

On the relationship between fire regime and vegetation structure in the tropics

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Summary

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- We assessed data from 11 experiments examining the effects of the timing and/or frequency of fire on tropical forest and/or savanna vegetation structure over one decade or more. The initial 'control treatment' in many such cases consisted of previously cleared land. This is as opposed to natural vegetation subject to some sort of endogenous fire regime before the imposition of fire treatments.
- Effects of fire on fractional foliar cover are up to 10-fold greater when clearing pre-treatments are imposed. Moreover, because many of the 'classic' fire trials were initialised with applied management questions in mind, most have also used burning regimes much more frequent and/or severe than those occurring in the absence of human activity.
- Once these factors are taken into account, our modelling analysis shows that nonanthropogenic fire regimes serve to reduce canopy vegetative cover to a much lower extent than has previously been argued to be the case.
- These results call into question the notion that fire effects on tropical vegetation can be of a sufficient magnitude to maintain open-type savanna ecosystems under climatic/soil regimes otherwise sufficient to give rise to a more luxuriant forest-type vegetation cover.

Introduction

The extent to which variations in the structure and function of tropical vegetation types can be explained solely by variations in climate and soil properties is a matter of active debate (Lloyd *et al.*, 2015; Staal & Flores, 2015; Veenendaal *et al.*, 2015; Lloyd & Veenendaal, 2016). At one end of the spectrum it has been argued on the basis of observational data that climate/soil interactions can, at least potentially, account for most of the variation observed (Lloyd *et al.*, 2015; Veenendaal *et al.*, 2015). Nevertheless, this 'deterministic' view has proved to be controversial. This is because, following on from the work of Bond *et al.* (2005), there have been several computer-based studies arguing for a role for fire as a paramount factor influencing large-scale variations in woody vegetation cover in the tropics (Lehmann *et al.*, 2011; Murphy & Bowman, 2012; Dantas *et al.*, 2015). This notion is now very much the accepted paradigm (Hoffmann *et al.*, 2012a; Lehmann *et al.*, 2014), and in support of this view there have been several recent analyses using the distribution of a remotely sensed woody canopy cover product (Hansen *et al.*, 2003). These studies have suggested that for all continents where both tropical

forest and savanna occur there are large areas for which the climate and soils are potentially suitable for forest, but with savannas actually the dominant vegetation type: see Hirota *et al.* (2011) and Staver *et al.* (2011), but also as regards methodological issues potentially undermining these analyses see Hanan *et al.* (2013), Staver & Hansen (2015), Gerard *et al.* (2017) and Wuyts *et al.* (2017).

Such *in silico* identified 'bi-stable' regions are argued to occur as a consequence of fire-mediated feedbacks thought to operate through a mechanism illustrated schematically as the red loop in Fig. 1. Here, according to the theory of alternative stable states (ASS) it is considered that, should a closed forest-type woody tropical system, by chance, be transformed to a more open vegetation type as a consequence of some major disturbance such as fire and/or prolonged drought, then a return to the pre-disturbance state may be not be possible – at least on timescales of centuries to millennia. Here, according to a hypothesis originally put forward to account for Tasmanian open woodlands and closed forest being found in close proximity to each other under apparently near identical $A \rightarrow B \rightarrow C$ climatic/edaphic conditions (Jackson, 1968), the basic idea is as follows: first, because the

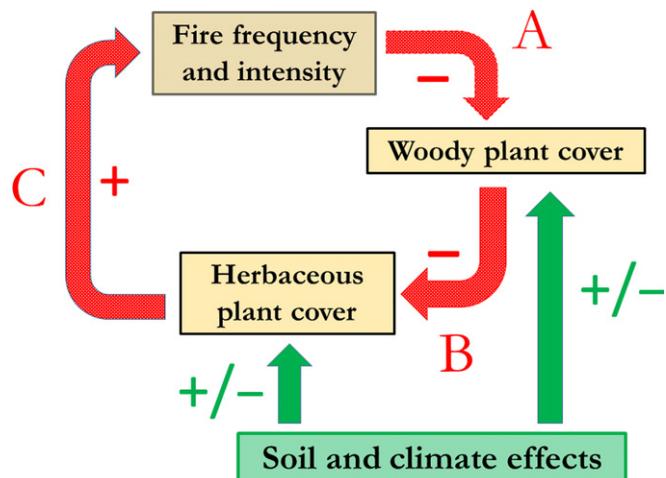


Fig. 1 Simplified diagram illustrating potential interacting roles of soil, climate and fire as factors influencing tropical vegetation structure.

According to this scheme, the potential vegetation structure is determined by soil and climate effects (green arrows) but with fire-mediated feedbacks (red arrows) potentially overriding these effects. Forming the red feedback loop are (A) new woody plant growth being impeded by more frequent and/or severe fires, (B) reduced woody plant cover allowing an increase in herbaceous plant cover and (C) increased herbaceous plant cover leading to an increased probability and/or severity of fire. For more information see the main text.

disturbance-affected canopy has many gaps with relatively high light penetration into the understorey, then there is a markedly greater abundance of grasses compared to the pre-disturbance forest-like state (reduced magnitude of negative effect B in Fig. 1) and so the probability and/or severity of fires is increased (increased magnitude of positive effect C in Fig. 1). With new woody plant growth then impeded by frequent fires (increased magnitude of negative effect A in Fig. 1), a positive feedback loop then emerges with a self-sustaining pyrogenic savanna-type ecosystem the end result. Implicit in the ASS argument is that, even in the absence of human intervention, a ‘natural fire’ regime can come in to play once a forest has been sufficiently ‘opened up’ by drought and/or fire or some other major perturbation and, importantly, with this fire regime of a sufficient regularity/severity to prevent the re-establishment of the ‘potential’ woody cover as dictated by soils and climate (green arrows in Fig. 1). It has also been suggested that it may be possible for savanna ecosystems to exist in two alternative states, each with its own unique fire regime (Van Langevelde *et al.*, 2003).

Whilst not disputing a role for fire as an important modulator of vegetation structure and function, one alternative view is that much of the variation observed in tropical vegetation structure both across and within the forest and savanna biomes can simply be accounted for by variations in soil and climate (Veenendaal *et al.*, 2015; Lloyd *et al.*, 2015: green arrows in Fig. 1) from which it follows that the fire-associated feedback loop of Fig. 1 may be less important than is generally considered to be the case. Specifically, it has been suggested by Lloyd & Veenendaal (2016) that fires act mostly as ‘a sharpening switch’ (Wilson & Agnew, 1992) where, rather than being the principal determinant of tropical vegetation structure across large regions of the terrestrial

tropics as is generally supposed, fire simply serves to reinforce potential vegetation patterns as determined by climate and/or soils. The above contrasting views are not, of course, necessarily mutually exclusive. For example, developing upon a hypothesis first presented by Kellman (1984), it has been suggested that reduced woody plant growth in nutrient-poor soils may serve to predispose the vegetation occurring on such soils to ASS-associated transitions (Hoffmann *et al.*, 2012a; Murphy & Bowman, 2012; Staal & Flores, 2015).

