot location to the following fuel measurements: (i) index of grass fuel abundance: total grass cover × height; (ii) litter cover; (iii) cover of shrubs < 50 cm tall; and (iv) index of coarse fuel

abundance: coarse fuel cover × height. We used a least-squares linear model ('lm' function in R) of fuel moisture as a function of fuel type, site and sample location (inside versus outside grove) to determine fuel moisture content for estimates of fuel biomass. Biomass of live graminoids, dead graminoids and litter were modelled as a function of sample location (inside versus outside grove) using non-spatial LMMs with site as a random factor.

To test the hypothesis that closed-canopy groves of *C. intratropica* are capable of reducing the spread of savanna fires, we used a binomial GLMM to examine the importance of canopy cover to the proportion of plot centres burnt, a binary response variable. Using canopy cover as a single, continuous explanatory variable in this analysis captured the key ecological feature distinguishing closed-canopy groves of *C. intratropica* from both open-canopy groves and eucalypt savanna (Fig. 1c).

The hypothesis that closed-canopy groves of *C. intratropica* reduce the intensity of fires was tested by modelling the amount of water vaporized from calorimeters as a function of plot location using LMMs. To see which of the fuel measurements were important to fire intensity, we also used LMMs to model water loss as a function of net change in fuel cover (i.e. fuel consumed) for the fuel variables described above.

Results

COMPOSITIONAL DIFFERENCES AMONG *C. INTRATROPICA* GROVES

Plotting the first two dimensions of the NMDS ordination illustrated a clear distinction between plots in closed-canopy groves and plots within the eucalypt savanna matrix, with those in open-canopy groves intermediate (Fig. 2a). The NMDS reached a stress level of 0.20, which suggested a ≤ 1% chance of the ordination having a random structure (Sturrock & Rocha 2000). The PERMANOVA also supported this pattern, with plot location supported as a significant factor explaining the separation of points ($F = 18.6$, $P < 0.01$). *Callitris intra-*

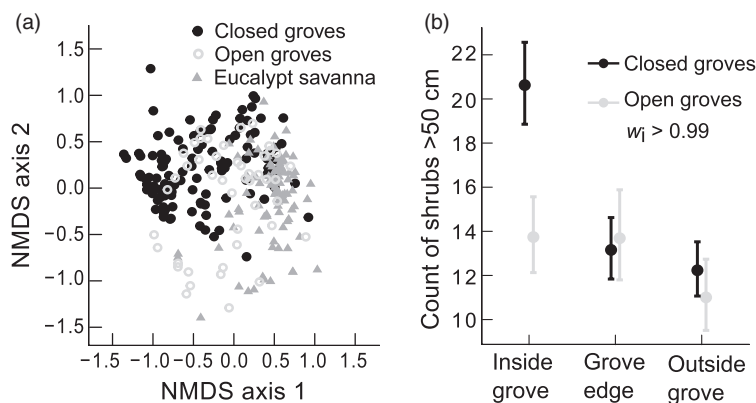


Fig. 2. The structural and compositional aspects of the woody plant community among closed-canopy and open-canopy *Callitris intratropica* groves and the surrounding eucalypt savanna matrix. (a) A scatterplot of the first two axes of an ordination using non-metric multidimensional scaling (stress = 0.20) is based on woody plant species composition (excluding *C. intratropica*) from 25-m² plots sampled among closed-canopy groves, open-canopy groves and eucalypt savanna. (b) GLMM predictions of counts of shrubs > 50 cm tall are presented as a function of plot location relative to *C. intratropica* and *C. intratropica* grove type. Error bars represent standard errors, and the Akaike weight (w_i) relative to the null model is presented.

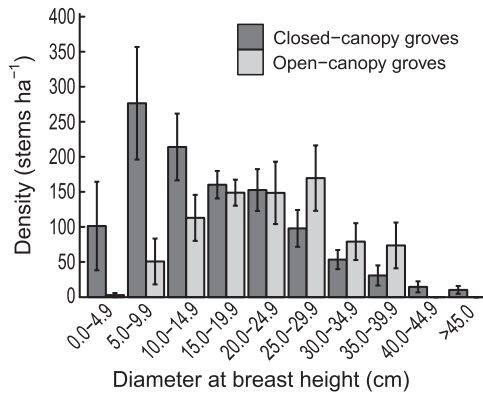


Fig. 3. Mean *Callitris intratropica* stem densities per diameter at breast height (d.b.h.) size class are shown for closed- and open-canopy groves. Error bars represent standard errors.

tropica groves and eucalypt savanna also differed structurally in their associated woody plant community, with higher stem counts of shrubs and small trees inside closed-canopy groves than inside open-canopy groves or outside groves ($w_i > 0.99$; Fig. 2b). In terms of regeneration patterns, closed- and open-canopy groves of *C. intratropica* showed clear differences with notably lower densities of *C. intratropica* individuals among smaller size classes in open-canopy groves (Fig. 3). Despite this difference, the mean total basal area of *C. intratropica* was similar between the two grove types [closed groves: 19.4 ± 2.9 (SE); open groves: 23.3 ± 3.8 (SE)].

