8 Appendix

Appendix 8.1: Recruitment, growth and mortality of trees in Australian savannas: predicting effects of fire management on tree biomass

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Peter J. Whitehead[1,2], Brett P. Murphy[3*], Jay Evans[1], Cameron P. Yates[1], Andrew C. Edwards[1], Harry J. MacDermott[1,3], Dominique C. Lynch[1] and Jeremy Russell-Smith[1,2]

[1] Darwin Centre for Bushfire Research, Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin NT 0909, Australia

[2]North Australia Indigenous Land and Sea Management Alliance Ltd, Brinkin NT 0810, Australia

[3] NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin NT 0909, Australia

Corresponding author: brett.murphy@cdu.edu.au

Running head: Savanna fire management and tree biomass

Abstract

Tropical savannas are characterised by high primary productivity and high fire frequency, such that much of the carbon captured by savanna vegetation is rapidly returned to the atmosphere. Hence, there have been suggestions that management-driven reductions in fire frequencies and/or intensities in savannas might significantly increase carbon storage in tree biomass. We analysed a large, long-term tree monitoring dataset (236 plots, monitored for 3–24 years, including 12,344 tagged trees) from the tropical savannas of northern Australia, in order to characterise relationships between fire regimes and key demographic rates of trees: recruitment into large sapling size classes (≥5 cm diameter at breast height); stem diameter growth; and mortality. We used these relationships to build a process-explicit demographic model of an Australian savanna tree population. We found that savanna fires, especially high-severity fires, significantly reduce tree recruitment, survival and growth. Despite these negative effects of fire on demographic rates, tree biomass appears to be suppressed by only a relatively small amount by ambient fire regimes. Nonetheless, there is substantial scope for fire managers to generate carbon credits from increased carbon storage in tree biomass. We found that plausible, management-driven reductions in fire frequency and severity could lead to increases in total tree biomass, of about 12.9 t DM ha^{-1} over a century. Accounting for this increase in carbon storage could generate significant tradeable carbon credits, worth on average 3–4 times those generated annually by current savanna greenhouse gas (methane and nitrous oxide) abatement projects, and potentially more on sites presently affected by high frequencies of severe fire. If appropriate carbon accounting methodologies can be developed, sequestration by tree biomass has the potential to significantly increase the economic viability of fire/carbon projects in Australian savannas. This burgeoning industry has the potential to bring much-needed economic activity to tropical savanna landscapes, without compromising important natural and cultural values.

Keywords: Australia; biomass; carbon; eucalypt; fire management; greenhouse gas; tree; tropical savanna

INTRODUCTION

Despite 150 years of extensive beef cattle pastoralism since European colonisation, the vast majority of Australia's tropical savannas remain structurally intact and comprise a globally significant carbon bank (Garnaut 2008). The mesic savannas (>1,000 mm mean annual rainfall) along the far northern coast have high woody biomass – amongst the most biomass dense savannas on Earth (Lehmann et al. 2014). However, tree height and density decrease markedly down a steep rainfall gradient running from the mesic coasts to the drier inland (Williams et al. 1999, Lehmann et al. 2014, Cook et al. 2015).

Like most of the Earth's savanna regions, fire frequencies are extremely high, typically ranging from once every 1–2 years in higher rainfall regions (>1,000 mm mean annual rainfall), to once every 3 or more years in drier regions (600–1,000 mm) (Fig. 1a; Russell-Smith et al. 2007, Whitehead et al. 2014). Such high fire frequencies are driven: bio-physically by an annual cycle of wet season growth of grasses that cure rapidly during a long (6–8 month) dry season with little or no rainfall, low humidity and often strong winds; and socially by ongoing traditions of Indigenous and pastoral use of fire as a land management tool (Williams et al. 2002, Russell-Smith et al. 2003b). In most of the savanna region, frequent fire is believed to reduce woody biomass below a climatically-determined upper bound (Sankaran et al. 2005, Lehmann et al. 2014, Murphy et al. 2015). Consistent with the disturbance-mediated, non-equilibrium status of woody vegetation, a number of studies suggest that reductions in fire frequency and/or intensity could cause northern Australia's savannas to act as substantial carbon sinks (Chen et al. 2003, Beringer et al. 2007, Murphy et al. 2010, Bristow et al. 2016).

Fire regimes influence savanna tree demography, and hence total tree biomass, in a number of ways. In northern Australia, despite significant observed variability in the responses of eucalypts (*Eucalyptus* and *Corymbia* spp.) and non-eucalypts to different fire regime characteristics (e.g. seasonality, frequency), high-intensity fires are observed to suppress growth rates in tree-sized stems (Murphy et al. 2010), and especially of non-eucalypt saplings (Russell-Smith et al. 2019). However, growth rates of adult trees exposed to low-intensity fires early in the dry season may be enhanced, relative to growth rates at unburned sites (Prior et al. 2006).

Growth rates determine rates of increase in biomass of existing stems (Murphy et al. 2009, Murphy et al. 2010) and, arguably more significantly, through their influence on the rate at which stems enter and leave more or less vulnerable size classes (Werner 2005, Werner and Prior 2013, Werner and Peacock 2019). In mesic savannas, faster-growing eucalypts escape the 'fire trap' by more quickly reaching heights and bark thickness that reduce susceptibility to fire-induced 'topkill' (death of aboveground parts) (e.g. Lawes et al. 2011a, Bond et al. 2012, Russell-Smith et al. 2019). Williams et al. (1999: Fig. 3) showed that survival after a single high-intensity fire was very low for the smallest and largest stems (<10 cm and >40 cm diameter at breast height [DBH], 130 cm), while uniformly high for intermediate-sized stems (15 to 40 cm DBH). The low survival of the largest trees was attributed to extensive hollowing of these individuals by termites, which renders trees susceptible to fire.

In a re-interpretation of the data of Williams et al. (1999), Cook et al. (2005: Fig. 3) present statistical models showing modest declines in survival of stems above about 15 cm for eucalypts and 30 cm DBH for non-eucalypts. These contrasting interpretations have not been satisfactorily reconciled, even though they might generate starkly contrasting predictions regarding the effects of fire on standing biomass. In particular, large, older, and more fire-susceptible trees contain a large proportion of the total live tree biomass at a site (Cook et al. 2015, Edwards et al. 2018). In drier (<1,000 mm annual rainfall), lower stature Australian savannas, fire effects on tree population dynamics are poorly studied. However, it has been recently shown that high-intensity fires can cause substantial adult tree mortality over large areas, including very substantial losses even of more fire-tolerant eucalypt stems across all stem size-classes (Edwards et al. 2018).

Tree competition for resources, especially available water, with both understorey plants and other woody vegetation, in addition to setting the biomass 'upper bound' (Hutley et al. 2001, Sankaran et al. 2005, Lehmann et al. 2014, Murphy et al. 2015), may affect growth and other demographic parameters on time-scales relevant to fire impacts. Long-term studies of tree growth rates in closely managed sites from which fire was excluded and located mostly in sub-tropical savannas indicate that some taxa common in drier tropical savannas have higher growth rates in higher rainfall areas (Ngugi et al. 2015). Prior et al. (2006) found that, in burned mesic savannas, growth rates of adult trees may be negatively correlated with annual rainfalls. They suggested that in drier years under-storey development is compromised relative to trees that can access deeper soil moisture. In these drier years, there is reduced competition for nutrients and lower biomass of grassy fuels, reducing the potential for fire to compromise tree growth.

In other situations, extended (multi-year) periods of below average rainfall (droughts) may cause adult tree death (Fensham et al. 2009). Observations from a semi-arid site (517 mm mean annual rainfall) also indicate that variable rainfall may have greater effects on tree demography, including reduced adult growth rates during periods of low rainfall, than fire (Fensham et al. 2017).

Clearly, interactions among climate, rainfall variability and fire may affect tree demography in complex ways. Disentangling anthropogenic, potentially manageable impacts of fire use from natural influences over such a large part (~20%) of the Australian continent is important to determine the extent to which improved land management can support reduction in Australia's emissions of greenhouse gases (Canadell et al. 2007). Fire regimes have been shown, through more than a decade of experience in commercial abatement of NO_x and CH_4 emissions, to be amenable to active management, particularly through the reduction of frequency and extent of more intense fires late in the dry season (Russell-Smith et al. 2013). *A priori*, such fire management is also likely to increase growth, recruitment and survival of savanna trees.

In this paper we examine effects of fire regimes on these key aspects of tree demography based on long-term observations of marked stems in plots sampling the northern savanna rainfall gradient from 600 to 1,700 mm mean annual rainfall. The study area encompasses regions covered by Australia's savanna burning method for generating tradable credits from reduced emissions of non-CO_2 greenhouse gases (methane and nitrous oxide), and carbon sequestration in coarse woody debris (Commonwealth of Australia 2018). That method quantifies reductions in emissions achieved essentially by shifting fire regimes dominated by intense late dry season fires to typically less severe and extensive early season fires, and by reducing fire frequency.

Our purpose is to: (1) quantify recruitment, mortality and stem diameter increment of savanna trees over a large rainfall gradient (600–1,700 mm mean annual rainfall); (2) use a simple demographic model to describe the effects of fire regimes on savanna tree populations; and (3) assess the potential for savanna fire management to increase carbon stored in live tree biomass, in order to generate tradeable carbon credits.

METHODS

Plot locations and establishment

Plot locations were chosen to sample the strong latitudinal rainfall gradient, from 600 to 1,700 mm, in the central region of the tropical savannas (Fig. 2). Plots were also chosen to represent all of the vegetation classes (Fig. 1b) eligible under Australia's existing GHG accounting methodologies for savanna fire management (Commonwealth of Australia 2018). These vegetation classes are all forms of the savanna biome, each having a woody overstorey, albeit of varying density, over a more-or-less continuous C_4 grass understorey.

Methods of plot establishment and sampling have been described in detail in several papers reporting earlier observations from monitoring plots in the high-rainfall zone (>1,000 mm per annum) (e.g. Edwards et al. 2003, Murphy et al. 2010, Russell-Smith et al. 2010). In brief, for the high-rainfall zone, permanent plots (40 × 20 m) were established from 1994 in three large conservation reserves (Kakadu, Nitmiluk and Litchfield National Parks). All live trees (≥5 cm DBH) were identified to species, and tagged. New recruits (≥5 cm DBH) were recorded and tagged at subsequent (~5-year) sampling intervals. DBH was measured for all tagged stems using standard methods and fate of individual stems recorded.

From 2006, additional plots were established in the low-rainfall zone (600–1,000 mm per annum) in three regions: Gulf of Carpentaria, Central Arnhem Land and Kimberley. At each low-rainfall site, three transects were established. Trees encountered within a 10 × 100 m transect were tagged and DBH of each stem recorded. If fewer than 20 trees were encountered within the transect, then it was widened to encompass at least 20 trees. Transects were laid out in groups of three, separated by up to 870 m (average 131 m). Each group of three transects constituted a 'plot'. Spatial clumping of transects within plots was taken into account in the statistical analysis, usually by combining observations into a single plot. During subsequent re-measures of tagged stems, new recruits (≥5 cm DBH) within the transects were also tagged and DBH measured.

Plot characterisation

The features of plots and/or their landscape context considered in developing statistical models are given in Table 1. There were 126 plots in the high-rainfall zone and 110 plots in the low-rainfall zone. While the high-rainfall plots were in conservation reserves, the low-rainfall plots were mostly on Aboriginal land used for subsistence and other traditional purposes, as well as areas of extensive cattle grazing. Most sites, including those in conservation reserves, are likely to have been disturbed by feral grazing animals (cattle [*Bos* spp.] and/or water buffalo [*Bubalus bubalis*) and pigs (*Sus scrofa*). Areas of severe disturbance by exotic animals (e.g. close to water sources) were avoided during plot selection.

Monthly rainfall at each plot, from 1970 to 2018 inclusive, were estimated using interpolated rainfall surfaces (Table 1; Australian Bureau of Meteorology 2018). Mean annual rainfall was calculated from the entire rainfall record. Rainfall anomalies (i.e. deviation of rainfall in a given period and mean annual rainfall) were calculated for all periods between observations.

Other variables for each plot were retrieved by intersecting plot locations with relevant broad scale digital mapping (Table1). Whilst these synthetic descriptors cannot be treated as accurate descriptions of individual plots, they summarise aspects of local landscape context that may influence vegetation patterns and local fire behaviour relevant to the study. No vegetation mapping at the scale needed for savanna-wide application appears applicable. Continental-scale vegetation mapping (Executive Steering Committee for Australian Vegetation Information 2003) included obvious misclassifications at plot scales and provided little additional information not incorporated in the primarily-structural vegetation classes used for savanna carbon accounting (Commonwealth of Australia 2018). Assignment of vegetation class was based on descriptions of tree stem density and cover and growth forms of dominant grasses made at plot establishment. An index of soil type and soil depth were recorded on site at each plot in 1 of 5 classes: skeletal sands, shallow sands, deep sands, shallow clays, and deep clays. Clay soils were collapsed into a single class before analysis because shallow clays were infrequently observed.

None of the plots support significant populations of exotic grasses of types that are likely to alter fuel loads, fire phenology, or understory competition with trees for water or other resources that might affect growth or other demographic rates.

Fire frequency and severity

Russell-Smith and Edwards (2006) describe assembly of fire histories for the monitoring plots in the high-rainfall zone. Fire histories for low-rainfall plots were derived similarly, as part of the same ongoing fire and vegetation monitoring program. Plots were not individually protected from fire nor managed to achieve particular patterns of burning; all plots were exposed to local ambient fire regimes.

Each monitoring plot was visited and photographed at least once each year. Using the photos and on-site observations, plots were scored as recently burned or unburned, and if burned, the fire was categorised as mild, moderate or severe, applying the following fire severity index based on leaf scorch height (Russell-Smith and Edwards 2006):

(1) mild fires: tree scorch heights <2 m, indicating fire intensities of <1 MW m^{-1};
(2) moderate fires: scorched to less than mid-height, indicating fire intensities of 1–2 MW m^{-1};
(3) severe fires: scorching the canopy to its full height, indicating intensities of >2 MW m^{-1}.

Fires were also classified by month of occurrence and hence season (early *versus* late dry season). Early dry season fires were those occurring from April to July, inclusive. Late dry season fires occurred from August–December, inclusive. In most north Australian landscape settings, fires in the early dry season characteristically extinguish by nightfall, whereas fires in the late dry season often are observed to continue through the night, albeit at lower intensities (Maier and Russell-Smith 2012). Assignments of timing were based on: (a) *in situ* observations like presence and distribution of fine, readily dispersed ash; leaf damage that would not be expected to persist across intervening wet seasons, and extent of resprouting of perennial grasses; and (b) interrogation of remotely sensed data sources including Landsat and Sentinel satellite imagery, and MODIS-derived regional fire mapping products derived from the North Australia Fire Information (NAFI) website (www.firenorth.org.au). Plot locations were intersected with all available monthly burnt area mapping for the period 1995–2016.

Arguably such mapping is too coarse to be used alone to determine whether relatively small plots were burned or not. Nonetheless, we consider it reasonable to use fire maps in combination with ground observations of recent fire to assign a burn date based on the month of mapping imagery showing fire at or close (<500 m, or <2 MODIS pixels) to those plots recorded by ground-based observers as burned during the relevant year. These assignments were in turn used to validate assignments of season (early versus late dry season) based on ground-based assessments. A few 'early' fires occurred in the wet season (*ca*. December–April). These were re-assigned to the subsequent early dry season for exploration of seasonal patterns.