Here, with an overall objective of addressing this debate, we provide a quantification of the extent to which variations in intensity and timing of fires serve to modulate woody vegetation structure in tropical ecosystems (path A in Fig. 1). We achieve this through the quantification of data from a range of fire manipulation experiments which have been undertaken in tropical regions over the last 80 or so years.

A short history of fire experiments in the tropics

Early observations of forest tree ‘islands’ occurring in areas otherwise dominated by savanna led to the idea – especially in West Africa – that many current savanna regions had originally been forest subsequently transformed through human action (Stebbing, 1937; Aubreville, 1949). This led to the first tree cover focused ‘fire experiment’ established in 1937 at Kokondekro (Ivory Coast). Here, different areas of what was considered ‘derived savanna’ (actually a cotton field area fallowed for several years before the experiment started; Aubreville, 1949; de la Mensbruge & Bergeroo-Campagne, 1961) were exposed to prescribed fire regimes (Louppe *et al.*, 1995). Many other fire experiments were initiated between the 1930s and 1950s (e.g. Hopkins & Jenkin, 1962; Trollope, 1974; Tainton *et al.*, 1978; Geldenhuys, 1977; Brookman-Amissah *et al.*, 1980; Carson & Abbiw, 1990; Swaine *et al.*, 1992; Chidumayo, 1997; Titshall *et al.*, 2000; Morris & Tainton, 2002; and see Supporting Information Notes S1), with the results from many of these experiments having subsequently been used to infer that fire may be just as important as climate as a determinant of vegetation structure and function in the tropics (Bond *et al.*, 2003, 2005). It is important to note that in almost all cases these experiments were not designed with this objective in mind; rather, they had the aim of investigating fire regime manipulation as a management tool. In some cases, the management question was protection of woody cover (Charter & Keay, 1960) and in others the use of prescribed fire regimes as a tool for the prevention of ‘bush encroachment’ into grazing lands (e.g. West, 1965).

As a result of different aims there was also a large diversity of characteristic pre-treatments. These included choosing fallow farmland with scattered large trees as a baseline ‘pre-treatment control’ (Aubreville, 1953), or the complete clearing of woody vegetation, inclusive of roots, before starting the experiment (Furley *et al.*, 2008). Other experiments simply applied different fire regimes to existing rangelands. Many fire experiments included ‘control’ areas from which fire was permanently excluded, but – as should be clear from the above – this was not always ‘natural vegetation’ when the experiment commenced.

Of note, many fire trials were simply intended as demonstration trials and, perhaps also due to the effort involved in their establishment and maintenance, many lack statistical finesse – for example with no replication of treatments (e.g. Louppe *et al.*, 1995). Variations in soil properties were also often ignored. For example, at Matopos (Zimbabwe) soil differences within plots caused difficulties in comparing treatments to the extent that Kennan (1972) went so far as to provide educated ‘guesses’ as to what some numbers should have been had soil heterogeneity not been a confounding factor. The original Kokondekro experiment discussed above also has similar design flaws (Laris & Wardell, 2006).

Bearing such complications in mind, the objective of the current study was to provide a synthesis of the fire experiment literature to determine if a general pattern can be established in terms of the magnitude of fire effects on vegetation structure in terms of (1) season and frequency of burning and (2) vegetation structure in the absence of fire.

Materials and Methods

We gathered all publications known to us where experiments had been established to examine effects of fire frequency and/or intensity on savanna/forest structure and function (Notes S1). Excluding experiments of duration < 10 yr to ensure robust conclusions on vegetation structure effects, we first chose a subset which included experiments specifically looking at different frequencies of burning. We then combined that dataset with single frequency studies to both verify our initial conclusions and to probe underlying causes of inter- and intra-study differences in magnitude of fire impacts on woody canopy cover.

Choice of units

Studies of tropical vegetation structure have used a range of different metrics, such as stem density (Bond, 2008), stem height class distribution (Kennan, 1972; Sweet, 1982), plot basal area (Lehmann *et al.*, 2014), biomass (Higgins *et al.*, 2007; Veenendaal *et al.*, 2015) and/or canopy cover measures (Sankaran *et al.*, 2005; Smit *et al.*, 2010). In bringing together the experiments selected from Notes S1, it was therefore necessary to choose a common metric. On the basis of woody vegetation effects on fire regimes most likely being mediated through a shading out of the potentially pyrogenic herbaceous layer by the vegetation above (Torello-Raventos *et al.*, 2013; Smit & Prins, 2015; Veenendaal *et al.*, 2015), and this then influencing fire spread rates and/or the frequency/intensity of fires (Govender *et al.*, 2006; Archibald *et al.*, 2010), we chose the fractional crown cover of woody species, ζ_w (Lloyd *et al.*, 2008; Veenendaal *et al.*, 2015), as our ‘common denominator’. Use of ζ_w as a woody cover metric also has the advantage that for many tropical vegetation classification systems crown or canopy cover are a key classification criterion (Eiten, 1972; White, 1983; Carnahan & Bullen, 1990; Torello-Raventos *et al.*, 2013).

To estimate ζ_w we used various continent-specific relationships relating tree and/or canopy height and diameter metrics as

described in Notes S2. With changes in ecosystem carbon stocks also being a key factor of any study of fire effects at the continental or regional scales (Langenfelds *et al.*, 2002; Bond *et al.*, 2005; van der Werf *et al.*, 2010) we also consider results in terms of changes in stand-level biomass (B).

Modelling approach

Although it is common to quantify fire frequencies with an average return time, T (typically as ‘once every T years’) we believe the frequency, f ($= 1/T$), is more useful, such that the model intercept corresponds to woody cover at $f=0$. This can conceptually be considered as the vegetation type that would be expected to occur in the long-term absence of recurring fires (namely fire return times of more than one decade).

Also taking into account effects of time of year (θ) of burning on the woody plant crown cover response, we developed a multi-level model as follows:

$$\zeta_{W(p,t)}^z = \beta_{0(t)} - \beta_{1(t)}f + s(\theta_t) + \varepsilon_{p,t}, \quad \text{Eqn 1}$$

where $\zeta_{W(p,t)}$ is the average canopy crown cover of the plot (p) exposed to a fire frequency f within fire trial t , z is an exponent, $\beta_{0(t)}$ is the predicted canopy crown cover in the absence of fire for trial t , $\beta_{1(t)}$ is a coefficient quantifying the dependence of ζ_w on f within each trial, s is a nonparametric smoother (centred on zero), θ is the month of burning (January = 1 to December = 12 for the southern hemisphere; July = 1 to June = 12 for the northern hemisphere to standardise for seasonality), and $\varepsilon_{p,t}$ represents the unexplained model error. Details of fitting procedures and an explanation for the power function used are provided in Notes S3.

Results

Multiple frequency fire trials

The best model fit of Eqn 1 was with $z=0.4$ with a minimal bias in the model fit and with reasonable predictions of fractional cover lost due to fire across a wide range of ζ_0 (Notes S3, S4). Here, with $\beta_0=0.74$ we obtain a modelled mean fractional crown cover in the absence of fire for our dataset $\zeta_{W(0)}$ of 0.74^{2.5}, which then gives $\zeta_{W(0)}=0.48$ (see also Fig. S4.1 in Notes S4). A consideration of the other terms is, however, less straight forward as with $z \neq 1$, interactions between f and magnitude of fractional canopy loss occur (Notes S5). Using the Kullback–Leibler divergence criterion we obtain $r^2=0.28$ as a best estimate of the proportionate reduction in uncertainty in magnitude of burning effects due to the inclusion of model regressors (Notes S3).

