Title: Continent-level drivers of African pyrodiversity

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Abstract

Pyrodiversity, which describes fire variability over space and time, is believed to increase habitat heterogeneity and thereby promote biodiversity. However, to date there is no standardised metric for quantifying pyrodiversity, and so broad geographic patterns and drivers of pyrodiversity remain unexplored. We present the first generalizable method to quantify pyrodiversity, and use it to address the fundamental questions of what drives pyrodiversity, which fire attributes constrain pyrodiversity under different conditions, and whether pyrodiversity is spatial grain-dependent. We linked the MODIS burned area and active fire products to measure fire size, seasonal timing, return interval, and intensity for 2.2 million individual fires in sub-Saharan Africa from 2000–2015. We then quantified pyrodiversity as a four-dimensional hypervolume described by fire attributes within a grid cell, for any spatial grain of analysis. Environmental (rainfall, vegetation, soils, and topography) and human-associated (cattle biomass, cropland area, and human population density) variables were assessed as potential drivers of pyrodiversity. Rainfall was the main environmental driver of pyrodiversity, with higher pyrodiversity in drier regions (< 650 mm yr^{-1}). Pyrodiversity was not strongly associated with human-associated variables across Africa. Rainfall and a human influence index had clear but contrasting effects on the variability of fire size, seasonal timing, return interval, and intensity. Our analyses show that fire size and seasonal timing constrain pyrodiversity in wetter regions, whereas none of the fire attributes pose a strong constraint in drier regions. We found no evidence that pyrodiversity was spatial grain-dependent when recalculated at 5-minute grain increments from 15 to 120 minutes. We hypothesise that the strongest positive effect of pyrodiversity on biodiversity in all its forms will occur at intermediate precipitation (650–1300 mm yr^{-1}),

where fire plays an important role in shaping vegetation structure and where pyrodiversity is still quite high.

Introduction

Fire characteristics vary considerably in response to climate, vegetation, herbivory, and human activities (Chuvieco et al. 2008, Archibald et al. 2009, Krawchuk et al. 2009, Le Page et al. 2010, Aldersley et al. 2011, Hantson et al. 2015), but distinct fire regimes nonetheless emerge at landscape to global extents (van Wilgen et al. 2004, Archibald et al. 2013). A fire regime is defined as the repeated pattern of fire at a location (Gill 1975, Bond and Keeley 2005), and is characterised by its typical combination of fire attributes, such as the frequency, intensity, size, season, and type of fire (e.g. ground, surface, or crown). Fire regime classifications thus tend to focus on average fire attribute values and not on the amount of variability in fire attributes over space and time – yet this variability, which is the core of pyrodiversity, is increasingly perceived as a fundamental ecological driver (Maravalhas and Vasconcelos 2014, Ponisio et al. 2016, Kelly and Brotons 2017).

Martin and Sapsis (1992) first defined pyrodiversity, proposing that the ‘variety in interval between fires, seasonality, dimensions and fire characteristics, [produces] biological diversity at the micro-site, stand, and landscape-level.’ This view is supported by evidence that variation in fire attributes can determine vegetation type and structure (Brockett et al. 2001, Bond and Keeley 2005, Higgins et al. 2007, Hoffmann et al. 2012), and thus habitat heterogeneity that promotes biodiversity in all its forms. Nonetheless, little consensus has so far emerged on the ecological consequences of pyrodiversity, in part due to the lack of a standard measure for quantifying pyrodiversity (Faivre et al. 2011). Recent work sought to redefine pyrodiversity as the ‘outcome of the trophic interactions and feedbacks between fire regimes, biodiversity and ecological processes’ (Bowman et al. 2016), which shifts emphasis away from how variation in fire attributes might affect ecosystems. In order to test Martin and Sapsis’ original hypothesis that pyrodiversity promotes biodiversity, it is necessary to establish a clear pyrodiversity definition and then a standard method for quantifying it. Here we propose an approach that is based on the original conceptualisation of pyrodiversity by Martin and Sapsis (1992) and derived from the fire attributes they identify (fire size, season, return interval, and intensity).

Fire affects the spatial and temporal patterns of abundance of fire-dependent or fire-sensitive species, and so the level of pyrodiversity in a system may have key implications for vegetation, trophic structure, and life-history evolution (Bond and Keeley 2005). A common management objective in protected areas is to increase pyrodiversity (e.g., with patch mosaic burns; Parr and Brockett 1999, Brockett et al. 2001), with the goal of increasing habitat heterogeneity and hence biodiversity (Keith et al. 2002). Support for the hypothesis that ‘pyrodiversity begets biodiversity’ (Martin and Sapsis 1992, Parr and Andersen 2006) remains limited at landscape extents (Davies et al. 2012, Kelly et al. 2012, Taylor et al. 2012, Farnsworth et al. 2014; but see Maravalhas and Vasconcelos 2014). Ambiguities arise because many taxa in fire-prone environments are resilient to at least some threshold level or form of pyrodiversity (Parr and Andersen 2006). Quantifying pyrodiversity patterns at macroecological scales, and exploring which fire traits are more variable under different environmental conditions, will allow for exploration of relations between fire and biodiversity over different timescales (evolutionary, ecological, and management).

Furthermore, an understanding of pyrodiversity patterns provides a tool for assessing the extent to which fire can be used to generate habitat diversity within protected areas (Parr and Andersen 2006), and to best match fire management resources to the variability of different fire attributes within a region. For example, it appears to be easier for people to manipulate fire season and fire intensity (which are affected by the by the timing of ignitions; Archibald 2016) than to manipulate total area burned (van Wilgen et al. 2004, but see also Price 2015).

Environmental context is likely to determine pyrodiversity at large extents, with the contribution of different fire attributes to pyrodiversity varying under different conditions. Fire characteristics are regulated by fuel attributes, weather conditions, and topography. Important fuel attributes include the amount, arrangement in space, and moisture content (Govender et al. 2006, Archibald et al. 2009, Bradstock 2010, Pausas and Ribeiro 2013). These elements affect whether fire spreads (fire size) and the intensity of a burn (radiative power). Environmental conditions constrain the distribution and abundance of different fuel types, and the abundance and flammability of fuels in space and time. Grass productivity is linked mainly to precipitation (O'Connor et al. 2001, Bai et al. 2008) but also to soil nutrients (Augustine et al. 2003), and is a major determinant of fuel accumulation rates, and hence fire return intervals and fire intensity. Herbivory can slow fuel accumulation rates, and even reduce fuel loads to below the fire-spread threshold, so observed patterns in herbivore rich areas will reflect these two factors (e.g. Holdo et al. 2009). Precipitation seasonality further constrains how long fuel moisture content is low enough that fire can occur, and thus the duration of flammability within a year (fire season length). Weather conditions during a fire (wind speed, relative humidity, temperature) influence the intensity, probability of spread, and potential size of a fire. Fire spread and intensity can also be affected by variation in topography, vegetation type, herbivore abundance, and land use (Archibald et al. 2010, Bowman et al. 2011, Wood et al. 2011, Little et al. 2012). The availability of ignition sources also contributes to pyrodiversity. Although currently ignition does not appear to limit burned area in human-occupied landscapes, the timing and number of ignitions can still strongly affect fire characteristics (Archibald 2016).

