DR. BRETT PATRICK MURPHY (Orcid ID : 0000-0002-8230-3069)

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Biomass consumption by surface fires across Earth's most fire-prone continent

Running head: Biomass consumption by fire

Brett P. Murphy[1]*

Lynda D. Prior[2]

Mark A. Cochrane[3]

Grant J. Williamson[2]

David M.J.S. Bowman[2]

1 Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, NT 0909, Australia

2 School of Biological Sciences, Private Bag 55, University of Tasmania, Hobart, TAS 7001, Australia

3 Appalachian Laboratory, University of Maryland Center for Environmental Science, Frostburg, MD 21532, USA

* Corresponding author:

brett.murphy@cdu.edu.au

ph: +61 8 8946 6049

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ABSTRACT

Landscape fire is a key but poorly understood component of the global carbon cycle. Predicting biomass consumption by fire at large spatial scales is essential to understanding carbon dynamics and hence how fire management can reduce greenhouse gas emissions and increase ecosystem carbon storage. An Australia-wide field-based survey (at 113 locations) across large-scale macroecological gradients (climate, productivity and fire regimes) enabled estimation of how biomass combustion by surface fire directly affects continental-scale carbon budgets. In terms of biomass consumption, we found clear trade-offs between the frequency and severity of surface fires. In temperate southern Australia, characterised by less frequent and more severe fires, biomass consumed per fire was typically very high. In contrast, surface fires in the tropical savannas of northern Australia were very frequent but less severe, with much lower consumption of biomass per fire (about a quarter of that in the far south). When biomass consumption was expressed on an annual basis, biomass consumed was far greater in the tropical savannas (>20 times that of the far south). This trade-off is also apparent in the ratio of annual carbon consumption to NPP. Across Australia's naturally vegetated land area, annual carbon consumption by surface fire is equivalent to about 11% of NPP, with a sharp contrast between temperate southern Australia (6%) and tropical northern Australia (46%). Our results emphasise that fire management to reduce greenhouse gas emissions should focus on fire-prone tropical savanna landscapes, where the vast bulk of biomass consumption occurs globally. In these landscapes, grass biomass is a key driver of frequency, intensity and combustion completeness of surface fires, and management actions

that increase grass biomass are likely to lead to increases in greenhouse gas emissions from savanna fires.

INTRODUCTION

Landscape fire is a key component of the global carbon cycle. Biomass consumed during landscape fires (excluding agricultural burning) accounts for carbon emissions of around 2.0 Gt C year^{-1} (van der Werf *et al.*, 2017), equivalent to about 20% of emissions from burning fossil fuels (Boden *et al.*, 2017). There are strong interactions between fire regimes and global environmental change, particularly climate and land use, though the outcomes of these interactions are difficult to generalise, let alone predict. Broadly, fire activity is limited in arid and semi-arid regions because of the scarcity of biomass to burn. Conversely, biomass-dense biomes burn less frequently because of the rarity of suitable fire weather. The highest fire frequencies occur in seasonally dry climates, where the weather is frequently suitable for fire and there is abundant biomass to burn (Bradstock, 2010, Krawchuk & Moritz, 2011, Boer *et al.*, 2016). Future climate-driven increases in the severity of fire weather – especially increased temperature and increased frequency and intensity of drought – and increased plant productivity due to atmospheric CO_2 enrichment might be expected to result in more frequent fires (Jolly *et al.*, 2015). However, uncertainties about the impacts of climate change on global fire regimes remain very large; statistical and process-based models of fire activity are hamstrung by complex interactions and feedbacks, which hamper reliable predictions (Bowman *et al.*, 2014c, Harris *et al.*, 2016). Superimposed on changing climate and fire weather are large-scale changes to land use, which can either increase fire frequency (e.g. through fragmentation or degradation of moist forests: Cochrane, 2003, Lindenmayer *et al.*, 2011) or decrease it (e.g. through clearing vegetation for agriculture, intensification of grazing: Archibald *et al.*, 2009, Andela *et al.*, 2017) at large spatial scales. For example, despite a warming climate over the last two decades, there has been a large decrease in the area burnt each year globally (24% decrease between 1997 and 2005) – a trend which is thought to be driven by agricultural expansion and intensification, especially in savanna landscapes (Andela *et al.*, 2017). Given these complexities, a research frontier is understanding the carbon dynamics and emissions associated with fires across biomes, and how management and land use affect these biogeochemical processes.

By burning biomass, landscape fires increase atmospheric greenhouse gas concentrations, and thereby contribute to climate change. With growing global pressure to offset carbon emissions from fossil fuel combustion, there is increasing interest in managing landscape fire regimes in ways that increase ecosystem carbon storage and/or reduce emissions of greenhouse gases, primarily by reducing the occurrence of uncontrolled wildfires (Grace *et al.*, 2006, Hurteau & Brooks, 2011, Russell-Smith *et al.*, 2015, Hurteau *et al.*, 2016). However, it is clear that technological attempts to subdue fire at large scales (fire suppression) are ecologically and economically unsustainable, and may even lead to greater long-term emissions due to infrequent high-severity wildfires, which can trigger enormous losses of carbon to the atmosphere (Hurteau & Brooks, 2011) and catastrophic switching from high-biomass to low-biomass biomes (Bowman *et al.*, 2013). In contrast to fire suppression, prescribed burning (also known as fuel reduction burning) has emerged as a potential means of reducing the incidence of uncontrolled wildfires and reducing greenhouse gas emissions (although with its own limitations and caveats).

Prescribed burning involves deliberately lighting fires at times when fire weather conditions are less severe (e.g. early in the fire season), under the assumption that such fires are considerably less intense and consume a smaller proportion of available fuel than wildfires. Frequent prescribed fires are variously assumed to have less negative impacts than infrequent uncontrolled wildfires, including reduced greenhouse gas emissions per unit of area burnt (Russell-Smith *et al.*, 2009) and tree mortality (Murphy *et al.*, 2009). Prescribed burning has been shown to significantly reduce the occurrence of uncontrolled wildfires in some landscapes (Boer *et al.*, 2009, Price *et al.*, 2012b), but there are many exceptions (e.g. Price *et al.*, 2012a, Price *et al.*, 2015). The question of whether prescribed burning can result in a net long-term decrease in emissions due to biomass consumption by fire remains controversial, because the cumulative carbon cost of frequent low-severity fires may exceed that of infrequent high-severity fires (Hurteau *et al.*, 2008, Hurteau & Brooks, 2011, Bradstock *et al.*, 2012, Campbell *et al.*, 2012, Hurteau *et al.*, 2016). Hence, trade-offs between fire frequency and severity in terms of biomass consumption and greenhouse gas emissions are central to optimising large-scale fire regimes for greenhouse gas abatement.

An unresolved question is how the benefits of prescribed burning vary across large-scale pyrogeographic gradients, from infrequently burnt, low productivity arid systems, through frequently burnt, intermediate productivity systems with seasonal climates, to infrequently burnt, moist productive systems (Bradstock, 2010). Answering this question hinges on the integration of remote-sensing and field-based observations. Analysis of satellite-derived records of fire activity (mainly fire frequency and, to a lesser extent, intensity) has driven the development of pyrogeographic theory (e.g. Archibald *et al.*, 2009, Krawchuk & Moritz, 2011, Archibald *et al.*, 2013, Boer *et al.*, 2016), yet there has been far more limited investigation of severity and biomass consumption, which is critical to developing and testing models of fire regimes, and hence understanding trade-offs between prescribed burning and the occurrence of wildfires. Such analyses require ground-based observations collected systematically at large spatial scales.