NEGATIVE FEEDBACK BETWEEN *C. INTRATROPICA* COVER AND FIRE

Fire weather and fuel conditions during our experimental burns resulted in low-intensity surface fires. Mean wind speed during the fires was moderate, ranging from 15 to 20 km h⁻¹ from the east to southeast; mean relative humidity was 38%; and temperature was 31 °C. ANOVAS of fuel moisture predicted differences among fuel types with no differences among sites [live graminoids: $57\% \pm 2$ (SE); dead graminoids: $27\% \pm 2$ (SE); litter: $15\% \pm 2$ (SE)]. ANOVAS of rate of spread [mean = $1.4 \text{ ms}^{-1} \pm 0.1$ (SE)] and flame height [mean = $0.81 \text{ m} \pm 0.15$ (SE)] indicated no significant differences among the seven fires intentionally lit at *C. intratropica* groves. The mean intensity along fire fronts outside *C. intratropica* stands was 640 kW m^{-1} (Byram 1959) based on rate of spread data, estimates of graminoid fuel consumption [mean = $261 \text{ kg ha}^{-1} \pm 74$ (SE)] from cover and biomass measurements along transects, and mean heat of combustion for grass fuels ($17\,781 \text{ kJ kg}^{-1}$; Trollope 1984). This estimate falls within the range of low-intensity savanna fires that are typical of the mid-dry season for the region (Russell-Smith & Edwards 2006).

The fuels data supported the hypothesis that closed-canopy groves of *C. intratropica* reduce the availability of fine fuels. LMMs predicted lower graminoid fuel abundance (% cover \times height) and lower graminoid biomass inside closed-canopy groves (Fig. 4a, d, e; abundance: $w_i = 0.98$; dead biomass: $***w_i > 0.99$; live biomass: $w_i > 0.99$). Our analyses indicated an increase in the abundance of coarse fuels (% cover \times

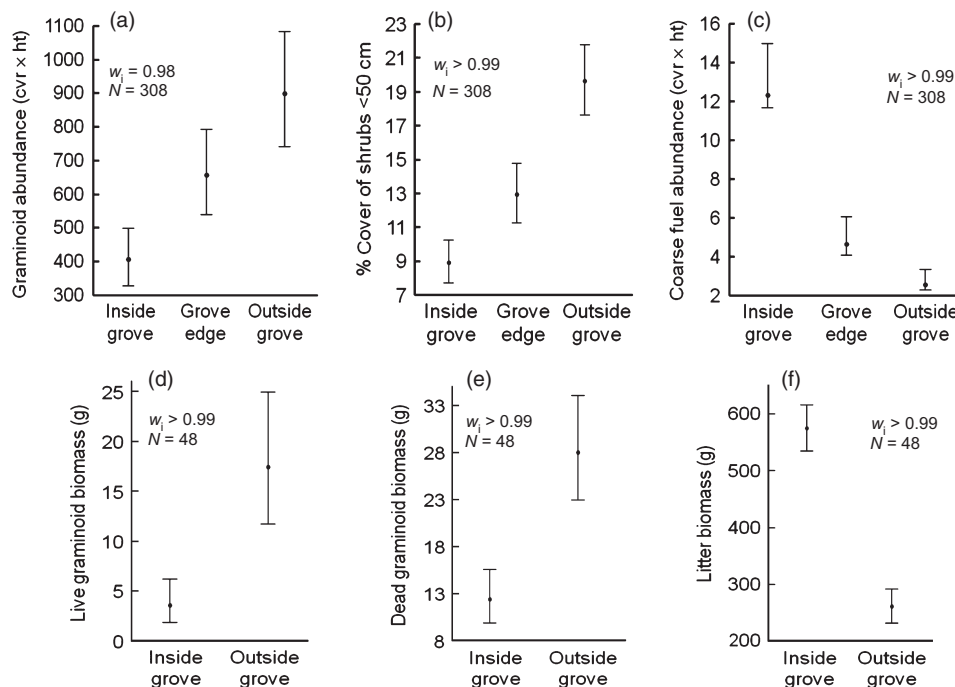


Fig. 4. Relationships between available fuels (i.e. before burning) and plot locations relative to *Callitris intratropica* groves. The upper panels present spatially explicit linear mixed model (LMM) predictions for fuel cover measurements taken along transects for (a) graminoid abundance, (b) low shrub cover and (c) coarse fuel abundance. The lower panels present LMM predictions based on biomass collected from $1 \times 1 \text{ m}$ plots inside and outside closed-canopy groves for (d) live graminoids, (e) dead graminoids and (f) litter. Error bars represent the standard error of model predictions, and Akaike weights (w_i) relative to the null model are presented.