We summarise fire regimes by plot in annual sequences within intervals between DBH measures and over the whole of the sample period, as annualised frequency of each of four categories (no fire, mild fire, moderate fire, severe fire) as well as total years with fire (of any intensity) within the interval for each plot. Additional metrics relating to timing of fires were also derived as appropriate. For low-rainfall plots that comprised up to three transects, we applied the maximum severity observed in any transect in a given year to the plot for that year.

Stem diameter increment and status

The diameter of the main stem of all tagged living trees ≥5 cm DBH was measured with a forestry tape. A number of stems slightly under this size were included in analysis where they were observed to attain the ≥5 cm DBH threshold in preceding or subsequent measurements. Numbers and sizes of secondary stems apparently associated with each tagged stem were also recorded to permit estimates of plot basal area. However, growth increments or decrements and mortalities are reported here only for tagged (primary) stems. New primary stems were added to the monitored population as they reached the 5-cm threshold and are described as 'recruits'. Monocotyledons (e.g. palms) and other arborescent groups (e.g. cycads) were excluded from all analyses.

All increments from DBH records taken while the tagged stem was described as living were used in summaries, including stems that subsequently died. Size at death was taken as the last DBH measure before the stem was recorded as dead. Presence of dead stems was also noted at plot establishment in relation to their position on the transect and DBH also measured. Details of standing dead stems will be reported elsewhere.

Assignments of stem death were made on absence of foliage, damage to bark or other evidence of loss of structural integrity. At the time of sampling, particularly in the low-rainfall zone when undertaken in the mid- to late dry season, stems were sometimes deciduous and/or damaged by fire, making assignments more ambiguous. In most cases, assignments of stem death subsequently proved reliable. However, in a few cases, stems showed evidence of recovery on subsequent visits, like flushing with leaves above breast height, suggesting that at least parts of the original stem remained functional. Most of these stems were again described as dead later in the study. Nonetheless, we excluded stems with ambiguous status from all analyses.

For plots in the high-rainfall zone, efforts were made to standardise re-measures at 5-year intervals but operational exigencies (national park staff availability, access difficulties, inclement weather) sometimes caused variation in timing. At low-rainfall plots, efforts were made to re-measure annually, but funding did not always permit this schedule to be followed. Although the low-rainfall sampling period was shorter (typically ≤10 years), measures were consequently more frequent, likely strengthening the precision of estimates of growth. Despite this relatively shorter sampling period, the wide geographic spread of low-rainfall plots also means that they were exposed to a wide array of fire regimes.

Grazing

Grazing animals may have direct and indirect effects on growth (Prior et al. 2006) and survival of savanna trees (Werner 2005, Werner et al. 2006). At most plots we have no direct measures of grazing intensity by native or, probably more significantly, managed or feral exotic herbivores. Feral stock are common over most of the savannas and local populations would often include water buffalo, horses, donkey and pigs.

Plot selections avoided sites where grazing impacts on the under-storey were clearly apparent or other indicators of significant grazing pressure (e.g. cattle or buffalo excreta, wallows, or pads) were conspicuous. However, many plots will have been subject to disturbance by grazing animals at levels typical of savannas outside lands actively managed for pastoral production. As such, we consider that information derived from these plots is broadly applicable to northern savannas outside the more intensively-managed pastoral estate under long-standing, and most likely continuing, land, fire and feral animal management regimes.

Statistical analysis of mortality rate

We used R (R Core Team 2018) for all statistical analysis. We used mixed effects models from R packages *lme4* (Bates et al. 2015) and *robustlmm* (Koller 2016) where application of robust methods appeared necessary.

Mortality of individual stems was treated as occurring within the interval between the last DBH measurement when recorded as alive and the first on which it was recorded as dead. The status of stems (dead or alive) was modelled statistically for all intervals over which their status and DBH were recorded as a binomial response with complementary log-log link as described by Bolker (2019), using the *glmer* command in *lme4*. Exposure time (the period in years between consecutive visits was entered to the regression formula as an ‘offset’, which generated predicted values as an annual probability of stem death. To account for repeated measures of individual stems within the same plots, both plot and stem identity were entered as random effects, with stem nested in plot in all candidate models.

There is a well-established unimodel relationship between DBH and mortality, with mortality highest in the smallest (<20 cm DBH) and largest stems (>40 cm DBH) (Williams et al. 1999, Prior et al. 2009). Hence, we included a quadratic function (DBH^2 + DBH) in all models of mortality. Exploratory analysis indicated that the relationship between mortality and DBH was asymmetrical, and hence we fit a ‘broken-stick’ model. We set the break at a DBH of 25 cm, and included an additional term in the model ‘DBH.large’, defined using the logical R function: ifelse(DBH>25, DBH–25, 0).

Fixed effects included in candidate models were those listed in Table 1, with the exception of time since last severe fire because uncertainty about time of stem death within the interval did not permit meaningful estimation. Continuous variables were centred and standardised prior to analysis, by subtracting the mean and then dividing by the standard error, such that the centred and standardised variables have mean of 0 and standard deviation of 1. The set of candidate models included all combinations of these variables, without interactions. We used model selection methods based on (Burnham and Anderson 2002). Because there was only one well-supported model (ΔAICc ≤2) we did not need to consider other techniques for narrowing selection nor use model averaging.

Statistical analysis of recruitment rate

We treated recruitment as the number of stems entering the population with DBH ≥5 cm in each plot over the whole of the observation period. Data exploration indicated over-dispersion apparently associated with episodic recruitment events: we modelled the response using a generalized linear model with negative binomial errors (*glm.nb* command in R package *MASS*). Because there was a single observation for each plot it was not necessary to include plot ID as a random effect. We examined the same suite of candidate predictor variables as used in other parts of the analysis, with the exception of time since last severe fire. Plot area (ha) and length of observation (years) were included as offsets, generating fitted values in units of stems ha^{-1} year^{-1}. We initially examined all combinations of predictor variables, with no interactions, and used AIC for selection of a preferred model. We re-ran that preferred model using R scripts from Aeberhard et al. (2014), as updated by the authors in *glmrob.nb*, version 0.4.

Statistical analysis of stem diameter increment

Changes in stem size were expressed as annualised DBH increments – the increase in stem diameter over the full period of observations divided by the length of that period in years – for all individual primary stems in all plots. In data exploration, we corrected observations where sources of error were obvious or excluded from growth analysis some values so extreme that they were clearly resulted from unresolvable errors or from structural change not reflective of regularly observed change (e.g. death and replacement of a stem). We did this by identifying increments that fell more than 2.58 standard deviations from the mean, resulting in exclusion of 1% of total observations. We did not exclude negative increments, which may arise from temporary change in stems dimensions related to water stress, minor bark loss or other structural change (e.g. Prior et al. 2006), but treated them in the same manner as positive increments.

We examined influences on stem increments in two stages. First, we modelled stem diameter increment as a function of 'stable' plot features including mean annual rainfall, soils and local topography. We did not consider plot floristics nor measures of stem density or basal area as explanatory variables. We did not consider interactions because such variables are inherently linked and interactions accordingly difficult to interpret.

The suite of stable fixed effects comprised:
(1) vegetation classes recognised in Australia's savanna burning carbon accounting methodology (Commonwealth of Australia 2018);
(2) slope, aspect and elevation;
(3) mean annual rainfall; and
(4) soil index (in four simple classes as described previously, reduced to two following data exploration).

We examined full subsets of a global model starting with all of these predictor variables using the R package *MuMIn* (Bartoń 2018). For comparing models, maximum likelihood methods were used. We used as necessary additional optimisers available through R package *optimx* (Nash and Varadhan 2011, Nash 2014) to achieve convergence. Where necessary to facilitate convergence of complex models and interpretation of model coefficients, we scaled and centred all continuous explanatory variables (Schielzeth 2010).

Because variance of residuals was found to be heterogeneous among classes of some categorical variables or vary with the value of continuous variables, we re-ran selected models using robust methods for mixed models (R package *robustlmm*: Koller 2016). Given that our goal was to avoid complex models that would create difficulties in use for prediction, we adopted a conservative approach to inclusion of predictor variables and did not use model averaging. This required that we adopt criteria for identifying a single preferred model despite multiple models being effectively equivalent fits to the data (ΔAICc<2).

We chose to select for further analysis a single best model with predictors appearing in all models with ΔAICc<2 or with importance scores exceeding 0.70 (R package *MuMIn*; Bartoń 2018). Our goal in adding the second criterion was to reduce the risk of entirely excluding from consideration some combinations of variables that may assume greater significance in another modelling environment. We recognise that importance scores say more about the relative importance of different models than the significance of predictor variables, especially in presence of multicollinearity, as arises in many ecological studies (Cade 2015).

A model log-likelihood is not defined for the robust estimates returned by *rlmer* so methods based on information-theory (AIC) could not be used to select the 'robust' model from those pointed to by the preceding AIC-based analysis. We therefore report and focus discussion on the robust model with the same structure as candidates from the *lmer* process ranked by AIC, checking the *rlmer* models against equivalent *lmer*-generated models using the *compare* process in *robustlmm*. We examined co-linearity of predictor variables using the variance inflation factor (VIF) in R package *car* (Fox and Weisberg 2011) and present no models where co-linearity is considered likely to cause problems with variance inflation.

After deriving a model for these more or less temporally invariant features, we considered effects of stem size and density. We introduced additional predictors for stem DBH at the beginning of the growth increment and plot basal area at the same time. Initial DBH was treated as a random effect.

We then added temporally dynamic, ‘disturbance’ variables for annual variations in rainfall and fire regimes (fire and rainfall anomalies) as fixed effect predictors. For rainfall variability the additional term added to the model was annualised rainfall anomaly. Predictors relating to fire exposure were annualised fire frequency during the observation period for each of mild, moderate and severe fires. Variables relating to intervals between fires and between fires and DBH measurements were fire-free period in years immediately preceding the last DBH measurement at each of the severity categories and collectively. We included quadratic transforms of fire frequency to model non-linearity.

In adding fire frequency and rainfall variation, we again examined all combinations of these subsets, but also specified that all variables from the ‘stable’ model should be retained in all members of the candidate set. Plots very rarely experienced fire more than once per year, so variables summarising frequencies are potentially inter-correlated; fire of any severity excludes fire of any other severity in the same plot in the same year. However, because overall frequency was 0.42 fires year^{-1}, and more severe fires were comparatively rare, inter-correlations of frequencies of fire of different severities did not appear to be associated with unacceptable risks of variance inflation.

Analyses of stem diameter increment based on aggregate change over the whole period of observations are not designed to provide information on temporal patterns of change in growth rate after fire. However, given that gross effects of a severe fire are conspicuous and these fires occur at relatively low frequency, there is much variation in years elapsed between last putative exposure and last measurement of DBH. Hence, we used time since last severe fire as an index of recovery time, and added this to the model including stable plot features and disturbance predictors. For re-running models using robust methods, we included only those disturbance variables satisfying the same criteria as above. We found in data exploration that seasonality of fire was too strongly associated with fire severity to permit inclusion in the same model as individual fire severity measures, so it was not considered further.

In all models we treated plot ID as a random effect. We initially sought to examine both random effect intercepts and slopes for interaction with each continuous predictor variable, but this most often resulted in models being identified as ‘singular’. Where models with random slopes did converge, command *rePCA* in package *lme4* indicated over-fitting. We therefore report only random-effect intercepts for plot ID.

We found no evidence of spatial autocorrelation of the response variable across plots (with low-rainfall transects pooled as single plots) and so made no related adjustments.

Demographic modelling

We developed a simple, individual-based demographic model, implemented in R, to explicitly simulate the processes of tree recruitment (into ≥5 cm DBH size classes), growth (stem diameter increment) and mortality, and make predictions of tree basal area and total biomass over time. The model simulates a 1-ha stand of savanna trees, initialising with a standardised DBH size class distribution, based on the mean size class distribution of the tree monitoring plots. The model runs on an annual time-step. It requires, as input variables, all the environmental variables used in the statistical modelling (i.e. listed in Table 1), such that estimates of growth, mortality and recruitment can be generated.

Each individual tree in the 1-ha stand grows (in terms of annual diameter increment) according to the statistical model of diameter increment. Each year, trees die according to a probability predicted by the statistical model of mortality. New saplings (≥5 cm DBH) are recruited each year according to the statistical model of recruitment. The statistical models require recent fire histories to be known. Hence, an annual fire history is simulated using input values of the annual frequency of mild, moderate and severe fires. The model assumes only one fire can occur each year.

Aboveground biomass of each tree is calculated from its DBH and mean annual rainfall (as this affects tree architecture), following Cook et al. (2015). Root biomass of each tree is calculated from aboveground biomass, according to the equation provided by (Eamus et al. 2002: Fig. 3a). Total tree biomass is calculated by summing aboveground and root biomass across all individuals in the stand.

Although we found no significant influence of initial basal area on recruitment or stem increment, there is much evidence that savanna tree basal area has an upper bound dictated by water availability (Cook et al. 2002, Lehmann et al. 2014). Hence, we used the large Australian savanna tree basal area dataset of Lehmann et al. (2014) to estimate the basal area carrying capacity in a given climate zone. Following Lehmann et al. (2014), we used non-parametric piecewise quantile regression (command *rqss* in R package *quantreg*, with lambda set at 1, and the constraints 'concave, increasing' specified) to estimate the upper bound (99th percentile) of tree basal area as a function of 'effective rainfall' (mean annual rainfall minus mean annual point potential evapotranspiration; Bureau of Meteorology 2019) (Fig. S3). In the demographic model, when basal area exceeds carrying capacity (i.e. the 99th percentile of basal area), recruitment and growth cease, until basal area is once again below carrying capacity due to mortality.

The demographic model was run with a 500-year 'spin up'. An additional 1,000 years was sufficient for basal area and biomass to reach a steady state under a constant set of environmental conditions.

We used the demographic model to investigate the long-term effects of savanna fire management. In northern Australia, fire management typically involves the use of low-severity prescribed burning in the early dry season (April–July, inclusive) to prevent high-severity wildfires in the late dry season (August–November, inclusive) (Fig. S2). Russell-Smith et al. (2013) showed that fire management in a 28,000 km^2 area of western Arnhem Land since 2005 (as part of a large greenhouse gas abatement project) led to a 66% reduction in the frequency of late dry season fires, and a 20% reduction in overall fire frequency. We are able to estimate the associated reduction in the frequency of mild, moderate and severe fires using data on fire severity and seasonality from the results of Russell-Smith and Edwards (2006). They showed that in the early dry season, 76% of fires (by area) are mild, 19% are moderate and 5% are severe. In the late dry season, 21% of fires are mild, 47% are moderate and 32% are severe. Hence, management in western Arnhem Land has most likely reduced moderate and severe fire frequencies by 44% and 53%, respectively.

We used this management-induced shift in fire regimes in western Arnhem Land to generate plausible fire management scenarios for the demographic model. To do so, we took the observed frequencies of mild, moderate and severe fire frequencies from the tree monitoring plots, and adjusted them according to the figures above, i.e. 44% and 53% reduction in moderate and severe fire frequencies, respectively, plus 20% reduction in overall fire frequency.