The effect of the timing of fire is highly significant (Table 1) with the modelled pattern of Fig. 2 showing greater effects of fire (a more positive s) for burning in the late dry season compared to earlier. It also seems that very early dry season burning may have a slightly more severe effect than those occurring in the early dry season proper. The effect of $s(\theta)$ is also strongly context-dependent. For example, at our data set average fire free cover of

Table 1 Mixed model predictions for the fit of Eqn 1 to the data set as shown in Figs 3 and 4

Parametric fixed effects	Coefficient	SE	T	Prob (> t)
β_0 = intercept	0.731	0.045	16.28	<0.0001
β_1 = coefficient of f	0.152	0.015	-10.41	<0.0001
Nonparametric fixed effect	Estimated d.f.		F	Prob (>F)
$s(\theta)$	3.95		2.99	0.017
Level 2 random terms	Estimate			
$\tau_0^2 = \text{var}(U_{0,t})$	0.0404			
Level 1 random terms				
$\varepsilon_{P,t} = \text{var}(S = \text{Brasilia})^*$	0.0010			

Full details of the random model components and their meaning can be found in Supporting Information Notes S3.

*Expressed relative to Brasilia (IBG plots), variances were estimated as: KNP-01 = 1.07; KNP-02 = 0.78; KNP-03 = 0.83; KNP-04 = 1.04; MAT-01 = 1.77; MAT-02 = 2.88; MDA-01 = 5.55 and MUN-01 = 1.18.

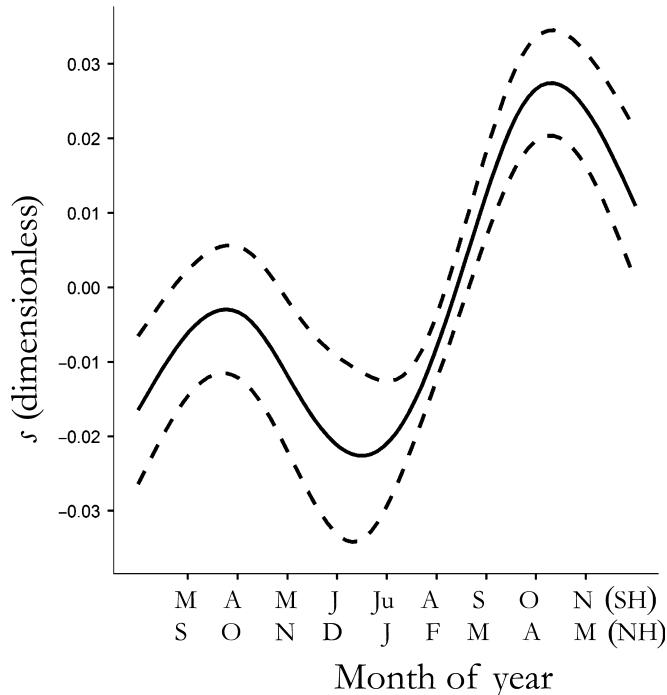


Fig. 2 Effect of time of fire occurrence on canopy cover loss according to Eqn 1. Simulation results are shown with month of the year indicated for both the southern and northern hemispheres (SH and NH, respectively), with the dimensionless s factor standardised to have an integral of 0. Positive values are associated with a greater reduction in fractional canopy cover. The solid line shows the nonparametric regression spline fit with the upper and lower dashed lines encompassing the 95% confidence interval.

$\zeta_{W(0)} = 0.48$, then for annual fires the model predicts $\zeta_W \approx 0.31$ and $\zeta_W \approx 0.21$ for fires occurring in June and October, respectively. For fires every 4 yr, the equivalent values are $\zeta_W \approx 0.47$ and $\zeta_W \approx 0.36$.

Noting the different scales for each panel's independent (y) axes, Fig. 3 shows the relationship between ζ_W and f as affected

by time of year for all sites analysed through Eqn 1 except for Brasilia which because of a different experimental design is shown separately in Fig. 4. In Fig. 3 each observation is indicated by the month of fire (with 'control' fire protected plots with $f=0$ denoted as N) and with the model prediction range as affected by time of year shown by the grey ribbon; the variation observable at any given f thus is attributable to different modelled magnitudes of burning impact for different times of year. Data include four different vegetation types from Kruger National Park in South Africa: KNP-01, KNP-02, KNP-03 and KNP-04 (Smit *et al.*, 2010), Marondera in Zimbabwe: MRA-01 (Furley *et al.*, 2008), two plots from Matopos in Zimbabwe: MAT-01 and MAT-02 (Kennan, 1972) and Munmalary in Australia: MUN-01 (Russell-Smith *et al.*, 2003).

Both model and data show increased effects of fire on ζ_W at higher burning frequencies and, generally speaking, effects of time of year are consistent with burns later in the dry season having a greater impact (Fig. 3). For all KNP sites and MUN-01 the model estimates observations well, but for MAR-01 reported reductions in woody cover are much greater than the other sites and consequently underestimated by the model. For MAT-01 and MAT-02 the data are considerably more variable than the other six sites. Problems with these latter three sites are also reflected in the modelled variances which are inferred to be unusually high (Table 1).

All the experiments of Fig. 3 included a fire-free control established at the same time as the fire-treatment plots. However, for the IBG plots at Brasilia (Fig. 4) fire treatments were imposed in an area that had previously been protected from fire for 17 yr (Miranda *et al.*, 2002). Thus the 'control' and 'treatment' results represent the same plot either before or after 12 subsequent years of exposure to a fire regime. Three physiognomic forms of cerrado were examined: *campo sujo* ('dirty field'), a shrub savanna; *cerrado sensu stricto*, a savanna woodland; and *cerrado denso*, a tall woodland. Here, as seen for the mid-season fire treatments (August 2 and 4 m in Fig. 4), a lower f leads to a lesser reduction in ζ_W but only for the *campo sujo* plots. As for the other sites, there is a clear tendency for reduced impacts when fires occur earlier in the dry season. Model simulations are in all cases reasonable, although we do acknowledge that with the data available for this experiment reflecting a period of only just over one decade, then some longer-term effects of the imposed fire regimes may not have been reflected in the data used here.