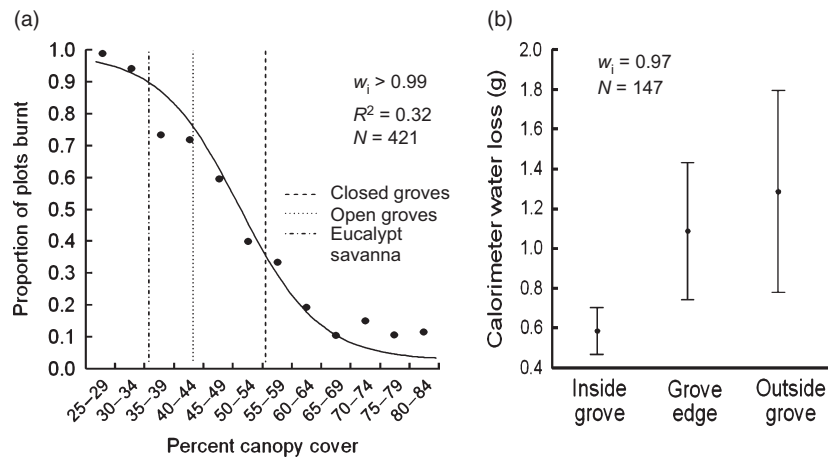


Fig. 5. Relationships between *Callitris intratropica* groves and savanna fires. Panel (a) presents the relationship between the proportion of plots burnt (binned in 5% cover increments) and canopy cover, which is a key factor distinguishing closed-canopy *C. intratropica* groves from open-canopy groves and the eucalypt savanna matrix. Dashed vertical lines show median canopy cover values for closed-canopy groves, open-canopy groves and eucalypt savanna. Panel (b) presents linear mixed model (LMM) predictions of fire intensity, measured by water loss from open calorimeters, as a function of plot location relative to closed-canopy *C. intratropica* groves. Error bars represent standard errors, and Akaike weights (w_i) are presented relative to the null model.

height; Fig. 4c; $w_i > 0.99$) and a decrease in low shrub cover inside closed-canopy groves (Fig. 4b; $w_i > 0.99$). Although no relationship was found between litter cover and the presence of a *C. intratropica* canopy, our analyses demonstrated higher litter biomass within closed-canopy *C. intratropica* groves (Fig. 4f; $w_i > 0.99$). Analyses of calorimeter water loss as a function of fuel consumed found the change in cover of low shrubs and litter were both important to fire intensity measurements ($w_i = 0.99$, $R^2 = 0.29$).

Our analyses showed that the probability of habitat burning decreases with increasing canopy cover based on the GLMM (Fig. 5a; $w_i > 0.99$; $R^2 = 0.32$), thus supporting our hypothesis that closed-canopy *C. intratropica* groves are able to limit the spread of fire. We present R^2 values calculated from model deviances based on log-likelihood (Nagelkerke 1991); however, it is important to note that deriving R^2 for models with random effects is problematic (e.g. Xu 2003). The analyses of the calorimeter data also supported the hypothesis that fire intensity is lower inside closed-canopy *C. intratropica* groves relative to open savanna (Fig. 5b; $w_i = 0.97$).

Discussion

Fire is considered a principal driver of habitat heterogeneity in savannas (e.g. Scholes & Archer 1997; Sankaran *et al.* 2005), yet the ways in which feedbacks between fire and woody vegetation affect the spatial patterns of disturbance within plant communities and ecosystems remain unclear. Here, we focussed on the occurrence of open- and closed-canopy groves of *C. intratropica* (Fig. 1), a fire-sensitive savanna conifer, in a highly fire-prone ecosystem to better understand the mechanisms that shape and maintain savanna heterogeneity. Our results showed marked differences in the floristics and community and population structures between closed-canopy groves and both open-canopy

groves and the surrounding savanna matrix. For example, the NMDS ordination (Fig. 2a) illustrates a clear pattern of separation among plots into closed-canopy *C. intratropica* groves and eucalypt savanna, indicating that the boundary between closed-canopy groves and savanna (Fig. 1a) is also characterized by differences in the woody plant community. These compositional patterns are mirrored by differences in the stem counts of woody plants over 50 cm tall (Fig. 2b), which was highest in closed-canopy groves and, importantly, very similar for open-canopy groves and eucalypt savanna.

Fire is the primary disturbance limiting woody plant establishment in Australian savannas, and therefore, the lack of juveniles and saplings (<15 cm d.b.h.) in open-canopy groves may be an indication that these groves are more likely to burn than groves with closed canopies (Fig. 3). Of course, fire can affect tree establishment in other ways, for example, by altering fecundity (Quintana-Ascencio & Menges 2000; Caddy & Gross 2006). However, high counts of *C. intratropica* seedlings have been observed to establish between fire events in both grove types (C. Trauernicht, unpublished data), indicating adult trees in open-canopy groves maintain their reproductive capacity. *Callitris intratropica* seedlings take many years to reach maturity and are much more vulnerable to fire than adult trees (C. Trauernicht, unpublished data; Russell-Smith 2006). Therefore, we argue that the population structure of open groves is ultimately shaped by higher rates of seedling and sapling mortality due to fire. Although an admittedly static representation of demography, the lower densities in smaller size classes for both open- and closed-canopy groves suggest that, at the patch scale, these populations may be declining (Rubin, Manion & Faber-Langendoen 2006). Gaps in size class structures may also reflect the fact that *C. intratropica* is a mast seeder and relies on episodic recruitment (e.g. Stocker 1966; Drewa