We used the demographic model to make predictions for the three most widespread vegetation classes in the vegetation mapping of Commonwealth of Australia (2018): *Open forest (mixed grasses)*; *Woodland (mixed grasses)*; *Open woodland (mixed grasses)*. We used the mean fire frequencies for these vegetation classes from the tree monitoring dataset. We compared a baseline scenario (i.e. ambient fire regimes) and a management scenario (reduced fire frequencies, especially of higher-severity fires).

RESULTS

Mortality

Tree mortality rate displayed a clear unimodal relationship with stem diameter, with mortality greatest in the smallest and largest stems (Fig. 3a). Mortality increased with increasing fire frequency, and this effect became more pronounced as severity increased (i.e. mild < moderate < severe) (Fig. 3b). All three fire frequency variables were included in all well-supported models of stem diameter increment (ΔAIC ≤2) (Table 2a).

In addition to fire regime variables, a number of environmental variables were clear correlates of mortality rate: mean annual rainfall (positively related); vegetation class; topography; and soil (Table 2a, Fig. S4). These variables were included in all well-supported models of mortality (ΔAIC ≤2).

Recruitment

Only one fire variable was related to recruitment rate, severe fire frequency, with this variable included in all well-supported models (ΔAIC ≤2) (Table 2b). The models suggested that recruitment was reduced as the frequency of severe fires increased (Fig. 4). Recruitment was also clearly influenced by mean annual rainfall (positively related) and vegetation class (Fig. S5; Table S4c–d).

Growth

Stem diameter increment was clearly affected by the frequency of mild, moderate and severe fires. All three of these variables were included in all well-supported models of stem diameter increment (ΔAIC ≤2) (Table 2c). There was evidence of a slight unimodal relationship between fire frequency and diameter increment, with diameter increment tending to peak when the frequency of moderate and severe fires was around 0.25 fires year−1 (Fig. 5b–c). The apparent peak may be an artefact of the quadratic model. At fire frequencies greater than this, diameter increment declined markedly, with the effect most pronounced as severity increased (i.e. mild < moderate < severe) (Fig. 5a–c).

There was also strong evidence of a longer-term reduction in diameter increment following severe fires. Time since severe fire was a highly significant term when added to the best model. Predicted diameter increment increased linearly by a relatively modest 0.023 mm year−1 for each year after the last severe fire in the plot (Fig. 5d), with no indication of a plateau after 25 years. In contrast, adding time since last mild or moderate fire did not improve the best model.

In addition to fire regime variables, there were a number of environmental variables that were clear correlates of diameter increment: mean annual rainfall and rainfall anomaly (both positively related to diameter increment); vegetation class; topography; and soil (Fig. S6a). These variables were included in all well-supported models of diameter increment (ΔAIC ≤2; Table 2c).

In none of the preferred statistical models for stem diameter increment or recruitment was basal area at the beginning of the interval over which responses were measured a substantial influence. Nor was stem size at the start of the response measurement period influential.

Demographic modelling

Our demographic model, integrating the relationships we have identified between fire regime variables and tree demographic rates, suggests that frequent moderate to severe fires lead to large reductions in tree abundance over time (Fig. 6). Annual severe fires reduce tree basal area and total biomass to near-zero (≥99% reduction relative to unburnt) at long-term equilibrium, in all three vegetation classes modelled: Open forest (mixed grasses), Woodland (mixed grasses) and Open woodland (mixed grasses). Annual moderate fires reduce tree basal area and total biomass by ≥41% (relative to unburnt) in Open forest (mixed grasses), ≥61% in Woodland (mixed grasses) and ≥75% in Open woodland (mixed grasses). However, annual mild fires have a much more modest effect: reducing tree basal area and total biomass by 2–47% (relative to unburnt).

Although frequent severe and moderate fires have a large negative effect on tree abundance, the relatively low frequencies of moderate and severe fires experienced by our monitoring plots have a relatively modest effect overall. For example, Woodland (mixed grasses) was the most frequently burnt vegetation class, with mild, moderate and severe fires experienced at a rate of 0.38, 0.16 and 0.04 fires year−1, respectively. The demographic model predicted that this would lead to a 19% reduction in both basal area and total biomass (relative to unburnt) (Fig. 6b).

The effect of ambient fire regimes on tree abundance was greatest, in relative terms, in the least productive vegetation classes (i.e. Open woodland > Woodland > Open forest). At the most productive open forest/mixed sites, tree abundance was not suppressed by the ambient fire regime, relative to unburnt (Fig. 6a). In this vegetation class, under this fire regime, tree basal area is expected to be at the water-limited upper bound (Fig. S3) (sensu Sankaran et al. 2005, Lehmann et al. 2014). In marked contrast, the demographic rates estimated from our monitoring data, suggest that Woodland (mixed grasses) and Open woodland (mixed grasses) could be expected to have tree basal area well below the water-limited upper bound under ambient fire regimes (Fig. 6b–c).

All three of the demographic processes in the model (mortality, recruitment, growth) made a substantial contribution to the negative effect of ambient fire regimes on tree basal area and total biomass (Fig. 7). The effect of a fire-driven reduction in recruitment was slightly larger than the effect of fire-driven mortality. The effect of a fire-driven reduction in growth was smallest of the three demographic effects, though still a substantial contributor to the overall impact of fire.

Our demographic model predicts that a realistic improvement in fire management (i.e. a 20% reduction in overall fire frequency, plus 44% and 53% reductions in the frequency of moderate and severe fires, respectively) would result in a substantial increase in tree abundance over time, in at least some vegetation classes (Fig. 8). In Woodland (mixed grasses), total tree biomass (including belowground biomass) is predicted to increase most, by 21.7 t DM ha–1 (18%) once a long-term equilibrium has been reached (Fig. 8b). However, our model predicts that such an equilibrium would take a very long time to reach: somewhere in the order of 200 years. Even so, a rapid increase in total tree biomass (12.9 t DM ha–1) in the first century following a shift in fire regimes due to improved fire management, would see Woodland (mixed grasses) sequester about 6.3 t C ha–1.

In both the most productive and least productive vegetation classes (Open forest [mixed grasses] and Open woodland [mixed grasses], respectively), increases in tree abundance, in absolute terms, due to improved fire management are likely to be much less than in woodland/mixed. In open forest/mixed, total tree biomass is predicted to increase by just 1.4 t DM ha–1 (<1%) once a long-term equilibrium has been reached (Fig. 8a). The small magnitude of this increase reflects that under ambient fire regimes, Open forest (mixed grasses) is already close to the water-limited upper bound to tree basal area (Fig. 6a). In Open woodland (mixed grasses), total tree biomass is predicted to increase by 6.8 t DM ha–1 (39%) once a long-term equilibrium has been reached (Fig. 8c).

Discussion

Tropical savanna biomes are characterised by both high primary productivity and high fire frequencies. Frequent fire causes much of the carbon captured by savanna vegetation to be rapidly returned to the atmosphere (Murphy et al. 2019), leading to suggestions that management-driven reductions in fire frequencies and/or intensities across the savannas might significantly increase biomass and carbon storage (Tilman et al. 2000, Grace et al. 2006, Russell-Smith et al. 2015). Our findings, based on analysis of a large, long-term tree monitoring dataset, coupled with a process-explicit demographic model, highlights that while individual high-intensity fires can have significant impacts on demographic rates –significantly reducing tree recruitment, growth and survival – tree biomass in northern Australian savannas appears to be relatively stable under ambient fire regimes. Our demographic model predicts that ambient fire regimes have only a modest long-term suppressive effect on tree basal area and biomass (*ca*. −25%), relative to unburnt savannas. The effects of fire on tree abundance appears to be strongly subordinate to resource availability, especially water (Fig. S3), consistent with earlier analyses (Lehmann et al. 2014, Murphy et al. 2015).

The pattern seen on other continents, of fire exclusion from mesic savannas leading to rapid and very large increases in woody biomass within a few decades (e.g. San Jose et al. 1998, Tilman et al. 2000), is inconsistent with our modelling results, as well as multi-decadal fire experiments in northern Australia (e.g. Russell-Smith et al. 2003a, Woinarski et al. 2004), both of which show only limited increases in tree abundance in response to fire suppression. A possible exception is provided by the recent work by Levick et al. (2019). They describe the results of a fire experiment implemented in a mesic savanna near Darwin, Australia, which had previously been protected from fire for at least 15 years. Experimental fires were then imposed over a period of just 9 years, resulting in significant differences in tree biomass between fire treatments at the end of that period: the greatest difference was between the unburnt treatment and the biennial late dry season fire treatment (fires were typically of moderate severity), with 45% less biomass under the biennial fire treatment. A possible explanation for the very rapid effect observed by Levick et al. (2019) is that fire-sensitive species had colonised the fire-excluded site (e.g. Woinarski et al. 2004), and the re-introduction of fire resulted in the rapid loss of biomass of those species.

The relatively muted response of Australian savanna trees to fire suppression is consistent with a recent meta-analysis of rates of 'woody thickening' in the savannas of Africa, Brazil and Australia by Stevens et al. (2017). Although those authors detected a clear trend of increasing woody biomass in all regions, in Australian savannas the effect was smaller and less variable than in Africa and Brazil. Stevens et al. (2017) were unable to identify the reason for the relative stability of woody biomass in Australian savannas, but identified some potential explanations, mainly related to environmental limitations to biomass accumulation (e.g. northern Australia's low nutrient availability and longer dry season). They also suggested that regional differences in tree architecture could play a role, with Australian savanna trees being notably taller for a given stem diameter (Moncrieff et al. 2014). It is also possible that the relative stability of tree abundance in Australian savannas reflects the dominance of fire-resistant taxa such as the Myrtaceae, including the eucalypts (*Eucalyptus* and *Corymbia* spp.). Eucalypts appear to be uniquely adapted to escaping the fire trap, even under regimes of very frequent fire, especially in situations where canopy competition is limited—whereas, for non-eucalypts recruitment is promoted under a variable canopy, but low-severity fire regime (Fensham and Bowman 1992, Woinarski et al. 2004, Bond et al. 2012, Murphy et al. 2015, Russell-Smith et al. 2019) – such that they are relatively unresponsive to variations in fire regimes characterised by frequent fires. The idea that trees (mostly eucalypts) in Australian savannas are not strongly suppressed by frequent fires is somewhat at odds with a number of authors emphasising the generality of a 'fire-mediated tree-recruitment bottleneck' in northern Australian savannas (Werner 2005, Prior et al. 2010, Werner 2012, Werner and Prior 2013). While our analysis of a long-term tree monitoring dataset shows that severe fires reduce tree recruitment rates (Fig. 4), it is most likely that the recruitment bottleneck is only intense (with significant demographic consequences) at less productive sites, e.g. *Open woodland (mixed grasses)* (Fig. 7).

Despite the apparent relative stability of tree biomass in northern Australian savannas under ambient fire regimes, there is significant scope for using fire management to increase carbon storage in tree biomass, using this carbon storage to generate tradeable carbon credits, and thereby providing a financial incentive for implementing effective and sustainable fire management at landscape scales (e.g. Russell-Smith et al. 2015). Our demographic model predicts that in the *Woodland (mixed grasses)* vegetation class – the most widespread vegetation in the high-rainfall parts of monsoonal northern Australia (Fig. 1b) – carbon storage in live trees (including belowground biomass) is expected to increase by 6.3 t C ha^{-1} in the first century following a plausible shift in fire regimes due to management, e.g. similar to the fire regime shift achieved by land managers in western Arnhem Land over the last 14 years (Evans and Russell-Smith 2019). The increase in carbon storage equates to 0.23 t CO_2-e ha^{-1} $year^{-1}$, currently worth about AU$3.45 ha^{-1} $year^{-1}$ (assuming a carbon price AU$15 / t CO_2-e on the Australian carbon market). To put this monetary value into perspective, the greenhouse gas (methane and nitrous oxide) abatement projects which have proliferated across northern Australian savannas over the last decade, now occupying more than 30 million ha (69% of the total land area) in the high-rainfall (>1,000 mm per annum) savanna zone, typically generate a carbon credit of *ca*. 0.06 t CO_2-e ha^{-1} $year^{-1}$, worth about AU$0.90 ha^{-1} $year^{-1}$ (Russell-Smith et al. 2015). Given that our savanna-wide projections include responses from sites with relatively benign fire regimes, sites chosen specifically because they warrant intervention to reduce frequency of severe fires might produce more carbon credits.

If carbon accounting methodologies can be extended to include carbon sequestration into tree biomass, the viability of savanna fire projects, and associated conservative land management, would increase dramatically, especially on Indigenously-owned lands which typically provide limited economically viable opportunities, including from mainstream cattle pastoralism (Russell-Smith and Sangha 2018). Savanna fire management projects that generate carbon credits have transformed the resourcing of fire management in northern Australian savannas, and brought much-needed economic activity to remote Indigenous communities (Russell-Smith et al. 2015, Lipsett-Moore et al. 2018). Beyond Australia, this business model has potential to bring environmentally sustainable economic activity to impoverished communities in tropical savanna landscapes elsewhere (Lipsett-Moore et al. 2018).

In order to generate plausible carbon credits from sequestration into the savanna tree biomass, a key challenge will be to develop an accounting framework that can adequately distinguish the effects of fire management from the effects of background global environmental change (e.g. climate change, elevated atmospheric CO_2 concentration). This is particularly important for savanna tree biomass, because of evidence that there is a global trend of increasing tree biomass in savannas (Stevens et al. 2017). This trend is possibly driven by elevated [CO_2] (Bond and Midgley 2000, Buitenwerf et al. 2012, but see van der Sleen et al. 2015), although there is still little consensus on the relative importance of local vs. global drivers (e.g. Venter et al. 2018). The existence of a background trend of increasing tree biomass (i.e. not the product of land management) is problematic, because an accounting framework would need to quantify what proportion of any observed increases in carbon storage is directly attributable to fire management, rather than the background trend. A carbon accounting methodology based entirely on the direct measurement of carbon stocks would not be able to distinguish the effects of fire management from the effects of background global environmental change. We consider that a modelling approach, such as dynamic global vegetation modelling (e.g. Scheiter et al. 2015), benchmarked with observations, can support separate accounting of management-driven change from underlying trends.

It is also important to consider the broader ecological consequences of managing savanna fire regimes to increase tree biomass. One of the main concerns amongst some ecologists is the potential for unintended negative consequences ('perverse outcomes') for biodiversity (e.g. Corey et al. 2019). For example, a notable recent study from Brazil has shown that several decades of fire exclusion has led to a dramatic increase in woody biomass in *Cerrado* (Brazilian savanna), and a severe loss in biodiversity, mostly from the ground layer (herbs and shrubs) (Abreu et al. 2017). Likewise, in many other savanna landscapes, increasing woody biomass is viewed as a threat to species requiring open, grassy habitats (e.g. Sirami et al. 2009, Parr et al. 2012). However, the style of fire management being implemented in northern Australia as part of savanna fire/carbon projects is not fire suppression (as occurs in some savanna regions where woody thickening threatens biodiversity), rather the active application of strategically-located prescribed burning to reduce typical fire intensities (by shifting the timing of fires from the late dry season to the early dry season), and to a lesser extent overall fire frequencies (Evans and Russell-Smith 2019). We consider it implausible that the modest increases in tree biomass (<28% in the long-term) predicted by our demographic model would have negative consequences for northern Australian savanna biodiversity. On the contrary, some of the groups of highest conservation concern, such as arboreal mammals, are likely to benefit from increases in the abundance of trees, and especially the retention of large, old trees under relatively mild fire regimes (Woinarski et al. 2011). There is strong evidence that reduced frequency of high-intensity fires benefits many declining plant communities (e.g. sandstone heathlands: Russell-Smith et al. 2002) and taxa (e.g. northern cypress-pine [*Callitris intratropica*] and other non-eucalypts: Lawes et al. 2011b, Trauernicht et al. 2016) within the northern Australian savanna matrix. Such is the apparent complementarity between fire management for carbon and biodiversity that many of the largest and most important properties in Australia's national reserve system are managed, wholly or in part, as fire/carbon projects, e.g. World Heritage-listed Kakadu National Park. Finally, an equally significant, albeit *indirect*, biodiversity benefit of fire management for carbon is that it provides a viable economic option for alleviating more intensive and environmentally destructive land uses in Australia's tropical savannas such as land clearing for marginal economic benefit (Russell-Smith et al. 2018; Northern Territory Government 2019).