The characteristics of individual fires are shaped by processes operating across diverse scales, and pyrodiversity is thus contingent on the spatial grain at which it is observed. Fuel characteristics, for example, can be determined at the local level by changes in soil moisture and nutrient availability along hill slopes (Venter et al. 2003), at the landscape level by the seasonal movements of migratory herbivores (McNaughton 1985), and at the continental level by El Niño Southern Oscillation effects on precipitation (Nicholson and Kim 1997). Investigating the spatial grain-dependence of pyrodiversity may thus provide insights into how ecological phenomena at different scales contribute to pyrodiversity. This is relevant to attempts to manage fire regimes, e.g. in protected areas – if pyrodiversity is driven at scales far larger than management units, then financial resources might be better spent on activities other than trying to manipulate pyrodiversity (Govender et al. 2006; Smit et al. 2013).

We developed a pyrodiversity index to explore how environmental conditions and human activities shape pyrodiversity across Africa, and how this changes with spatial grain. It is useful to examine factors that drive pyrodiversity in Africa because many ecosystems across the continent are fire-prone (Bond and Keeley 2005), and burn frequently enough to provide sufficient fire data over the 15-year period for which remotely sensed information is available. We linked data from the Moderate Resolution Imaging Spectroradiometer (MODIS) on the seasonal timing and size of individual fires to information on the time since fire and the energy released from the fire. These novel data (we are not aware of other studies linking MODIS products to examine individual fires) allow us to address fundamental questions about the drivers and continent-level patterns of pyrodiversity.

We hypothesized that pyrodiversity would be higher in low rainfall areas because longer fire return intervals are possible, the dry season is longer, and fire size and intensity can range from very large (in years with high rainfall and high grass fuel loads) to very small (low, discontinuous fuel loads in dry years). By contrast, we anticipated low pyrodiversity in high rainfall areas because fires are frequent (few areas remain unburned for long periods), the dry season (period when grasses are flammable) is shorter, and because fire size is more likely to be limited by constant factors, such as drainage lines, than by variation in fuel loads. We hypothesised that the effects of soil nutrient levels on pyrodiversity would be analogous effects to those of rainfall, with positive correlations among soil fertility, the amount and continuity of grass fuel loads, and the homogeneity of fire histories. We hypothesized that topographic diversity would be positively correlated with pyrodiversity because as topographic diversity increases, so does the variety of plant growth conditions and the diversity of fire histories. We also hypothesized that local pyrodiversity would increase as human population density increases because humans extend the length of the fire season (Le Page et al. 2010) and suppress or increase the likelihood and variability of fire (e.g., by direct suppression, indirect suppression via high cattle biomass, or burning for grazing or cropland preparation) beyond the ecological range of variation in different regions (Bird et al. 2008).

Methods

Fire data

We used 15 years of remotely sensed data on fires to derive data that summarised the characteristics of individual fires across sub-Saharan Africa (south of 10° North). Data were available from April 2000 through June 2015 (with one missing month, June 2001). The 500 m resolution MODIS MCD45A1 burned area product identifies the location and date (accurate to within 8 days) when the area represented by individual pixels burned. These data can be used to identify individual fires and calculate the size and timing of fires (Roy et al. 2008). Validation against higher-resolution LANDSAT data has indicated that the MCD45A1 product underestimates total area burned, especially in systems where trees obscure detection of fires burning in the ground layer (Tsela et al. 2010). The MODIS MCD14ML product (1 km resolution) uses the brightness temperatures of the sensor's infrared bands to locate actively burning fire fronts (Giglio et al. 2003), and can quantify the energy released from these fires (Ellicott et al. 2009). The MCD45A1 and MCD14ML products have been used to describe various fire characteristics (Archibald 2010, Le Page et al. 2010, Hantson et al. 2015), and we linked them to create data on the size, date of burn, time since last fire, and intensity of individual fires.

We identified individual fires with a flood-fill algorithm (Archibald et al. 2009): all pixels burned within 5 days of an adjacent pixel were considered one fire event (Fig. 1). This algorithm was validated by Hantson et al. (2015) against LANDSAT data: small fires (< 125 ha) are not well identified but the range of fire sizes is well described by the MODIS data. We calculated the size of these fires in km^2. We calculated the date of each fire as the earliest burn date of all pixels within the fire area (probable date of ignition) and converted to cosine of radians for analysis. We quantified fire return period as the mean time since last burn across all of the pixels within the fire. Fires early in the time series for which there were no data on previous burns or for which fewer than 50% of cells had burned before were excluded. This added an element of temporal bias to our data (early fires would have shorter intervals than later ones due to censoring), but did not systematically bias the spatial pattern that was the focus of this work. This conservative approach also allowed us to somewhat mitigate the data that were missing due to cloud cover in the MODIS images, which may have led to overestimation of time since last fire. Finally, we linked fire radiative power (kW m^{-1} s^{-1}) from the MODIS active fire product (MCD14ML) to the burned area data and used this as an index of fire intensity (see Archibald et al. 2010, Smith and Wooster 2005).

MCD45A1 and MCD14ML are produced with different methods: MCD45A1 uses changes in reflectance after a burn event to identify a burn scar, and MCD14ML uses thermal bands to identify energy released by an actively burning fire. Therefore, some active fires are not associated with a burn pixel (fire too small to be identified by the MCD45A1 algorithm), and many burn pixels do not have active fires (fire was not actively burning in the pixel when the TERRA or AQUA satellite passed above). Because our focus was individual fires, we used the maximum fire radiative power (fire intensity) of all active fires within 1 km of a burned pixel, and within five days of the estimated burn date, for each pixel within the individual fire. Each pixel in the fire potentially can be associated with four fire radiative power records each day (TERRA and AQUA satellites each circumnavigate the globe twice daily). Therefore, we used the maximum to represent the fire radiative power of the head fire, which generally burns the greatest area of any fire. Due to errors of commission and omission in both data products (Krawchuk and Moritz 2014, Hantson et al. 2015), not all fires were associated with a fire radiative power value, and not all fire radiative power values were associated with a fire. In these cases, we omitted the fire from our analysis. Because small fires were least likely to have a fire radiative power allocated, some degree of bias was introduced (Supplementary material, Appendix 1, Fig. A1).