Australia is an ideal model system to explore how variation in fire regimes across large-scale gradients in climate and productivity (Murphy *et al.*, 2013) impacts continental-scale carbon budgets by consuming biomass. Australia is ideal because it is generally highly fire-prone and prescribed burning is widely practised. Despite comprising just 6% of the Earth's land area (excluding Antarctica), it is responsible for 14.4% of annual burnt area (Giglio *et al.*, 2013). It is also dominated by strongly contrasting biomes, ranging from temperate moist forests and heathlands to tropical savannas and deserts, positioned along strong gradients of annual rainfall and rainfall seasonality, and, consequently, fire activity (Bradstock, 2010, Murphy *et al.*, 2013, Williamson *et al.*, 2016). We conducted an Australia-wide field-based survey of biomass consumption by 113 recent fires, and use these data to identify the regions in geographic and environmental space where fire consumes the greatest amount of biomass, both in absolute terms, and expressed as the ratio of annual carbon consumption to NPP. Our survey included both prescribed fires and wildfires. However, it did not include crown fires, which consume the leaves and fine twigs of the canopy, but rather focused on the more geographically common surface fires, which consume ground-level fuels including shrubs. Our study makes a substantial contribution by estimating biomass consumption and carbon emissions at a continental scale, in order to better understand large-scale pyrogeographic patterns and the impacts of fire on the global carbon cycle. We frame our results in the context of global pressure to manage fire regimes to reduce biomass consumption by fire, and hence greenhouse gas emissions (e.g. Russell-Smith *et al.*, 2013, Lipsett-Moore *et al.*, 2018).

MATERIALS AND METHODS

Fuel biomass

At 113 locations we identified a recent fire scar (<<1 year, and no full growing season, since fire) in relatively natural vegetation (i.e. uncleared), across a range of biomes and climate zones (Table 1; Figure 1a). We did not attempt – given no reliable method for doing so – to distinguish between fire scars due to prescribed fires or wildfires. There are no records kept of the timing and location of prescribed burning across the vast majority of the Australian continent.

At each fire scar we established a survey site, consisting of six 30-m transects close to a burnt–unburnt boundary in otherwise homogeneous vegetation: three transects outside the fire scar (i.e. unburnt fuel transects) and three inside (i.e. burnt fuel transects). Transects were located at least 100 m from the burnt–unburnt boundary, and all transects were separated by at least 100 m. Measurements of surface fuel biomass along the unburnt transects provided an approximation of the pre-fire fuel load, and comparing this to fuel biomass measured along the burnt transects allowed us to estimate consumption of different fuel components by the fire. We acknowledge that this space-for-time substitution has potential limitations, most notably that by establishing transects close to the burnt–unburnt boundary we could bias our sampling towards areas that burnt with lower intensity and severity.

We did not measure overstorey fuel biomass or fuel consumption as none of the fire scars we encountered was due to a crown fire. A focus on surface fires enabled a consistent, actionable field protocol, because of the relative rarity of crown fires and their restriction to vegetation types that cover just 7% of Australia's land area (Murphy *et al.*, 2013).

At 10-m intervals along each transect, fine litter (≤6 mm minimum diameter) and aboveground biomass (AGB) of grass and herbs were completely removed from four 1-m^2 quadrats, separated and immediately weighed in a bucket on a 3-kg electronic balance. At each survey site, a single bulked sample (i.e. from the four 1-m^2 quadrats, combined) of each fuel type (fine litter, grass, herbs) was collected and weighed. These samples were later oven-dried (at 70°C for 48 hours) and weighed to estimate moisture content, in order to convert fresh weights of fuel biomass, measured in the field, to dry weight.

The biomass of woody debris (>6 mm minimum diameter) was measured using a modified planar-intercept method, based on that of Brown (1974). Along each 30-m transect, a vertical plane was visualised. Each time a piece of woody debris intercepted the vertical plane, its diameter was noted. Each intercept was classified according to the diameter of the woody debris: (1) twigs (>6–25 mm); (2) sticks (>25–76 mm); and (3) logs (>76 mm). Twig intercepts were counted in two 2-m sections of the transect (0–2 m and 13–15 m). Stick intercepts were counted in two 4-m sections of the transect (0–4 m and 11–15 m). Log intercepts were counted along the entire length of the 30-m transect, and the diameter of each intercept was recorded, as was the estimated diameter of the hollow centre, if present.

For each individual plane-intercept, the cross-sectional area of the woody debris was estimated from its diameter, assuming it was circular in cross-section (i.e. cross-sectional area = π (diameter/2)^2). For twigs and sticks, mean diameters of 1.37 and 4.22 cm, respectively, were assumed (Brown, 1974). For logs, the measured diameter was used, and if the core of the log was hollow, the cross-sectional area of the hollow was deducted. Hence the total cross-sectional area of all plane-intercepts in each diameter class could be estimated. For each diameter class, total cross-sectional area was converted to biomass of woody debris (t DM ha^{-1}) according to the formula:

$$Biomass = \frac{CSA}{L} \times AC \times SG ,$$

where *CSA* is total cross-sectional area (cm^2) of the woody debris and *L* is the length (m) of the transect. *AC* is the angle correction factor, assumed to be 1.13 for twigs and sticks and 1.00 for logs (Brown, 1974); *SG* is the specific gravity of the woody debris, assumed to be

0.63 for all diameter classes, based on the median of wood *SG* values for 1,925 Australian tree species (Ilic *et al.*, 2000). Brown (1974) reduced SG by 25% in instances where logs (>76 mm diameter) were obviously rotten. We found it impossible to assess, with any acceptable level of confidence or objectivity, whether logs were rotten, and hence we did not use this correction for rotten logs.

Shrub aboveground biomass was estimated using one of two methods, depending on shrub density and its variability:

(1) Where shrub density was low or variable, our measurement of pre- and post-fire aboveground biomass followed the general approach of Russell-Smith *et al.* (2009). Shrub density was assessed in a 2 × 15 m belt transect (1 m either side of the first 15 m of the main transect). The height of each shrub in the swath was recorded, and whether it was covered in leaves or leafless. We harvested individual shrubs at each site (total 234 individual shrubs) to develop a general allometric relationship between shrub height and aboveground biomass ($R^2 = 0.55$):

$$\log_{10} AGB = 1.55 \log_{10} H - 1.14,$$

where *AGB* and *H* are the aboveground biomass (g) and height (cm) of the individual shrub, respectively (see Supporting Information, Figure S1a). Hence, we estimated the aboveground biomass of each shrub in the belt transect from its measured height.

In some cases, shrubs were leafless, e.g. due to drought or fire. We accounted for this by multiplying the estimated biomass of the shrub with leaves (based on shrub height alone) by the estimated proportion of biomass contributed by stem (in an individual shrub with leaves). This was estimated by separating, oven-drying (at 70°C for 48 hours) and weighing the leaves and stems of 37 individual shrubs, and developing a general allometric relationship between shrub height and the proportion of aboveground biomass contributed by stems (R^2 =

0.16):

$$\text{logit}\, p_{stem} = 0.84 \log_{10} H - 0.82,$$

where p_{stem} is the proportion of total aboveground biomass contributed by stem biomass (Figure S1b).

We consider the approach of using allometric equations to estimate shrub biomass is justified for a large survey across diverse vegetation communities, because there is little variation in allometric relationships within plant functional types between ecoregions across Australia (Paul *et al.*, 2016). However, the generality of our two allometric equations, especially under varying environmental conditions such as light and water availability, is a potential source of uncertainty which we are unable to resolve.

(2) Where shrub density was high and homogeneous, shrub biomass was assessed by harvesting and weighing all aboveground shrub biomass in four 1-m^2 quadrats at 10-m intervals along each main transect. At each survey site, a single bulked sample of shrub biomass was collected and weighed in a bucket on a 3-kg electronic balance. This was later oven-dried and weighed to estimate moisture content, in order to convert fresh weights of shrub biomass, measured in the field, to dry weight.

The slope of the ground between the start and end of each transect was measured with a clinometer. Slope angle was used to estimate a correction factor (c) to convert biomass per unit of area of sloping ground to biomass per unit of horizontal area:

$$c = \sqrt{1 + (0.01\, slope)^2},$$

where *slope* is the slope angle in percent (Brown, 1974). The correction factor was applied to all components of fuel biomass.