et al. 2008; Prior *et al.* 2010). However, the temporal variability among the processes limiting seedling recruitment can make population structures difficult to interpret and a forthcoming paper will examine *C. intratropica* demography in greater detail. Modelling long-term population stability at the patch scale will be critical in determining whether *C. intratropica* groves are expanding and/or whether the species relies on the initiation of new patches in a meta-population context. Given the longevity of *C. intratropica* adults (>200 years), population dynamics may also provide a strong indication of the degree to which current fire regimes have changed since extant groves established. Yet the key aspect of the data we present here is that the higher density of seedlings and saplings in closed-canopy groves (Fig. 3) strongly implies that some kind of feedback mechanism is reducing the likelihood of disturbance within these groves (e.g. Stevens & Beckage 2009), thereby allowing smaller trees to escape mortality.

Previous anecdotal descriptions have linked fire exclusion by *C. intratropica* to the litter layer forming within groves (Stocker & Mott 1981; Bowman & Wilson 1988). Our results support this assertion with closed-canopy groves having greater litter biomass than the surrounding savanna (Fig. 4f). However, it is more likely the reduction in fine fuel cover and biomass – specifically graminoids and low shrubs (Fig. 4a, b, d, f) – within groves that ultimately reduces the probability of habitat burning. Grasses are the primary fuel source for fires in these savannas (e.g. Setterfield *et al.* 2010), and our analyses found low shrubs to be an important factor driving observed fire intensities. Increased litter cover has been shown to negatively affect grass establishment (Schramm & Ehrenfeld 2010; Scott *et al.* 2010; Viard-Cretat *et al.* 2010). Alternatively, multiple studies have found shading to be a limiting factor to the growth and survival of C_4 grasses, which are dominant fuels in temperate and tropical savannas (Veenendaal, Shushu & Scurlock 1993; Lett & Knapp 2003; Scott *et al.* 2010). Light limitation is an obvious physical effect of closed-canopy *C. intratropica* groves on the local environment (Fig. 1c). However, it is difficult to disentangle the effects of shading and litter on fuels with our data and both processes may be important. Regardless of the mechanism, the reduction in grass biomass within *C. intratropica* groves has direct consequences for limiting both fire intensity, critical for adult survival and stand persistence, and fire occurrence, critical for juvenile recruitment (e.g. Thaxton & Platt 2006; Engber *et al.* 2011).

We examined the potential for a feedback between fire and *C. intratropica* more explicitly by measuring the extent of habitat burnt along transects extending across the boundary of eucalypt savanna and closed- and open-canopy groves after fires had passed through our field sites. Our data provide compelling evidence that closed-canopy groves of *C. intratropica* have a lower probability of being burnt (Fig. 5a). In addition, calorimeter measurements suggest that those areas that do burn within closed-canopy *C. intratropica* groves experience fires of lower intensity than outside or along the edges of groves (Fig. 5b). These results have important implications for understanding how *C. intratropica* persists in such a flammable ecosystem. The apparent feed-

back between closed-canopy *C. intratropica* groves and fire has the potential to maintain long fire-free intervals within groves even under frequent, low-intensity, ambient fire conditions. From a demographic perspective, the ability of these groves to exclude fires would be critical to maintaining recruitment among smaller, highly fire-sensitive size classes (Russell-Smith 2006). This not only provides an explanation of observed differences in population structure among grove types (Fig. 3), but also suggests the mechanism by which the species self-organizes into groves. The persistence of *C. intratropica* in the landscape requires further examination to determine the ultimate fate of damaged groves, as well as the degree to which the species depends on the tree cover–fire feedback we describe versus the initiation of new groves. Nonetheless, our results suggest the decline and degradation of *C. intratropica* groves are due to increases in fire intensity rather than in fire frequency (Russell-Smith *et al.* 2010), although establishing specific thresholds for fire impacts on canopy cover and tree survival would require observations of fires at varying intensities (e.g. Cohn *et al.* 2011).

A growing body of literature has explored the potential of woody plants to both facilitate and impede fire in flammable ecosystems (Bond & Midgley 1995; Schwilk 2003; Kane, Varner & Hiers 2008). On broader scales, alternative stable state theory has been invoked to explain how vegetation–fire feedbacks maintain contrasting disturbance regimes across ecosystem boundaries (Hoffmann *et al.* 2009; Odion, Moritz & DellaSala 2010; Staver, Archibald & Levin 2011). We argue that the potential for a feedback between fire and closed-canopy groves of *C. intratropica* suggests a similar mechanism may be operating at the patch level and community level in savannas. A canopy cover–fire feedback has obvious and direct implications for the demography and persistence of *C. intratropica*. However, the community composition data (Fig. 2a, b) also suggest that fire exclusion by *C. intratropica* has implications for broader patterns of vegetation structural complexity and diversity. At larger spatial scales, the persistence of closed-canopy *C. intratropica* groves essentially maintains a mosaic of small-scale forest or woodland patches within the wider eucalypt savanna matrix. Unfortunately, establishing a longitudinal decline due to fire damage from closed-canopy to open-canopy groves and eventually to isolated, individual trees is beyond the temporal scope of the present study. However, we hypothesize that open-canopy groves provide evidence of a state change, in terms of canopy cover (Fig. 1c), community structure (Fig. 2b) and habitat flammability (Fig. 5a), from *C. intratropica* woodland to eucalypt savanna conditions, despite the survival of *C. intratropica* adults.