In conclusion, our study provides new insights into fire-driven tree biomass dynamics in Australian savannas. Despite fire regimes having clear negative effects on the key demographic rates (recruitment, growth and survival), tree biomass appears to be suppressed by only a small amount by ambient fire regimes. This is in contrast to observations from other savanna regions, where experimental fire exclusion has been shown to cause large and rapid increases in biomass. Despite this relative stability, increases in tree biomass with demonstrably achievable changes in fire management are cumulatively significant at the spatial and temporal scales relevant to fire management projects. There is substantial scope for fire managers to generate carbon credits from increased carbon storage in tree biomass. If appropriate carbon accounting methodologies can be developed, sequestration by tree biomass has the potential to significantly extend the economic viability of burgeoning fire/carbon projects in Australian savannas. Such industries have the potential to: (1) bring much-needed environmentally sustainable economic activity to impoverished human communities in tropical savanna landscapes; and (2) create ecological benefits from improved capacity of land managers to address carbon management obligations in tandem with other conservation goals.

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TABLE 1. Plot-level predictor variables used in models of demographic rates: mortality, recruitment and/or growth.

Variable	Details	Source
(a) 'Stable' environmental variables		
Mean annual rainfall	Mean annual rainfall (mm) (rain-year: July–June). Average over the period 1970 to 2018 from monthly rainfall grids (0.05° × 0.05°).	Jones et al. (2009), Australian Bureau of Meteorology (2018)
Vegetation class	Six classes: *Open forest with mixed grasses*; *Woodland with mixed grasses*; *Woodland with hummock grasses*; *Woodland with tussock grasses*; *Open woodland with mixed grasses*; *Shrubland (heath) with hummock grasses*.	Field observations: this study
Topography class	Six broad topographic units: plains or gently undulating; broad plateaus; dissected plateaus; stony hills; dissected lowlands; and floodplains and margins. For analysis a dissected lowland site with one member was grouped with plains/gently undulating.	National Resource Information Centre (1991)
Slope	Slope in degrees	90-m digital elevation model: NASA (2015)
Aspect	Aspect (orientation of slope) in four categories (north, east, south, west)	90-m digital elevation model: NASA (2015)
Elevation	Elevation (m) above mean sea level	90-m digital elevation model: NASA (2015)
Soil class	Four categories: deep, shallow or skeletal sands, and clay	Field observations: this study
Basal area	Live tree basal area (m^2 ha^{-1}) at beginning of plot observations	Field observations: this study

TABLE 1. Continued.

Variable	Details	Source
(b) 'Disturbance' variables		
Rainfall anomaly	Annualised difference between long term average rainfalls for the period between DBH measurements and actual falls (adjusted for beginning and end dates by estimated daily rainfalls), divided by the number of years between DBH measurements.	Australian Bureau of Meteorology (2018)
Frequencies of mild, moderate and severe fires	Number of mild, moderate and severe fires in the interval, divided by period in years in the measurement interval.	Field observations and satellite data: this study
Time since severe fire	Number of years since severe fire at the plot.	Field observations and satellite data: this study

TABLE 2. Model ranking table for the three response variables: (a) tree mortality rate; and (b) recruitment rate; and (c) stem diameter increment. Each line represents a model, with asterisk indicating the variables included in each model. Models were ranked according to AIC. ΔAIC represents the difference between a model's AIC value and the minimum AIC value in the set of candidate models. w_i is the Akaike weight, equivalent to the probability of that model being the best in the candidate set. Only well-supported models (ΔAIC ≤2) are shown. The shading indicates variables for which there is clear evidence of a relationship (i.e. the variable appears in all well-supported models).

Fire frequency			Mean annual rainfall	Rainfall anomaly	Vegetation class	Topography class	Soil class	ΔAIC	w_i
Mild fires	Moderate fires	Severe fires							
(a) Mortality rate									
*	*	*	*		*	*		0.00	0.35
*	*	*	*		*	*	*	0.35	0.29
*	*	*	*	*	*	*		1.22	0.19
*	*	*	*	*	*	*	*	1.54	0.16
(b) Recruitment rate									
*		*	*	*	*			0.0	0.30
		*	*	*	*			0.5	0.23
*	*	*	*	*	*			1.8	0.12
(c) Stem diameter increment									
*	*	*	*	*	*	*	*	0.0	0.96

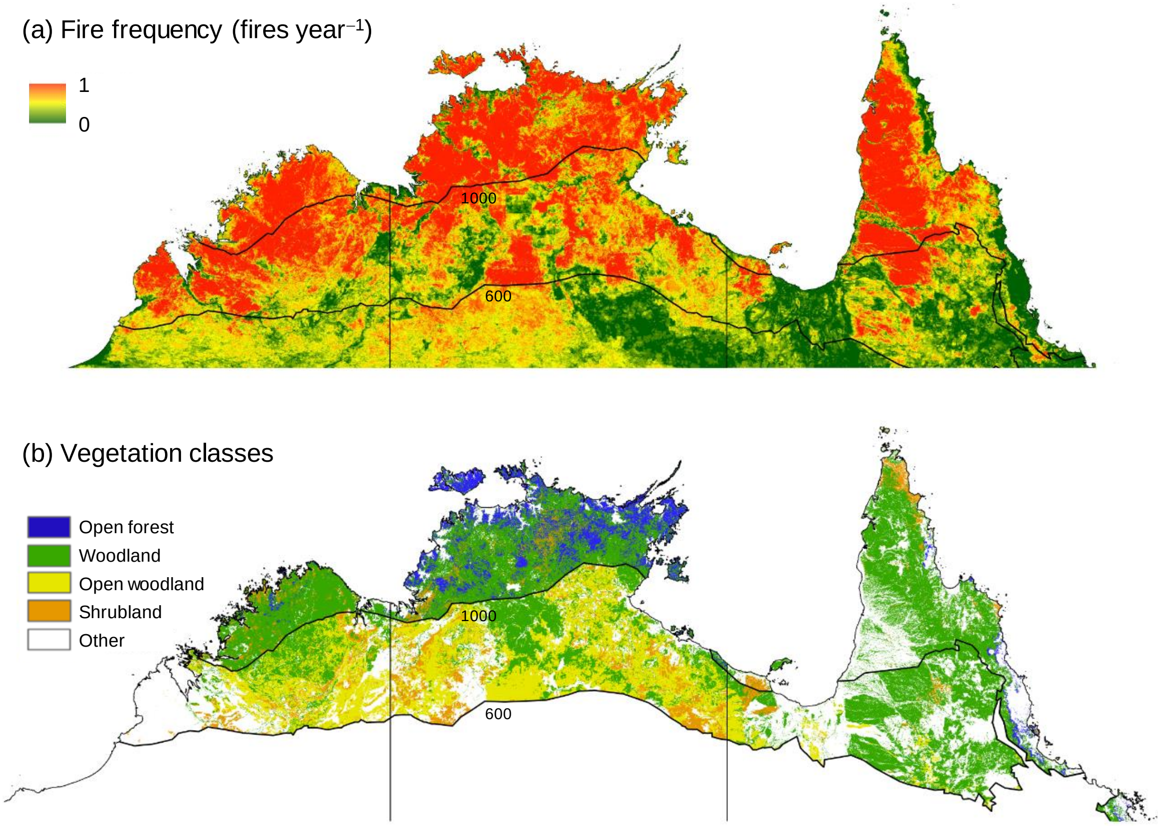


FIG. 1. (a) Fire frequency (fires year^{-1}) in northern Australia for the period 2000–2018, inclusive, from the MODIS satellite record (www.firenorth.org.au). (b) Major vegetation classes in the high- and low-rainfall zones (600–1,000 mm and ≥1,000 mm annual rainfall), used in Australian savanna carbon accounting methodologies (Commonwealth of Australia 2018). In (b) 'Other' indicates areas of non-savanna vegetation, not eligible as savanna carbon projects, such as grasslands and closed forests.

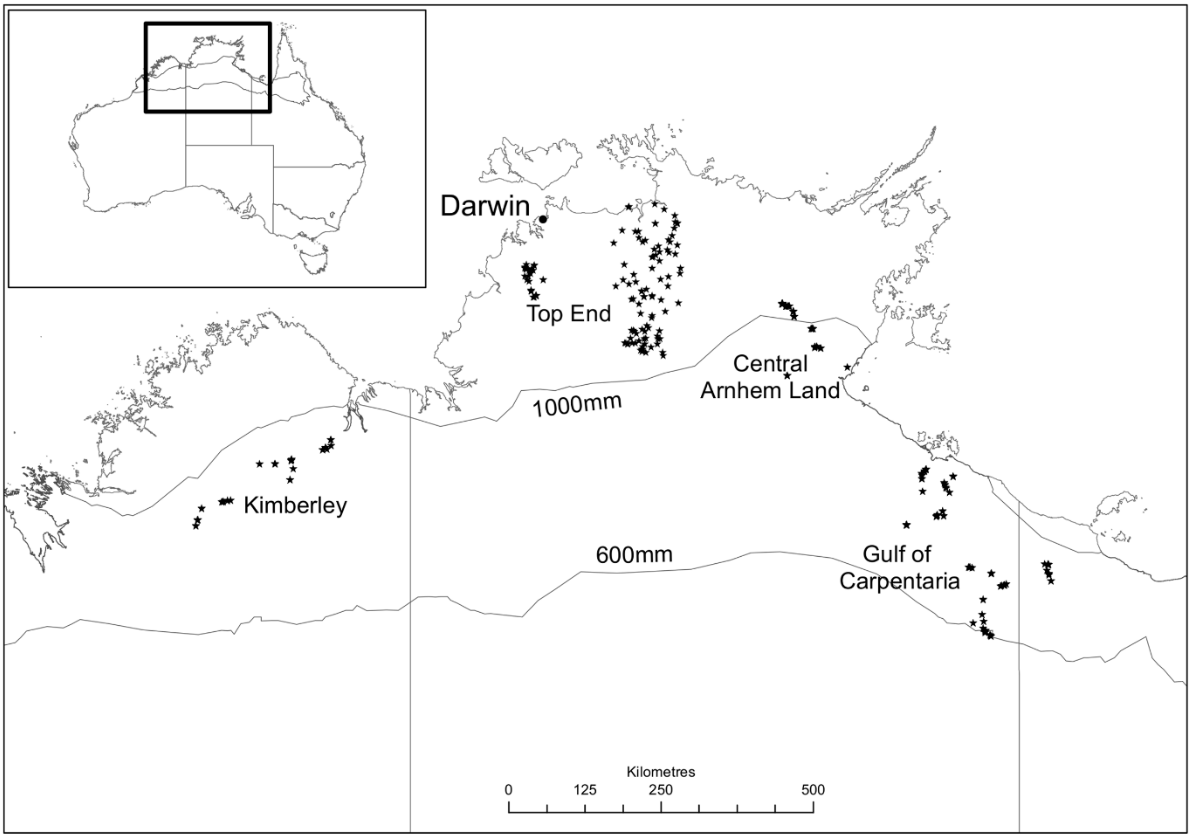
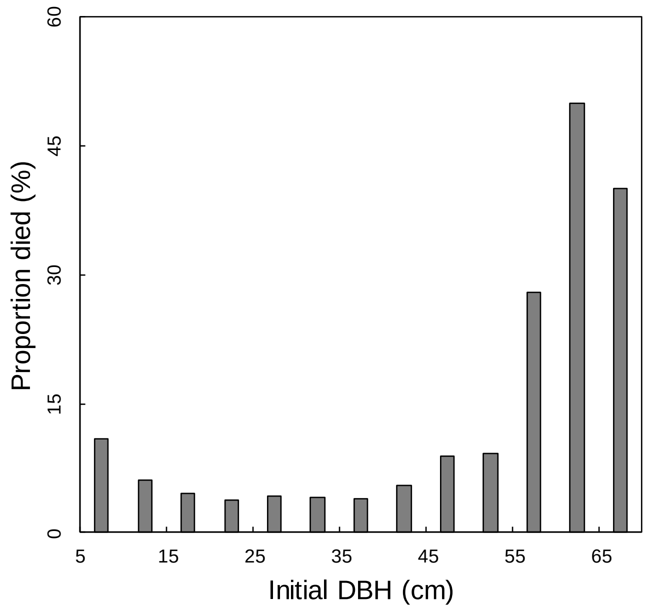


FIG. 2. Location of study plots in the savannas region in relation to 1,000 and 600 mm mean annual rainfall isohyets, corresponding to the high- and low-rainfall zones.

(a)



(b)

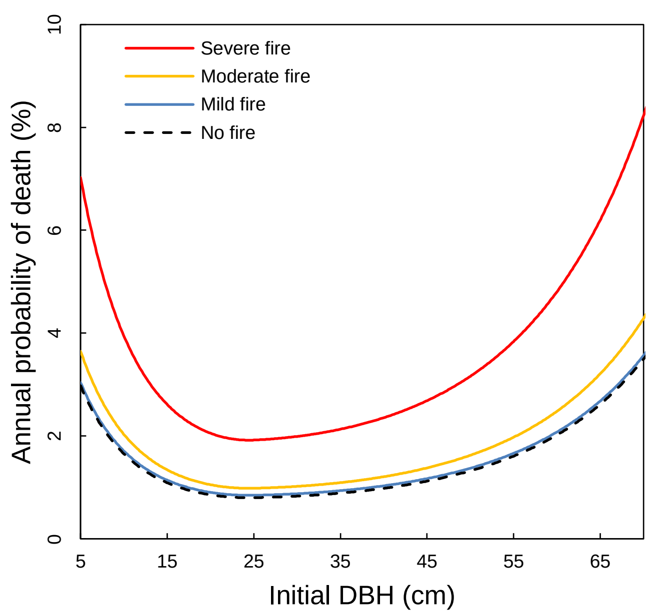


FIG. 3. Relationship between tree mortality rate and stem diameter at breast height (DBH). The raw data are shown in (a) and the modelled relationship in (b). In (b), the modelled effect of a single mild, moderate or severe fire on the probability of death are shown.