Biomass consumption by fire

To estimate the amount of biomass consumed by a single fire, we compared the biomass of fuel between the unburnt and burnt transects:

$$fuel\ consumed_{single\ fire} = fuel_{unburnt} - fuel_{burnt},$$

where $fuel_{unburnt}$ and $fuel_{burnt}$ are the measured fuel biomass in unburnt and burnt areas, respectively. In two cases $fuel_{burnt}$ exceeded $fuel_{unburnt}$ (i.e. giving a negative number for biomass consumed), so we assumed that no fuel was consumed.

To estimate the amount of biomass consumed on an annual basis, we multiplied the fuel biomass consumed by a single fire by mean fire frequency, expressed as the mean annual proportion of the surrounding landscape (50-km radius) which is burnt, based on global burnt area data from MODIS satellite imagery for the 17-year period November 2000–November 2017, inclusive (Collection 6, described by Giglio *et al.*, 2016). In doing so, we assume that that the sampled fire is representative of typical fuel consumption in the region. We feel this is a valid assumption because we sampled fires quasi-randomly (i.e. as we came across them, without targeting particular fire or fuel attributes). In calculating annual proportion burnt, we excluded areas within the 50-km radius which were either permanent water (e.g. sea, lakes, rivers), or had vegetation which was heavily modified (e.g. by agricultural clearing), according to a recent high-resolution vegetation map of Australia (National Vegetation Information System, 2016).

We compared the amount of carbon consumed by fire on an annual basis to the amount of carbon captured through photosynthesis (i.e. net primary production: NPP). We first converted annual biomass consumption to carbon consumption by multiplying by 0.49 (i.e. the approximate carbon content of dry biomass: Cook *et al.*, 2005, Russell-Smith *et al.*, 2009). We estimated NPP from using a global NPP layer derived from MODIS satellite imagery for the 15-year period 2000–2014, inclusive (Running & Zhao, 2015). We took the mean NPP of the area surrounding each survey location (within a 50-km radius), again excluding parts of this area which were permanent water or heavily modified vegetation. Estimates of NPP at continental scales are uncertain, and various models produce widely varying estimates (Roxburgh *et al.*, 2004). The MODIS-based NPP layer we used gave a mid-range estimate of total NPP for Australia (2.1 Gt C year^{-1}), close to the median of estimates from the 12 models examined by Roxburgh *et al.* (2004) (1.8 Gt C year^{-1}).

Fire severity

To express fire severity (*sensu* Keeley, 2009), we used an index based on the proportion of fine woody debris (twigs: 6–25 mm diameter) that was consumed by fire. Estimates of the abundance of fine woody debris in burnt and unburnt areas were made using the planar-intercept method described above (in *Fuel biomass*), in two 2-m sections of the 30-m transect (0–2 m and 13–15 m). The fire severity index (range: 0–100) was expressed as:

$$Fire\ severity\ index = 100 - 100 \times \frac{FWD_{unburnt}}{FWD_{unburnt} + FWD_{burnt}},$$

where $FWD_{unburnt}$ and FWD_{burnt} are the counts of fine woody debris intercepts in unburnt and burnt areas, respectively. Focussing on a single fuel component allowed us to consistently compare severity across strongly contrasting vegetation types. Fine woody debris was chosen because it: (1) was present at virtually all sites, unlike the coarser woody components that tended to be absent from grasslands; (2) showed wide variation in the proportion consumed, unlike the finer fuel components (e.g. grass or fine litter), which tended to be almost entirely consumed by any fire. Using proportional consumption of twigs also has strong parallels with the use of minimum twig diameter as a post-hoc fire-severity index (e.g. Keeley, 2009).

Statistical analysis

We examined variation across the continent in a range of attributes related to fire regimes:

(1) fuel biomass (separately for grass, fine litter [mainly leaves and woody fuels <6 mm diameter] and all fuel components combined);

(2) mass of biomass consumed by a single fire;

(3) annualised mass of biomass consumed fire;

(4) ratio of annual carbon combustion by fire to NPP;

(5) the fire severity index.

Response variables (1) to (4) were continuous, and were modelled as least-squares linear regression models in the computer program R (R Core Team, 2015). Where necessary, the response variables were transformed prior to analysis to ensure normality of model residuals. Response variable (5), the fire severity index, was analysed as proportion data, i.e. $FWD_{unburnt}$ / ($FWD_{unburnt}$ + FWD_{burnt}) (see earlier explanation of terms), so it was most appropriate to model using a generalized linear model (GLM) with binomial errors.

All fire regime response variables were modelled as a function of (1) latitude and (2) mean annual proportion of the surrounding landscape (50-km radius) which is burnt, based on the 17-year (2000–2017) MODIS satellite-derived fire history.

We generated a continent-wide map of predicted values of the amount of biomass consumed by a single fire. The first step was to use our field data to develop a predictive model of biomass consumption as a function of environmental predictor variables. As predictor variables we used tree cover and summer rainfall concentration (proportion of mean annual rainfall falling in the austral summer months); these variables adequately described the strong gradients in biomass consumption associated with both latitude and aridity, despite being unable to account for temporal variability in biomass consumption within regions (e.g. due to fine-scale temporal variability in fire weather). The model was implemented as a generalized least-squares linear regression model (GLS) in R. GLS has the advantage of being able to adequately deal with spatially autocorrelated errors. There was strong spatial autocorrelation in our biomass consumption dataset, so we accounted for it in the GLS models using an exponential correlation structure (Crawley, 2012). All combinations of the predictor variables, including their interaction, were evaluated and the best model selected using Akaike's Information Criterion (AIC) (Burnham & Anderson, 2003) (Table S1). We used the best model (Figure S2) to predict the amount of biomass consumed by a single fire, across the entire continent. We also modelled the residual spatial autocorrelation using universal kriging (with an exponential variogram model) (Cressie, 2015), and predicted residuals across the entire continent. Our final map of predicted values of the amount of biomass consumed by a single fire was generated by taking the sum of the map of the GLS model predictions and the map of the kriged residuals.

The map of predicted values of the amount of biomass consumed by a single fire was multiplied by annual proportion burnt (within a 50-km radius) to generate a map of annual biomass consumption by fire. This was then divided by NPP (mean of a 50-km radius) to generate a map of the ratio of annual carbon consumption by fire to NPP (both with units: t C ha^{-1} year^{-1}). In some cases, the predicted ratio exceeded 1 (i.e. carbon emissions via fire exceed carbon inputs via NPP), which is highly unrealistic. Potential causes for this discrepancy include error in the modelled NPP layer, burnt area data or our statistical model. While it has limitations, the map of the ratio of annual carbon consumption by fire to NPP provides an indication of the parts of Australia where fire is most likely to strongly dominate carbon losses from terrestrial ecosystems.

We characterised uncertainty in the total amount of biomass consumed by fire across the Australian continent using a Monte Carlo simulation approach (bootstrapping). We sought to identify: (i) the uncertainty associated with variation in fuel biomass between transects at a single site; and (ii) the uncertainty due to the statistical model underpinning the total estimate. To achieve (i), we randomly selected combinations of the three burnt and unburnt transects (with replacement) at each site 10,000 times, and recalculated the total based on each randomisation. To achieve (ii), we randomly selected combinations of the sites 10,000 times (with replacement), and recalculated the total based on each randomisation. We undertook a third set of randomisations, where both the combinations of sites, and transects within sites were randomised 10,000 times. For the third set of 10,000 randomisations, we calculated the 2.5% and 97.5% quantiles of the total estimate of biomass consumption by fire, and use these as 95% confidence limits.

RESULTS

The strong latitudinal gradient in fire frequency (Figure 2a) was paralleled – but inversely – by a gradient in fire severity, expressed as the proportion of twigs (>6–25 mm) consumed by fire (Figure 2b). In the tropical north, where fire frequency tends to be extremely high (typically 10–40% burnt per annum), fire severity tended to be relatively low (fire severity index: 60–80% of twigs consumed), and highly variable. Moving south through the deserts, and into the temperate zone, fire severity increased significantly (to >90% of twigs consumed) and became less variable. Low-severity fires (<50% of twigs consumed), which were frequently observed in the tropics, were not observed in the temperate zone. This pattern strongly suggests a trade-off between fire frequency and fire severity across the continent.