While the fire feedback we describe is critical to the persistence of *C. intratropica* and potentially other fire-sensitive species, continued regional declines in *C. intratropica* abundance suggest that this mechanism cannot withstand the high-intensity fires typical of current fire regimes (Bowman & Panton 1993; Edwards & Russell-Smith 2009; Cohn *et al.* 2011). There is a strong case that the prevailing pattern of landscape-scale habitat degradation in northern Australia (Russell-Smith *et al.* 1998; Bowman *et al.* 2001; Franklin *et al.* 2005; Woinarski

et al. 2010) is related to the breakdown of Aboriginal fire management. The life histories of extant *C. intratropica* groves in this region span the transition across much of the region from > 50 000 years of Aboriginal management to what can be aptly described as modern wilderness (Bowman *et al.* 2001). Thus, the spatial patterns of *C. intratropica* groves and their potential to tolerate frequent, low-intensity burning likely hold further clues to disentangling the complex relationships between people and savanna landscapes (e.g. Price & Bowman 1994). We hope that by establishing the mechanism by which *C. intratropica* can exclude fire, we can better understand the species' potential as an indicator of fine-grain landscape heterogeneity, the availability of long-unburnt habitat and the system's response to changing fire regimes. Although still a contentious issue, the maintenance of habitat heterogeneity by fire is currently thought to be crucial for the integrity of communities across multiple guilds of species (Schwilk, Keeley & Bond 1997; Bradstock *et al.* 2005; Van Dyke *et al.* 2007; Yarnell *et al.* 2007; Clarke 2008; Fuhlendorf *et al.* 2009). Our research on vegetation–fire feedbacks at the patch scale provides further insight into the processes driving habitat complexity in Australian savannas and raises the question of how alternative stable state dynamics may shape patterns of savanna structure and burning world-wide.

Acknowledgements

We are very grateful to the Rostron family, Wesley Campion and the Djelk Aboriginal Ranger group for their support. Many thanks to the staff at the Northern Territory Herbarium for help with plant identification. The comments of Thomas Kitzberger, Dick Williams and two anonymous referees greatly improved earlier versions of the manuscript. Grants from the ANZ Holsworth Endowment, Australian Geographic, the Ecological Society of Australia and the Australian Research Council (Linkage project LP110200006) funded this research.