Model predictions and single frequency fire trials

In addition to the multiple frequency fire trials analysed above, many trials involving only annual burns (i.e. $f=1.0 \text{ yr}^{-1}$) and with the appropriate fire-exclusion control exist. Those suitable for analysis include Kokondekro on the Ivory Coast: KOK-01 (Louppe *et al.*, 1995), Mwekera in Zambia: MWE-01 (Chidumayo, 1997), Ndola in Zambia: NDO-01 (Trapnell, 1959; Chidumayo, 1997), Olokomeji in Nigeria: OLO-01 (Charter & Keay, 1960; Hopkins & Jenkin, 1962), Red Volta in Ghana: RED-01 (Ramsay & Rose Innes, 1963; Brookman-Amissah *et al.*, 1980) and Solar Village in Australia: SOL-01 (Woinarski

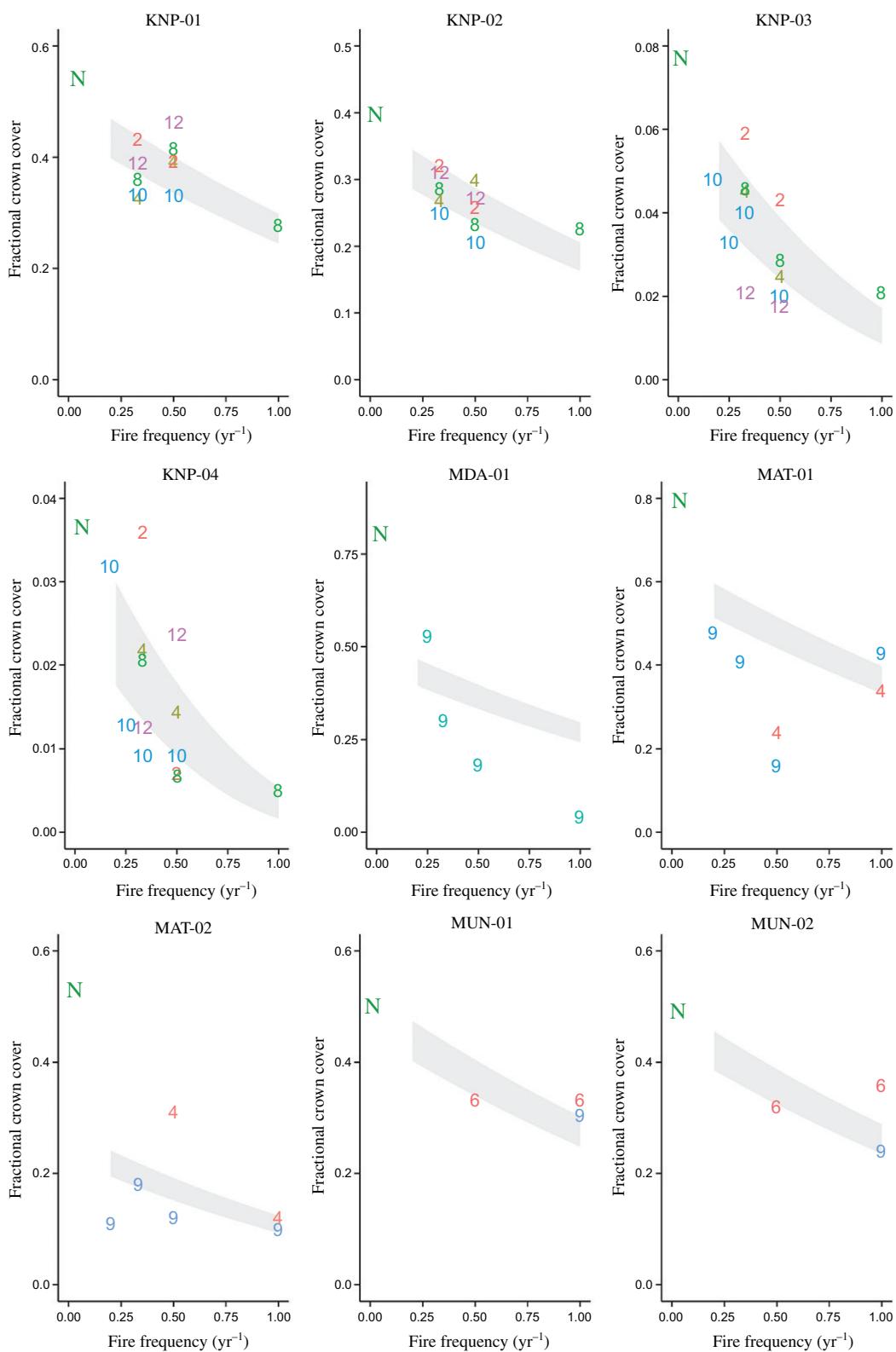


Fig. 3 Fractional crown cover in relation to month of burning and fire frequency. Each panel represents a different plot with the numbered symbol representing the month of burning and the grey shaded area showing the model predictions across a range of burning dates spanning the maximum to minimum s (see also Table 1 and Fig. 2). Control (unburned) plots are designated 'N'. For more details on the plots used see Supporting Information Notes S1.

et al., 2004). With the exception of SOL-01 all these studies investigated the effects of early- vs late-season annual burns and combining these data with the multiple frequency trials (with

$f = 1 \text{ yr}^{-1}$: IBG values back-calculated from their $f = 0.5 \text{ yr}^{-1}$ assuming $z = 2.5$) the relationship between the fire-free fractional canopy cover, $\zeta_{W(0)}$, and the fractional canopy cover in the

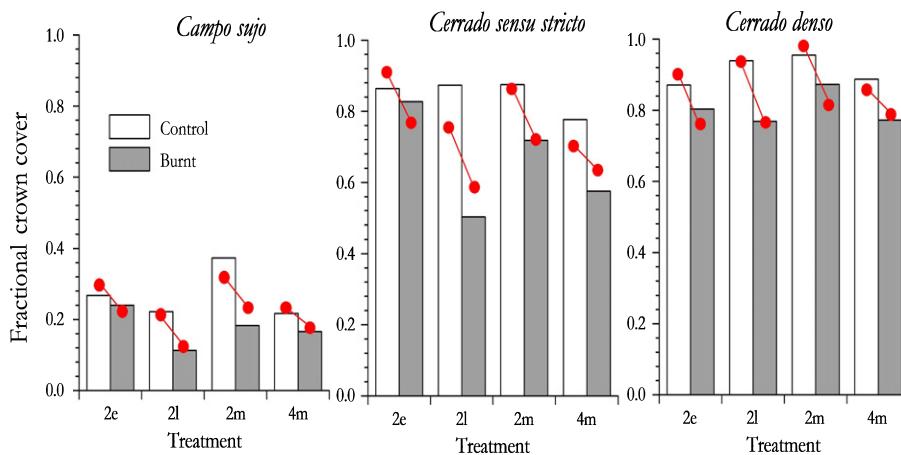


Fig. 4 Effect of fire frequency and date of burning on fractional crown cover of three vegetation types at Brasilia (Brazil). Treatment codes: 2e, burnt every 2 yr early in the dry season; 2l, burnt every 2 yr late in the dry season; 2m, burnt every 2 yr in the middle of the dry season; 4m, burnt every 4 yr in the middle of the dry season. Vertical bars, data; red circles and lines, model predictions according to Eqn 1.

