Aboriginal fire management, patch mosaics, and the population stability of a fire-sensitive conifer in northern Australia

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ABSTRACT

Differences among woody plant species in their adaptive responses to fire provide important insight into shifts in ecosystem composition due to changing fire regimes. In Australian tropical savannas, the switch from patchy landscape burning by Aborigines to unmanaged wildfires across much of the region within the past century has been implicated in widespread declines of the fire-sensitive conifer, *Callitris intratropica*. The species occurs as singleton trees but also commonly forms small, closed-canopy groves that are capable of excluding fire and thereby contributing both to conspecific recruitment and the persistence of a distinct community of fire-sensitive woody plants. Despite C. intratropica’s contribution to savanna heterogeneity, the mechanisms underlying its persistence and decline at the population level remain poorly understood. In this paper, we examined the hypothesis that the presence of C. intratropica in highly flammable, open savanna is dependent upon a regime of low-intensity fires maintained by Aboriginal management. We combined integral projection models of *C. intratropica* population behavior with an environmental state change matrix to examine how the contributions of demography, grove dynamics, and the frequency of high and low intensity fires contribute to the species’ long-term population stability. As expected, our patch-based population model projected negative population growth rates under current fire probabilities. We found that closed canopy C. intratropica groves make a disproportionately large contribution to population stability by promoting seedling/sapling recruitment. Conversely, singleton trees accounted for a larger proportion of adult mortality. Our results suggest that C. intratropica decline is a successional process likely requiring multiple, high intensity fire events and that the recruitment of new groves plays a critical role in the species’ persistence. Manipulating fire disturbance probabilities also suggested that reductions in fire intensity – a primary outcome of Aboriginal burning – lead to positive *C. intratropica* population growth. These findings provide critical insight into the role of human management as a driver of the vegetation mosaics encountered in flammable ecosystems.

INTRODUCTION

The accumulation of woody biomass provides a key signal of the role of fire in driving the composition of savannas (Bond and Keeley 2005, Murphy and Bowman 2012). Fire can affect the growth, survival, and fecundity of woody species which, in turn, shape ecosystem biomass and structural complexity (Quintana-Ascencio and Morales-Hernández 1997, Murphy et al. 2010). Importantly, differences among plant species in their adaptive response to fire have provided insight into compositional shifts related to changes in fire disturbance regimes. For instance, fire suppression has been implicated in the encroachment of fire-sensitive shrubs into African and North American grasslands (Roques 2001, Heisler et al. 2004) as well as continental-scale increases in the abundance of fire-sensitive trees in North America (Nowacki and Abrams 2008), while increases in fire intensity have been linked to the degradation of forest patches in South American and Australian savannas (Bilbao et al. 2010, Russell-Smith et al. 2012). Modeling the effects of fire on woody plants at the population level can therefore provide critical insight into how fire disturbance affects and interacts with the spatial heterogeneity of vegetation (Hoffmann 1999, Caswell and Kaye 2001, Keeley et al. 2006, Hoffmann et al. 2009b).

*Callitris* *intratropica* is a long-lived, fire-sensitive conifer that has persisted in Australian tropical savannas despite being one of the most fire-prone environments on Earth. *Callitris intratropica* is one of the few non-eucalypt overstory trees in these savannas and it provides a model system with which to understand the effects of fire disturbance on ecosystem composition. Widespread declines in *C. intratropica* have coincided with declines in other species assemblages, notably small mammals (Woinarski et al. 2010), and provide some of the best, direct evidence of landscape scale ecological degradation wrought by changing fire regimes in recent decades (Bowman and Panton 1993, Edwards and Russell-Smith 2009). Research on the interactions between fire and *C. intratropica* regeneration, mortality, and patch dynamics has led to the hypothesis that the species' establishment and persistence in open savanna vegetation is largely dependent upon a regime of low-intensity, patchy fires maintained by Aboriginal burning (Price and Bowman 1994, Russell-Smith 2006, Trauernicht et al. 2012). The species occurs as singleton trees but is also commonly found in small (0.01-0.3 ha) and abundant groves (c. 1 grove ha-1), within the savanna matrix (Trauernicht et al. submitted). Structurally intact *C. intratropica* groves form closed canopies that alter fuel availability and exclude low-intensity savanna fires (Figure 1a). This feedback allows for conspecific recruitment (Figure 1c) as well as the establishment of a distinct woody plant community with a greater abundance of other fire-sensitive species than occur in the savanna matrix (Trauernicht et al. 2012). Canopy damage from high intensity fires disrupts this feedback, however, causing a state change among degraded groves in which the abundance of grass fuel, probability of fire, and plant community composition are equivalent to open savanna, even though adult *C. intratropica* individuals persist (Figure 1b). Thus the proportions of intact and degraded *C. intratropica* groves across the landscape provide insight into changes in the structural complexity and diversity of savanna plant communities. For example, a greater prevalence of intact *C. intratropica* groves in central Arnhem Land (CAL) – one of the few regions of Australian savanna still under direct Aboriginal management – than in neighboring Kakadu National Park (KNP) indicates greater structural complexity and plant species diversity in CAL savannas (Trauernicht et al. 2013). Importantly, the presence of degraded groves in KNP indicates that the ecological integrity of KNP savannas has degraded over time. Examining the potential of humans to influence *C. intratropica* establishment and persistence ultimately requires an understanding of the relationship between the patch dynamics of *C. intratropica* groves and the species’ population behavior.

The cessation of Aboriginal burning regimes across much of northern Australia following widespread depopulation within the last century has been a major driver of fire regime change (Bowman and Panton 1993, Russell-Smith et al. 1997, Whitehead et al. 2003, Trauernicht et al. 2013). Proactive landscape burning to manipulate resources, ‘clean’ country and mitigate destructive fires is prevalent among indigenous management systems worldwide, often providing templates for contemporary land management (Trauernicht et al. submitted). In regions with pronounced rainfall seasonality, indigenous and contemporary managers effectively 'jumpstart' the process of landscape burning in the early dry season (EDS) before fuels have completely cured, thereby disrupting fuel continuity and reducing the occurrence and extent of higher intensity, larger fires in the late dry season (LDS; Gill et al. 2000, Mbow et al. 2000, Laris 2002, Bowman et al. 2004, Bird et al. 2008, van Wilgen et al. 2008, Price et al. 2012). For example, the relatively recent adoption of strict EDS-only burning in Kakadu, conducted largely from helicopters, is explicitly an attempt to re-impose Aboriginal burning practices and mitigate the ‘wilderness effect’ of decades of unmanaged, large scale and high intensity LDS wildfires (Kakadu National Park Board of Management 2007). More even distributions of fire ignitions throughout the dry season on lands under the tenure of indigenous people in both Africa and Australia suggest that the implementation of EDS fires allows for the continuation of controlled burning into the LDS (Laris 2002, Petty and Bowman 2007, Franklin et al. 2008). Thus, the extent to which modern, 'remedial' EDS burning and 'traditional' Aboriginal fire management overlap remains debated (Lewis 1989).