Further paralleling the latitudinal gradients in fire frequency and severity were clear gradients in fuel type and biomass. There was a very marked shift from dominance by grassy fuels in the tropical north and central deserts to dominance by litter fuels in the temperate south (Figure S3). There was a five-fold increase in grass biomass moving from south to north (Figure 3a), and a six-fold increase in litter biomass moving in the opposite direction – north to south (Figure 3b). Summing across all surface fuel types, fuel biomass was highest in the far south, with about six times the fuel biomass of the north (Figure 3c).

Commensurate with the high total fuel biomass in southern Australia, biomass consumption by a single surface fire (expressed on a per hectare basis) was highest in the south, with four times the biomass consumption of the far north (Figure 4a). However, when biomass consumption is expressed on an annual basis, i.e. by multiplying biomass consumption per fire by annual area burnt, it is clear that biomass consumption over time is far greater in northern Australia (Figure 4b). Annual biomass consumption in the far north was more than an order of magnitude (>20 times) greater than that of the far south (1.4 *vs* 0.1 t DM ha^{-1} $year^{-1}$).

In terms of fire frequency and rate of biomass consumption by fire, there was a dramatic contrast in the fire regimes of tropical and temperate sites. The tropical savanna sites typically had extremely high fire frequencies, and consistently low biomass consumption per single fire (Figure 4a). Temperate sites on the other hand had consistently low fire frequencies, but biomass consumption per single fire was typically very high.

At many of our survey sites in the tropical savannas of northern Australia and the deserts of central Australia, we estimate that much of the carbon captured via NPP is consumed by fire. Fire consumed about 25% of NPP at the northernmost sites (annual carbon combustion/NPP), but only about 0.4% of NPP at the southernmost sites (Figure 5a). There was a very strong relationship between annual proportion burnt and the ratio of annual carbon consumption by fire to NPP, suggesting that high fires frequencies – rather than high biomass consumption per fire – are responsible for driving the continent's highest rates of carbon turnover.

The parts of northern Australia where the ratio of annual carbon consumption by fire to NPP is greatest are not the highly fire-prone mesic tropical savannas (i.e. along the northern coast), but rather the semi-arid savannas to hot deserts of northwestern Australia (Figure 6c). In these regions, most of the carbon captured by NPP appears to be consumed by fire – despite fire frequency being substantially lower than in the mesic savannas further north.

We estimate that across Australia's naturally vegetated land area (6.56×10^6 km^2), fire consumes biomass of 0.50 t DM ha^{-1} each year, containing carbon of 0.25 t C ha^{-1}. Hence, total fuel biomass consumed by fire across Australia in a typical year is estimated to be 329 Mt (95% confidence interval: 257–475; Figure S4), containing about 161 Mt of carbon (83% of which is consumed in the tropics). Across this area, NPP averages around 2.3 t C ha^{-1} year^{-1}. Therefore, in a typical year, fire consumes the equivalent of about 11% of the carbon captured by Australia's natural vegetation. North of the Tropic of Capricorn this figure rises dramatically, equivalent to 46% of carbon captured – compared to just 6% of carbon captured south of the Tropical of Capricorn.

At our tropical survey sites, the dominance of fine fuels by grass was a strong predictor of the proportion of fine fuels and total fuels consumed by fire (R^2 = 0.54 and 0.35, respectively; Figure 7). At sites with fine fuel dominated by grass, about 99% and 93% of fine fuel and total fuel, respectively, was consumed by fire. However, at sites with fine fuel dominated by litter, these were reduced to about 76% and 39% of fine fuel and total fuel, respectively. The magnitude of this effect was substantially larger than the estimated reduction in biomass consumption that would be achieved by switching from all late dry season fires (60% of biomass consumed) to all early dry season fires (46% and 38%, in the low and high rainfall zones; 600–1000 mm and ≥1000 mean annual rainfall, respectively) (Australian Government, 2015, Russell-Smith *et al.*, 2015).

DISCUSSION

We have conducted a continental-scale analysis which integrates detailed field data on fuels and fire effects from 113 locations across the Australian continent with satellite-derived estimates of fire frequency and NPP. Our findings extend previous pyrogeographic analyses of Australia (Murphy *et al.*, 2013), and provide empirical evidence of the critical role of fire in the carbon cycle, including the trade-offs between fuel types and fire frequency/severity, which affect greenhouse gas emissions.

Australia's strong latitudinal gradient in fire frequency, from the monsoon tropics (40% burnt per annum) to the extreme southern extremities of the continent (<1% burnt per annum) (Figure 2a), has been well described previously (e.g. Russell-Smith *et al.*, 2007, Murphy *et al.*, 2013). However, our understanding that this gradient is also paralleled by a strong gradient in fire severity (i.e. generally frequent, low-severity fires in the north; infrequent, high-severity fires in the south) has been based on qualitative observations or inferred from conceptual models, as described by two recent syntheses of Australian pyrogeography (Bradstock, 2010, Murphy *et al.*, 2013). We have used extensive field data to demonstrate that severity of surface fires increases markedly from north to south (Figure 2b). Despite a trade-off between fire frequency and severity across the continent, it is clear that frequency is the key driver of annual biomass consumption by surface fire, rather than severity. The high biomass consumption per fire in the far south of the continent (Figure 4a), does not come close to compensating for the effect of very high frequencies in the far north (Figure 4b). The strength of the relationship between total biomass consumption (and hence carbon emissions) and surface fire frequency – and the relative unimportance of other fire regimes attributes such as typical fire severity – is central to understanding how land management by humans impacts the global carbon cycle. Recently, Andela *et al.* (2017) have demonstrated that global burnt area decreased by almost a quarter (*c.* 24%) over 18 years (1998–2015), apparently driven by land use changes in tropical savannas. One region with the greatest reduction in burnt area was Australia (*c.* 37%), particularly in the sparsely populated Western Desert region. The cause of the reduction in that region remains unclear, but may be related to marked fluctuations in fuel availability in the extensive *Triodia* grasslands, as a result of high-rainfall years and subsequent wildfires associated with La Niña conditions (Burrows *et al.*, 2009, Bliege Bird *et al.*, 2012). Overall, our finding of a positive relationship between annual biomass consumption by surface fires and annual proportion burnt is consistent with the notion that a trend of decreasing area burnt by surface fires could be associated with a large reduction in emissions from landscape fires globally (Andela *et al.*, 2017). In savannas, it is unlikely that an associated increase in fire severity could completely compensate for the decrease in burnt area. However, an important counterpoint is provided by recurrent crown fires in temperate regions, which can cause state change from biomass-dense forest to a treeless state (e.g. Bowman *et al.*, 2013).

Our study is the first comprehensive, field-based estimate of biomass consumption by fire – and the relative contribution of fire to carbon cycling – across an entire continent. Previous work to characterise biomass consumption by fire at very large spatial scales has utilised detailed process-based models (e.g. van der Werf *et al.*, 2010, van der Werf *et al.*, 2017) or model-based estimates from satellite-derived data (Andela *et al.*, 2016), rather than relying primarily on field data, which have limited spatial coverage and are typically collected idiosyncratically (van Leeuwen *et al.*, 2014). For example, the most recent and comprehensive global estimates of biomass consumption by fire have been made by van der Werf *et al.* (2017). Comparing their estimates of carbon consumption by fire (available at http://www.globalfiredata.org/) with ours, we see strong agreement in terms of regional patterns (R^2 = 0.74; Figure S5). However, our total estimate of biomass consumption across Australia is somewhat higher than that of van der Werf *et al.* (2017); they estimated that fires (excluding agricultural burning) consume biomass totalling 220 Mt DM year^{-1}, while we estimated 328 Mt DM year^{-1}. The satellite-derived estimates of biomass consumption of Andela *et al.* (2016) compare well with ours in terms of broad patterns – most notably, the increase in biomass consumption per fire from north to south. Our findings – derived by integrating detailed field data from 113 locations across the Australian continent with satellite-derived estimates of fire frequency and NPP – demonstrate that frequent fires drive very high rates of carbon turnover in the seasonally wet–dry tropical savanna landscapes. Across the continent, the equivalent of about 11% of the carbon captured via NPP is consumed by surface fire, but we found strong geographic variation in this figure. Frequent fires characteristic of seasonally wet–dry tropical savanna landscapes were found to drive very high rates of carbon turnover, such that the equivalent of almost a quarter of the carbon captured via NPP in tropical Australia is consumed by surface fire. By contrast, only a small proportion is consumed by surface fire in the mid-latitudes (6%).