References

- Anderson, D.R. & Burnham, K.P. (2002) Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management*, **66**, 912–918.
- Beckage, B., Platt, W.J. & Gross, L.J. (2009) Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. *American Naturalist*, **174**, 805–818.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.
- Bond, W.J. & Midgley, J.J. (1995) Kill thy neighbor – an individualistic argument for the evolution of flammability. *Oikos*, **73**, 79–85.
- Bowman, D.M.J.S. & Panton, W.J. (1993) Decline of *Callitris intratropica* R. T. Baker & H. G. Smith in the Northern Territory: implications for pre- and post-European colonization fire regimes. *Journal of Biogeography*, **20**, 373–381.
- Bowman, D.M.J.S. & Wilson, B.A. (1988) Fuel characteristics of coastal monsoon forests, Northern Territory, Australia. *Journal of Biogeography*, **15**, 807–817.
- Bowman, D.M.J.S., Wilson, B.A. & Davis, G.W. (1988) Response of *Callitris intratropica* R.T. Baker & H.G. Smith to fire protection, Murguella, northern Australia. *Australian Journal of Ecology*, **13**, 147–159.
- Bowman, D.M.J.S., Price, O., Whitehead, P.J. & Walsh, A. (2001) The 'wilderness effect' and the decline of *Callitris intratropica* on the Arnhem Land Plateau, Northern Australia. *Australian Journal of Botany*, **49**, 665–672.
- Bradstock, R.A., Bedward, M., Gill, A.M. & Cohn, J.S. (2005) Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research*, **32**, 409–423.
- Buckley, Y.M., Bolker, B.M. & Rees, M. (2007) Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters*, **10**, 809–817.
- Byram, G.M. (1959) Combustion of forest fuels. *Forest Fire: Control and Use*, pp. 61–89. McGraw-Hill, New York, NY.
- Caddy, H.A.R. & Gross, C.L. (2006) Population structure and fecundity in the putative sterile shrub, *Grevillea rhizomatosa* Olde & Marriott (Proteaceae). *Proceedings of the Linnean Society of New South Wales*, **127**, 11–18.
- Clarke, M.F. (2008) Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research*, **35**, 385–394.
- Cohn, J.S., Lunt, I.D., Ross, K.A. & Bradstock, R.A. (2011) How do slow-growing, fire-sensitive conifers survive in flammable eucalypt woodlands? *Journal of Vegetation Science*, **22**, 425–435.
- Collins, S.L. & Smith, M.D. (2006) Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology*, **87**, 2058–2067.
- Couteron, P. & Kokou, K. (1997) Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecology*, **132**, 211–227.
- Crawley, M.J. (2007) *The R Book*. John Wiley & Sons Ltd, Chichester.
- D'Antonio, C.M., Hughes, R.F. & Vitousek, P.M. (2001) Factors influencing dynamics of two invasive C-4 grasses in seasonally dry Hawaiian woodlands. *Ecology*, **82**, 89–104.
- Denslow, J.S. (1995) Disturbance and diversity in tropical rain-forests – the density effect. *Ecological Applications*, **5**, 962–968.
- Drewa, P.B., Platt, W.J., Kwit, C. & Doyle, T.W. (2008) Stand structure and dynamics of sand pine differ between the Florida panhandle and peninsula. *Plant Ecology*, **196**, 15–25.
- Easton, R. (1922) *Report on the North Kimberley District of Western Australia by William R. Easton, LS etc., in Command of Kimberley Expedition, 1921*. Publication 3. Government Printer, Perth.
- Edwards, A.C. & Russell-Smith, J. (2009) Ecological thresholds and the status of fire-sensitive vegetation in western Arnhem Land, northern Australia: implications for management. *International Journal of Wildland Fire*, **18**, 127–146.
- Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C. & Lambin, X. (2001) Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology*, **122**, 563–569.
- Engber, E.A., Varner III, J.M., Arguello, L.A. & Sugihara, N.G. (2011) The effects of conifer encroachment and overstorey structure on fuels and fire in an oak woodland landscape. *Fire Ecology*, **7**, 32–50.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology Evolution and Systematics*, **35**, 557–581.
- Franklin, D.C. (1999) Evidence of disarray amongst granivorous bird assemblages in the savannas of northern Australia, a region of sparse human settlement. *Biological Conservation*, **90**, 53–68.
- Franklin, D.C., Whitehead, P.J., Pardon, G., Matthews, J., McMahon, P. & McIntyre, D. (2005) Geographic patterns and correlates of the decline of granivorous birds in northern Australia. *Wildlife Research*, **32**, 399–408.
- Frazer, G.W., Canham, C.D. & Lertzman, K.P. (1999) *Gap Light Analyzer (GLA)*. Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, NY.
- Fuhlendorf, S.D., Engle, D.M., Kerby, J. & Hamilton, R. (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, **23**, 588–598.
- Furley, P.A. (2007) Tropical savannas and associated forests: vegetation and plant ecology. *Progress in Physical Geography*, **31**, 203–211.
- Gill, A.M., Ryan, P.G., Moore, P.H.R. & Gibson, M. (2000) Fire regimes of world heritage Kakadu National Park, Australia. *Austral Ecology*, **25**, 616–625.
- Guerin, D.N. (1993) Oak dome clonal structure and fire ecology in a Florida longleaf pine dominated community. *Bulletin of the Torrey Botanical Club*, **120**, 107–114.
- Haynes, C. (1985) The pattern and ecology of munwag: traditional aboriginal fire regimes of north central Arnhemland. *Proceedings of the Ecological Society of Australia*, **13**, 203–214.
- Hobbs, N.T. (1996) Modification of ecosystems by ungulates. *Journal of Wildlife Management*, **60**, 695–713.
- Hoffmann, W.A., Adasme, R., Haridasan, M., de Carvalho, M.T., Geiger, E.L., Pereira, M.A.B., Gotsch, S.G. & Franco, A.C. (2009) Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology*, **90**, 1326–1337.
- Hood, S.M. (2010) Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis. *General Technical Report RMRS-GTR-238*, pp. 71. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Kane, J.M., Varner, J.M. & Hiers, J.K. (2008) The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeters. *Forest Ecology and Management*, **256**, 2039–2045.