The EDS/LDS dichotomy provides a useful proxy for relative fire intensity, which can be combined with frequency to refine our characterization of fire regimes (Knapp and Keeley 2005, Govender 2006, Russell-Smith and Edwards 2006). Fire frequency alone remains, by far, the more common metric. For example, tropical savannas worldwide are generally characterized by their short (1-3 years) fire return times (Coutinho and Goldammer 1990, Gill et al. 2000, Trollope 2008) and changes in fire frequencies are used to frame anthropogenic effects on landscape burning such as fire suppression or increased frequency of ignitions (Guyette et al. 2002, Hoffmann and Solbrig 2003). Fire frequency also lends itself well to modeling disturbance effects on plant demography by sequencing population vital rates recorded before and after fire events (Menges and Kimmich 1996, Hoffmann 1999, Caswell and Kaye 2001, Caswell 2006). Frequency alone, however, may be inadequate to assess both the effects of fire on vegetation and how human management has altered fire regimes. Fire intensity has variable and critical effects on woody plant survival, growth, and reproduction (Knapp and Keeley 2006, Hoffmann et al. 2009b) and is positively correlated with the spatial extent of fire, affecting heterogeneity and diversity of savanna vegetation at broader spatial scales (Bessie and Johnson 1995, Yates and Russell-Smith 2003). In addition, research in savannas suggests that the annual extent of landscape burnt (the equivalent of fire frequency) is largely unaffected by human management (Gill et al. 2000, Van Wilgen et al. 2004, Archibald et al. 2009).

Given the difficulties apparent in altering fire frequency via management intervention, we instead consider how Aboriginal burning may have affected the establishment and persistence of *C. intratropica* by altering the intensity of fires in open savanna vegetation. We hypothesize that on a landscape scale, intact groves make a disproportionately large contribution to population stability, and that the decline of *C. intratropica* is a successional process from intact to degraded groves, then to singleton trees and eventually to local extirpation. In this paper, we combine integral projection models of *C. intratropica* population behavior with an environmental state change matrix to examine how the contributions of demography, the grove dynamics described above, and the frequency of high and low intensity fires contribute to the species’ long term stability in savanna vegetation. By manipulating patterns of fire disturbance in this patch-based population model, we intend to shed light on how the cessation of Aboriginal burning may be implicated in *C. intratropica* declines, as well as the general, contemporary trend of homogenization of savanna vegetation in northern Australia (Russell-Smith et al. 2010a, 2012).

METHODS

Study Species and Location

*Callitris* *intratropica* (Cupressaceae) is the only conifer species in tropical savannas, occurring as singleton trees and in small, scattered groves often in fire-protected rocky areas and rainforest patches. However, the species is also common in open, fire-prone savanna where it co-occurs as an overstory tree with the dominant eucalypts (*Eucalyptus miniata* and *E. tetrodonta*). Relative to the eucalypts, however, *C. intratropica* is much more vulnerable to fire damage, with low-growing crowns and a poor ability to resprout new shoots after burning (Prior et al. 2007, Lawes et al. 2011). Whereas *C. intratropica* adults can survive lower intensity surface fires, any burning may result in high mortality among seedlings and saplings (Russell-Smith 2006, Lawes et al. 2011). *C. intratropica* is monoecious and although cone and seed production may vary considerably year to year (Hawkins 1966), the species does not form persistent seed banks either in the soil or in cones retained in the canopy. Thus, recruitment in a given year depends on cone production and short-distance (i.e. <25 m) dispersal of seeds by wind during the wet season (Russell-Smith 2006).

Censuses of *C. intratropica* growth and survival were conducted at Dukladjarranj, an Aboriginal ‘estate’ on the Cadell River on the northeastern edge of the Arnhem Plateau and owned and managed by a Gunei-speaking clan within the Djelk Indigenous Protected Area of Arnhem Land, Northern Territory, Australia (Figure 2a). The Arnhem Plateau is a low massif (<400 m elevation) of deeply dissected Middle Proterozoic quartzose sandstone and is a regional centre of species endemism (Freeland et al. 1988, Woinarski et al. 2006). The region is dominated by mesic savanna with annual rainfall (c. 1500 mm) driven by the Asian monsoon, with 90% of precipitation occurring from November to May. The region is characterized by very short fire return times of 1–3 years (Gill et al. 2000, Russell-Smith et al. 2003). Detailed descriptions of the study area are provided elsewhere (Yibarbuk et al. 2001, Murphy and Bowman 2007). Observations of cone and seed production used to estimate fecundity were made in a climatically and compositionally similar savanna in Litchfield National Park, about 200 km west of Dukladjarranj (Lawes et al. 2013).

Demographic Surveys

We recorded the growth and survival of 722 *C. intratropica* individuals ranging from 1 to 650 mm in stem diameter (measured at 1 m from the ground) and 563 *C. intratropica* seedlings ranging from 35 to 1300 mm in height over three growing seasons between 2006-2009. The former, hereafter referred to as ‘adults’, were scattered across a 2.5 km stretch of open savanna dominated by *Eucalyptus tetrodonta* and *E. miniata* with a grass understory (Figure 2b). Seedlings were tagged and monitored in thirteen 30 m2 circular plots in the same area. Sampling encompassed a range of grove conditions and fire disturbances. Adult trees were identified as occurring within an intact, closed-canopy grove (N=215 among 12 groves), within a degraded, open-canopy grove (N=208 among 24 groves), or as lone, singleton trees (>5 m from any adult conspecific; N=299) following Trauernicht et al. (2012). LANDSAT satellite-derived fire scar maps (~30 m resolution; Edwards and Russell-Smith 2009) were used to establish whether adult trees and seedling plots were exposed to low intensity EDS fires (May-July), high intensity LDS fires (August-October), or no fire in the year prior to measurements. These data were corroborated on the ground by recording fire damage for each individual. Fecundity was determined by measuring cone and seed production and seed germination rates from 31 trees sampled from closed-canopy (‘dense’) groves, open-canopy (‘open’) groves, and singleton trees (Lawes et al. 2013).