Pyrodiversity quantification

Of the approximately 6.8 million fires identified over the 15 years, we had the necessary information on size, date (in radians), intensity, and time since last fire for about 2.2 million individual fires (Fig. 1). These are analogous to the attributes identified by Martin and Sapsis (1992) for characterising pyrodiversity (fire size = spatial extent dimension, date = seasonality, intensity = a proxy for severity, which is also associated with their fire patchiness dimension, and time since last burn = fire frequency). We first calculated logarithms of fire size, intensity, and time since last burning, then centred and scaled each attribute. Any given fire therefore can be located as a point within the four-dimensional space described by the four fire attributes. For any given spatial grain of analysis, we aggregated all fires within a cell, and used the QHull algorithm (Barber et al. 1996) to compute the minimum convex hull of the four-dimensional space. The greater the variation among fires on the four axes, the greater the hypervolume. In the absence of external forcing, we expected the attributes of individual fires within a cell to have a multivariate normal distribution, which would result in an increase in the volume of the enclosing convex hull as a simple function of the number of fires recorded. Consequently, we used a nonparametric bootstrap to correct the volume: we divided the calculated volume by the median of 1000 volume calculations that were based on an equivalent number of fires selected at random from the entire dataset. This final pyrodiversity index was scaled to have a mean of zero such that cells with positive values had relatively high pyrodiversity and cells with negative values had relatively low pyrodiversity. We calculated pyrodiversity for all cells in sub-Saharan Africa with more than four fires for which all attributes were available, starting with a grid of 15 minutes (approximately 28 × 28 km at the equator) and increasing the spatial grain in 5 minute increments to 120 minutes (i.e., 2 degrees or 221 × 221 km). We used the 30-minute spatial grain for all analyses other than the spatial grain dependence analysis.

Drivers of pyrodiversity

To identify the environmental drivers of pyrodiversity, we fitted a spatially explicit conditional autoregressive model explaining pyrodiversity as a function of mean annual rainfall (from the WorldClim version 1 dataset, 0.5 minute native resolution, aggregated to mean value at 30 minute resolution; Hijmans et al. 2005), vegetation type (derived from White 1983; Supplementary material, Appendix 1, Table A1), soil nutrient status (from FAO 2009; Harmonised World Soils Database version 1.2: SQ1 Nutrient availability, 5 minute native resolution, aggregated to mean value at 30 minute resolution) and topographic roughness (R raster package: 'terrain' function with 'roughness' option and 'neighbours' = 8; Hijmans 2015; calculated at 0.5 minute resolution with elevation data from the U.S. Geological Survey, and then aggregated to mean value at 30 minute resolution). We used integrated nested Laplace approximation (INLA: Rue et al. 2009) to obtain parameter estimates. INLA provides a computationally efficient and accurate approximation to the posterior distribution of parameters in a wide range of Bayesian models, in a fraction of the time of other estimation methods such as Markov Chain Monte Carlo (Rue et al. 2009). We fitted continuous variables as generalised additive models with two knots (Crainiceanu et al. 2005). To test hypotheses concerning human associations with pyrodiversity, we fitted similar models with cattle density (Robinson et al. 2014), proportion of land used for crops (FAO 2006), and human population density (CIESIN 2005) as independent variables. Conditional-autoregressive models fitted in INLA allow fitting of complex Bayesian models that can account for spatial autocorrelation.

Fire attribute constraints

Fire attributes have different levels of variability along gradients of rainfall and human-associated variables, and thus promote or constrain pyrodiversity by varying amounts as conditions change. For each of the four fire attributes (i.e. fire size, season, time since last fire and intensity), we calculated an index describing the extent to which it constrained pyrodiversity in each cell, and then assessed whether the level of constraint varied predictably with rainfall or an index of human influence (from Sanderson et al. 2002). The degree of constraint on pyrodiversity imposed by each fire attribute is determined by the attribute with the smallest range of scaled values in the cell: as the range on any single axis approaches zero, so too does the volume, irrespective of variation in other dimensions. Thus, to estimate constraint for each focal fire attribute we divided the range of the scaled focal attribute by the minimum range of all other scaled attributes for each cell. We then used the constraint index for each fire attribute as the response variable in a conditional-autoregressive model with either mean annual rainfall or the human influence index (Sanderson et al. 2002) as predictors.

Spatial grain dependence

We assessed spatial grain dependency by calculating the pyrodiversity at a range of spatial grains: every five minutes from 15 minutes to 120 minutes (i.e. two degrees). The extent of the analysis at all spatial grains was limited to the geographic area in which 2 degree cells contained a minimum of seven 15 minute cells (i.e. > 10%) for which pyrodiversity had been calculated (at finer grain cells may not meet the minimum threshold number of fires for inclusion). We grouped estimates by three levels of ecologically relevant mean annual rainfall ranges (< 650, 650–1300 and > 1300 mm; 650 mm ≈ xeric/mesic savanna transition, and 1300 mm approaches the upper rainfall limit of mesic savannas in Africa) and computed the mean and 25–75% confidence interval for each spatial grain.

Results

Drivers of pyrodiversity

Pyrodiversity index calculations at 30 minute spatial grain were possible for ~65% of sub-Saharan Africa, and revealed clear structure in the associations with fires across this region (Fig. 2). Rainfall emerged as a major driver of pyrodiversity on the continent (Fig. 3A), with strong support that pyrodiversity increased as rainfall decreased (i.e. < 650 mm MAR; neither credible interval for parameter estimate in spatially explicit restricted GAM overlapped zero; Table 1). Although overall pyrodiversity was strongly associated with rainfall, the amount of variation in pyrodiversity was similar along the rainfall gradient. Vegetation type did not have a consistent effect on the overarching rainfall-pyrodiversity relation (Fig. 3B). For example, there was no indication that pyrodiversity in forest-grassland mosaics was greater than expected for their rainfall range. Similarly, there was limited support for an effect of soil nutrients (Fig. 3C) or topography (Fig. 3D) on pyrodiversity at this spatial grain (Table 1). At this grain, the human-associated variables we measured appeared to have minimal association with pyrodiversity (Table 2, Fig. 4), despite the fact that they are undoubtedly able to shape local- and regional-scale fire regimes (Bowman et al. 2011, Le Page et al. 2010, Archibald et al. 2013, Hantson et al. 2015). Neither cattle biomass (Fig. 4A) nor the extent of cropland (Fig. 4B) were associated with pyrodiversity, whereas human population density had a slight negative association with pyrodiversity (Fig. 4C).