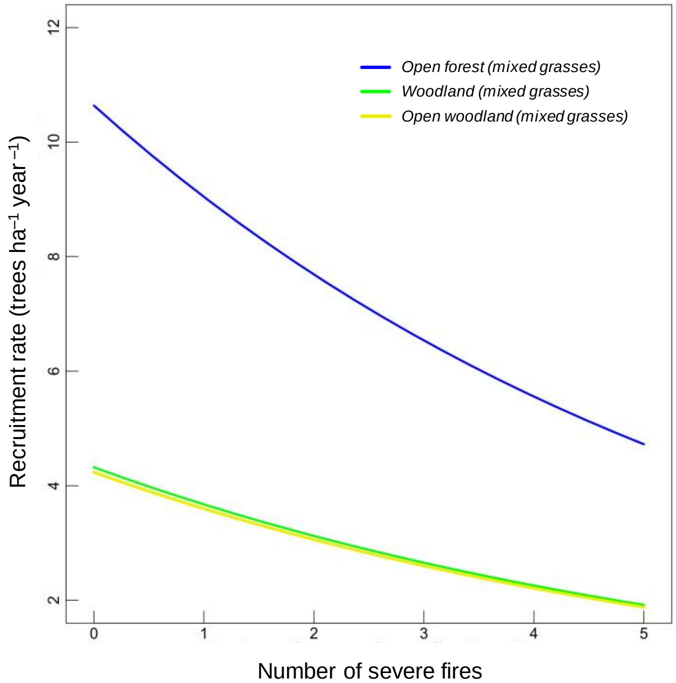


FIG. 4. Modelled relationship between tree recruitment rate and the number of severe fires experienced at the plot during the monitoring period. Separate predictions are shown for the three vegetation classes used in the demographic modelling: *Open forest (mixed grasses)*, *Woodland (mixed grasses)* and *Open woodland (mixed grasses)*. The mean monitoring period was 14.8 years (range: 3.2–23.7 years).

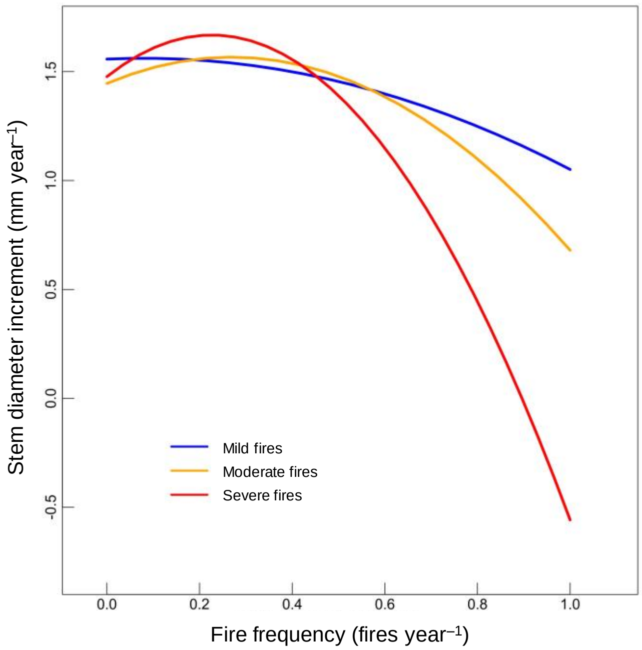
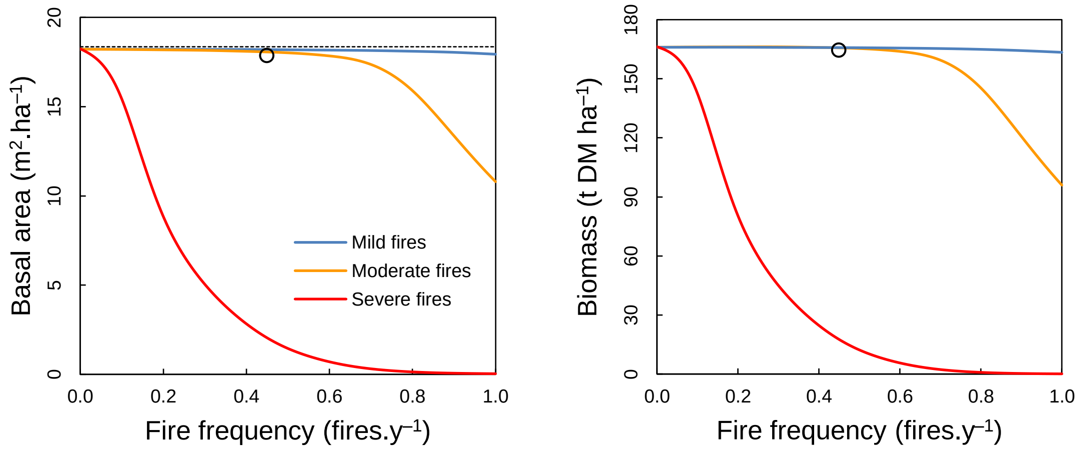
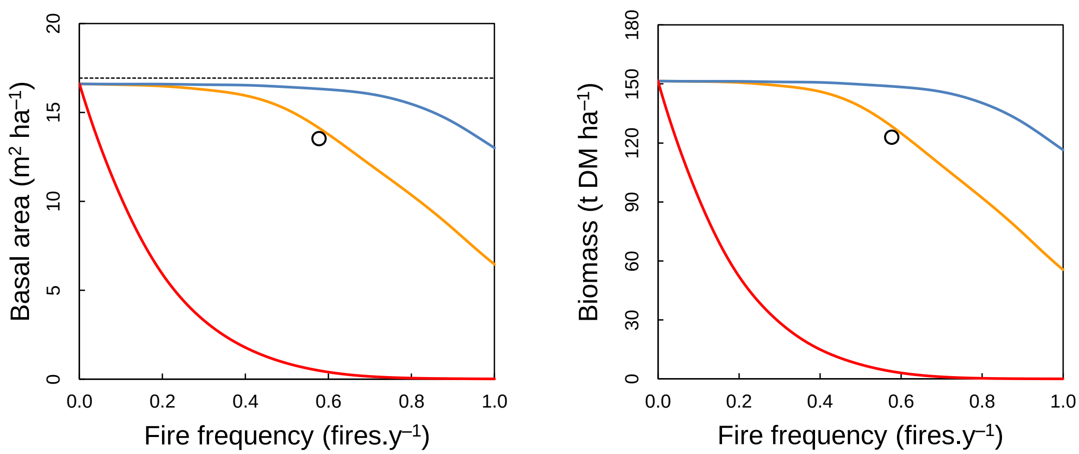


FIG. 5. Modelled relationship between annual stem diameter increment and the frequency of mild, moderate and severe fires.

(a) *Open forest (mixed grasses)*



(b) *Woodland (mixed grasses)*



(c) *Open woodland (mixed grasses)*

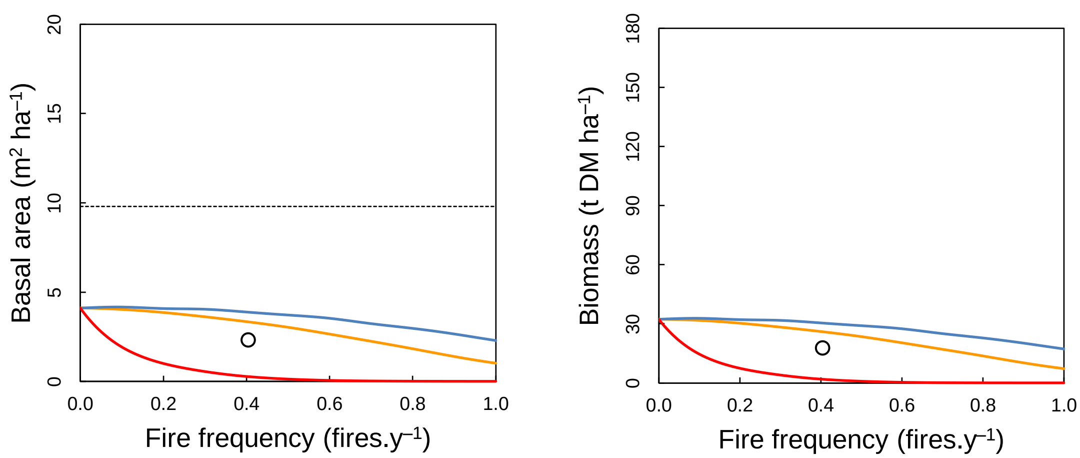
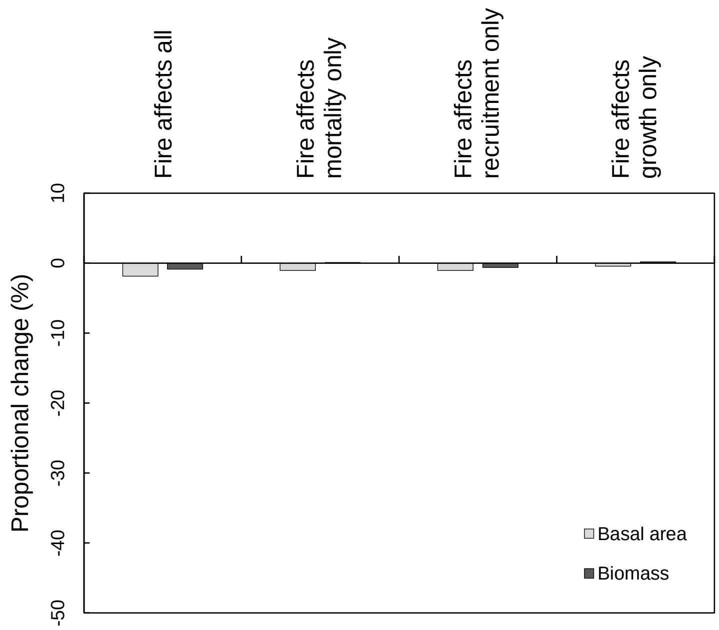
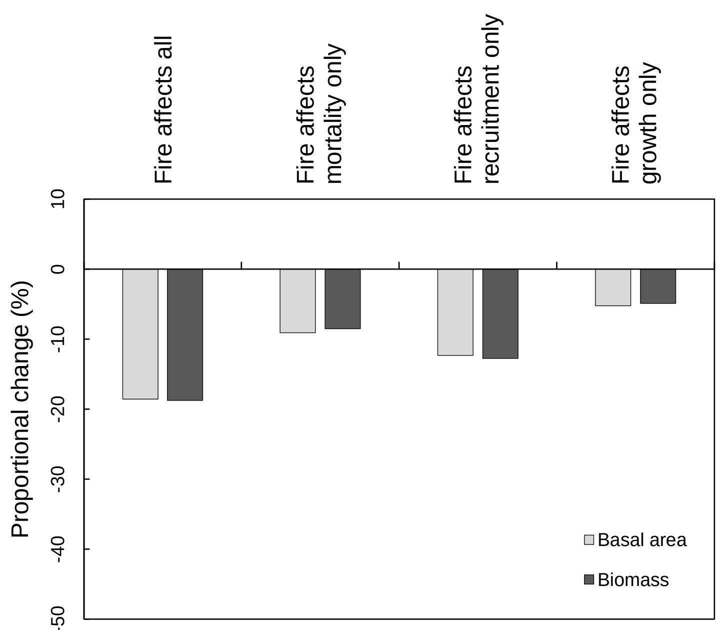


FIG. 6. Predicted tree abundance at long-term equilibrium, expressed as basal area (left) and biomass (right), under varying frequencies of mild, moderate and severe fires. For each line, all fires are assumed to be of a single severity class (i.e. low, moderate or high). Predictions for different vegetation classes are shown separately: (a) *Open forest (mixed grasses)*; (b) *Woodland (mixed grasses)*; and (c) *Open woodland (mixed grasses)*. The horizontal dashed lines on the basal area graphs indicate the climatically-determined upper bound to basal area. The circles indicate the mean fire frequency experienced at the monitoring plots over the study period (comprising a mix of mild, moderate and severe fires) and the predicted tree abundance at long-term equilibrium under that fire regime. These projections represent the median of 10,000 replicate simulations.

(a) *Open forest (mixed grasses)*



(b) *Woodland (mixed grasses)*



(c) *Open woodland (mixed grasses)*

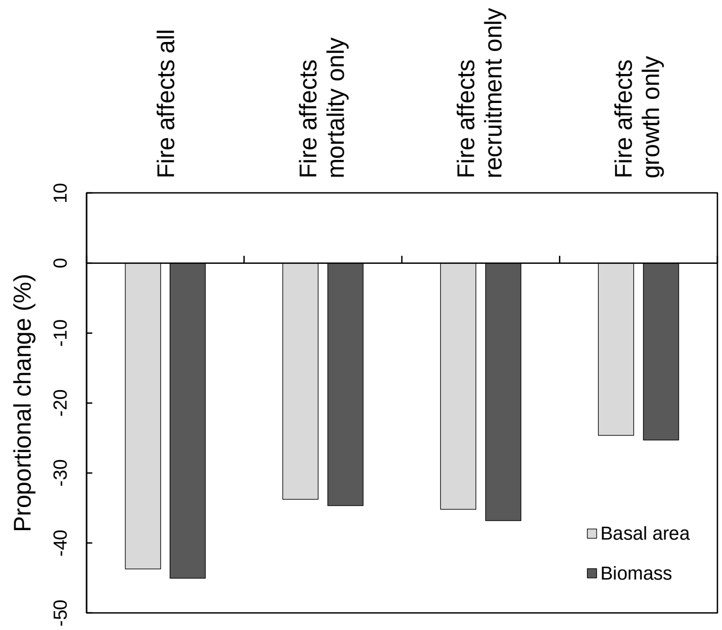


FIG. 7. Predicted proportional change in tree basal area and biomass, from unburnt to the ambient fire regime. The model was run in four configurations: (i) with fire affecting mortality, recruitment and growth; (ii) fire affecting mortality only; (iii) fire affecting recruitment only; and (iv) fire affecting growth only. Predictions for different vegetation communities are shown separately: (a) *Open forest (mixed grasses)*; (b) *Woodland (mixed grasses)*; and (c) *Open woodland (mixed grasses)*.

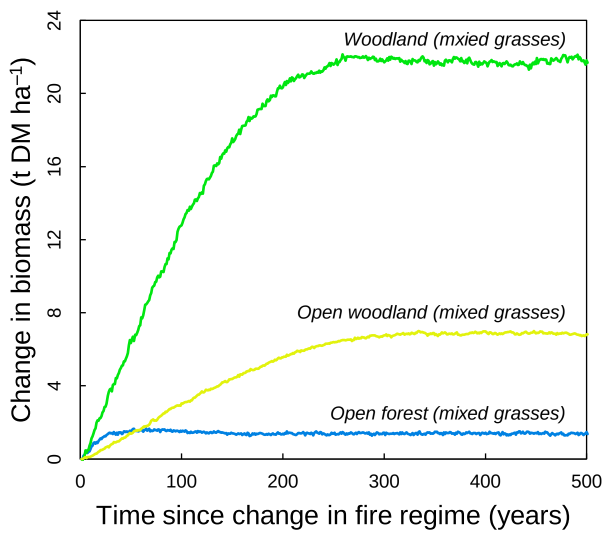


FIG. 8. Predicted change in biomass due to a management-driven moderation of fire regimes, namely a 20% reduction in overall fire frequency, plus 44% and 53% reductions in the frequency of moderate and severe fires, respectively. These projections represent the median of 10,000 replicate simulations.

TABLE S1. Rainfall at sampled plots summarised by vegetation classes recognised under methods for recognising emissions abatement from interventions in savanna fire regimes (Commonwealth of Australia 2018). Groups of up to three transects at low-rainfall (<600 mm per annum) sites have been treated as one plot.