Analyses of Vital Rates

We modeled *C. intratropica* adult survival and growth increment and seedling survival and size at time *t+1* as continuous functions of tree diameter or seedling height at time *t* using linear and generalized linear models, including random effects where possible. We included (i) fire disturbance (unburnt, low intensity burn, high intensity burn) and (ii) grove state (intact grove, degraded grove, singleton tree) as categorical covariates in our global models wherever appropriate (Table S1). Adult growth and survival models included both fire disturbance and grove state as covariates. Seedling growth included fire disturbance and stand density (basal area of adult *C. intratropica* per seedling plot), whereas seedling survival included only fire disturbance as a covariate (Table S1). Wherever possible, we included individual and year as random effects to account for pseudo-replication in re-censusing individuals and annual climatic variation, respectively. Global models of adult growth and survival included two-way interactions between fire disturbance and grove state and size at time *t* and grove state. Linear mixed models of growth included exponential variance structures to account for heterogeneous variance in the relationship between diameter at time *t* and diameter increment for adults and height at time *t* and height at time *t+1* for seedlings (Zuur et al. 2009).

Fecundity models were constructed using the count of cones produced as a function of adult tree diameter and grove state, including an interaction term. These models were combined with mean counts of seeds per cone and percentage of seed germination for each grove type (Lawes et al. 2013) to construct a size-based predictive model of viable seed production for adult *C. intratropica* trees. We also incorporated the effects of fire on fecundity in the IPMs described below using the findings of Hawkins (1966), in which severe fires were found to reduce seed production of *C. columellaris* – considered synonymous with *C. intratropica* by some authorities (Farjon 2005) – by 98.4%. We determined the probability of seedling establishment as the proportion of newly established seedlings in our Arnhem Land seedling plots to the total *potential* seed production of the *C. intratropica* adults in each plot based on this predictive model. The best-supported models of growth, survival, and cone production were determined via multi-model inference based on the Akaike Information Criterion (AICc) according to the Information-Theoretic approach (Anderson and Burnham 2002). All analyses were completed in R using the lme4 (Bates et al. 2011) and nlme packages (Pinheiro et al. 2010).

Modeling Population behavior

We used an integral projection model (IPM) that combined the continuous, size-based functions of *C. intratropica* growth, survival, and fecundity described above into a single function - the kernel – to project population behavior (see Supplementary Methods; Easterling et al. 2000, Ellner and Rees 2006). IPMs provide the same projections as traditional matrix models, such as long-term population stability, or lambda (λ), long-term population structure, or stable stage distribution (SSD), in addition to sensitivity and elasticity analyses, but are considered more accurate for slow-growing plant species (Zuidema et al. 2010). The use of fire disturbance and grove state (see above) as categorical covariates in our IPM kernel function effectively resulted in nine separate IPMs, corresponding to each of the possible combinations of the three levels in the covariates. We calculated the projected, long-term population growth rate (λ) for each IPM with the popbio package in R (Stubben and Milligan 2007). Values of λ>1 indicate a growing population whereas λ<1 indicates a population expected to decline, although lambda values may provide a better measure of relative growth rate among populations than a prediction of actual future population growth (Menges 2000).

Environmental State Change Transition Matrix

To model *C. intratropica* patch dynamics relative to fire disturbance, we constructed matrix *F*, a 9 × 9 discrete state Markov chain of transition probabilities from time *t* to time *t+1* for all grove state categories across all fire disturbance categories (see Supplemenrary Methods; Horvitz and Schemske 1986, Valverde and Silvertown 1997, Pascarella and Horvitz 1998). Grove state transitions were derived from the responses of intact groves, degraded groves and singleton *C. intratropica* trees to low and high intensity fires observed from surveys and experimental burns (Figure 3; Prior et al. 2011, Trauernicht et al. 2012, 2013). We calculated the probability of fire disturbance from LANDSAT satellite imagery (~30 m resolution) of early and late dry season fire scars for each annual time-step between 1990 and 2011 across the entire 28,000 km2 region encompassing our field site and comprising the Western Arnhem Land Fire Abatement project (Edwards and Russell-Smith 2009). We used matrix *F* to project stable stage distributions (SSDs) of each of the nine possible 'fire-states', from which we derived the predicted proportions of grove states across the landscape under known or hypothetical fire disturbance probabilities. We also used grove state SSDs to examine the sensitivity of these outputs to changes in the grove state transition parameters (see Supplementary Methods).

The Megamatrix

Finally, we combined our environmental state change matrix, *F,* with the IPMs derived for each of the nine combinations of fire disturbance and grove state using a 'megamatrix’ to project population demography across different environmental patches (Figure 4 & Supplementary Methods; Valverde and Silvertown 1997, Pascarella and Horvitz 1998). This approach produced the probabilities of a plant of a given size within a given environmental state (i.e. grove type × fire disturbance) transitioning to another combination of size and state. Thus this model describes individuals moving from patch to patch as opposed to patches ‘carrying’ populations through successional states (Caswell 2006). The megamatrix enabled us to project long-term stability (lambda) for the entire population across all environmental states, thereby incorporating demography, patch dynamics and fire disturbance into a single model. To our knowledge, this is the first application of this approach to patch-based environmental state changes using IPMs in place of traditional population matrix models.

Fire regime scenarios

In order to examine the effects of changing fire frequencies on our model projections, we maintained the probabilities of no fire occurring at time *t+1* (established from the LANDSAT data in matrix *D* above), while altering the probabilities of fire occurring as a low intensity or high intensity burn at time *t+1*. Thus, we varied the transition probabilities in our fire disturbance matrix *D* such that the total proportion of the landscape burnt annually remained unchanged (c. 40%), enabling us to test only the effects of changing the proportion of fires occurring as low or high intensity fires. Maintaining the overall frequency of fire occurrence better reflects the effects of actual savanna fire management which alters fire seasonality and thus intensity (Gill et al. 2000, Van Wilgen et al. 2004). However, we also created hypothetical fire regime scenarios in which we compare the effects of varying both overall fire frequency (the probability of fire occurring) as well as the probability of fire occurring as a low vs. high intensity burn.