Fire attribute constraints

The contribution of different fire attributes to pyrodiversity is contingent on rainfall (Fig. 5 and Supplementary material, Appendix 1, Fig. A2 and Table A2). Fire size was a stronger constraint on pyrodiversity in wetter regions, and was more clearly evident after accounting for spatial autocorrelation (Fig. 5A vs. Supplementary material, Appendix 1, Fig. A2A; Supplementary material, Appendix 1, Table A2). The seasonal timing of fires was also less variable in wetter regions (Fig. 5B), although support for a quadratic term suggested that seasonal timing becomes less of a constraint on pyrodiversity in the very wettest parts of the continent (Appendix 1, Fig. A2B and Table A2). Fire frequency (Fig. 5C) and intensity (Fig. 5D) both had weak negative relations with mean annual rainfall, suggesting that these fire attributes are more likely to constrain pyrodiversity in dry regions (Supplementary material, Appendix 1, Table A2). Overall, however, the strongest patterns in fire attribute constraints on pyrodiversity were the limited variability in fire size and seasonal timing of fires in high rainfall areas.

Fire size places a greater constraint on pyrodiversity as the human influence index increased, suggesting that humans tend to homogenise this fire attribute more than others (Supplementary material, Appendix 1, Fig. A3A and Table A3). Fire season, frequency, and intensity had weak negative relations with the human influence index (Supplementary material, Appendix 1, Fig. A3B-D and Table A3). These fire attributes showed slightly higher relative variability as human influence index increased, and thus placed less constraint on overall pyrodiversity. Although the models provide support for an effect of humans on the extent to which different fire attributes shape pyrodiversity, the sizes of these effects are small.

Spatial grain dependence

Pyrodiversity was largely independent of the grain at which it was measured (Fig. 6). If anything, there was a subtle decrease in pyrodiversity as spatial grain increased in the intermediate (650-1300 mm yr^{-1}; $y = -0.002*x – 0.023$, $p < 0.001$, $r^2 = 0.77$) and high rainfall regions (> 1300 mm yr^{-1}; $y = -0.001*x – 0.278$, $p = 0.003$, $r^2 = 0.35$). If that trend is consistent at smaller spatial grains, pyrodiversity may peak at grains smaller than the minimum of approximately 28 × 28 km we considered.

Discussion

Our analysis of the attributes of individual fires produced a novel, generalised index of pyrodiversity using widely available metrics of principal fire attributes. This marks an advance in understanding of pyrodiversity and provides a template for future research in savannas and other flammable biomes. We weighted fire size, season, frequency, and intensity equally, but future work might consider whether some fire attributes warrant more weight than others. For example, it could be argued that variability in the seasonal timing of fire (which results in variation in fire intensity, patchiness, plant phenology etc.) should be given greater weight than variability in fire size.

The value of retaining the original definition of pyrodiversity from Martin and Sapsis (1992) is highlighted by our analyses of the drivers and spatial grain dependence of pyrodiversity, which would not have been possible under the definition recently proposed by Bowman et al. (2016). We suggest that redefining pyrodiversity to be entirely contingent on context makes quantification difficult and risks losing insights available from directly considering the variability of fire attributes within an ecosystem. The approach we present here allows for pyrodiversity and its effects on ecosystems to be compared among regions, which in turn will inform the holistic perspective on the trophic dynamics of fire encouraged by Bowman et al. (2016).

Our analysis of pyrodiversity across sub-Saharan Africa is to some extent constrained by the quality of the remotely sensed data products that we used. For example, these products limit the range of fire sizes and time since last fire that we could record. This constraint will diminish with longer recording periods and better sensors, but is unlikely to a change the general patterns we observe. Nonetheless, the value of developing a pyrodiversity index that incorporates individual fire characteristics into one metric is independent of the data quality used in this study. Landscape-scale analyses, for example, might choose to use LANDSAT data or field records to quantify pyrodiversity.

Environment–pyrodiversity relationships

Of the environmental variables we measured, mean annual rainfall was the most strongly associated with pyrodiversity across sub-Saharan Africa. However, there was substantial variability in the level of pyrodiversity at any range of annual precipitation (Fig. 3A), which suggests that it may be possible to manipulate pyrodiversity under most environmental conditions. Our results suggest that manipulating the size and the seasonal timing of fires will produce the greatest increases in pyrodiversity in high-rainfall areas (Fig. 5), although the feasibility of doing so may be limited by high grass fuel loads and moisture content (Govender et al. 2006). In contrast, the weak negative relations between fire frequency and intensity constraints on pyrodiversity suggest that in dry regions, it may be possible to manipulate pyrodiversity via any of the four fire attributes we assessed. Nonetheless, careful consideration should be given to whether pyrodiversity is being promoted within a basis of naturally occurring bounds – and to which local plant and animal communities should be adapted – or whether novel fire regimes are being created that may in fact prove counter to conservation objectives.

The lack of spatial grain dependence of pyrodiversity could suggest that environmental factors replace each other at different grains, or that pyrodiversity is determined by processes operating at smaller grains (i.e. < 15 min). For example, fine-grained interspersion of low- or non-flammable vegetation associations such as riparian zones (Pettit and Naiman 2007), forest patches (Staver et al. 2011), or grazing lawns (Waldram et al. 2008, Leonard et al. 2010) can have strong effects on fire attributes. These features restrict fire spread and thus directly affect fire size, but also allow fuel accumulation (or grazing and decomposition) to continue in unburned patches, which may considerably alter the intensity and frequency of fires in areas in which ignition events are limited (Govender et al. 2006).

Humans and pyrodiversity

In our analyses, human-associated variables had little association with pyrodiversity, in contrast to our expectations (Fig. 4). Human activity often is hypothesized to diversify fire regimes (Bowman et al. 2011, Bird et al. 2012). However, global analyses suggest that humans have homogenised fire regimes, creating very similar fire patterns across very different parts of the globe (Archibald 2016). Our data indicated weak support of homogenisation at high population densities (Fig. 4C), and no evidence that humans recently acted as a diversifying force. This is probably because humans reduce the variability of some parameters (e.g. fire size; Supplementary material, Appendix 1, Fig. A3A; Hantson et al. 2015), but increase the variability of other parameters (e.g. fire season; Supplementary material, Appendix 1, Fig. A3B; Le Page et al. 2010). Assessing human effects on pyrodiversity thus may require value judgments about which fire attributes are most relevant. Humans can extend fire seasons both by extending the seasonal timing of ignitions beyond that of lightning and by intentional ignitions in locations and during weather conditions when fires are likely to result. That fire size increasingly constrains pyrodiversity as the human influence index increases is likely due to human limitation of fire sizes, either by active suppression or by fragmentation that limits fire spread (Archibald 2016). Humans may well have stronger effects on pyrodiversity at spatial grains smaller than those studied here.