Over the last few decades, there has been an increasing appreciation of the importance of fire as a driver of ecosystem function in tropical savannas, e.g. regulating biogeochemical cycles (Cook, 1994, Chen *et al.*, 2003), vegetation structure (Moreira, 2000, Murphy & Bowman, 2012), and biodiversity (Russell-Smith *et al.*, 2010, Andersen *et al.*, 2012). However, our analysis emphasises the potential importance of fire in tropical deserts, such as those of northwestern Australia. These systems burn much less frequently than the mesic savannas (Figure 1b), yet the direct effects of fire are likely to dominate many aspects of ecosystem function to a far greater extent, because a much greater proportion of incoming carbon (i.e. via NPP) is eventually consumed by fire. Our analysis suggests that in parts of arid northwestern Australia (<450 mm mean annual rainfall), which burn at a rate of about 10% per annum, almost all of the carbon captured via NPP is consumed by fire. In contrast, in the mesic tropical savannas (>1000 mm mean annual rainfall), which burn at a rate of about 40% per annum, only 46% of the carbon captured via NPP is consumed by fire. It is likely that in tropical deserts, fire has a more significant effect on carbon and nitrogen cycling than in the productive, albeit highly fire-prone, mesic savannas. Importantly, in these environments there is evidence that Indigenous patch burning can substantially reduce the area burnt by damping inter-annual variation in moisture supply that affects grass fuel production (Bliege Bird *et al.*, 2012), thus affecting carbon cycling as well as biodiversity (Bird *et al.*, 2013).

The magnitude of biomass consumption by surface fire across a continent – consuming carbon equivalent to 11% of continental NPP – underscores the significant impact that broad-scale fire management can have on the global carbon budget (Grace *et al.*, 2006). That carbon emissions are so strongly concentrated in the mesic savannas of northern Australia highlights that this is the region where the greatest carbon benefits can be derived. Indeed, earlier work has suggested that opportunities for emissions abatement through fire management (namely prescribed burning under mild fire weather conditions) in eucalypt forests and woodlands are largely restricted to Australia's monsoon tropics (Russell-Smith *et al.*, 2009); in temperate forests, the emissions generated by low-severity prescribed burning tend to far exceed those avoided by preventing high-severity wildfires (Bradstock *et al.*, 2012). Our findings are consistent with the notion that if prescribed burning increases overall fire frequencies, there will be a net increase in emissions, even if typical fire severity is significantly lower. However, we acknowledge that high-severity crown fires can cause significant carbon losses (e.g. Bowman *et al.*, 2014a), and note that our study focussed on surface fire regimes – we did not sample crown fires. The Australian debate about the ability of prescribed burning of dry *Eucalyptus* forests to deliver emissions abatement is mirrored in North American *Pinus* forests (Hurteau & Brooks, 2011, Campbell *et al.*, 2012, Hurteau *et al.*, 2016).

In Australia's mesic tropical savannas, prescribed burning in the early dry season (April–July, inclusive) reduces the extent of subsequent late dry season wildfires (Russell-Smith *et al.*, 2009, Price *et al.*, 2012b, Price *et al.*, 2015). However, whether prescribed burning can occur without increasing *overall* fire frequency (i.e. the sum of prescribed fires and wildfires) remains uncertain (Price, 2015). Vast areas of Australia's savannas are being deliberately burnt in the early dry season in an attempt to reduce the amount of biomass consumed by fire each year, primarily by reducing fire severity, thereby reducing emissions of the greenhouse gases methane and nitrous oxide, which can be traded on carbon markets (Russell-Smith *et al.*, 2013, Murphy *et al.*, 2015). However, our study suggests that reducing carbon emissions from northern Australian savanna landscapes requires close management of grass and litter biomass, and not just the seasonal timing of ignitions (Figure 7). A feature of northern Australian pyrogeography is the lower frequency of fires in pastoral landscapes due to cattle grazing reducing grass biomass (Russell-Smith *et al.*, 2007). Grazing by large herbivores has been shown to reduce grass biomass and subsequent fire frequencies and/or severities in mesic and semi-arid savannas. For instance, high densities of swamp buffalo (*Bubalus bubalis*) in Kakadu National Park have been correlated with lower fire activity (Russell-Smith *et al.*, 1997, Lehmann *et al.*, 2008). Conversely, grassy weeds – typically introduced as fodder for domestic stock – have the potential to increase fire frequency and severity following the establishment of a grass–fire cycle (D'Antonio & Vitousek, 1992). This process is occurring in parts of central and northern Australia with the invasion of the African grasses buffel (*Cenchrus ciliaris*) and gamba (*Andropogon gayanus*) grass, leading to increases in fire frequency and severity, driving substantial loss of woody cover (Butler & Fairfax, 2003, Setterfield *et al.*, 2010, Bowman *et al.*, 2014b). Bowman *et al.* (2007, 2014b) have suggested that a native grass–fire cycle has become established in parts of northern Australia under non-Indigenous fire management, where native annual grasses, especially *Sorghum* (also known as *Sarga*) spp., have increased in abundance, leading to increased fire frequencies and severities. There are few feasible options for reducing grassy fuels loads, and consequently fire frequency and severity, at large spatial scales once a grass–fire cycle has become established. However, approaches which have been suggested are the careful use of grazing (e.g. Bowman, 2012) and 'wet season' burning to kill immature annual grasses shortly after germination (Dyer *et al.*, 2001, Russell-Smith, 2010). Any such intervention must be accompanied by appropriate risk analysis and, if implemented, be closely monitored and evaluated to identify perverse outcomes, both in terms of greenhouse gas emissions and biodiversity impacts. For example, while cattle grazing can reduce grass biomass, and hence fire activity, reduced greenhouse emissions from landscape fires may well be offset by increased methane emissions from enteric fermentation by cattle. Likewise, cattle grazing has been demonstrated to have negative impacts on biodiversity in northern Australia (e.g. Woinarski & Ash, 2002, Legge *et al.*, 2011).

A key unanswered question is whether extensive prescribed burning in the early dry season might promote the establishment of a grass–fire cycle in mesic savannas, as postulated by Bowman *et al.* (2007). They argued that extensive early dry season burning might cut short the growing season of perennial grasses and woody understorey plants, thereby favouring annual grasses, especially annual *Sorghum*, which senesce very early in the dry season. We recommend that a cautious approach to fire management in tropical savannas be adopted, whereby the mid- to long-term effects of prescribed burning are closely monitored, to minimise the risk of perverse outcomes (particularly the promotion of a grass–fire cycle). Providing long-term reductions in carbon emissions from savanna landscapes requires close management and monitoring of grass and litter biomass, not just the seasonal timing of ignitions.

Through the integration of field-based and remote-sensing data, we have demonstrated the pivotal role fire plays in the carbon cycle of Australia, with an estimated 11% of NPP being consumed by surface fire. We show that there are strong geographic patterns in carbon consumption reflecting the interplay of fire frequency and grass and litter fuel types – 46% of NPP is consumed by fire in tropical sites compared to 6% in mid-latitude sites. Because of this geographic pattern, we argue that manipulation of fire regimes has the greatest effect on carbon emissions in the tropical savannas. Our findings also highlight that if management actions inadvertently switch the predominant fuel type from litter to grass, savings in greenhouse gas emissions due to manipulating the predominant season of burning may be negated. Our findings, based on an Australia-wide survey, would likely hold for other continents, given our estimates of total biomass consumed by fire tally with recent global estimates based on process-based models (van der Werf *et al.*, 2017). There is a need to validate such assumptions using field-based studies on other continents.