RESULTS

Vital Rates

Our analyses confirmed tree diameter, fire disturbance and grove state as important predictors of both growth increment and survival of *C. intratropica* adults (Growth increment: Akaike weight (Wi) = 0.95, R2 = 0.45, N = 2112, Table 1, Figure 5; Survival: Wi =0.65, R2=0.11, N = 2342, Figure 6). The slight but significant effect of tree diameter on growth increment differed among grove types, with a positive relationship in intact groves, a small negative relationship among singleton trees, and with almost no size effect among degraded groves. Low intensity fires actually increased growth increment among trees in intact groves but had very little effect on singletons and trees in degraded groves. High intensity fires decreased growth increment across all grove types, however, they had the greatest deleterious effect on intact groves (Figure 5c). For survival, fire disturbance increased *C. intratropica* mortality across all grove types, with high intensity fires having the strongest effect on tree mortality (Figure 6). Degraded groves experienced slightly higher mortality than intact groves, whereas singleton trees experienced much higher rates of mortality across all disturbance types, with the difference being most pronounced for high intensity fires (Figure 6c). Although we did not explicitly include density effects in adult vital rate functions, *C. intratropica* basal area correlated with grove state (e.g., mean of 12.65 m2/ha for intact groves, 12.18 m2/ha for degraded groves, and 4.99 m2/ha for singletons; Figure 1d) and therefore adult density effects were implicitly modeled by including the grove state covariate.

Our seedling plots experienced only low intensity fires over the census period, thus we included two levels of fire disturbance (unburnt vs. low intensity burn) in our global models of seedling growth and survival. Our analysis of *C. intratropica* seedling growth only supported height at time *t* and ‘adult competition’ (i.e., basal area of adult *C. intratropica* trees within seedling plots) as important factors affecting seedling size at time *t+1*, but we found no effect of fire on growth (Wi =0.82, R2=0.91, N=367). The effect of adult density on seedling growth was incorporated into the IPM using the mean adult density values for each grove type. Analyses of seedling survival identified both height at time *t* and fire disturbance as important predictors (Wi =0.70, R2=0.08, N=972, Figure 7a), with early dry season fires negatively affecting survival. We assumed no seedling survival under high intensity fires in the parameterization of our IPMs (Russell-Smith 2006). In our models of fecundity, only adult tree size was supported as an important predictor the count of cones produced with no effect of grove state (Wi =0.55, R2=0.024, N=31, Figure 7b).

Population dynamics

The individual IPMs enabled us to examine population behavior for each grove state under each fire disturbance. On their own, these models assumed a continuous state of fire disturbance and are therefore unsuitable for projecting the overall population stability of *C. intratropica*, which would experience variable probabilities of disturbance among patches across the landscape. The lambda values from these individual IPMs (Figure 8a), however, are useful for understanding how the different grove states contribute to overall population stability as well as susceptibility of each grove state to different conditions of burning. Our models indicated population growth (λ>1) among all grove states under conditions of no fire and for intact groves under low intensity burns. IPMs projected negative population growth (λ<1) for all other combinations of grove state and fire disturbance, with high intensity fires having a strongly negative effect on the stability of degraded groves and singleton trees.

Patch dynamics and the megamatrix

The grove state SSDs projected from the environmental state change matrix, *F*, were robust to changes in the transition probabilities of intact groves under low intensity burns, and for both intact and degraded groves under high intensity burns (Supplementary Methods; Figure S1). Grove state SSDs were sensitive to changes in the recruitment of intact groves (i.e., increasing contributions to intact groves from degraded groves and singleton trees; Figure S1d). However the probabilities used in matrix *F*, based on actual observed frequencies of occurrence of newly recruiting *C. intratropica* groves (i.e., patches of seedling/sapling cohorts), provided very conservative estimates for this value.

Altering the probability of fire occurring as a low intensity fire had effects on both the projected proportion of grove states and the overall population stability projected by the megamatrix (Figures 8b, 9). Thus, although the total projected proportion of the landscape burnt (total fire frequency) remained unchanged, Figure 6b illustrates how, as the proportion of fire occurring as low intensity burns increases, so does the projected proportion of intact *C. intratropica* groves. The SSD of grove states under current fire probabilities projected higher proportions of singleton trees and lower proportions of intact and degraded groves (Intact: 5%, Degraded: 11%, Singletons: 84%) than the actual proportions of the population among grove states observed in the field (Intact: 30%, Degraded: 29%, Singletons: 41%). It must be noted, however, that the environmental state change matrix alone does not include singleton mortality – this is accounted for in the megamatrix by including singleton tree mortality from the IPM. Therefore, some of the singleton grove state proportion in the SSD actually represent patches that are unoccupied by *C. intratropica*. The megamatrix projected negative population growth (λ=0.97) for the overall *C. intratropica* population across all grove types under observed probabilities of fire disturbance. The values of projected overall *C. intratropica* population stability, λ, increased as the prevalence of low intensity increased relative to high intensity fires (Figure 9a). Altering both the probability of fire occurrence and low vs. high intensity burns, indicated that decreasing total fire frequency in the model also increased *C. intratropica* population stability. However, these results also suggested that increasing the prevalence of low intensity fires may increase *C. intratropica* population growth even under very high total fire frequencies (Figure 9b)

DISCUSSION

The recruitment bottleneck imposed by fire is a major determinant of the demography of woody plants and, therefore, the composition and structural complexity of savannas and other grassland mosaic systems worldwide (Bond 2008, Hoffmann et al. 2009a, Wood et al. 2011, Murphy and Bowman 2012, Ellair and Platt 2013). Our analyses of population behavior using grove state and fire disturbance as categorical variables simplify complex ecological processes into a heuristic model (Figure 3). Yet given the high fire frequencies in some Australian savannas (eg. 1-3 years between fires) and the high sensitivity of *C. intratropica* seedlings and saplings to burning, the negative fire feedback/alternative state imposed by intact groves is obviously a major factor in shaping the species’ demography (Trauernicht et al. 2012). Importantly, our findings suggest that this feedback, when coupled with a predominance of low intensity fires, has the potential to allow *C. intratropica* expansion in one of the world’s most flammable ecosystems. Evidence that human intervention largely influences the seasonality, intensity and spatial extent of fire, as opposed to fire frequency (Gill et al. 2000, Van Wilgen et al. 2004, Archibald et al. 2009), suggests that the use of fire intensity and *C. intratropica* spatial configuration as covariates in our demographic analyses targets the parameters that are most critical to elucidating the relationship between Aboriginal patch burning and *C. intratropica* persistence (Price and Bowman 1994, Trauernicht et al. 2012).