Pyrodiversity–biodiversity relationships

Research interest in pyrodiversity has largely stemmed from the hypothesis that 'pyrodiversity begets biodiversity' (Martin and Sapsis 1992, Parr and Andersen 2006). Data for African savannas indicate that fire has more effect on vegetation structure in mesic systems, where tree cover and height are determined by fire frequency and fire intensity (Higgins et al. 2007, Bond 2008). In arid systems, although fires occur, they have minimal impacts on woody structure because of relatively low fuel loads; instead, woody cover is controlled by establishment opportunities (density), browsing (sapling escape) and water availability (height/biomass; Bond 2008). Shifts in vegetation structure and composition have myriad cascading direct and indirect effects on ecosystems, and can strongly reshape the array of ecological niches (Bond and Keely 2005, Bowman et al. 2016). Although pyrodiversity increased as rainfall decreased, we expect that its effect on biodiversity will be greatest in locations with intermediate rainfall, where fire has greater influence on habitat heterogeneity. This hypothesis is consistent more broadly with the lack of relation between pyrodiversity and the diversity of birds (species richness; Taylor et al. 2012), small mammals (species richness; Kelly et al. 2012), and reptiles (alpha, beta and gamma diversity; Farnsworth et al. 2014) in the dry parts of south-eastern Australia (220–330 mm yr^{-1}), some evidence of a positive relation between pyrodiversity and ant and termite species richness in South Africa as rainfall increases from 450 to 550 to 750 mm yr^{-1} (Parr et al. 2004, Davies et al. 2012), and a positive association between pyrodiversity and ant species richness in Brazil (1387 mm yr^{-1}; Maravalhas and Vasconcelos 2014). Tests of our hypothesis that rainfall mediates the effect of pyrodiversity on biodiversity will need to span a wide rainfall gradient and make use of a consistent measure of pyrodiversity.

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Tables

Table 1. Median and 95% credible intervals of parameter estimates for environmental variables as predictors of pyrodiversity at 30 minute spatial resolution. Mean annual rainfall (MAR; mm), soil nutrient availability (SNA) and topographic roughness (TOPO) were fitted as generalised additive models with two knots, and vegetation type was fitted as a categorical variable. Conditional autoregressive models were fitted in INLA and account for spatial autocorrelation within a Bayesian framework. ΔWAIC is provided based on difference in WAIC between full model and models lacking particular terms; values below -2 are usually considered to indicate strong support.

Environmental variable	Model term	0.025 quantile	0.5 quantile	0.975 quantile	ΔWAIC
	Intercept	0.4782	0.6120	0.7456	
Mean annual rainfall	MAR 1	0.1830	0.2517	0.3204	-111.8
	MAR 2	-0.4320	-0.3451	-0.2583	
Vegetation type	Mixed savanna	-0.7156	-0.5812	-0.4467	-346.7
	Grassland	-0.6659	-0.5110	-0.3562	
	Caesalpinioid savanna	-0.8256	-0.6850	-0.5445	
	Forest-grassland	-0.7871	-0.6415	-0.4959	
	Forest	-0.8875	-0.7195	-0.5515	
Soil nutrient availability	SNA 1	-0.0182	0.0078	0.0338	-7.09
	SNA 2	-0.0390	-0.0159	0.0070	
Topographic roughness	TOPO 1	-0.0226	0.0042	0.0310	8.34
	TOPO 2	-0.0271	-0.0005	0.0262	

Table 2. Median and 95% credible intervals of parameter estimates for human-associated variables as predictors of pyrodiversity at 30 minute spatial resolution, while accounting for mean annual rainfall. Mean annual rainfall (MAR; mm), cattle biomass (CAT; kg km^{-2}), proportion of cropland (CROP) and population density (POP; log(people km^{-2})) were fitted as generalised additive models with two knots. Conditional autoregressive models were fitted in INLA and account for spatial autocorrelation within a Bayesian framework. ΔWAIC is provided based on difference in WAIC between full model and models lacking particular terms; values below -2 are usually considered to indicate strong support.

Environmental variable	Model term	0.025 quantile	0.5 quantile	0.975 quantile	ΔWAIC
	Intercept	-0.0186	-0.0102	-0.0017	
Mean annual rainfall (mm)	MAR 1	0.2821	0.3276	0.3732	-562.1
	MAR 2	-0.4394	-0.3745	-0.3096	
Cattle biomass (kg km^{-2})	CAT 1	-0.0321	0.0516	0.1352	7.64
	CAT 2	-0.1661	-0.0712	0.0236	
Cropland (proportion of area)	CROP 1	-0.0157	0.0089	0.0335	7.64
	CROP 2	-0.0185	0.001	0.0205	
Population density (log scale)	POP 1	0.0366	0.1576	0.2786	-139.4
	POP 2	-0.1958	-0.0807	0.0343	