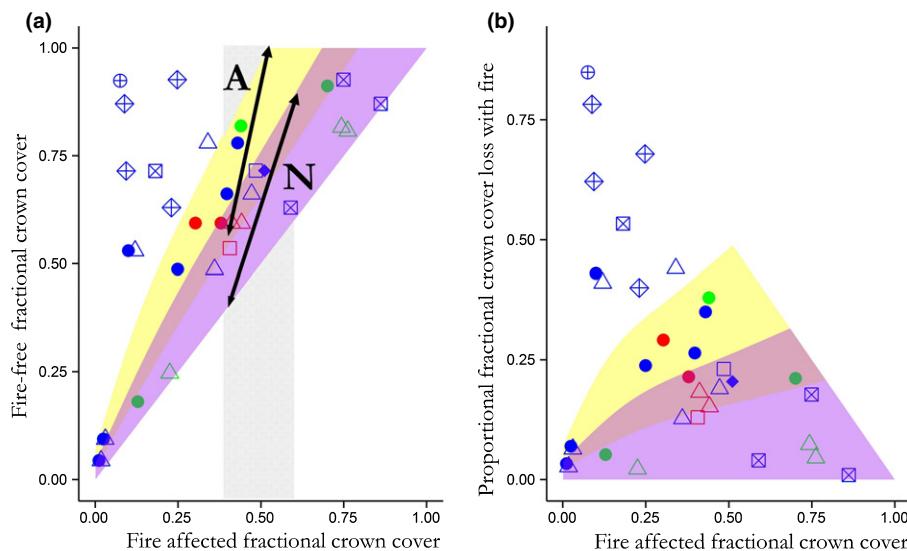


Fig. 5 Observed and modelled effects of time of year, and modelled effects of frequency of burning on savanna fractional crown covers shown in terms of (a) absolute reductions in canopy cover due to fire and (b) proportional reduction in canopy cover. Squares and triangles, data for early annual dry season fires; circles and diamonds, data for late annual dry season fires; circles and triangles, data used in original Eqn 1 model fit; squares and diamonds, data not used for initial model parameterisation. Symbols: circle + cross, square + cross and diamond + cross represent sites that had been cleared immediately before the imposition of the first burning treatment. The different colours represent different continents: blue, Africa; red, Australia; green, South America. Yellow ribbon, model predictions (0.95 quantile confidence interval) for annual fires (i.e. $f = 1 \text{ yr}^{-1}$ in Eqn 1) encompassing all possible dates of burning across the dry season. Light purple ribbon, model predictions (0.95 quantile confidence interval) for quadrennial fires (i.e. $f = 0.25 \text{ yr}^{-1}$ in Eqn 1) encompassing all possible dates of burning across the dry season. The light pink region shows the area of overlap between the early dry-season annual fires and late dry-season quadrennial fires. Also shown in (a) are likely threshold ranges for fire/nonfire regimes and associated transition points for high-intensity anthropogenic (A) and natural (N) fire regimes with the grey shaded area indicating the probable associated range of canopy cover (for further explanation see the main text). The vertical bar indicates uncertainties in the fractional woody canopy threshold differentiating tree–grass mixtures that easily burn from those that do not (see also Supporting Information Notes S6, Fig. S6.1).

presence of annual burning is shown in Fig. 5. Here we have not only separated out those data used to fit the model vs the single frequency sites as well as early vs late dry season burning treatment, but have also indicated (as open symbols with internal cross (\blacksquare , \oplus and \diamond)) those studies for which there was clearing of both the control and the fire treatment plots before the commencement of the experiment. Also shown as coloured ‘ribbons’ are 0.95 quantile intervals of the predictions of the fit to Eqn 1 for $f = 1 \text{ yr}^{-1}$ and $f = 0.25 \text{ yr}^{-1}$.

From both Fig. 5(a) and (b) it can be seen that all late dry-season burn treatments with clearing before imposition of

treatments fall outside the main population, with a considerably greater fire-free canopy cover at any given (inevitably much lower) fire-affected ζ_w (MDA-01, MWE-01, RED-01 and OLO-01). Also falling outside the main population are the Matopos sites, especially MAT-02, which as mentioned already had severe problems with the initial experimental set up. For the other sites examined – for all of which we believe methodological issues to be less of a consideration – the largest response is seen at an annual late burning, with a maximum reduction in fractional canopy cover of < 0.4 (Fig. 5b). On the other hand, a clear ‘pre-treatment’ fire effect was only observed in one case when annual

fires were early in the dry season (RED-01). All other sites had annual early dry-season fires reducing fractional canopy cover by < 0.15, even with prior clearing of the land.

Also shown as a 'ribbon' in Fig. 5 is the modelled effect of $f=0.25 \text{ yr}^{-1}$, the minimum value of which occurs at $\zeta_w = \zeta_{w(0)}$. This suggests that, even when exposed only to high-intensity late season burns, quadrennial fires are likely to reduce fractional canopy cover by < 0.2, and if occurring early in the dry season with fires every 4 yr likely to cause reductions in ζ_w of < 0.1. These are all data-based predicted long-term average effects of the fire frequency and timing and include inter-annual climate effects; in many cases the experimental periods including extreme events such as El Niño.

Further included in Fig. 5(a) is a shaded bar providing an uncertainty estimate of the fire-affected crown cover (ζ_w^*) associated with the delineation of readily flammable vs potentially nonflammable savanna-type ecosystems. This threshold woody canopy cover is usually taken as $\zeta_w^* \sim 0.5$ as suggested by Hennenberg *et al.* (2006), but here with some uncertainty accounted for with the shaded bar encompassing a range $0.4 < \zeta_w^* < 0.6$ as suggested by our own unpublished data: see Notes S6). For both $f=0.25 \text{ yr}^{-1}$ and $f=1.0 \text{ yr}^{-1}$ also shown in this figure and connected by arrows are the intersects of the mutually low $\zeta_w^*/0.95$ confidence interval estimates. Similarly, intersects where both the ζ_w^* and 0.95 confidence interval estimates are at their maximum value are also shown. Taking the associated fire-free fractional crown cover values on the y -axis, this in turn provides an estimate for the maximum ζ_w that could have occurred under any given fire regime (itself potentially self-sustaining and regularly burning because $\zeta_w \leq \zeta_w^*$). Taking an intensive anthropogenic annual burning 'A' (i.e. with $f=1.0 \text{ yr}^{-1}$) we then find that it is quite possible for even fully closed stands for which $\zeta_{w(0)} \rightarrow 1.0$ to be maintained in an open state by annual fires. But if one takes $f=0.25 \text{ yr}^{-1}$ as broadly representative of a more natural (nonanthropogenic) savanna fire regime (Laris & Wardell, 2006; Furley *et al.*,

2008), then the upper estimate (corresponding to repeated late season burns) is only *c.* 0.8 with a best estimate (half way along the 'N' arrow) of *c.* 0.62.

Contrasting responses for fractional canopy cover vs biomass

While woody cover is most relevant to understand fire-mediated feedbacks, carbon stocks are also important: as shown in Fig. 6 very different patterns emerge between these two metrics when compared on a common scale using data for $f=1 \text{ yr}^{-1}$ (here as a fraction of the fire-free value). Specifically, there is a marked decline in the fractional cover loss as $\zeta_{w(0)}$ declines for both early and late dry season fires but with no such pattern observable when fractional biomass losses are expressed relative to the fire-free biomass (B_0). These different patterns arise not only because of differences in $\zeta_w; B_0$ allometry between continents (Fig. S2.1 in Notes S2), but also because of the very rapid increase in B with ζ_w as the latter approaches unity (see Veenendaal *et al.*, 2015).