The decline of *C. intratropica* has provided a strong signal of change in both the fire regime and in the structural complexity and plant diversity of Australian savannas over the course of radical changes in the social-ecological relationships shaping this ecosystem (Bowman and Panton 1993, Edwards and Russell-Smith 2009, Russell-Smith et al. 2012, Trauernicht et al. 2013). Importantly, the life history of extant *C. intratropica* groves span the shift from widespread Aboriginal landscape burning to what has become, largely, a ‘modern wilderness’ within the past century (Bowman et al. 2001). Widespread contemporary declines in *C. intratropica* pose an evocative hypothesis that prescribed burning by humans enabled this relatively fire-sensitive conifer to ‘invade’ and persist in highly fire-prone vegetation. The negative feedback between *C. intratropica* adult canopy cover and savanna fires illustrates how, under low to moderate intensity fires, intact groves contribute to fine-scale ecological heterogeneity across the landscape, promoting both conspecific recruitment as well as the maintenance of fire-sensitive plant communities (Trauernicht et al. 2012, 2013). By including the difference in this feedback – effectively an ecological state change – among intact and degraded groves, our patch-based modeling approach provides critical insight into whether and how the establishment and persistence of intact groves contributes to the long-term persistence of the *C. intratropica* population as a whole. Equally compelling, the integration of the frequency of low and high intensity burns allow us to explore how, by altering the occurrence of high intensity burns, patchy landscape burning by Aboriginal managers may have contributed to the current distribution of *C. intratropica* in these savannas. Thus, *C. intratropica* provides a window into a management legacy that extends back over 40 millennia and, arguably, must underlie any attempt to understand the current and grave declines in biodiversity across the region.

It is clear from previous research that the strongest impacts of fire on *C. intratropica* demography is via seedling and sapling mortality (Bowman and Panton 1993, Price and Bowman 1994, Russell-Smith 2006, Prior et al. 2007, 2011). *C. intratropica* populations are not limited by reproductive capacity, as illustrated by fecundity measurements (Figure 7b) and reports of abundant recruitment when protected from fire (Bowman et al. 1988, Lawes et al. 2013). Yet even low intensity fires can have major effects on seedling survival (Figure 7a; Russell-Smith 2006), reinforcing the importance to *C. intratropica* demography of the negative fire feedback among intact groves. Although the effects of this recruitment bottleneck due to fire on *C. intratropica* population dynamics have been demonstrated and discussed elsewhere (Price and Bowman 1994, Prior et al. 2007), the critical role of the species’ patch dynamics has been missing from previous models. Similarly, our approach of constructing separate IPMs for each combination of fire disturbance and grove state provides an incomplete picture of *C. intratropica* demography. Yet the IPMs do illustrate how under conditions of no fire, all grove types are capable of maintaining similar positive population growth rates (Figure 8a). The IPMs also reveal that despite little change in growth rates among degraded groves and singletons exposed to low intensity fires (Figure 5b), the reduction in seedling survival (Figure 7a) is sufficient to project negative population growth (λ<1; Figure 8a). Assumptions of complete seedling mortality under high intensity (LDS) fires drove IPM projections well below levels of stable population behavior across all grove states.

Although we expected greater survival among trees in intact than in degraded groves (Trauernicht et al. 2012), our survival models clearly support the importance of grove formation to *C. intratropica* persistence, even under high intensity fires (Figure 6). Just as intact groves contribute disproportionately to seedling and sapling recruitment (Figure 1c), singleton trees conversely account for a larger proportion of the mortality events among adult trees (Figure 6c). These findings support our hypothesis that degraded groves and singleton trees represent successional stages in the process of *C. intratropica* decline. In the absence of the negative fire feedback found in intact groves, degraded groves and singleton trees do little to promote seedling/sapling survival and therefore do not represent intermediate stages of grove formation. Moreover, the dependence of seedling/sapling recruitment on this fire feedback suggests that most extant *C. intratropica* adults in open savanna vegetation – whether currently part of a grove or a singleton tree – originated through this process of grove formation.

The establishment of new groves is occasionally observed in the field as patches of seedling/sapling cohorts (C. Trauernicht, pers. obs.). Any extant adult tree may therefore contribute to the process of grove formation as a seed source – indeed, our patch dynamic model allows for this via the contribution to intact groves from degraded groves and singleton trees (Figure 3). However, we hypothesize that the ultimate driver of grove formation is the availability of habitat patches remaining unburnt long enough for seedling cohorts to establish, suppress fuels, and thereby alter the local disturbance regime. Although the availability of long-unburnt habitat in highly fire-prone savannas seems an unlikely phenomenon, the presence of new *C. intratropica* groves demonstrates that it does occur. Even if low-intensity burns predominate, the inevitable occurrence of intense fires means that *C. intratropica* groves will not persist indefinitely and, thus, the rate of grove establishment is a likely a critical driver of grove dynamics (Figure S1d; see below) and long-term population stability. Yet, whereas low fire intensity fire is critical to the persistence of established *C. intratropica* groves, the creation and maintenance of long-unburnt patches – and thus the formation of new groves – is more difficult to explain. Habitat modeling, however, suggests increasing the spatial heterogeneity of fire disturbance – which is also correlated with lower intensity fire regimes – may increase the age diversity of available habitat patches (Trauernicht et al., submitted).