Figures

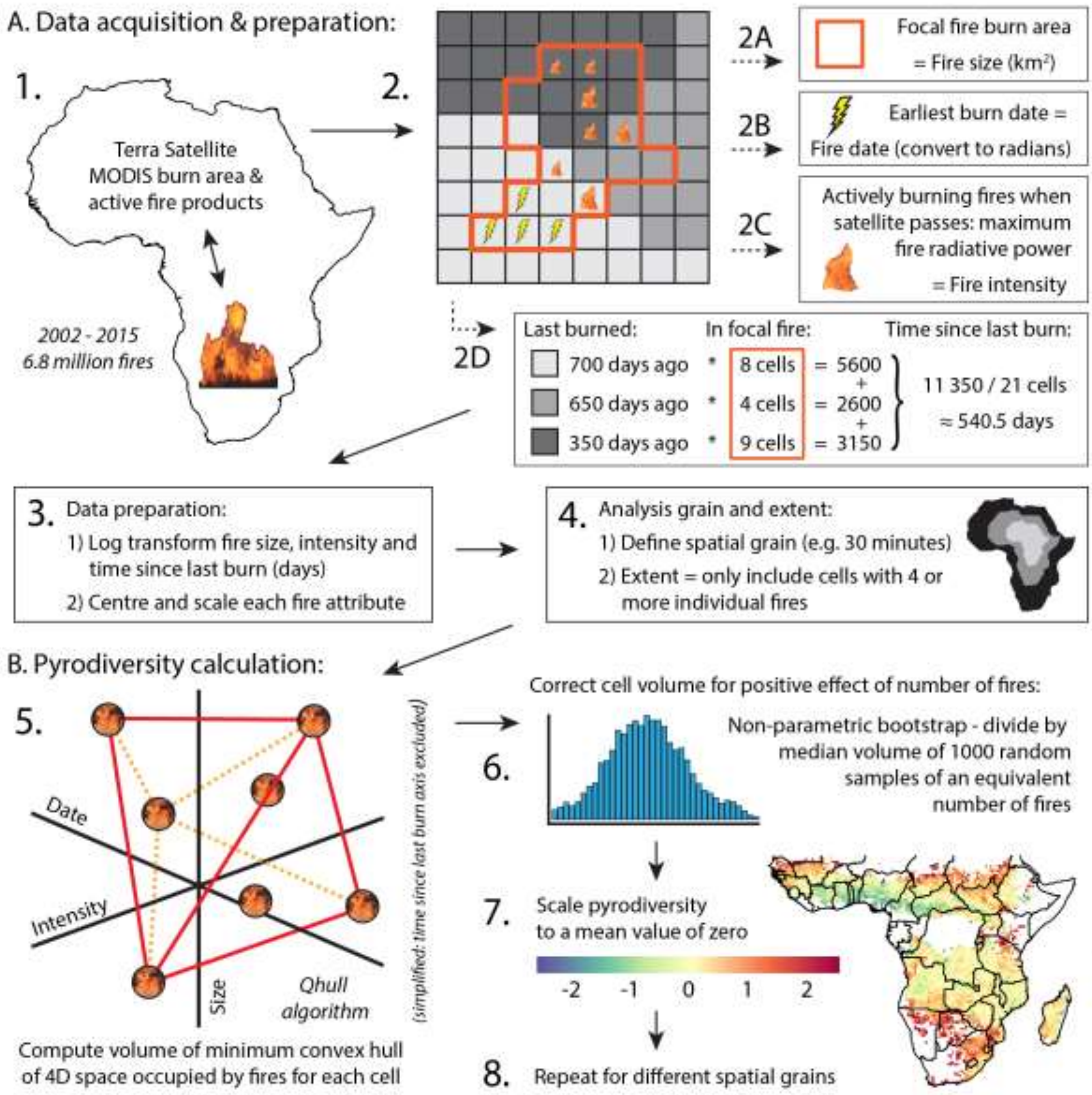

Figure 1. The data and methods we used to quantify pyrodiversity. Three fire attribute axes are illustrated in part 5 (i.e. time since last burn is excluded), but note that we quantified pyrodiversity as the minimum volume in four-dimensional space.

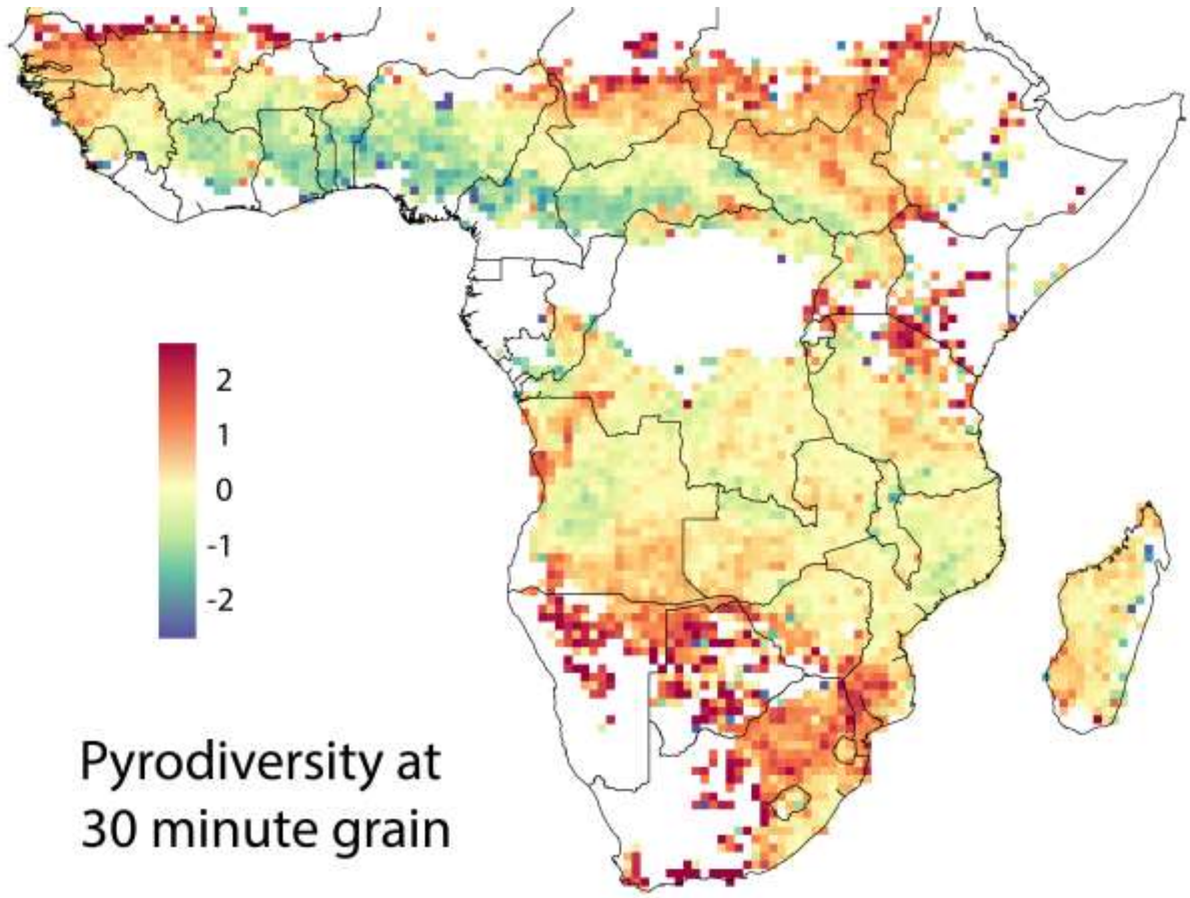

Figure 2. Pyrodiversity at 30 minute spatial grain across sub-Saharan Africa. Regions with no values did not meet the analysis criteria of having more than four fires for which all fire attribute information was available during the 2000–2015 data availability period.