- Kitzberger, T., Araújo, E., Gowda, J.H., Mermox, M. & Morales, J.M. (2012) Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. *Ecosystems*, **15**, 97–112.
- de Knegt, H.J., Groen, T.A., van de Vijver, C., Prins, H.H.T. & van Langevelde, F. (2008) Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. *Oikos*, **117**, 543–554.
- Laycock, W.A. (1991) Stable states and thresholds of range condition on North American rangelands – a viewpoint. *Journal of Range Management*, **44**, 427–433.
- Lett, M.S. & Knapp, A.K. (2003) Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. *Journal of Vegetation Science*, **14**, 487–496.
- Mandle, L., Bufford, J.L., Schmidt, I.B. & Daehler, C.C. (2011) Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. *Biological Invasions*, **13**, 1815–1827.
- Mayer, A.L. & Khalyani, A.H. (2011) Grass trumps trees with fire. *Science*, **334**, 188–189.
- Mohandass, D. & Davidar, P. (2009) Floristic structure and diversity of a tropical montane evergreen forest (shola) of the Nilgiri Mountains, southern India. *Tropical Ecology*, **50**, 219–229.
- Mourik, A.A., van Langevelde, F., van Tellingen, E., Heitkönig, I.M.A. & Gaijgher, I. (2007) Stability of wooded patches in a South African nutrient-poor grassland: do nutrients, fire or herbivores limit their expansion? *Journal of Tropical Ecology*, **23**, 529–537.
- Murphy, B.P. & Bowman, D.M.J.S. (2007) The interdependence of fire, grass, kangaroos and Australian Aborigines: a case study from central Arnhem Land, northern Australia. *Journal of Biogeography*, **34**, 237–250.
- Nagelkerke, N.J.D. (1991) A note on a general definition of the coefficient of determination. *Biometrika*, **78**, 691–692.
- Nowacki, G.J. & Abrams, M.D. (2008) The demise of fire and “Mesophication” of forests in the eastern United States. *BioScience*, **58**, 123–138.
- Odion, D.C., Moritz, M.A. & DellaSala, D.A. (2010) Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, **98**, 96–105.
- Oksanen, J., Blanchet, F.G., Legendre, P., O’Hara, R.B., Simpson, G.L., Peter Solymos, M., Stevens, H.H. & Wagner, H. (2011) vegan: Community Ecology Package. R package version 1.17-4. <http://vegan.r-forge.r-project.org/>.
- Perez, B. & Moreno, J.M. (1998) Methods for quantifying fire severity in shrubland-fires. *Plant Ecology*, **139**, 91–101.
- Perry, G.L.W. & Enright, N.J. (2002) Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial ‘state-and-transition’ model. *Journal of Biogeography*, **29**, 1143–1158.
- Peterson, D.W. & Reich, P.B. (2008) Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. *Plant Ecology*, **194**, 5–16.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Development Core Team (2009) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-91. <http://cran.r-project.org/web/packages/nlme/index.html>.
- Platt, W.J. (1999) Southeastern pine savannas. *Savannas, Barrens and Rock Outcrop Plant Communities of North America* (eds R.C. Anderson, J.S. Fralish & J.M. Baskin), pp. 23–51. Cambridge University Press, New York.
- Price, O. & Bowman, D.M.J.S. (1994) Fire-stick forestry: a matrix model in support of skillful fire management of *Callitris intratropica* R.T. Baker by north Australian Aborigines. *Journal of Biogeography*, **21**, 573–580.
- Prior, L.D., Bowman, D.M.J.S. & Brook, B.W. (2007) Growth and survival of two north Australian relictual tree species, *Allosyncarpia ternata* (Myrtaceae) and *Callitris intratropica* (Cupressaceae). *Ecological Research*, **22**, 228–236.
- Prior, L.D., Lee, Z., Brock, C., Williamson, G.J. & Bowman, D. (2010) What limits the distribution and abundance of the native conifer *Callitris glauco-phylla* (Cupressaceae) in the West MacDonnell Ranges, central Australia? *Australian Journal of Botany*, **58**, 554–564.
- Prior, L.D., McCaw, W.L., Grierson, P.F., Murphy, B.P. & Bowman, D. (2011) Population structures of the widespread Australian conifer *Callitris columellaris* are a bio-indicator of continental environmental change. *Forest Ecology and Management*, **262**, 252–262.
- Quintana-Ascencio, P.F. & Menges, E.S. (2000) Competitive abilities of three narrowly endemic plant species in experimental neighborhoods along a fire gradient. *American Journal of Botany*, **87**, 690–699.
- Rubin, B.D., Manion, P.D. & Faber-Langendoen, D. (2006) Diameter distributions and structural sustainability in forests. *Forest Ecology and Management*, **222**, 427–438.
- Russell-Smith, J. (2006) Recruitment dynamics of the long-lived obligate seeders *Callitris intratropica* (Cupressaceae) and *Petraeomyrtus pumicea* (Myrtaceae). *Australian Journal of Botany*, **54**, 479–485.
- Russell-Smith, J. & Edwards, A.C. (2006) Seasonality and fire severity in savanna landscapes of monsoonal northern Australia. *International Journal of Wildland Fire*, **15**, 541–550.
- Russell-Smith, J., Ryan, P.G., Klessa, D., Waight, G. & Harwood, R. (1998) Fire regimes, fire-sensitive vegetation and fire management of the sandstone Arnhem Plateau, monsoonal northern Australia. *Journal of Applied Ecology*, **35**, 829–846.
- Russell-Smith, J., Yates, C.P., Whitehead, P.J., Smith, R., Craig, R., Allan, G.E., Thackway, R., Frakes, I., Cridland, S., Meyer, M.C.P. & Gill, M. (2007) Bushfires ‘down under’: patterns and implications of contemporary Australian landscape burning. *International Journal of Wildland Fire*, **16**, 361–377.
- Russell-Smith, J., Yates, C.P., Brock, C. & Westcott, V.C. (2010) Fire regimes and interval-sensitive vegetation in semiarid Gregory National Park, northern Australia. *Australian Journal of Botany*, **58**, 300–317.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S. *et al.* (2005) Determinants of woody cover in African savannas. *Nature*, **438**, 846–849.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.
- Scholes, R.J. & Archer, S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.
- Schramm, J.W. & Ehrenfeld, J.G. (2010) Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. *Biological Invasions*, **12**, 3195–3204.
- Schwilk, D.W. (2003) Flammability is a niche construction trait: canopy architecture affects fire intensity. *American Naturalist*, **162**, 725–733.
- Schwilk, D.W., Keeley, J.E. & Bond, W.J. (1997) The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. *Plant Ecology*, **132**, 77–84.
- Scott, K.A., Setterfield, S.A., Douglas, M.M. & Andersen, A.N. (2010) Environmental factors influencing the establishment, height and fecundity of the annual grass *Sorghum intrans* in an Australian tropical savanna. *Journal of Tropical Ecology*, **26**, 313–322.
- Setterfield, S.A., Rossiter-Rachor, N.A., Hutley, L.B., Douglas, M.M. & Williams, R.J. (2010) Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. *Diversity and Distributions*, **16**, 854–861.
- Staver, A.C., Archibald, S. & Levin, S. (2011) Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. *Ecology*, **92**, 1062–1072.
- Stevens, J.T. & Beckage, B. (2009) Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). *New Phytologist*, **184**, 365–375.
- Stocker, G.C. (1966) Aspects of the seeding habits of *Callitris intratropica*. *Forestry and Timber Bureau Leaflet*. Department of National Development, Canberra, SA.
- Stocker, G.C. & Mott, J.J. (1981) Fire in the tropical forests and woodlands of northern Australia. *Fire and the Australian Biota* (ed A.M. Gill), pp. 425–439. Australian Academy of Science, Canberra, SA.
- Sturrock, K. & Rocha, J. (2000) A multidimensional scaling stress evaluation table. *Field Methods*, **12**, 49–60.
- Thaxton, J.M. & Platt, W.J. (2006) Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. *Ecology*, **87**, 1331–1337.
- Trollope, W.S.W. (1984) Fire behavior. *Ecological Effects of Fire in South African Ecosystems*, pp. 199–217. Springer-Verlag, New York, NY.
- Turner, M.G. (2005) Landscape ecology: what is the state of the science? *Annual Review of Ecology Evolution and Systematics*, **36**, 319–344.
- Van Dyke, F., Schmeling, J.D., Starkenburg, S., Yoo, S.H. & Stewart, P.W. (2007) Responses of plant and bird communities to prescribed burning in tallgrass prairies. *Biodiversity and Conservation*, **16**, 827–839.
- Veenendaal, E.M., Shushu, D.D. & Scurlock, J.M.O. (1993) Responses to shading of seedlings of savanna grasses (with different C4 photosynthetic pathways) in Botswana. *Journal of Tropical Ecology*, **9**, 213–229.
- Viard-Cretat, F., Gross, N., Colace, M.P. & Lavorel, S. (2010) Litter and living plants have contrasting effects on seedling recruitment in subalpine grasslands. *Preslia*, **82**, 483–496.
- Warman, L. & Moles, A.T. (2009) Alternative stable states in Australia’s Wet Tropics: a theoretical framework for the field data and a field-case for the theory. *Landscape Ecology*, **24**, 1–13.
- Williams, R.J., Gill, A.M. & Moore, P.H.R. (1998) Seasonal changes in fire behaviour in a tropical savanna in northern Australia. *International Journal of Wildland Fire*, **8**, 227–239.