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TABLES

Table 1 Summary of climate zones and biome types sampled in the fuel and fire characteristics survey (113 sites).

Climate zone	Biome	Number of sites
Tropical	Savanna	47
	Grassland	7
Desert	Grassland	12
	Shrubland	9
Temperate	Forest	19
	Shrubland	10
	Woodland	6
	Heathland	3

FIGURE CAPTIONS

Figure 1 Locations of field measurements of fuel biomass and fire characteristics (n = 113). The climate zone of each survey site is shown, over maps of: (a) rainfall seasonality, defined here as the proportion of annual rainfall occurring in the wettest six consecutive months; and (b) mean annual proportion of the surrounding landscape (50-km radius) that is burnt, from the MODIS satellite record (2000–2017). The dashed line indicates the Tropic of Capricorn. In (c), the relationship between fire frequency and rainfall seasonality for the survey sites is shown. The regression line shows the predictions of a least-squares linear model (with 95% confidence intervals).

Figure 2 Variation in (a) the mean annual proportion burnt (within 50-km radius) and (b) the fire severity index, across the latitudinal gradient. The fire severity index is the proportion of twigs (6–25 mm diameter) consumed by fire. The regression lines in (a) and (b) show the predictions of a least-squares linear model and generalized linear model (binomial errors), respectively (both with 95% confidence intervals).

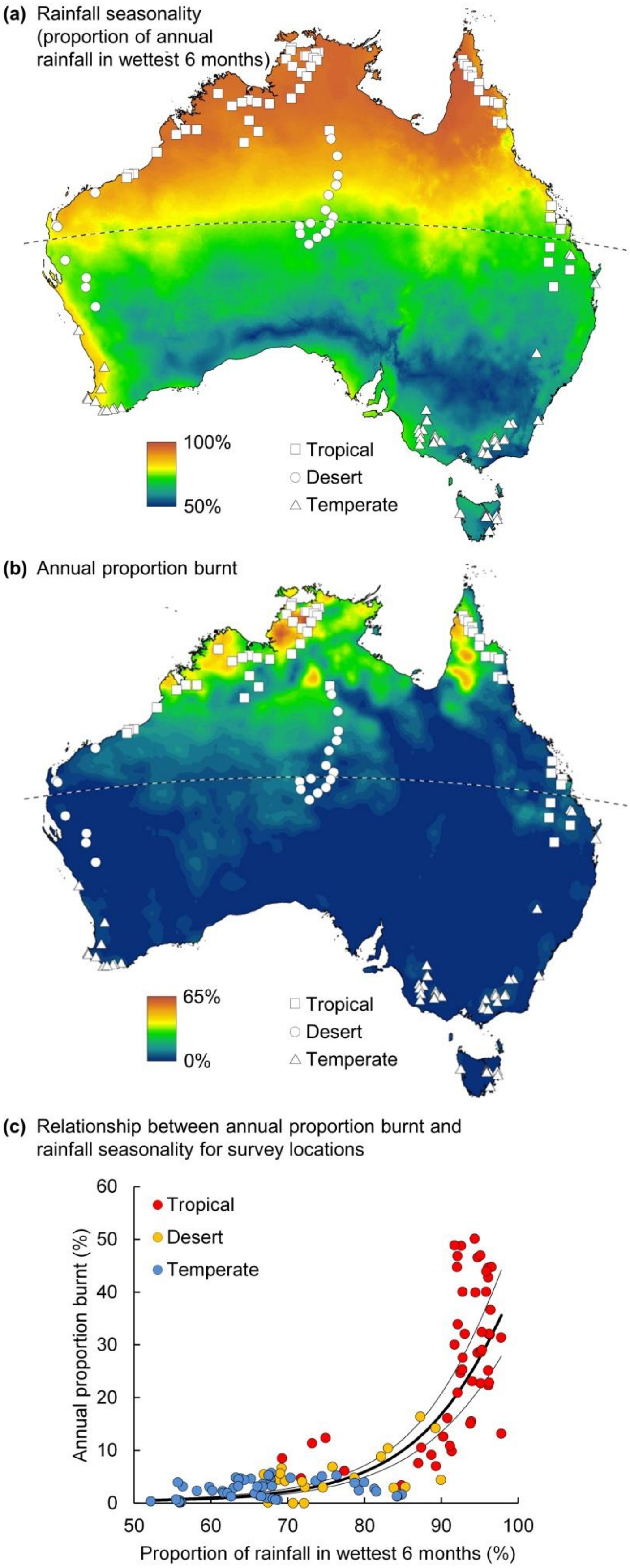
Figure 3 Variation in fuel biomass across the latitudinal gradient: (a) grass; (b) fine litter (mainly leaves and woody fuels <6 mm diameter) and (c) all surface fuel components combined. The regression lines show the predictions of least-squares linear models (with 95% confidence intervals).

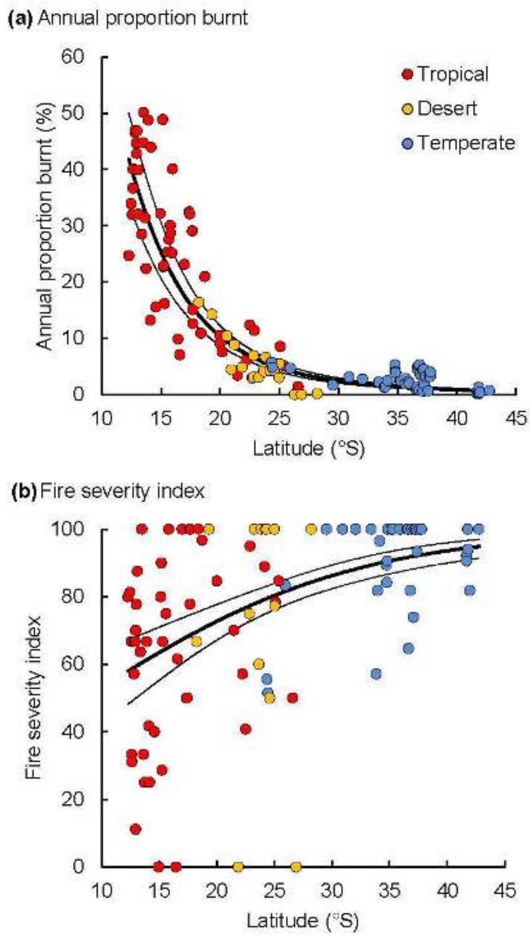
Figure 4 Biomass consumption (a) by a single surface fire and (b) by repeated surface fires over time (expressed on an annual basis), in relation to latitude (left column) and annual proportion burnt (within 50-km radius) (right column). The regression lines show the predictions of generalized least-squares linear models (with 95% confidence intervals).