Vegetation class	Count	Annual rainfall (mm)			Rainfall of the driest quarter (mm)		
		Mean	SD	Range	Mean	SD	Range
Open forest (mixed grasses)	14	1476	84	1254–1537	5.4	0.2	5.2–6.0
Woodland (mixed grasses)	112	1323	237	659–1689	5.3	0.6	4.2–7.9
Shrubland (heath) (hummock grasses)	7	1269	367	624–1683	5.6	1.5	5.0–9.1
Woodland (hummock grasses)	23	1254	244	815–1683	5.5	0.7	4.3–7.4
Woodland (tussock grasses)	14	908	39	831–949	6.6	1.8	4.9–10.0
Open woodland (mixed grasses)	66	834	102	599–967	6.8	1.7	4.9–12.6

TABLE S2. Distribution of marked stems (and plots) among landscape types and vegetation classes. Coding of landscape types is from National Resource Information Centre (1991).

Landscape setting	Landscape type	Vegetation class					
		Open forest (mixed grasses)	*Open woodland (mixed grasses)*	*Shrubland (heath) (hummock grasses)*	*Woodland (hummock grasses)*	*Woodland (mixed grasses)*	*Woodland (tussock grasses)*
Sand plains	AB	79 (3)	34 (2)	0	0	182 (9)	0
	AC	0	443 (5)	0	192 (3)	293 (5)	0
Broad or dissected sandstone plateau	BA	87 (3)	599 (15)	92 (6)	177 (9)	524 (20)	0
	BY	0	46 (1)	0	50 (1)	0	0
Undulating sandy plains with laterite	Cd	0	121 (2)	0	0	67 (1)	359 (6)
Hills on basalt with shallow loams	Fz	0	48 (2)	0	0	0	124 (3)
Hills and sandstone ridges and plateau	JJ	0	454 (9)	0	0	625 (11)	73 (1)
	JK	0	369 (10)	0	52 (1)	0	0
Plateau to gently undulating plains with laterised soils	JV	0	205 (4)	5 (1)	0	87 (4)	0
Coastal plans with dunes	Jw	0	36 (1)	0	0	0	0
Rolling lowlands with ironstone gravels and yellow earths	JY	96 (3)	0	0	0	369 (14)	0
Steep hills with shallow stony and gravelly loams	LK	0	0	0	127 (5)	778 (28)	0
Undulating plains on basalt (Mo) or laterite	Mo	0	59 (1)	0	0	0	137 (3)

TABLE S2. Continued.

Landscape setting	Landscape type	Vegetation class					
		Open forest (mixed grasses)	*Open woodland (mixed grasses)*	*Shrubland (heath) (hummock grasses)*	*Woodland (hummock grasses)*	*Woodland (mixed grasses)*	*Woodland (tussock grasses)*
	MP	0	86 (3)	0	0	0	0
Undulating plains with yellow earths, grey clays in depressions	Mt	0	55 (1)	0	0	59 (2)	59 (1)
Undulating plains with sandy and loamy red earths	Mw	164 (5)	0	0	0	75 (3)	0
Undulating plains on basalt with sandstone exposures	My	0	40 (1)	0	0	0	0
Fringes of coastal or inland floodplains	NN	0	0	0	0	56 (1)	0
	CC	0	0	0	129 (2)	259 (4)	0
	Mb	0	205 (4)	0	0	37 (1)	58 (1)
Low outcropping hills, loamy red earths	Qd	0	87 (4)	0	0	0	0
Undulating to hilly with rock outcrops, shallow stony soils	Tb	0	0	0	0	54 (1)	0
Undulating on shales and sandstone, hard yellow soils or shallow sands on basal slopes	Ui	0	216 (4)	0	0	0	0

TABLE S2. Continued.

Landscape setting	Landscape type	Vegetation class					
		Open forest (mixed grasses)	*Open woodland (mixed grasses)*	*Shrubland (heath) (hummock grasses)*	*Woodland (hummock grasses)*	*Woodland (mixed grasses)*	*Woodland (tussock grasses)*
Flat plains with streams and floodplain areas, yellow earths	Va	0	0	0	13 (1)	94 (3)	0
Undulating to hilly on granite, sandy yellow mottled earths	Wd	0	0	0	31 (1)	144 (6)	0

TABLE S3a. Top 20 statistical models of tree mortality rate. Candidate models represent all combinations of the predictors, and are ranked by ΔAIC_c. All models also included stem DBH. MILD, MOD and SEV were always included together in the same model (i.e. they represented a composite variable).

	Predictors										
	MAR[2]	VEG[3]	SOIL[4]	TOP[5]	RAn[6]	MILD[7]	MOD[8]	SEV[9]	DF[10]	ΔAIC_c[11]	w_i[12]
$w+$[1]:	1.00	1.00	0.46	1.00	0.35	1.00	1.00	1.00			
	+	+		+		+	+	+	19	0.00	0.35
	+	+	+	+		+	+	+	20	0.35	0.29
	+	+		+	+	+	+	+	20	1.22	0.19
	+	+	+	+	+	+	+	+	21	1.54	0.16
	+		+	+		+	+	+	15	17.63	0.00
	+	+				+	+	+	15	17.67	0.00
	+	+	+			+	+	+	16	17.82	0.00
	+			+		+	+	+	14	18.31	0.00
	+	+			+	+	+	+	16	18.99	0.00
	+	+	+		+	+	+	+	17	19.10	0.00
	+		+	+	+	+	+	+	16	19.29	0.00
	+			+	+	+	+	+	15	20.02	0.00
			+	+		+	+	+	14	22.66	0.00
				+		+	+	+	13	22.75	0.00
			+	+	+	+	+	+	15	24.44	0.00
				+	+	+	+	+	14	24.56	0.00
		+		+		+	+	+	18	24.68	0.00
		+	+	+		+	+	+	19	24.76	0.00
		+		+	+	+	+	+	19	26.42	0.00
		+	+	+	+	+	+	+	20	26.49	0.00

1 The importance value, equivalent to the probability of that variable being in the 'best' model in the candidate set. Shading indicates those variables with a high level of support ($w+ \geq 0.72$).

2 Mean annual rainfall (mm).

3 Vegetation class.

4 Soil class, reduced to two levels: shallow/skeletal sands; and clays or deep sands.

5 Topography class.

6 Rainfall anomaly (deviation from mean rainfall) over the 3 years preceding the end of the observation period (mm).

7 The annual frequency of mild fires (fires $year^{-1}$).

8 The annual frequency of moderate fires (fires $year^{-1}$).

9 The annual frequency of severe fires (fires $year^{-1}$).

10 Degrees of freedom of the model.

[11] The difference between the model's AIC_c value and the minimum AIC_c value in the entire candidate set.

[12] The model's Akaike weight, equivalent to the probability of the model being the 'best' in the candidate set.

TABLE S3b. Model parameters for tree mortality rate, derived using multi-model averaging of the entire candidate set. Aliased categories are 'Open forest (mixed grasses)' in vegetation class, 'Clays and deep sands' in soil class, and 'Floodplain margin' in topography class. DBH.large is used to position of the 'break' in the broken stick model (assumed here as 25 cm DBH). DBH.large is defined using the logical function: ifelse(DBH>25, DBH-25, 0). Centred and standardised predictors are indicates by the suffix '.CS', and are defined as: (predictor – mean(predictor))/sd(predictor) (see TABLE S3c for means and standard deviations of the predictors).

Model term	Estimate	SE
Intercept	-2.756	0.256
DBH	-0.171	0.013
DBH^2	0.004	0.000
$DBH.large^2$	-0.003	0.001
MAR.CS	0.285	0.060
RAn.CS	-0.006	0.007
MILD.CS	0.001	0.026
MOD.CS	0.076	0.023
SEV.CS	0.177	0.019
Vegetation: Open woodland (mixed grasses)	0.496	0.230
Vegetation: Shrubland (heath) (hummock grasses)	0.170	0.336
Vegetation: Woodland (hummock grasses)	0.139	0.226
Vegetation: Woodland (mixed grasses)	-0.146	0.193
Vegetation: Woodland (tussock grasses)	0.523	0.247
Soil: Shallow–skeletal sands	-0.050	0.039
Topography: Plain	0.274	0.155
Topography: Plateau broad	0.857	0.212
Topography: Plateau dissected	0.782	0.229
Topography: Stony hill	0.400	0.153

TABLE S3c. Means and standard deviations of predictors that were centred and standardised for the analysis of tree mortality rate.

Predictor	Mean	SD
MAR	1063	284
Ran	91.1	178.9
MILD	0.36	0.48
MOD	0.21	0.36
SEV	0.06	0.20

TABLE S4a. Top 20 statistical models of tree recruitment rate. Candidate models represent all combinations of the predictors, and are ranked by ΔAIC_c.

	Predictors										
	ASP[2]	BA[3]	VEG[4]	ELV[5]	MAR[6]	SOIL[7]	SLO[8]	TOP[9]	DF[10]	ΔAIC_c[11]	w_i[12]
w+[1]:	0.43	0.26	0.74	0.53	1.00	0.60	0.35	0.10			
			+	+	+	+			10	0.00	0.08
	+		+		+	+			12	0.13	0.08
			+		+	+			9	0.21	0.08
	+		+	+	+	+			13	0.34	0.07
	+		+	+	+				12	0.58	0.06
			+	+	+				9	0.63	0.06
	+		+		+				11	0.68	0.06
				+	+	+			5	0.85	0.05
					+	+			4	0.95	0.05
			+	+	+		+		10	1.09	0.05
			+		+				8	1.23	0.05
	+		+	+	+		+		13	1.40	0.04
	+		+		+		+		12	1.49	0.04
			+	+	+	+	+		11	1.60	0.04
			+		+		+		9	1.69	0.04
			+		+	+	+		10	1.87	0.03
		+	+	+	+	+			11	1.88	0.03
	+		+		+	+	+		13	1.95	0.03
		+	+		+	+			10	2.09	0.03
	+		+	+	+	+	+		14	2.13	0.03

1 The importance value, equivalent to the probability of that variable being in the 'best' model in the candidate set. Shading indicates those variables with a high level of support (*w*+ ≥0.72).

2 Aspect, in four categories: north; south; east; west.

3 Initial plot basal area (m^2 ha^{-1}).

4 Vegetation class.

5 Elevation (m).

6 Mean annual rainfall (mm).

7 Soil class, reduced to two levels: shallow/skeletal sands; and clays or deep sands.

8 Slope in degrees.

9 Topography class.

10 Degrees of freedom of the model

11 The difference between the model's AIC_c value and the minimum AIC_c value in the entire candidate set.

[12] The model's Akaike weight, equivalent to the probability of the model being the 'best' in the candidate set.

TABLE S4b. Top 20 statistical models of tree recruitment rate, with disturbance vectors added to the model based on 'stable' predictors (Table S4a). Candidate models represent all combinations of the disturbance-related predictors (with VEG, and MAR included in all models). Models are ranked by ΔAIC_c.

	Predictors								
	MILD[2]	MOD[3]	SEV[4]	RAn[5]	VEG[6]	MAR[7]	DF[8]	ΔAIC_c[9]	w_i[10]
w+[1]:	0.56	0.29	0.87	0.94	0.99	0.94			
	+		+	+	+	+	11	0.00	0.30
			+	+	+	+	10	0.51	0.23
	+	+	+	+	+	+	12	1.77	0.12
		+	+	+	+	+	11	2.50	0.08
	+			+	+	+	10	3.80	0.04
	+		+		+	+	6	4.41	0.03
			+	+	+		9	4.48	0.03
				+	+	+	9	4.59	0.03
			+		+	+	5	4.77	0.03
	+	+		+	+	+	11	5.11	0.02
	+	+	+		+	+	7	6.08	0.01
		+		+	+	+	10	6.24	0.01
	+		+	+	+		10	6.36	0.01
		+	+	+	+		10	6.59	0.01
		+	+		+	+	6	6.61	0.01
	+				+	+	5	8.30	0.00
	+	+	+	+	+		11	8.49	0.00
					+	+	4	9.27	0.00
	+	+			+	+	6	9.46	0.00
				+	+		8	9.56	0.00

[1] The importance value, equivalent to the probability of that variable being in the 'best' model in the candidate set. Shading indicates those variables with a high level of support (*w*+ ≥0.72).

[2] The raw count of mild fires in the period of observation.

[3] The raw count of moderate fires in the period of observation.

[4] The raw count of severe fires in the period of observation.

[5] Rainfall anomaly (deviation from mean rainfall) over the period of observation (mm).

[6] Vegetation class.

[7] Mean annual rainfall (mm).

[8] Degrees of freedom of the model

[9] The difference between the model's AIC_c value and the minimum AIC_c value in the entire candidate set.

[10] The model's Akaike weight, equivalent to the probability of the model being the 'best' in the candidate set.

TABLE S4c. Comparison of parameters of robust model (*glmrob.nb*) with non-robust (*glm.nb*), for tree recruitment rate. An important difference is the substantial increase in the standard error for the robust model coefficient for annualised rainfall anomaly. Given the intent to retain only variables that are unambiguously influential, this vector was dropped from the model used in demographic simulations (Table S4d below). The only aliased category is 'Open forest (mixed grasses)' in vegetation class.

Model term	*glm.nb*				*glmrob.nb*	
	Estimate	SE	z-value	*p*	Estimate	SE
Intercept	0.890044	0.539478	1.65	0.0990	0.771653	0.564171
Vegetation: Open woodland (mixed grasses)	-0.639057	0.348790	-1.83	0.0669	-0.999181	0.363401
Vegetation: Shrubland (heath) (hummock grasses)	-0.627605	0.450755	-1.39	0.1638	-0.660673	0.466223
Vegetation: Woodland (hummock grasses)	-0.974604	0.330870	-2.95	0.0032	-1.018923	0.341521
Vegetation: Woodland (mixed grasses)	-0.475204	0.268160	-1.77	0.0764	-0.611218	0.276409
Vegetation: Woodland (tussock grasses)	-1.437765	0.436270	-3.30	0.0010	-1.207453	0.455570
Mean annual rainfall (mm)	0.001006	0.000347	2.90	0.0037	0.001328	0.000367
Annualised rainfall anomaly (mm)	0.004021	0.001093	3.68	0.0002	0.001374	0.001174
Raw count of severe fires	-0.197389	0.078545	-2.51	0.0120	-0.161323	0.081564

TABLE S4d. Comparison of parameters of robust (*glmrob.nb*) and non-robust (*glm.nb*) models for tree recruitment rate, after dropping annualised rainfall anomaly. The coefficient for raw count of severe fires was little affected in the reduced model.

Model term	*glm.nb*				*glmrob.nb*	
	Estimate	SE	z-value	*p*	Estimate	SE
Intercept	0.504022	0.551739	0.91	0.3610	0.672076	0.563213
Vegetation: Open woodland (mixed grasses)	-0.322267	0.354345	-0.91	0.3631	-0.921432	0.361773
Vegetation: Shrubland (heath) (hummock grasses)	-0.622707	0.462439	-1.35	0.1781	-0.658089	0.468500
Vegetation: Woodland (hummock grasses)	-0.985963	0.338552	-2.91	0.0036	-1.025889	0.343067
Vegetation: Woodland (mixed grasses)	-0.482872	0.274816	-1.76	0.0789	-0.619732	0.277811
Vegetation: Woodland (tussock grasses)	-0.981253	0.424956	-2.31	0.0209	-1.057140	0.433569
Mean annual rainfall (mm)	0.001558	0.000336	4.63	0.0000	0.001496	0.000344
Raw count of severe fires	-0.192171	0.080081	-2.40	0.0164	-0.162351	0.081882

TABLE S5a. Top 20 statistical models of stem diameter increment (mm year^{-1}). Candidate models represent all combinations of the predictors, and are ranked by ΔAIC_c. Plot ID was included as random effect.