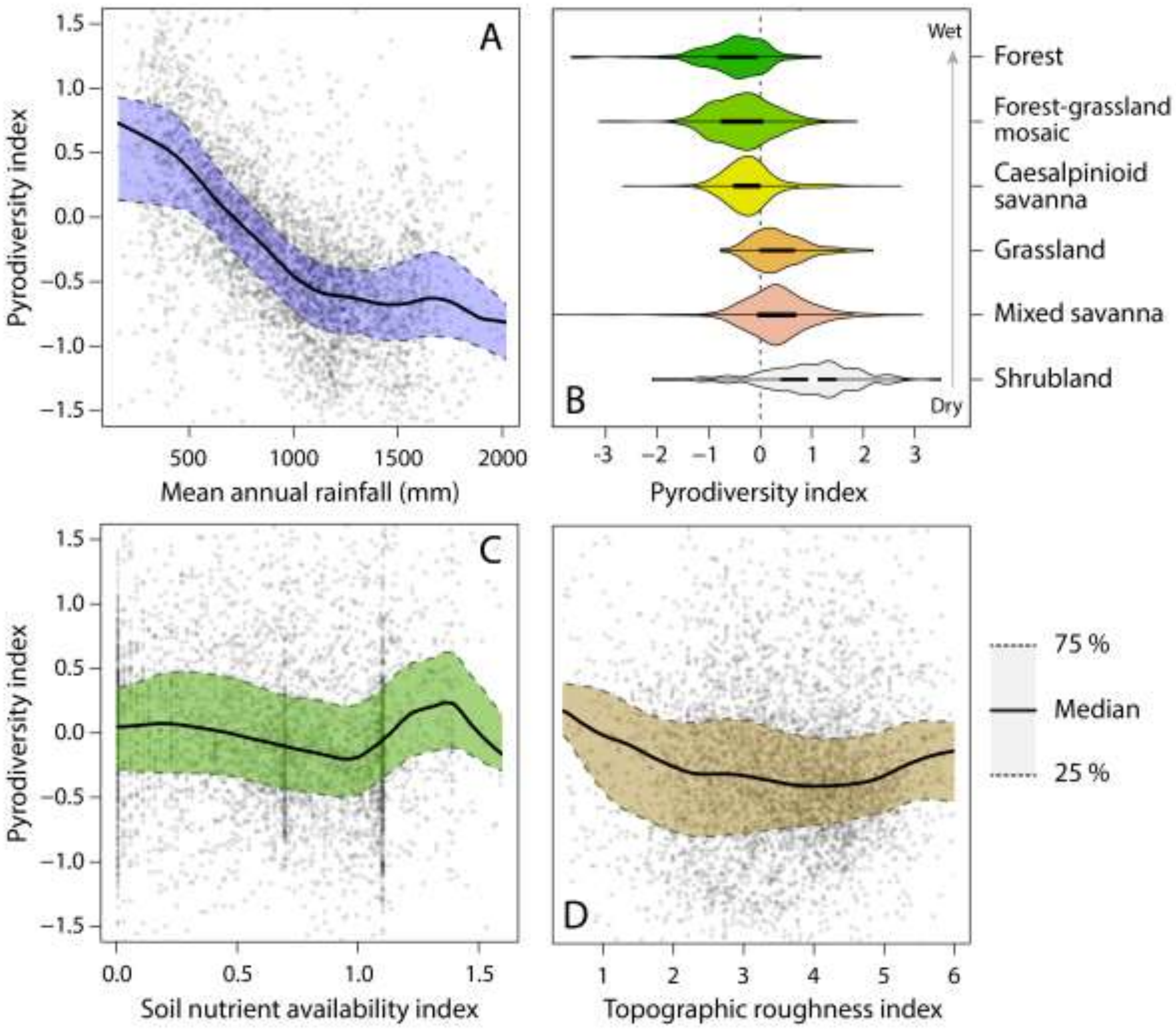

Figure 3. Relations between pyrodiversity and A) rainfall, B) vegetation types, C) soil nutrients and D) topography. Vegetation types are presented in increasing order of mean annual rainfall. Values are medians and interquartile ranges for binned values (rainfall: 10 mm, soil nutrients and topographic roughness: 0.1) and displayed with locally weighted scatterplot smoothing regression lines. All variables were assessed at 30 minute spatial grain.

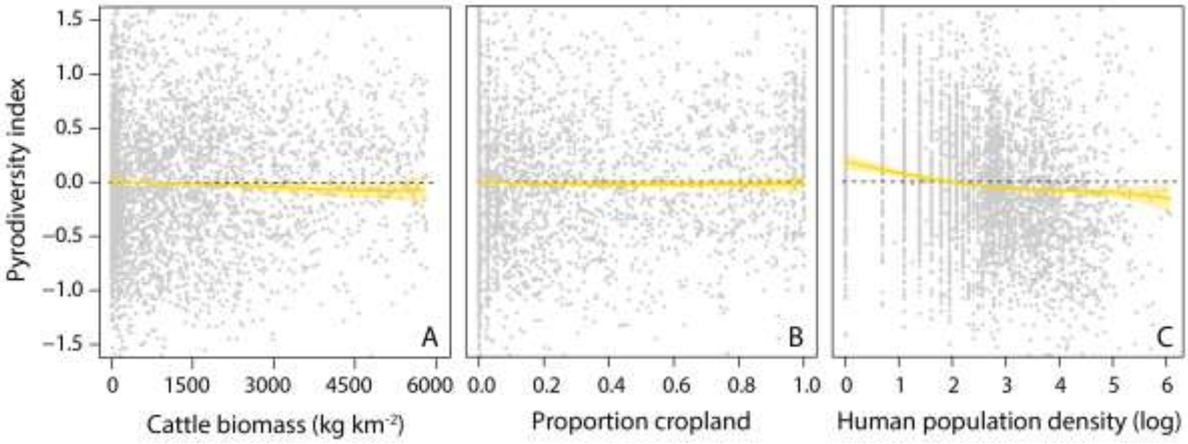

Figure 4. Modelled relations between human activity and pyrodiversity: A) cattle biomass (kg km^{-2}), B) proportion of cropland area, and C) the log of human population density (people km^{-2}). Grey points represent the raw data, solid yellow lines the median model projections, and shaded regions the 95% credible intervals. Analyses were conducted at 30 minute spatial grain.