Discussion

Most early fire experiments started with the aim of determining the appropriate frequency and/or timing of fire events for the prevention of woody plant invasion of pastoral systems (Kennan, 1972; Harrington, 1974; Sweet, 1982; Sawadogo *et al.*, 2005; Trollope & Tainton, 2007). This is as opposed to being designed to evaluate the effect of fire in 'naturally occurring' savanna as initiated in recent decades, such as Kruger National Park in South Africa (Govender *et al.*, 2006; Higgins *et al.*, 2007), northern Australia (Russell-Smith *et al.*, 2003; Woinarski *et al.*, 2004) and South America (Miranda *et al.*, 2002). This – as we argue below – is a difference especially marked in terms of the frequency and intensity of the fires imposed and with associated differences in the apparent fire sensitivities.

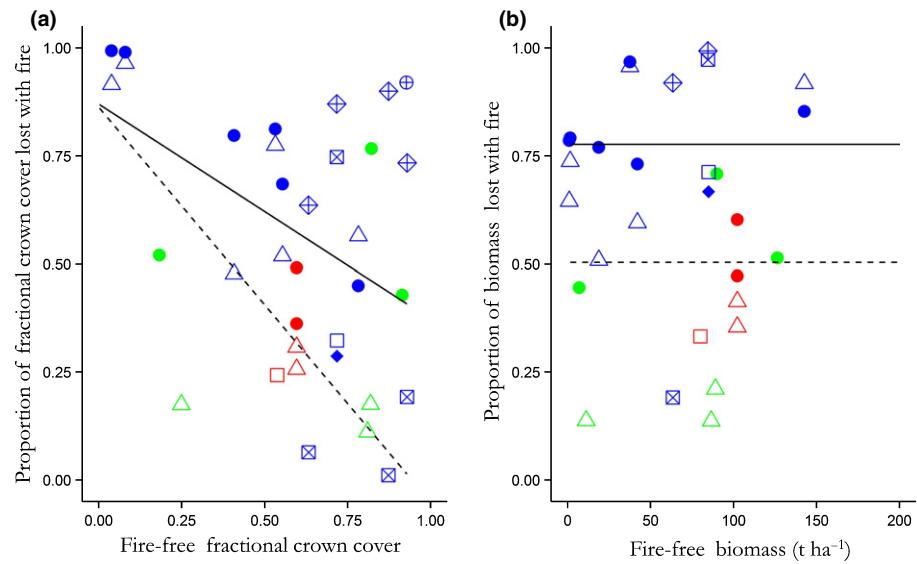


Fig. 6 Effects of time of year of burning on (a) woody vegetation fractional crown cover and (b) biomass. Squares and triangles, early dry-season fires; circles and diamonds, late dry-season fires; circles and triangles, used in original Eqn 1 model fit; squares and diamonds, not used for initial model parameterisation. Symbols: circle + cross, square + cross and diamond + cross represent sites that had been cleared immediately before the imposition of the first burning treatment. Dashed lines, early dry-season burn ordinary least squares (OLS) regression (pre-cleared sites not included), in (a): slope = $-0.92, P = 0.004$. Solid lines, late dry-season fire OLS regression (pre-cleared sites not included), slope = $-0.50, P = 0.028$.

Effects of pre-treatment, frequency and timing

Our first and most obvious result is that where there was some sort of clearing pre-treatment of the vegetation then the observed effects on stand structure were much greater than when the vegetation was initially in some sort of ‘equilibrium’ with the local natural fire regime. This conclusion is unlikely to have been significantly affected by allometric equation uncertainties (Notes S2) and is also a difference that has been noted before (Russell-Smith *et al.*, 2003). It does not necessarily reflect some sort of preconceived bias by the investigators involved. Rather, as noted already, most early fire experiments were primarily designed to investigate the use of prescribed fire regimes as part of an overall pastoral range management strategy.

That pre-clearing of land before imposition of fire treatments can lead to much greater effects is not surprising. This is because fire is generally accepted to exert an effect on tropical vegetation structure primarily through dissimilar effects at different stages of tree development (Higgins *et al.*, 2000) with younger small trees prevented from reaching maturity with regular and/or intense fires, but with mature trees much more resistant (Swaine, 1992). Nevertheless, with the exception of hurricane/cyclone-induced damage we know of no cases where natural disturbances – even when involving a combination of fire and drought effects – have been reported to lead to anything approximating total canopy destruction. For example, for tropical forests typical (absolute) drought-induced increases in mortality rates in association with individual drought events are generally <10% (Leighton & Wirawan, 1986; Swaine, 1992; Nakagawa *et al.*, 2000; Williamson *et al.*, 2000; Slik *et al.*, 2008; Baker & Bunyavejchewin, 2009; Phillips *et al.*, 2009, 2010; Granzow-de la Cerda *et al.*, 2012; Feldpausch *et al.*, 2016) with the most severe case we know of being *c.* 22% (Van Nieuwstadt & Sheil, 2005). Moreover, in none of these studies has there been any suggestion that a subsequent transformation to some sort of savanna occurred. Indeed, two studies in the Amazon have shown that even after >7 yr of continuous experimental drought, increases in tree mortality and litter-fall rates have been surprisingly modest (Nepstad *et al.*, 2007; da Costa *et al.*, 2010). Tellingly, in the one case where a marked increased canopy openness in drought years has been reported, this has been only in conjunction with a concerted high-intensity fire regime maintained over nearly a decade in an area not previously experiencing fires (Silvério *et al.*, 2013; Brando *et al.*, 2014; Balch *et al.*, 2015). Indeed, rather than arising through ‘catastrophic events’ past forest–savanna transitions have usually been interpreted as arising because of a drying climate, often coupled with increased anthropogenic activity, and without ASS necessarily being involved (Cavelier *et al.*, 1998; Mayle *et al.*, 2000; Ledru, 2002; Ledru *et al.*, 2006, 2008; Kershaw *et al.*, 2007; Gu *et al.*, 2008; Mayle & Power, 2008; Rull *et al.*, 2015).

That the timing of fires can have a large effect on woody vegetation cover (Fig. 3) has also long been known. In particular, later on in the dry season when fuels are typically at their driest fires are also more intense and with more damaging effects (Dundas,

1944; Ramsay & Rose Innes, 1963; West, 1965; Pivello *et al.*, 2010). Our analysis also suggests that fires very early in the dry season might have larger than average effects. This is perhaps due to shoot lateral extension growth capabilities of woody plants not having been lost completely at this time, so highly susceptible but still physiologically active primordia are present (Kozlowski & Pallardy, 2002). Young regenerating seedlings still in the grass layer would be especially susceptible as they tend to cease growth later in the growing season than more mature adults (Doorenbos, 1965).

Why such modest effects?

A general estimate for fire return time in savannas is often taken to be 4 yr (Laris & Wardell, 2006; Furley *et al.*, 2008) and our data suggest, taking the associated $f=0.25$ as some sort of ‘generic value’, that a typical tropical vegetation burning regime should reduce the canopy cover by at most 0.2 (Fig. 5a). This represents a proportional loss of ζ_w of <0.5 except at the lowest ζ_w where losses are higher (Fig. 5b). Contributing to this low sensitivity must be the minimal overlap in the species composition of forest vs savanna (Torello-Raventos *et al.*, 2013). In particular for experiments in the forest–savanna zone, forest species are usually found to eventually dominate fire exclusion plots but with inherently fire-resistant savanna species more abundant where fire is present (Ramsay & Rose Innes, 1963; Devineau *et al.*, 1984; Louppe *et al.*, 1995; Russell-Smith *et al.*, 2003). This means that reductions in canopy cover and biomass associated with fire should be much less than would be expected should fire-specific trait adaptations not occur.