- Woinarski, J.C.Z., Hempel, C., Cowie, I., Brennan, K., Kerrigan, R., Leach, G. & Russell-Smith, J. (2006) Distributional pattern of plant species endemic to the Northern Territory, Australia. *Australian Journal of Botany*, **54**, 627–640.
- Woinarski, J.C.Z., Armstrong, M., Brennan, K., Fisher, A., Griffiths, A.D., Hill, B., Milne, D.J., Palmer, C., Ward, S., Watson, M., Winderlich, S. & Young, S. (2010) Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildlife Research*, **37**, 116–126.
- Xu, R.H. (2003) Measuring explained variation in linear mixed effects models. *Statistics in Medicine*, **22**, 3527–3541.
- Yarnell, R.W., Scott, D.M., Chimimba, C.T. & Metcalfe, D.J. (2007) Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. *Oecologia*, **154**, 387–402.
- Yibarbuk, D., Whitehead, P.J., Russell-Smith, J., Jackson, D., Godjuwa, C., Fisher, A., Cooke, P., Choquenot, D. & Bowman, D.M.J.S. (2001) Fire ecology and aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. *Journal of Biogeography*, **28**, 325–343.

Received 24 October 2011; accepted 28 February 2012

Handling Editor: Thomas Kitzberger

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Summary of statistical models.

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