	Predictors										
	DBH[2]	MAR[3]	BA[4]	VEG[5]	ELV[6]	SOIL[7]	SLO[8]	TOP[9]	DF[10]	ΔAIC_c[11]	w_i[12]
w+[1]:	0.36	0.88	0.29	1.00	0.31	0.99	0.29	0.87			
		+		+		+		+	14	0.0	0.20
	+	+		+		+		+	15	1.1	0.11
		+		+	+	+		+	15	1.6	0.09
		+		+		+	+	+	15	1.8	0.08
		+	+	+		+		+	15	1.9	0.08
	+	+		+	+	+		+	16	2.8	0.05
	+	+	+	+		+		+	16	2.9	0.05
	+	+		+		+	+	+	16	2.9	0.05
	+	+		+	+	+	+	+	16	3.4	0.04
		+	+	+	+	+		+	16	3.4	0.04
		+	+	+		+	+	+	16	3.6	0.03
				+		+		+	13	3.8	0.03
		+		+		+			10	4.1	0.03
	+	+	+	+	+	+		+	17	4.4	0.02
	+	+		+	+	+	+	+	17	4.5	0.02
	+	+	+	+		+	+	+	17	4.6	0.02
	+			+		+		+	14	4.9	0.02
		+		+	+	+			11	5.0	0.02
		+	+	+	+	+	+	+	17	5.1	0.02
	+	+		+		+			11	5.4	0.01

1 The importance value (*w*+), equivalent to the probability of that variable being in the 'best' model in the candidate set. Shading indicates those variables with a high level of support (*w*+ ≥0.72).

2 Initial DBH (cm).

3 Mean annual rainfall (mm).

4 Initial plot basal area (m^2 ha^{-1}).

5 Vegetation class.

6 Elevation (m).

7 Soil class, reduced to two levels: shallow/skeletal sands; and clays or deep sands.

8 Slope in degrees.

9 Topography class.

10 Degrees of freedom of the model

11 The difference between the model's AIC_c value and the minimum AIC_c value in the entire candidate set.

12 The model's Akaike weight, equivalent to the probability of the model being the 'best' in the candidate set.

TABLE S5b. Top 20 statistical models of stem diameter increment (mm year^{-1}), with disturbance vectors added to the model based on 'stable' predictors (Table S5a). Candidate models represent all combinations of the disturbance-related predictors (with VEG, MAR, SOIL and TOP included in all models). Models are ranked by ΔAIC_c. Plot ID was included as random effect.

	Predictors										
	MILD[2]	MOD[3]	SEV[4]	RAn[5]	VEG[6]	MAR[7]	SOIL[8]	TOP[9]	DF[10]	ΔAIC_c[11]	w_i[12]
w+[1]:	0.99	0.99	0.99	1.00	-	-	-	-			
	+	+	+	+	+	+	+	+	21	0.00	0.96
	+		+	+	+	+	+	+	19	8.40	0.01
	+	+		+	+	+	+	+	19	8.68	0.01
		+	+	+	+	+	+	+	19	9.34	0.01
	+	+	+		+	+	+	+	20	11.98	0.00
	+		+		+	+	+	+	18	16.55	0.00
		+	+		+	+	+	+	18	17.89	0.00
	+			+	+	+	+	+	17	18.72	0.00
		+		+	+	+	+	+	17	19.14	0.00
	+	+			+	+	+	+	18	19.70	0.00
			+	+	+	+	+	+	17	22.84	0.00
	+				+	+	+	+	16	25.81	0.00
		+			+	+	+	+	16	26.68	0.00
			+		+	+	+	+	16	27.01	0.00
				+	+	+	+	+	15	34.67	0.00
					+	+	+	+	14	37.82	0.00
	+	+	+	+	+	+	+	+	21	0.00	0.96
	+		+	+	+	+	+	+	19	8.40	0.01
	+	+		+	+	+	+	+	19	8.68	0.01
		+	+	+	+	+	+	+	19	9.34	0.01

[1] The importance value (*w*+), equivalent to the probability of that variable being in the 'best' model in the candidate set. Shading indicates those variables with a high level of support (*w*+ ≥0.72).

[2] The annual frequency of mild fires (fires year^{-1}). This term was fit as using the function *poly* in R: poly(MILD, 2).

[3] The annual frequency of moderate fires (fires year^{-1}). This term was fit as using the function *poly* in R: poly(MOD, 2).

[4] The annual frequency of severe fires (fires year^{-1}). This term was fit as using the function *poly* in R: poly(SEV, 2).

[5] Rainfall anomaly (deviation from mean rainfall) over the period of observation (mm).

[6] Vegetation class.

[7] Mean annual rainfall (mm).

[8] Soil class, reduced to two levels: shallow/skeletal sands; and clays or deep sands.

[9] Topography class.

[10] Degrees of freedom of the model

[11] The difference between the model's AIC_c value and the minimum AIC_c value in the entire candidate set.

[12] The model's Akaike weight, equivalent to the probability of the model being the 'best' in the candidate set.

TABLE S5c. Comparison of the robust model for 'stable' predictors of stem diameter increment (mm year^{-1}) with the equivalent *lmer*-generated model using REML and run on unscaled variables. The most conspicuous difference in the robust model is narrower standard errors rather than substantial relative shifts in coefficients. Aliased categories are 'Open forest (mixed grasses)' in vegetation class, 'Clays and deep sands' in the soil class, and 'Plain' in topography class. The coefficients for the quadratics for MILD, MOD and SEV are based on 'raw' linear and squared terms (not the orthogonal squared terms generated by the *poly* function in R).

Model term	Coefficient (SE)	
	robustlmm::rlmer	*lme4::lmer*
Intercept	1.580300 (0.305306)	1.581971 (0.347169)
Vegetation: Woodland (hummock grasses)	-0.649960 (0.185353)	-0.610646 (0.210953)
Vegetation: Woodland (mixed grasses)	-0.438502 (0.154201)	-0.370032 (0.175413)
Vegetation: Woodland (tussock grasses)	-0.538012 (0.213524)	-0.592248 (0.243454)
Vegetation: Open woodland (mixed grasses)	-0.493760 (0.188684)	-0.483319 (0.214953)
Vegetation: Shrubland (heath) (hummock grasses)	-0.707852 (0.272295)	-0.622557 (0.307620)
Soil: Shallow–skeletal sands	-0.294811 (0.073493)	-0.291641 (0.083696)
Topography: Plateau dissected	0.540812 (0.233011)	0.449402 (0.265113)
Topography: Plateau broad	-0.220251 (0.150034)	-0.181104 (0.170337)
Topography: Stony hill	-0.089017 (0.148575)	-0.094872 (0.168625)
Topography: Floodplain margin	-0.373711 (0.191366)	-0.318041 (0.218062)
Mean annual rainfall (mm)	0.000280 (0.000178)	0.000312 (0.000203)
Annualised rainfall anomaly (mm)	0.000679 (0.000182)	0.000722 (0.000198)
Mild fire frequency (fires year^{-1}) (MILD)	0.174582 (0.265110)	0.350295 (0.289929)
MILD^2	-0.704455 (0.332650)	-0.851355 (0.362619)
Moderate fire frequency (fires year^{-1}) (MOD)	0.676032 (0.274987)	0.697898 (0.300940)
MOD^2	-1.326279 (0.414249)	-1.214936 (0.450115)
Severe fire frequency (fires year^{-1}) (SEV)	1.624424 (0.409654)	1.488276 (0.447627)
SEV^2	-3.228033 (0.646295)	-2.948015 (0.702115)
Time since severe fire (years)	0.023342 (0.004305)	0.019652 (0.004694)
Variance components		
(Intercept) xplotid	0.426	0.505
σ	1.26	1.39
rho.e	smoothed Huber (k=1.345, s=10)	
rho.σ.e	smoothed Huber, Proposal II (k=1.345, s=10)	
rho.b_1	smoothed Huber (k=1.345, s=10)	
rho.σ.b_1	smoothed Huber, Proposal II (k=1.345, s=10)	
deviance		31353
Pseudo-R^2		Conditional: 0.157 Marginal: 0.047

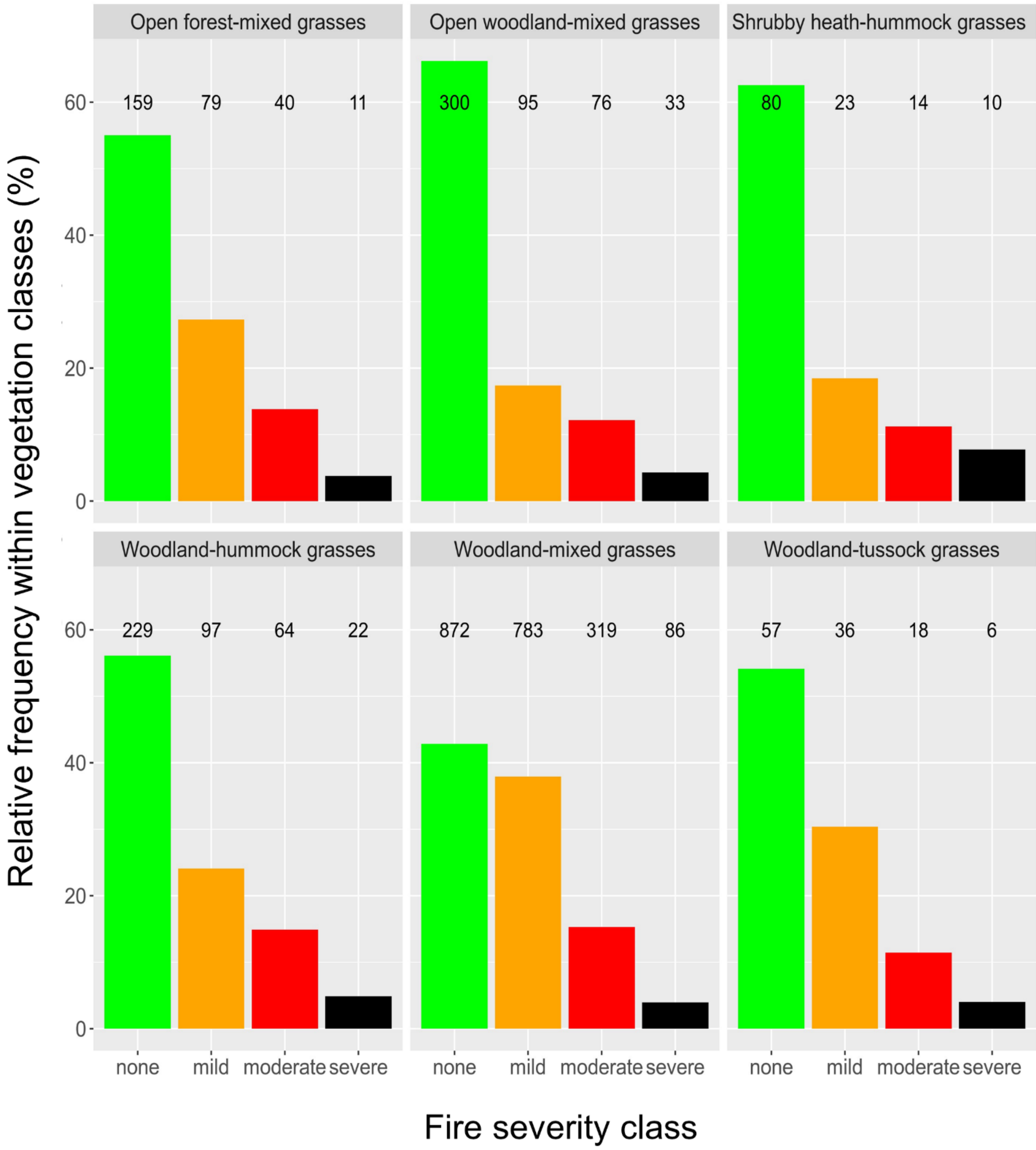


FIG. S1. Relative frequencies of mild, moderate and severe fires at plots in the different vegetation classes. Numbers above bars are the number of fires of each severity over the period of study (including years unburned).

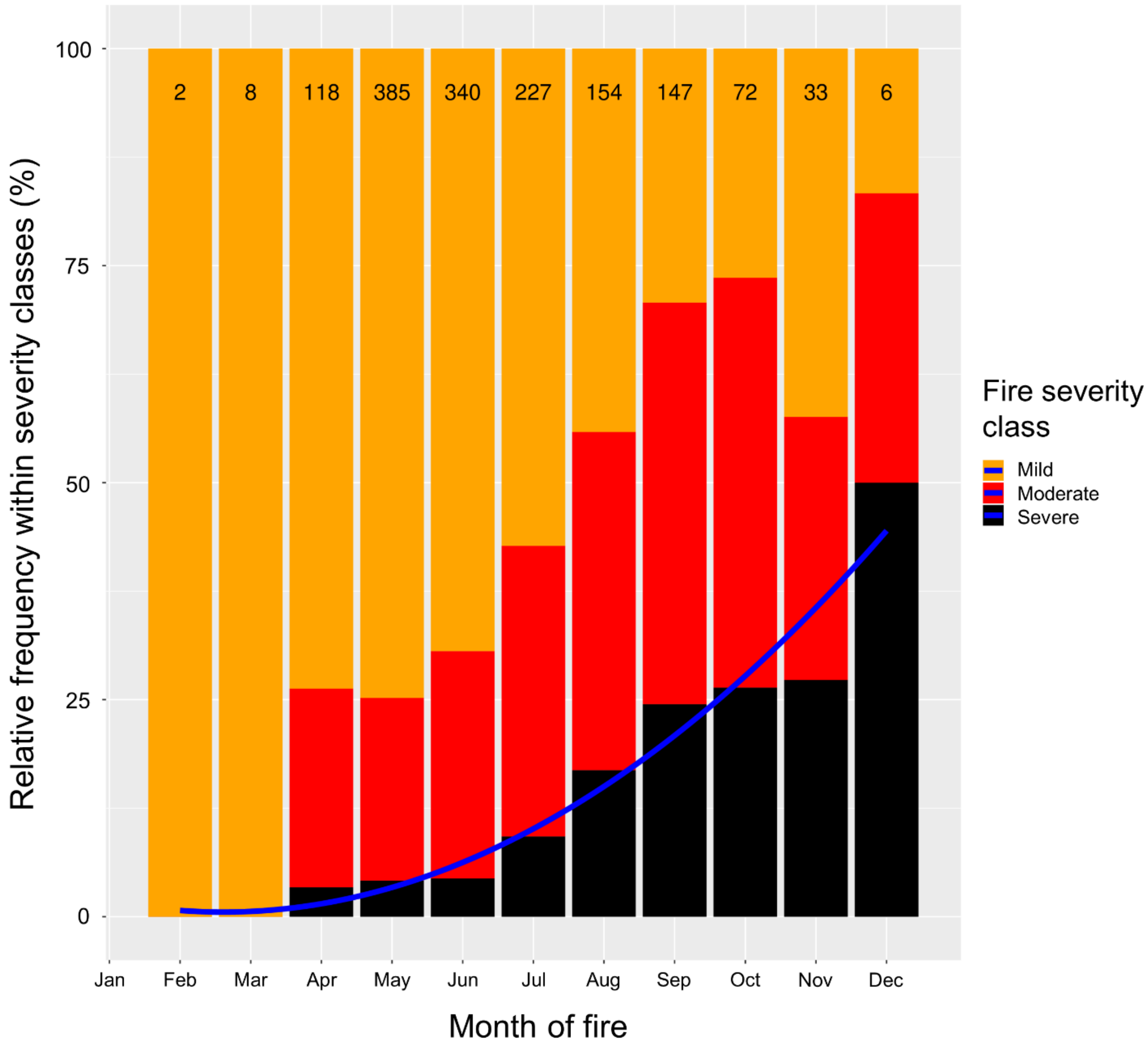


FIG. S2. Within-year changes in the relative frequency of fires of different severity. No January fires were recorded. The blue line is a second order polynomial regression of best fit to the proportion of fires rated as severe by month (R^2 = 0.93, F2,,8 = 72.6, *p*<0.0001).