Putting it a different way, because there are the many differences between forest and savanna species associated with the ability of the latter to tolerate fire – for example a greater bark thickness (Hoffmann & Franco, 2003; Ratnam *et al.*, 2011) – upon imposition of burning treatments it would be expected that the replacement of forest species with savanna species would result in much less of an effect on woody canopy cover than would be the case were this species change not to occur.

Fire can, however, only be maintained where the canopy cover is typically less than *c.* 0.5 (Notes S6) where inter-tree competition for light is also not such an issue. Thus in savannas there is also no need for trees to grow to heights similar to that of the fire-free forest (Veenendaal *et al.*, 2015). Proportional differences in woody canopy cover associated with fire are therefore much less than is the case for biomass cover, especially at high ζ_w (Fig. 6b).

Fire experiments and the real fire world

According to our results, the magnitude of fire effects in tropical woody systems is strongly dependent on both frequency and timing. Thus, in translating our results to the ‘real world’ it is necessary to ascertain at what time of year, and how often, fires occur.

This has been studied in many different tropical regions and for a diversity of land uses (e.g. Archibald *et al.*, 2010; Alencar *et al.*, 2011; Oliveras *et al.*, 2013; Smit *et al.*, 2013; Beringer

et al., 2015; Smit & Prins, 2015) with methods varying from remote-sensing to (more commonly) field studies. In general, for open savannas (grasslands and shrub savannas), fire return times usually oscillate between 1 and 5 yr (Oliveras *et al.*, 2013). In savanna woodlands, fire frequencies vary widely (e.g. Archibald *et al.*, 2010), having been quoted in the range of 2–5 yr in Africa and Australia, and 6–12 yr in South America (Periera Júnior *et al.*, 2014). Regional variation in fire return intervals is largest for tall savanna woodlands and dry forests, with values ranging from c. 1–4 yr in West Africa to 10 yr in southern Africa. A general estimate for fire return time in savannas is often taken to be 4 yr (Laris & Wardell, 2006; Furley *et al.*, 2008). Tropical forests usually have long fire return intervals, with estimates in West Africa and the Amazon varying from 10 yr to decades (Hall & Swaine, 1981; Cochrane *et al.*, 1999; Archibald *et al.*, 2010).

Worldwide, most fires observed in savannas and tropical forests are a direct consequence of human activity (e.g. Russell-Smith *et al.*, 2009; Cochrane *et al.*, 1999). Such ‘anthropogenic’ fires generally occur early in the dry season, as part of arable land management practices (Hough, 1993; Mistry, 1998; Andersen *et al.*, 2005; França *et al.*, 2007). Late dry season fires are generally set for maximum impact when opening new land and reducing tree cover, or perhaps more commonly, occurring accidentally. This is because of their higher intensity and impact (Fig. 2) making them harder to manage and with their occurrence sometimes even being associated with substantial loss of life (Bowman *et al.*, 2011). Fires associated with lightning occur mostly during the late dry season/early wet season and with a less clear pattern as they are also dependent upon fuel loads of affected areas (Andersen *et al.*, 2005; França *et al.*, 2007; Devineau *et al.*, 2010).

The above considerations lead us to suggest that either a 1 yr return time early dry-season fire regime (typical of managed savannas) or a 4 yr return time late dry-season burn for natural fires (as for example in ‘protected areas’) should present a credible ‘best estimate’ average fire regime. And here, noting that there is significant overlap in the magnitude of the effects of $f=1.0\text{ yr}^{-1}$ (early) and $f=0.25\text{ yr}^{-1}$ (late) on canopy cover (Fig. 5), it would seem reasonable to take our estimates of an average fractional biomass loss for the former (c. 0.4) as a best estimate of the maximum extent to which the presence of fire reduces tropical tree cover below that which would occur in its total absence.

There are considerable uncertainties in our biomass loss estimates as these have come from continent-specific allometric equations (Notes S2). Nevertheless, we can, for the relatively high fractional crown cover plots KNP-01 and KNP-02, check our estimates with those recently reported for the same sites using the methodology of Colgan *et al.* (2012). For the control plots and estimating stand-level biomass by first back calculating the basal area from the supplied fractional cover (Fig. S2.1a in Notes S2), then using that basal area to predict the biomass (Fig. S2.1b in Notes S2), we obtain estimates for KNP-01 and KNP-02 of 64 and 30 t ha^{-1} as compared with the Colgan *et al.* (2012) estimates of 45 and 33 t ha^{-1} , respectively. More importantly, comparing the fractional reductions, we find quite similar estimates. For example, for the annual mid-season (August) burn Colgan

et al. (2012) estimates biomass reductions of 42 and 37%, respectively, with our analysis suggesting reductions of 57 and 52%. Estimating biomass directly from fractional cover (Veenendaal *et al.*, 2015), we obtain similar but somewhat lower estimates for the proportional reductions of this annual middle of the dry season fire regime of 35 and 25%, respectively.

Despite such uncertainties, allometric equation errors cannot account for the contrast in typical biomass reductions of c. 50% presented here when compared to reductions of >90% as implied by Bond *et al.* (2005). That analysis is, however, biased as it includes not only the flawed Matopos sites (MAT-01 and MAT-02), but also MAR-01 which as well as being pre-cleared had been deliberately exposed to high-intensity late dry-season burns to maximise treatment effects (Furley *et al.*, 2008). A comparison of the Bond *et al.* (2005) values for the Kruger National Park experiment (cited from Shackleton & Scholes, 2000) also suggests an over-estimation of the average effect: with their illustrated fire-associated reduction in biomass of c. 75% for KNP-03 for the upper extreme of the landscape-averaged values for the same experiment as given in fig. 1 of Higgins *et al.* (2007). That publication – effectively summarising biomass data for the KNP sites as also used in this analysis – suggests a typical fire-induced biomass reduction of c. 40% when averaged across the 1, 2 and 3 yr fire return time treatments (see also KNP-03 in our Fig. 3) – quite close to the c. 50% suggested here. Bond and colleagues similarly seem to have overestimated treatment effects for the Venezuelan fire exclusion study of San José *et al.* (1998) where a ‘control’ (nonfire) value for comparison with an annually burned savanna (above-ground biomass $\sim 0.4\text{ t DW ha}^{-1}$) was that of a nearby semi-deciduous forest (c. 160 t DW ha^{-1}), even though a nearby plot in the same experiment that had been exposed to 30 yr of total fire protection had a total above-ground biomass increase (including woody plants) over those 30 yr of only 4 t ha^{-1} .