The differences in growth rates of adult trees among grove states and fire disturbance types were also significant, albeit small (Figure 5). There are likely several processes shaping these growth relationships. For example, the inverse effects of diameter on growth among singletons versus trees in intact groves are possibly due to differences in intraspecific competition. Higher *C. intratropica* density in fire-protected areas can reportedly arrest growth, especially among smaller individuals (Bowman et al. 1988, Lawes et al. 2013). Thus the smaller singleton trees may be experiencing faster growth rates due to reduced competition. Although we did not explicitly model density-dependent growth, *C. intratropica* basal area was clearly greater among degraded and intact groves (Figure 1d). In addition, reduced growth rates for larger singleton trees than for trees in intact groves may be due to canopy damage from greater exposure to repeated fires. Degraded groves may simply be experiencing the worst of both worlds, with competition and canopy damage reducing growth for trees across all size classes. The negligible impacts of high intensity fires on degraded groves and singleton trees, relative to the effect on intact groves, also suggests that tree growth may be permanently impaired from accumulated canopy damage from previous fires.

The environmental state Markov chain (matrix *F*) provided a broader context from which to interpret the individual IPM results discussed above. The SSDs, or projected proportions, of grove states derived from matrix *F* under observed LANDSAT fire frequencies were fairly robust to changes in the transition probabilities among *C. intratropica* grove states (Figure S1). For example, plotting the projected grove state SSDs against changing probabilities of intact and degraded groves remaining in their respective states under high fire intensities (Figure S1b,c) suggested our parameterizations of grove state transitions were conservative with respect to the process of transitioning to singleton trees. Increasing ‘recruitment’ rates of intact groves (modeled as the transitions to intact groves from degraded groves and singleton trees) dramatically altered projections of grove state proportions (Figure S1d). The grove recruitment rates used in our parameterization of matrix *F* (Figure 3) were based on field observations of the frequency of seedling/sapling cohorts establishing new groves relative to counts of mature degraded and intact groves sampled across a landscape of variable fire conditions (Trauernicht et al. submitted). Thus our model parameterizations for recruitment were similarly conservative because they likely underestimate the potential for grove establishment under conditions of no fire. The sensitivity of grove state SSDs to grove recruitment also indicates the potential of *C. intratropica* to expand under conditions that favor seedling/sapling survival and thus the establishment of new groves. The effects of altering the probability of fire occurring as a low intensity vs. high intensity burn on grove state SSDs in the environmental state change matrix *F* revealed two important patterns. First, the difference between projected and observed proportions of grove states under observed fire probabilities suggests that grove state proportions are ‘drifting’ towards lower proportions of intact and degraded groves and higher proportions of singleton trees (Figure 8b). Although this patch dynamic model alone does not account for ‘mortality’ among singleton patches (see Methods), the dominance of this grove state corroborates field observations of *C. intratropica* declines and, more generally, the homogenization of Australian savannas under contemporary fire regimes (Russell-Smith et al. 2010b, 2012, Trauernicht et al. 2013). However, the patch dynamic model also suggests that increasing the prevalence of low intensity burns may increase the abundance of intact *C. intratropica* groves (Figure 8b), which has been linked to greater structural heterogeneity and diversity of savanna vegetation (Trauernicht et al. 2013).

The megamatrix approach allowed us to effectively ‘insert’ the demographic models of *C. intratropica* (the IPMs) into the environmental state change matrix *F* (Horvitz and Schemske 1986, Valverde and Silvertown 1997, Pascarella and Horvitz 1998). We do not presume to model the reality of complex savanna dynamics. However, the megamatrix, *M*, provides a synthetic model of patch-based population behavior, which incorporates the negative fire feedback in intact groves, and is ultimately driven by the probabilities of low and high intensity fire occurrence. Therefore, our model has important implications for distinguishing the ecological effects of *how* a landscape burns from simply *how much* of it burns. In other words, evidence suggests management has little influence on the proportion of landscape burnt annually – directly analogous to overall fire frequency – but has major effects on fire seasonality and thus, the intensity and heterogeneity of fire events (Gill et al. 2000, Knapp and Keeley 2006, Russell-Smith and Edwards 2006, Archibald et al. 2009). Thus, understanding the influence of Aboriginal burning on Australian savannas requires exploring metrics of fire regimes other than overall frequency. Given the well documented declines in *C. intratropica* across northern Australia (Bowman and Panton 1993, Bowman et al. 2001, Edwards and Russell-Smith 2009, Trauernicht et al. 2013), the negative population growth (λ = 0.97) projected by the megamatrix under current frequencies of low and high intensity fires is no surprise. However, the critical finding here is that increasing the frequency of low intensity burns relative to high intensity burns, without altering total fire frequency, increases the overall stability of *C. intratropica* populations (Figure 9a). Further, this relationship appears to hold even under conditions of very high total fire frequencies (Figure 9b). Thus, our results not only suggest that managing fire intensity can contribute to *C. intratropica* persistence, but that this practice may also mitigate shifts in overall fire frequency which may be climate driven (e.g., Bliege Bird et al. 2012).

The relationship between fire intensity and *C. intratropica* persistence evident in our patch-based population model has implications beyond understanding the potential of Aboriginal burning to influence the distribution of a single, fire-sensitive tree species. It also suggests a potential mechanism by which fire feedbacks may drive mosaics of fire-sensitive and fire-tolerant vegetation in other systems. In Australian savannas, there is a clear relationship between the abundance of intact *C. intratropica* groves and the heterogeneity of fire disturbance, availability of refugia for other fire-sensitive species, and overall structural complexity and plant diversity (Trauernicht et al. 2012, 2013). Thus, in addition to linking biodiversity to pyrodiversity (ie, landscape heterogeneity wrought by fire), our findings also suggest that human management has the potential to engineer fundamental aspects of ecosystem composition. The use of proactive landscape burning to mitigate destructive fires is widespread among indigenous land management systems in flammable ecosystems worldwide (Trauernicht, submitted). Therefore, understanding the relationship between disturbance and species composition/conservation may require reshaping our perspective of what constitutes the ecological baseline in these systems. For instance, it may be coincidental that the current species declines among birds, mammals, and fire-sensitive plants in northern Australia have occurred within decades of the abandonment of Aboriginal lands (Franklin 1999, Edwards and Russell-Smith 2009, Woinarski et al. 2010). However, the persistence of these species through more than 40,000 years of Aboriginal management strongly implicates the ‘wilderness effect’ as a contributing factor to these declines. Our findings therefore provide critical insight into a millennial-scale relationship between human–fire interactions and ecosystem composition. Although we maintain that this interaction is critical to rehabilitating Australian savannas as social-ecological systems, the role of humans in ‘natural systems’ will, doubtless, continue to raise contentious debate.