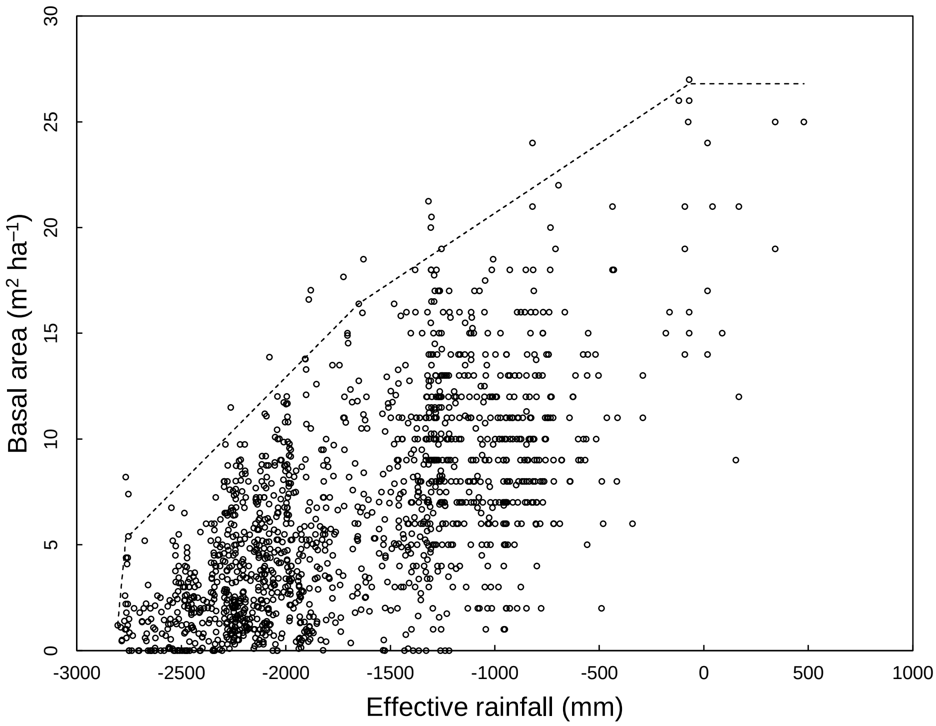


FIG. S3. The relationship between tree basal area and effective rainfall (mean annual rainfall – mean annual point potential evapotranspiration) in Australian savannas. The dashed line represents the predictions of a non-parametric piecewise quantile regression (99th percentile), approximating the 'upper bound' of basal area. The basal area data are from Lehmann et al. (2014).

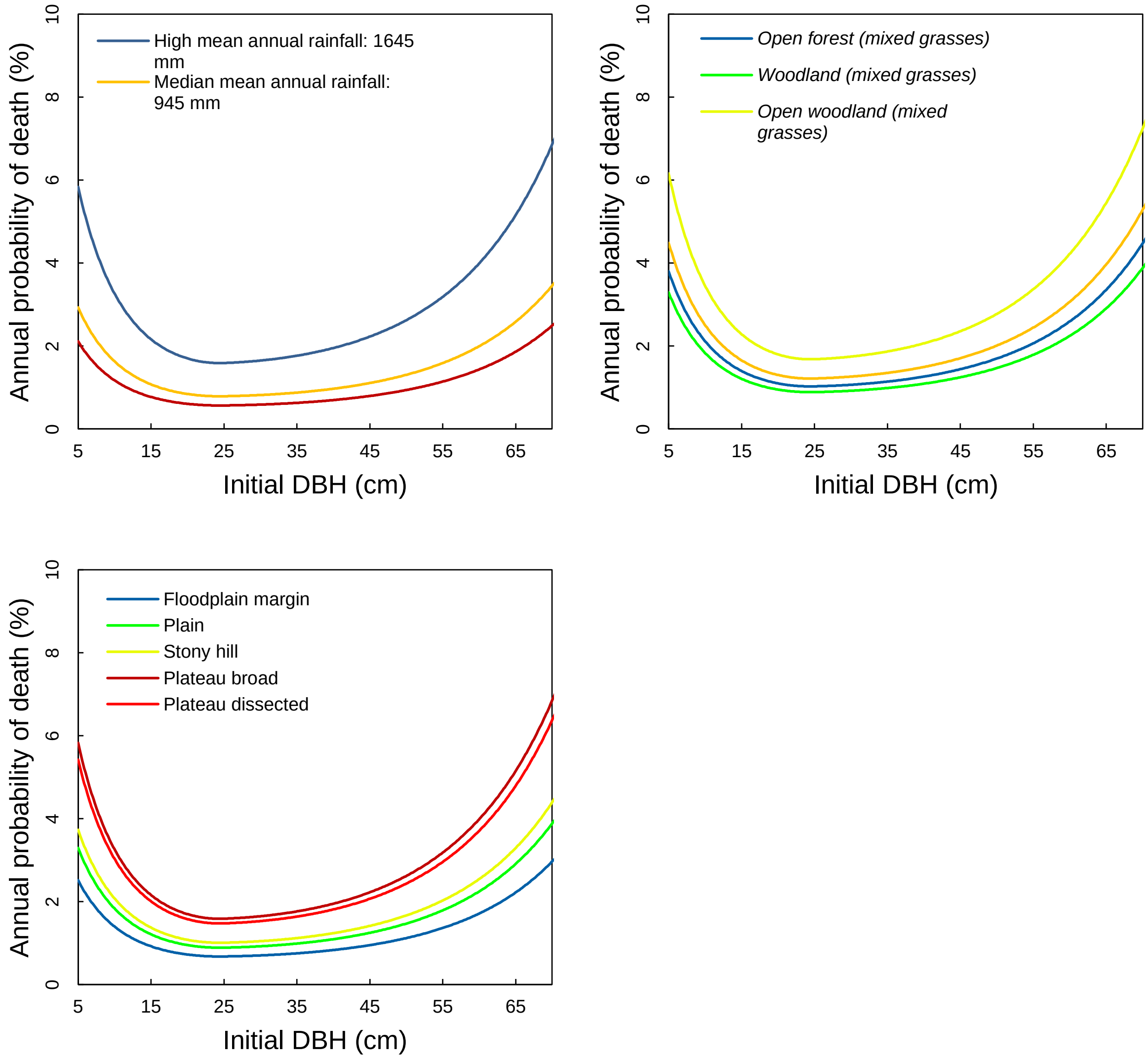


FIG. S4. Modelled variation in mortality rate in response to varying mean annual rainfall, vegetation class, and topography class.

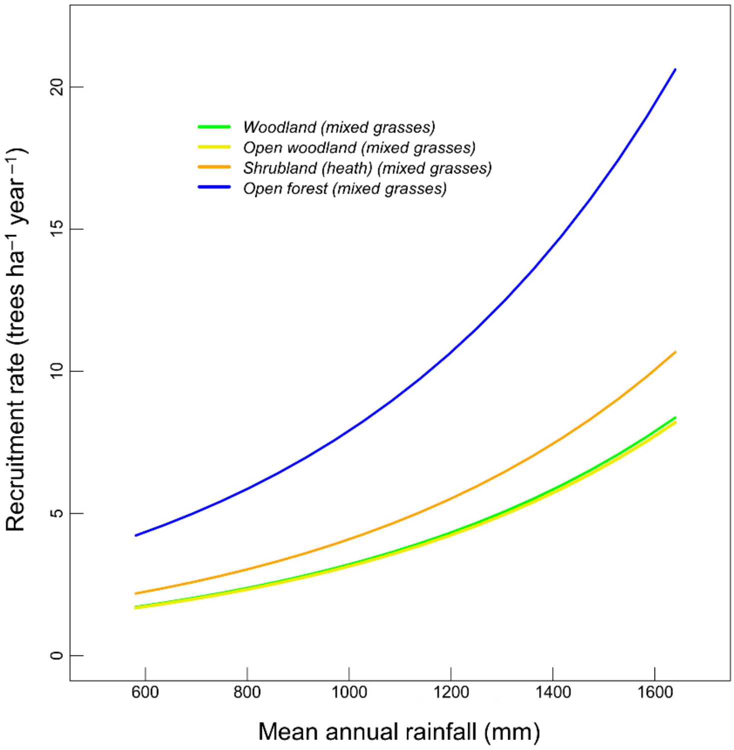


FIG. S5. Modelled differences in recruitment rate between major vegetation classes.

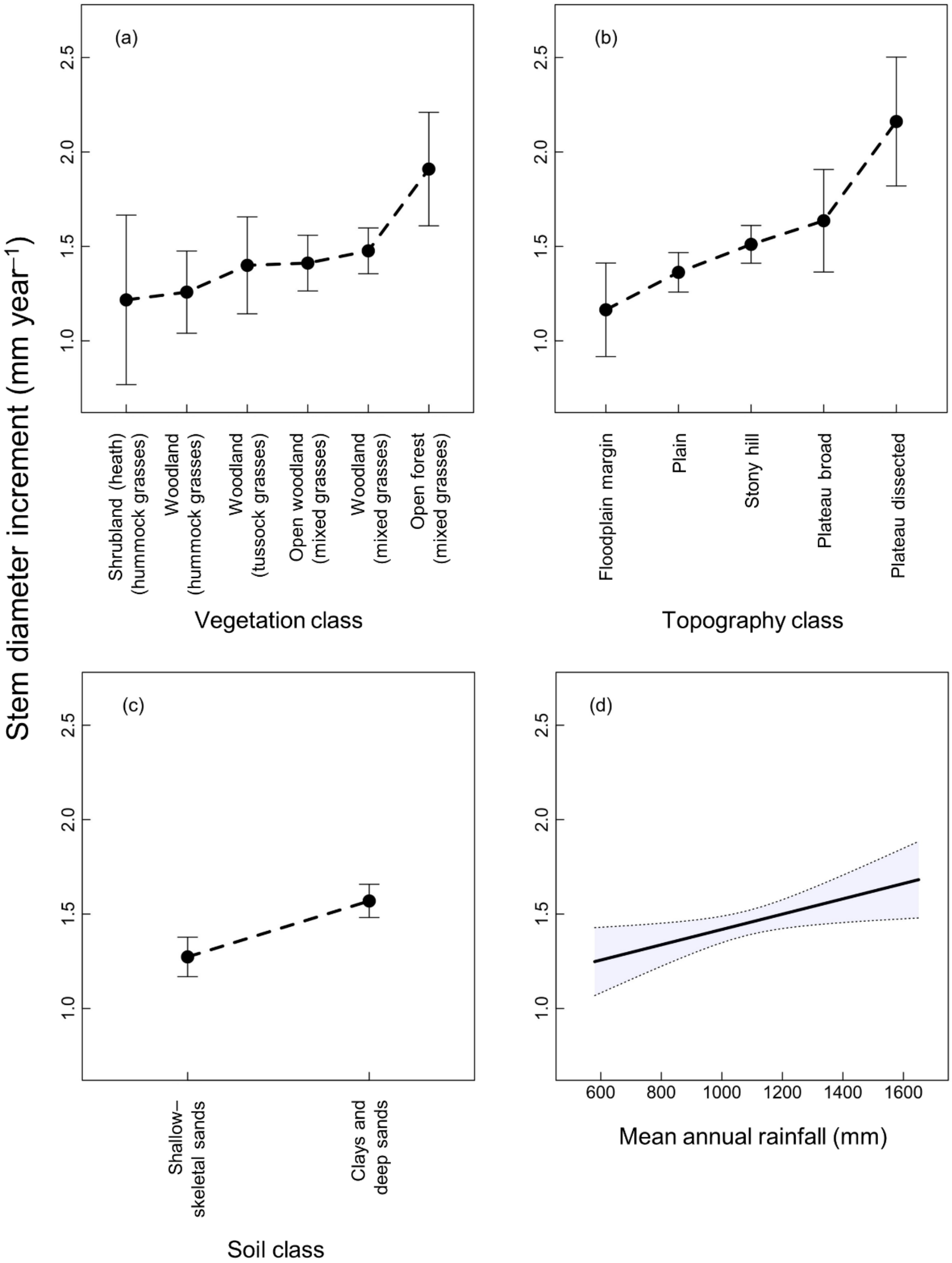
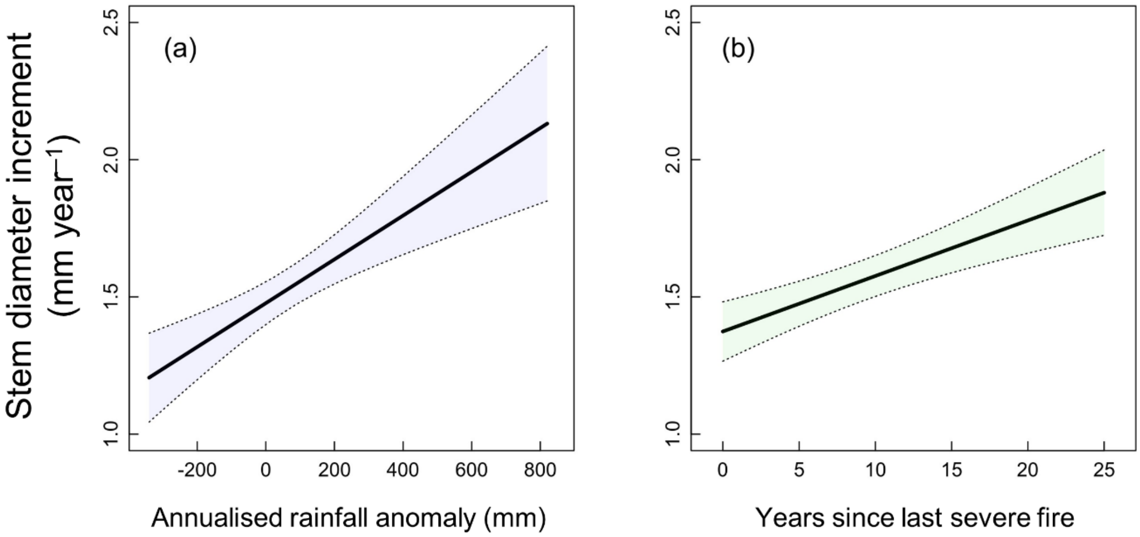


FIG. S6a. Effects plots for 'stable' variables for annual stem diameter increments, not shown graphically in the main paper. All predicted values are conditioned on all other variables in relevant statistical models.


Stem diameter increment
(mm year⁻¹)
(a)
2.5
2.0
1.5
1.0
-200
0
200
400
600
800
Annualised rainfall anomaly (mm)
(b)
0
5
10
15
20
25
Years since last severe fire