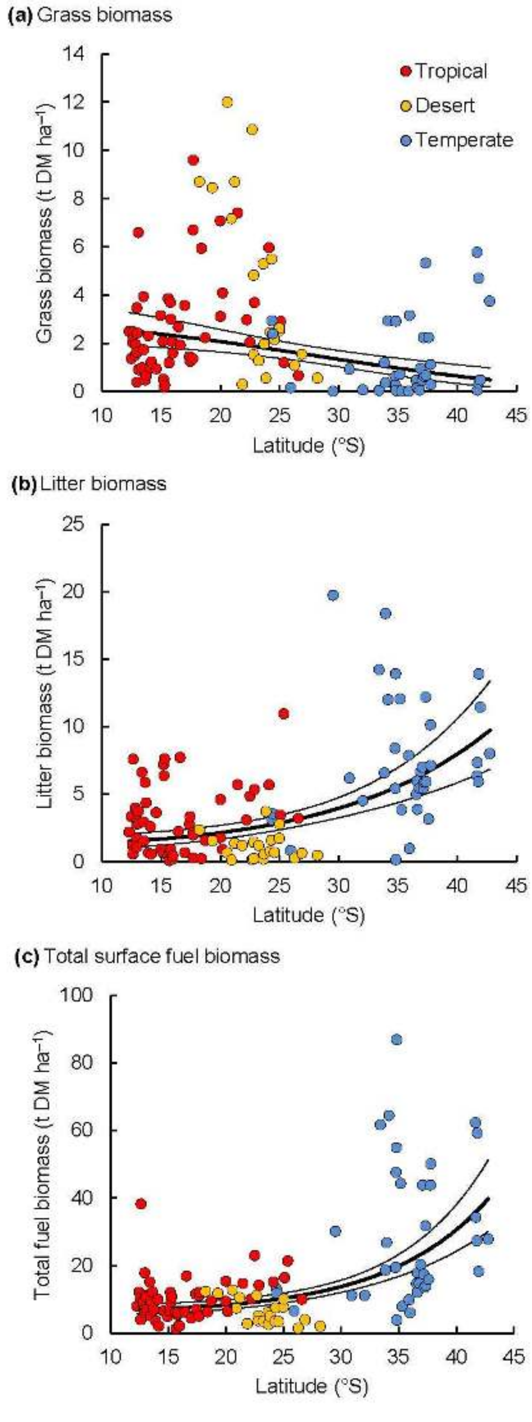
Figure 5 The ratio of annual carbon consumption by surface fire to net primary production, in relation to the latitudinal gradient in fire frequency, with latitude shown in (a) and annual proportion burnt (within 50-km radius) in (b). Note that both the y-axes and the x-axis in (b) are plotted on a $\log_{10}$ scale. The regression lines show the predictions of least-squares linear models (with 95% confidence intervals).

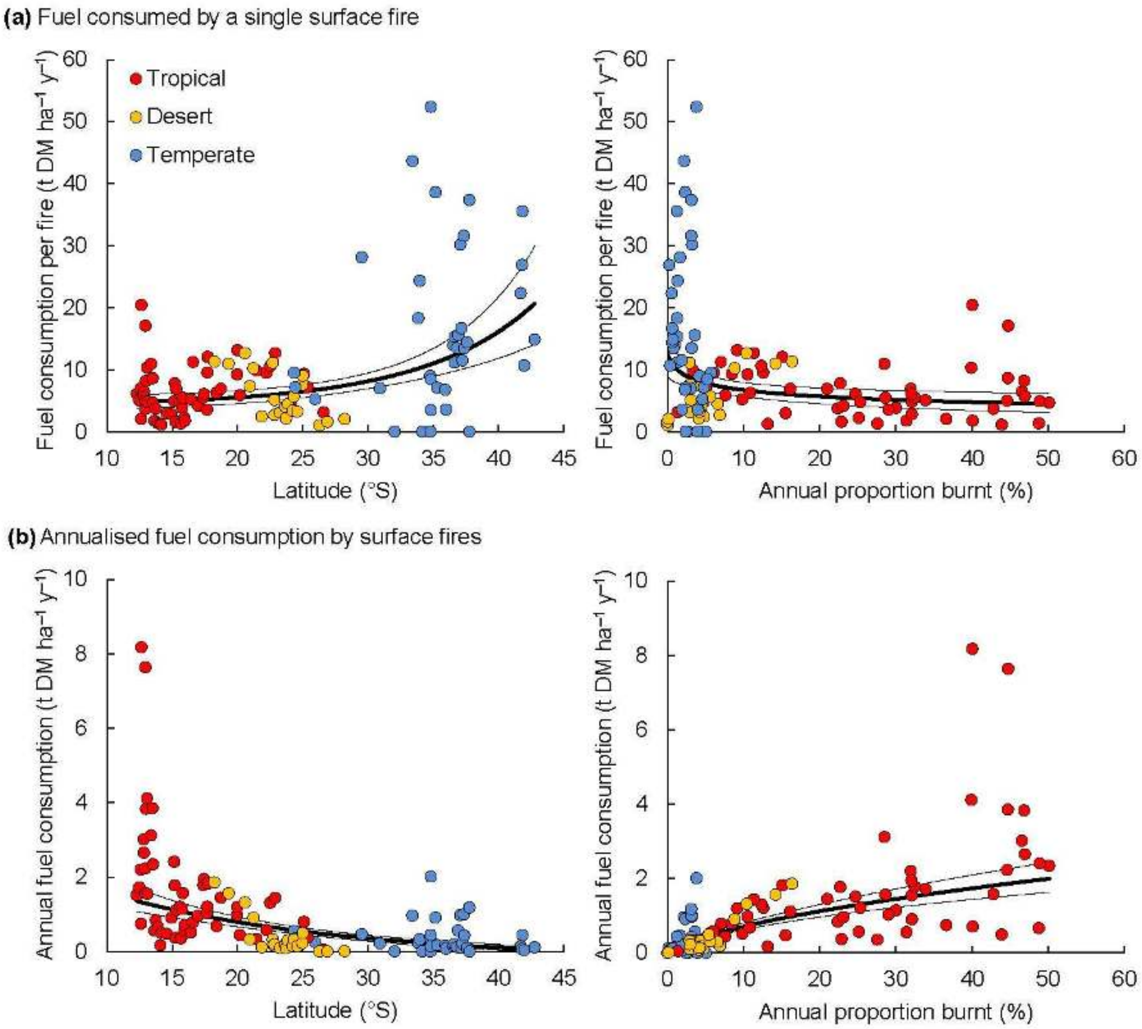
Figure 6 Rates of biomass consumption by surface fires across Australia. The modelled distribution of biomass consumed by a single surface fire is shown in (a). Annual biomass consumption, derived by multiplying (a) by annual proportion burnt (within 50-km radius), is shown in (b). The ratio of carbon consumption by surface fires to NPP is shown in (c). The black areas are either cleared or very heavily modified vegetation, or naturally non-vegetated (e.g. waterbodies and saltpans). The dashed line indicates the Tropic of Capricorn.

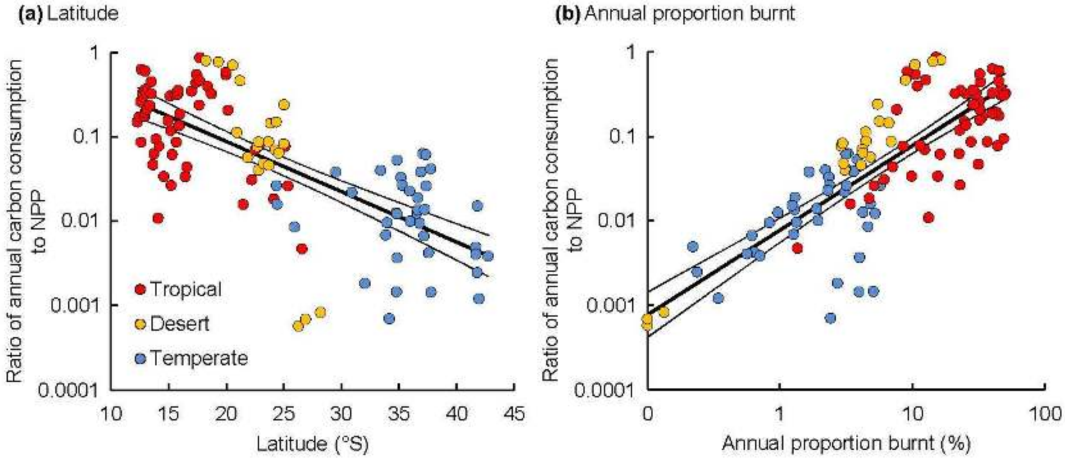
Figure 7 The proportion of (a) fine fuel biomass (grass, herbaceous and fine litter [<6 mm]) and (b) total surface fuel biomass consumed by a single surface fire, in relation to the proportion of fine fuel biomass contributed by grass, for sites in the tropical climate zone. The regression lines show the predictions of least-squares regression models (with 95% confidence intervals). The filled circles indicate sites with mean annual rainfall ≥1000 mm; unfilled circles indicate sites with mean annual rainfall <1000 mm. To the right of (b) is the magnitude of the reduction in biomass consumption expected due to a management-driven shift from early dry season (EDS: April–July) to late dry season (LDS: August–November) fires (Australian Government, 2015, Russell-Smith *et al.*, 2015).