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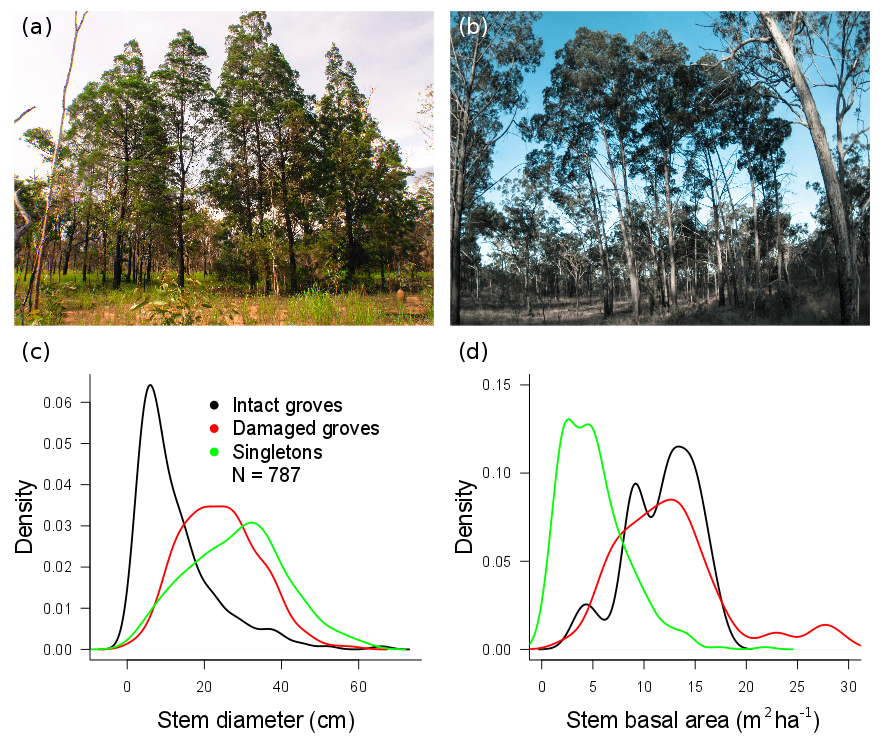


Figure 1. Characteristics of *C. intratropica* groves sampled in open eucalypt savanna vegetation. (a) A typical intact grove with closed canopy and woody understory development. (b) Example of a degraded grove with damaged canopy and open, grassy understory. The bottom panels are kernel density plots showing the distributions of *C. intratropica* (c) stem diameter and (d) basal area (sampled within a 10 m radius of each individual) for each of the *C. intratropica* grove states: (i) intact groves, (ii) degraded groves, and (iii) singleton trees.

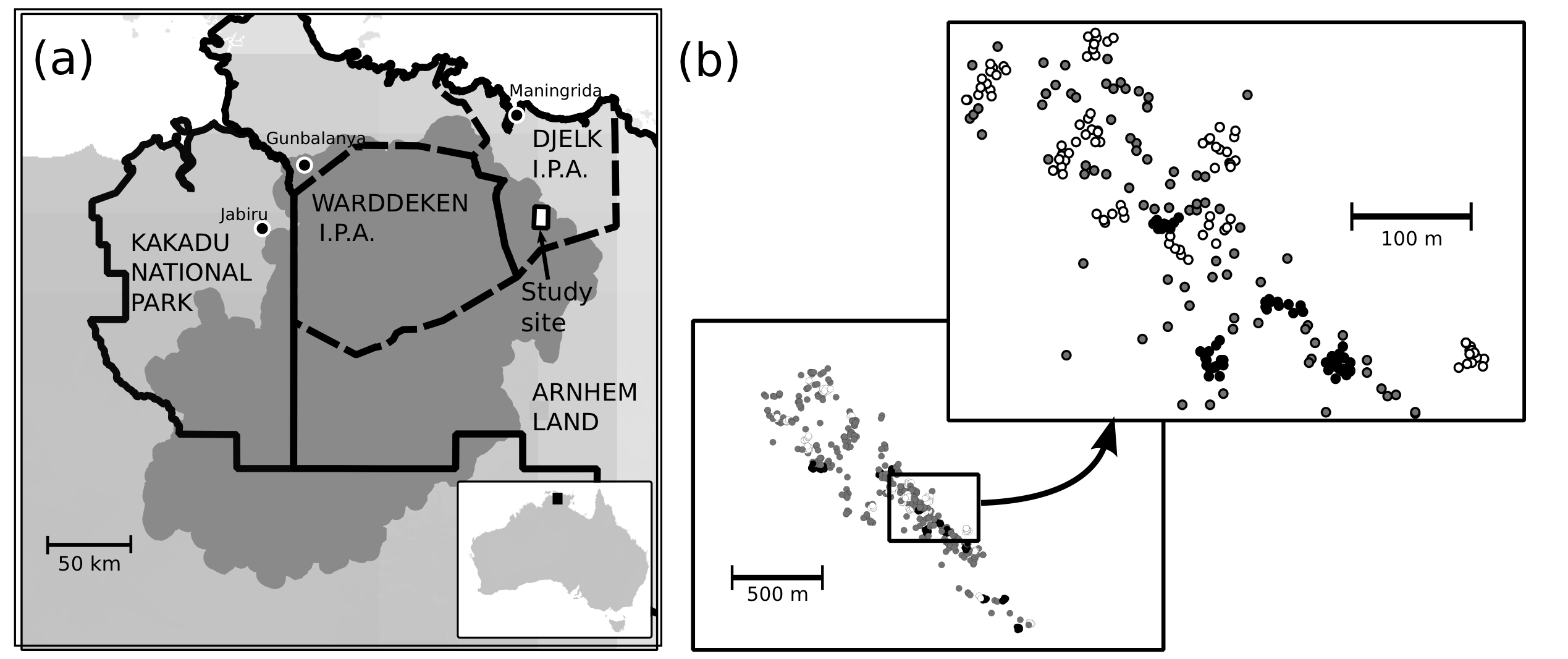


Figure 2. Maps of (a) the study site in Arnhem Land (the shading indicates the extent of the Arnhem Plateau ‘Stone Country’) and (b) the trees surveyed the Callitris intratropica census. Black circles show the location of trees classified as intact groves, white circles are trees classified as degraded groves, and grey circles are singleton trees.