Implications for fire-mediated feedbacks

Some authors are clearly of the view that there are many parts of the tropical world where relatively luxuriant tropical forests should exist but do not because their ‘climate space’ is occupied by more-open savanna-type vegetation types with their own endogenous fire regime (Hirota *et al.*, 2011; Staver *et al.*, 2011). Here, according to the theory of ASS it is considered that, should a closed forest-type woody tropical system become fire affected, then with subsequent woody plant growth impeded by fires grasses attain a dominance otherwise not possible. Importantly, the subsequent grass-dominated ecosystem is itself more susceptible to fire than was the forest due to the higher herbaceous fuel load: this then gives rise to a self-sustaining pyrogenic savanna-type ecosystem. Implicit in the ASS argument is that even in the absence of human intervention, a ‘natural fire’ regime can come in to play once a forest has been sufficiently ‘opened up’ by drought and/or fire or some other major disturbance, this fire regime being of a sufficient regularity to prevent the re-establishment of the ‘potential’ woody cover. But importantly, should a closed canopy become re-established, then due to

shading out of grasses and a less suitable microclimate for the permeation of fire, the alternative fire-free ‘forest’ formation is itself also highly stable (Hoffmann *et al.*, 2012a,b).

The extent to which the distributions of forest and savanna can, in many parts of the world, be taken as indicative of alternative stable states is, however, currently a matter of active debate (Hanen *et al.*, 2013; Staal & Flores, 2015; Staver & Hansen, 2015; Veenendaal *et al.*, 2015; Lloyd & Veenendaal, 2016) and in what follows we consider the extent to which the magnitude of effects for ‘natural fire’ regimes as revealed by our analysis can help contribute to this argument. Given that our results suggest that along with canopy cover in the absence of fire, it is also the extent of disturbance before imposition and frequency/timing of the fire regime that determine the magnitude of the fire response, we consider all factors together.

First, we note that although severe pre-clearing treatments should not be considered as representative of actual forest–savanna transition, it also seems that a naturally fire-free completely closed canopy can potentially be maintained in an open state by fire, but only with annual late-season burns (upper yellow ribbon in Fig. 5a). Such high frequencies are, however, only representative of an intensive anthropogenic burning regime. Nevertheless, when a more realistic natural (endogenous) fire return time of 4 yr is considered, it does seem possible for regular late-season fires to maintain what would otherwise be a fire-free closed canopy as high as $\zeta_{W(0)} = 0.8$ as open savanna (upper right side on ‘N’ arrow in Fig. 5a). But a more reasonable estimate of the maximum fire-free canopy cover that could be maintained under some sort of natural fire regime is $\zeta_{W(0)} = 0.6$ (median point of N arrow in Fig. 5a), by which time a canopy can already be considered to be partially open and, more likely than not, already consisting of trees typically found in savanna formation types (Torello-Raventos *et al.*, 2013).

Because natural world fire frequencies reflect an average fire return time as opposed to a continually repeated experimentally imposed interval, results from the fire-trial experiments analysed here might actually be severe overestimates of the relative impact at any given f . This can be illustrated by taking fire as a simple binomial process where the probability of burning is independent of time since the last burn (McCarthy *et al.*, 2001; Pueyo *et al.*, 2010; Hoffmann *et al.*, 2012a). Here, according to theory, the relationship between f (now treated as a probability) and the expected total time required to observe a single fire interval (T) is $[1 - (1 - f)^T]/[(1 - f)^T f]$ (Johnson *et al.*, 2005). This means, for example, that for $f = 0.25 \text{ yr}^{-1}$ a period of 10 yr without fires (which based on the experiments analysed here should be long enough for a ‘fire-protected savanna’ to grow back to a relatively closed forest-type formation) should be observed on average every 67 yr and a 20 yr fire period (certainly long enough for a fire-maintained savanna to revert to forest) every 1250 or so years. Whilst the latter might seem a long time (as suggested by Hoffmann *et al.* (2012a) who made a similar back-of-the-envelope calculation for the more severe $f = 0.33 \text{ yr}^{-1}$ and for which one obtains $T = 63 \text{ yr}$ and $T = 9117 \text{ yr}$ for 10 and 20 yr fire-free periods, respectively), the real question is ‘a long or short time relative to what?’ To which we suggest the answer is ‘relative to

return times for the opposite transition from forest to savanna’. But the latter must be at least several millennia because, as mentioned above, we know of no recorded occurrence of such a transformation having ever naturally occurred worldwide. That is to say, even if a forest were to be somehow transformed to savanna through a major disturbance (the existence of such disturbances we emphasise being purely hypothetical), then due to the probabilistic nature of fire frequencies one would expect that within centuries, if not decades, a fire-free period long enough to allow the return to the natural forested ‘fire-free’ state should occur.

Of course, in many forest–savanna transition zones all vegetation types are actively managed with frequent burning by the local populations. And because of this – as was the original hypothesis giving rise to many of the fire trials in the first place – it is quite likely that some areas in the ‘derived savannah zone’ were indeed originally forest (Charter & Keay, 1960; Clayton, 1961; Ramsay & Rose Innes, 1963; Phillips, 1965; Egunjobi, 1971). Thus, it should not be surprising that long-term protection from fire in such regions allows a return to the woodier vegetation types originally there. Hence, assertions that because such experiments have shown that a transformation of savanna to forest occurring when fire is excluded is supportive evidence for the existence of ASS (Murphy & Bowman, 2012) are flawed. This is because such logic assumes (contrary to the notions of those who established many of the experiments in the first place) that the vegetation before the imposition of the fire exclusion experiment was not human-influenced at the time of treatment imposition.

Indeed, perhaps we should not think of nonanthropic fire regimes as being in any way representative of the current fire regime of the savanna lands with, in particular in Africa, human influences on fire patterns now being the dominating effect for all but the most strictly protected areas (Hough, 1993; Mbow *et al.*, 2000; Sheuyange *et al.*, 2005; Laris, 2011; Kamau & Medley, 2014; Laris *et al.*, 2015). Here, rather than thinking of most savanna formations as typically existing in some sort of natural fire-mediated equilibrium state, a far more realistic notion is that of a myriad of highly dynamic systems which, in the absence of significant fire interventions, are always tending towards their own unique soil/climatic optimum (Laris, 2011; Laris *et al.*, 2015). In the natural state this tendency is counteracted by the occasional set back by fire, but – in the situation typical of much of modern-day Africa at least – most savannas are maintained in a much more open state than would otherwise be the case through the active interventions of the local populations.

Conclusions

The analysis here shows that effects of fire on tropical vegetation structure have often been overstated in the past with classical fire experiments, almost all of which were not designed to evaluate the effects of natural fire regimes on unmanaged ecosystems, having been misinterpreted. This is because they purposely utilised pre-treatments and high-intensity burning regimes that do not reflect those occurring in natural ecosystems.

The analysis here does not imply that there are no effects of fire. Rather, with the modest effects observed – as shown by the relatively benign effects of early season fires even when imposed on an annual basis – this means that it is unlikely that a self-sustaining nonanthropic fire regime could ever emerge of a strength sufficient to maintain some open savanna-type vegetation in areas that would otherwise be forest.

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Author contributions

J.L. and E.M.V. conceived the study, analysed data and wrote the paper; M.T.-R., F.v.L. and I.O. assisted with data analysis and contributed substantially to the writing and discussion of the paper; H.S.M, N.M.S. and G.P.A. provided data and contributed to the writing and discussion of the paper.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Notes S1 Details of the fire trials examined.

Notes S2 Estimation of fractional canopy cover and biomass.

Notes S3 Model description, fitting procedure and test statistics.

Notes S4 Goodness of model fit.

Notes S5 Model interpretation.

Notes S6 Relationship between herbaceous and woody vegetation cover.

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