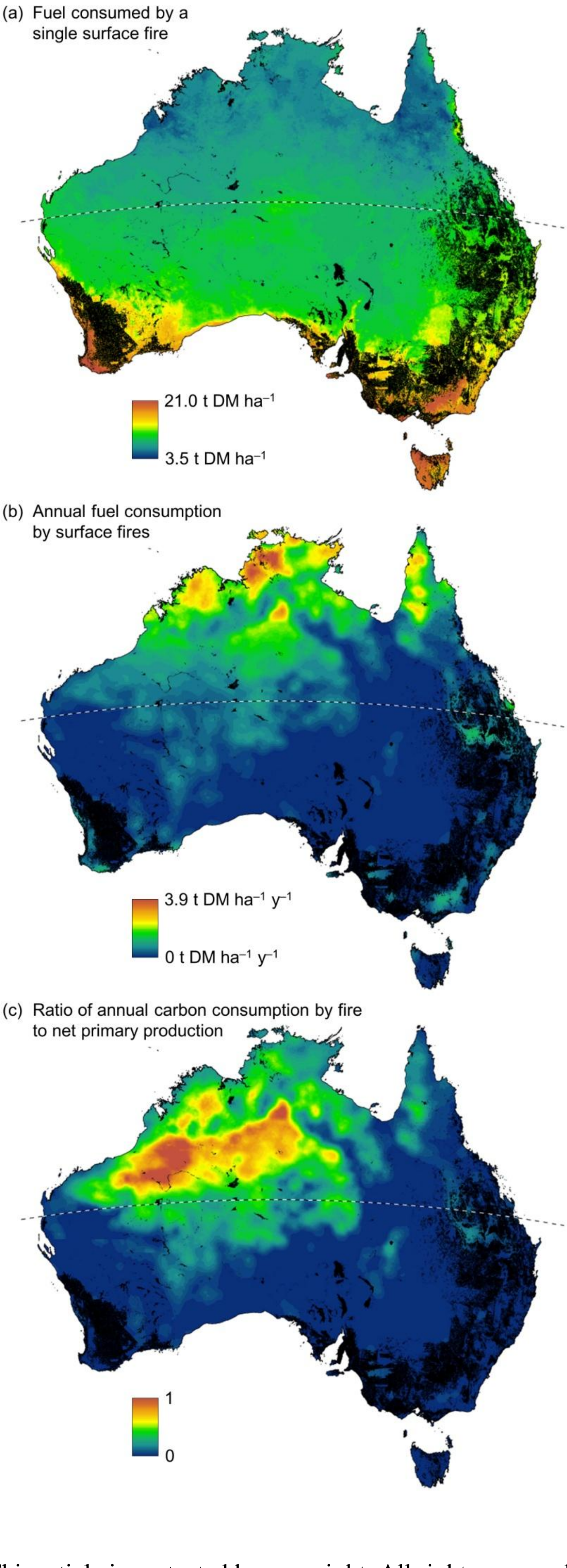

(a) Rainfall seasonality (proportion of annual rainfall in wettest 6 months)
100%
50%
Tropical
Desert
Temperate
(b) Annual proportion burnt
65%
0%
Tropical
Desert
Temperate
(c) Relationship between annual proportion burnt and rainfall seasonality for survey locations
Tropical
Desert
Temperate
Annual proportion burnt (%)
0
10
20
30
40
50
60
Proportion of rainfall in wettest 6 months (%)
50
60
70
80
90
100

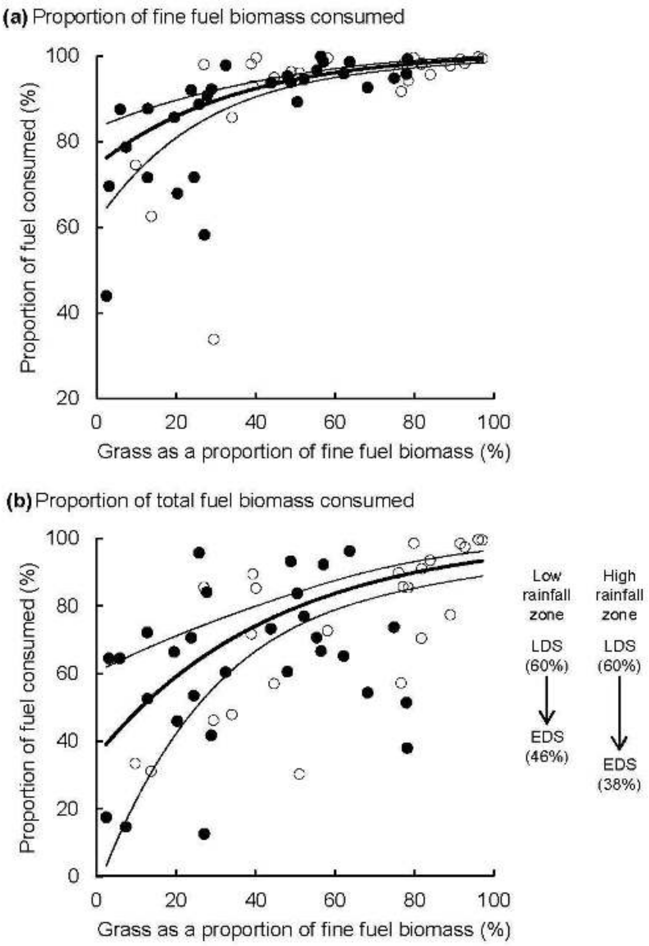

(a) Annual proportion burnt
Tropical
Desert
Temperate
Annual proportion burnt (%)
Latitude (°S)
(b) Fire severity index
Fire severity index
Latitude (°S)


(a) Grass biomass
Tropical
Desert
Temperate
Grass biomass (t DM ha^{-1})
Latitude (°S)
(b) Litter biomass
Litter biomass (t DM ha^{-1})
Latitude (°S)
(c) Total surface fuel biomass
Total fuel biomass (t DM ha^{-1})
Latitude (°S)


(a) Fuel consumed by a single surface fire
Tropical
Desert
Temperate
Fuel consumption per fire (t DM ha−1 y−1)
Latitude (°S)
Annual proportion burnt (%)
(b) Annualised fuel consumption by surface fires
Annual fuel consumption (t DM ha−1 y−1)
Latitude (°S)
Annual proportion burnt (%)


(a) Latitude
Ratio of annual carbon consumption to NPP
1
0.1
0.01
0.001
0.0001
Tropical
Desert
Temperate
10
15
20
25
30
35
40
45
Latitude (°S)
(b) Annual proportion burnt
Ratio of annual carbon consumption to NPP
1
0.1
0.01
0.001
0.0001
0
1
10
100
Annual proportion burnt (%)


(a) Fuel consumed by a single surface fire
21.0 t DM ha^{-1}
3.5 t DM ha^{-1}
(b) Annual fuel consumption by surface fires
3.9 t DM ha^{-1} y^{-1}
0 t DM ha^{-1} y^{-1}
(c) Ratio of annual carbon consumption by fire to net primary production
1
0


(a) Proportion of fine fuel biomass consumed
Proportion of fuel consumed (%)
Grass as a proportion of fine fuel biomass (%)
(b) Proportion of total fuel biomass consumed
Proportion of fuel consumed (%)
Grass as a proportion of fine fuel biomass (%)
Low rainfall zone
LDS (60%)
EDS (46%)
High rainfall zone
LDS (60%)
EDS (38%)