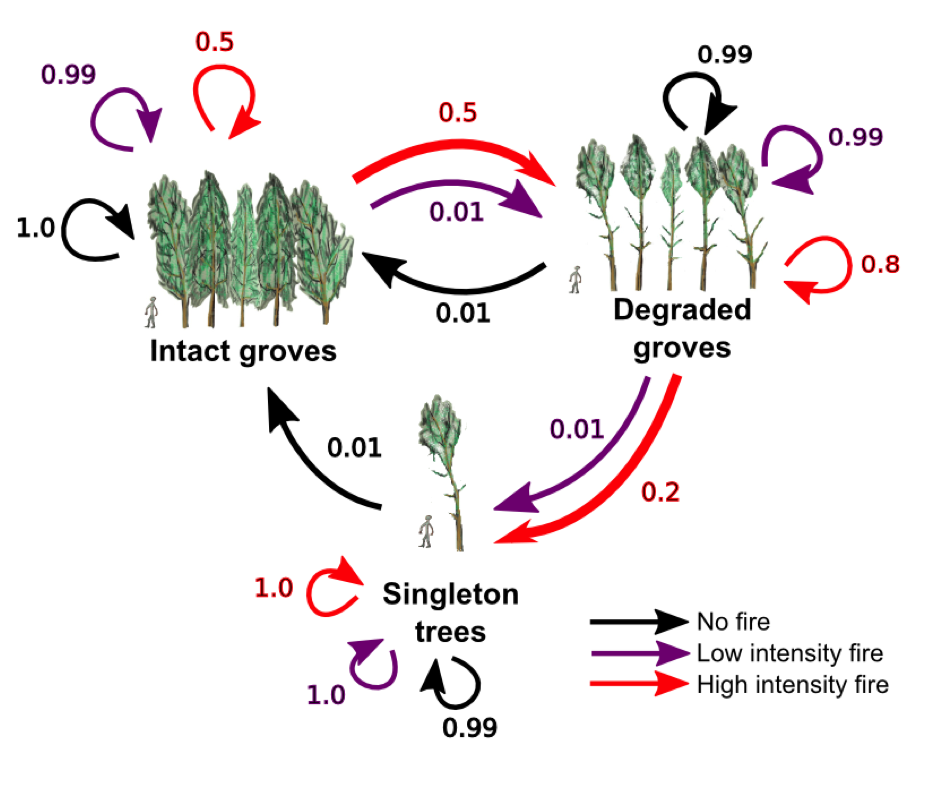


Figure 3. A model of *Callitris* *intratropica* ‘grove state’ transitions under conditions of no fire, low intensity fire and high intensity fire. Values adjacent to arrows indicate the fire-dependent probabilities used in the construction of Markov chain probability matrices of patch dynamics. These probabilities were based on field observations of the response of groves to fire events in Kakadu National Park and central Arnhem Land. Low frequencies of grove ‘recruitment’ is allowed via ‘transitions’ to intact groves from degraded groves and singleton trees. There is no grove ‘extinction’ category because we are not modeling the entire landscape – only patches occupied by *C. intratropica*. However, grove ‘extinction’ was included in our final patch-based model by integrating the population vital rates of *C. intratropica*. Thus, survival models of singleton trees under each fire disturbance type ultimately defined the proportion of singleton ‘patches’ remaining after high and low intensity fires.



Figure 4. Flow chart of analyses employed to develop a patch-based model of *Callitris intratropica* population behavior. Markov chains of C. intratropica grove state transition probabilities were developed for each type of fire disturbance and then combined with a Markov chain of actual fire disturbance probabilities (derived from LANDSAT satellite imagery) to contruct the environmental state change matrix. This matrix was then combined with matrices of size-based transition probabilities derived from integral projection models of C. intratropica population behavior to construct an integrated ‘megamatrix’ accounting for the transition of individual trees among size classes and environmental states. The megamatrix was use to project overall population stability (Lambda) across grove states and disturbance types. Probabilities in the fire disturbance Markov chain were manipulated to examine the response of population stability to hypothetical changes in fire disturbance.



Figure 5. *Callitris* *intratropica* diameter growth increment as a function of diameter at time *t* for (a) unburnt conditions, (b) low intensity burns, and (c) high intensity burns. Akaike weight (Wi) are presented relative to the null model.



Figure 6. Probability of *C. intratropica* survival under (a) unburnt conditions, (b) low intensity burns, and (c) high intensity burns. Akaike weights (Wi) are presented relative to the null model.



Figure 7. *Callitris* *intratropica* (a) seedling survival under no fire and low intensity burns and (b) adult cone production as a function of stem diameter. Akaike weights (Wi) are presented relative to the null model.



Figure 8. *Callitris intratropica* (a) population stability (lambda) derived from integral projection models for each combination of fire disturbance type (unburnt, low intensity, and high intensity burns) grove state (intact groves, degraded groves, and singleton trees) and (b) stable stage proportions of grove states derived from the environmental state change matrix. Lambda>1 indicates positive population growth and lambda<1 indicates populations are declining. The vertical dashed lines indicate the actual observed probability of fire occurring as a low intensity burn, derived from LANDSAT data for western Arnhem Land. ‘Observed groves’ are the actual proportions of the surveyed *C. intratropica* population occurring among the three grove states. The environmental state change matrix is a Markov chain transition matrix integrating the probabilities of each fire disturbance type above with the fire-dependent transition probabilities among *C. intratropica* groves states.



Figure 9. Overall *C. intratropica* population stability (lambda) projections from the megamatrix integrating patch-level (i.e., grove) dynamics and population behavior from integral projection models. Panel (a) illustrates the response of lambda to changing the probability that fire occurs as a low intensity burn, keeping total fire frequency constant (c. 40%; observed from LANDSAT data for western Arnhem Land). The dashed vertical line indicates that under actual observed probabilities of low intensity burns, lambda is 0.97. Panel (b) is a surface plot of the response of lambda to hypothetical changes in both total fire frequency (y-axis) and the probability that fire occurs as a low-intensity burn (x-axis). In both panels, lambda<1 indicates declining populations and lambda>1 indicates population growth.