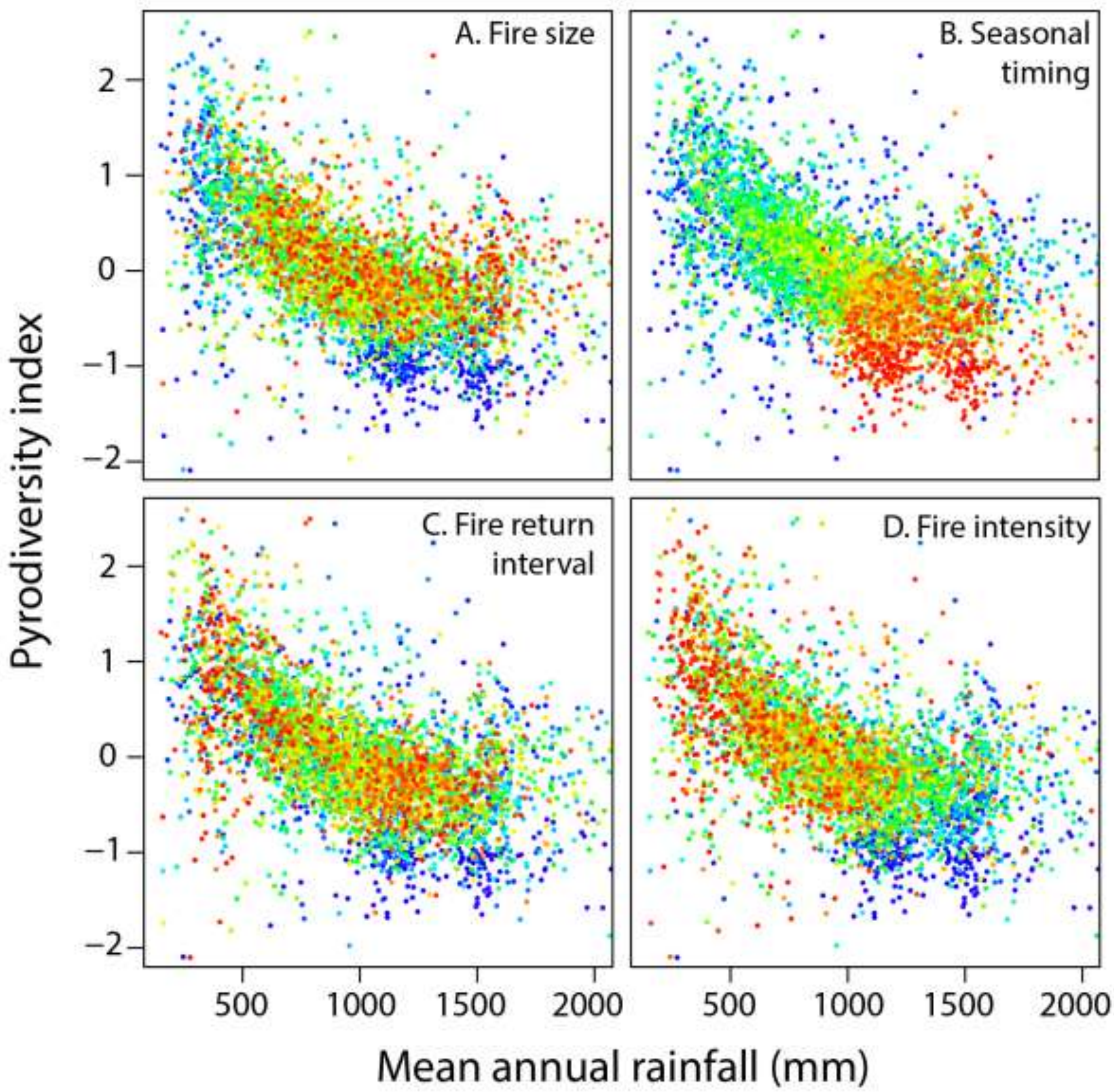

Figure 5. Contribution of different fire attributes to generating pyrodiversity in relation to mean annual rainfall (mm). The colour gradient ramp indicates the strength with which each fire attribute acts as a constraint on pyrodiversity. Blue is weak, green is intermediate, and red is strong. All variables were quantified at 30 minute spatial grain.

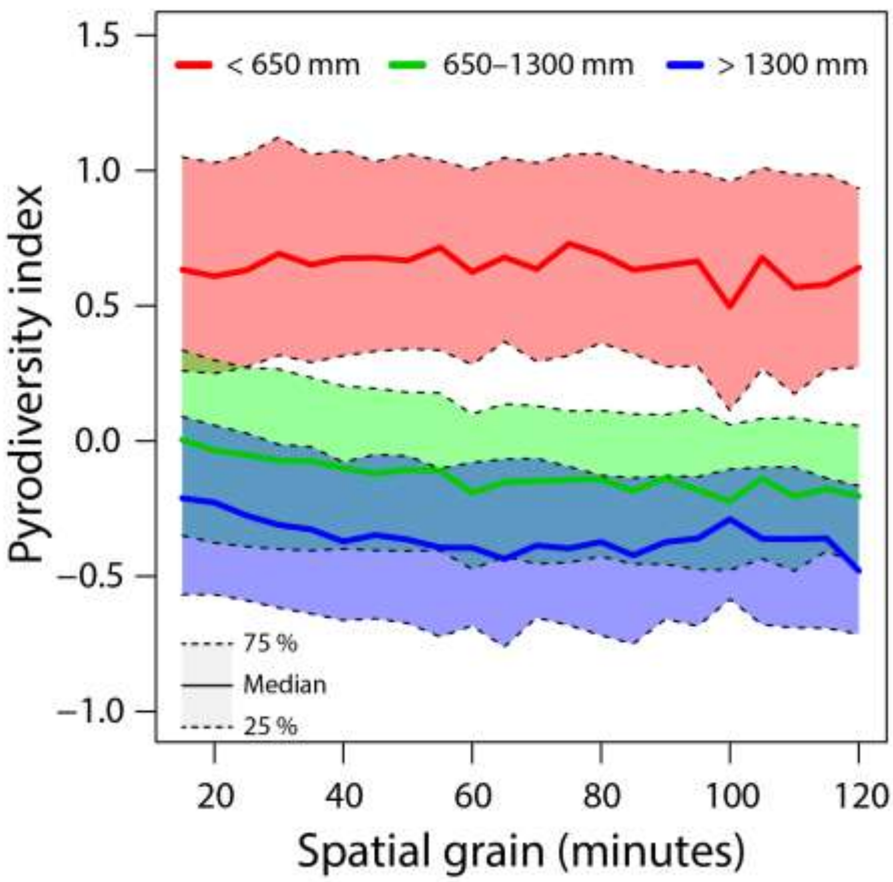

Figure 6. Values of the pyrodiversity index at different spatial grains and three levels of mean annual rainfall. Pyrodiversity was quantified at 5 minute increments and corrected for the number of fires per pixel. Median index values and interquartile ranges were calculated for areas with mean annual rainfall of < 650, 650–1300, and > 1300 mm.

Supplementary material

Appendix 1

Supplementary figures

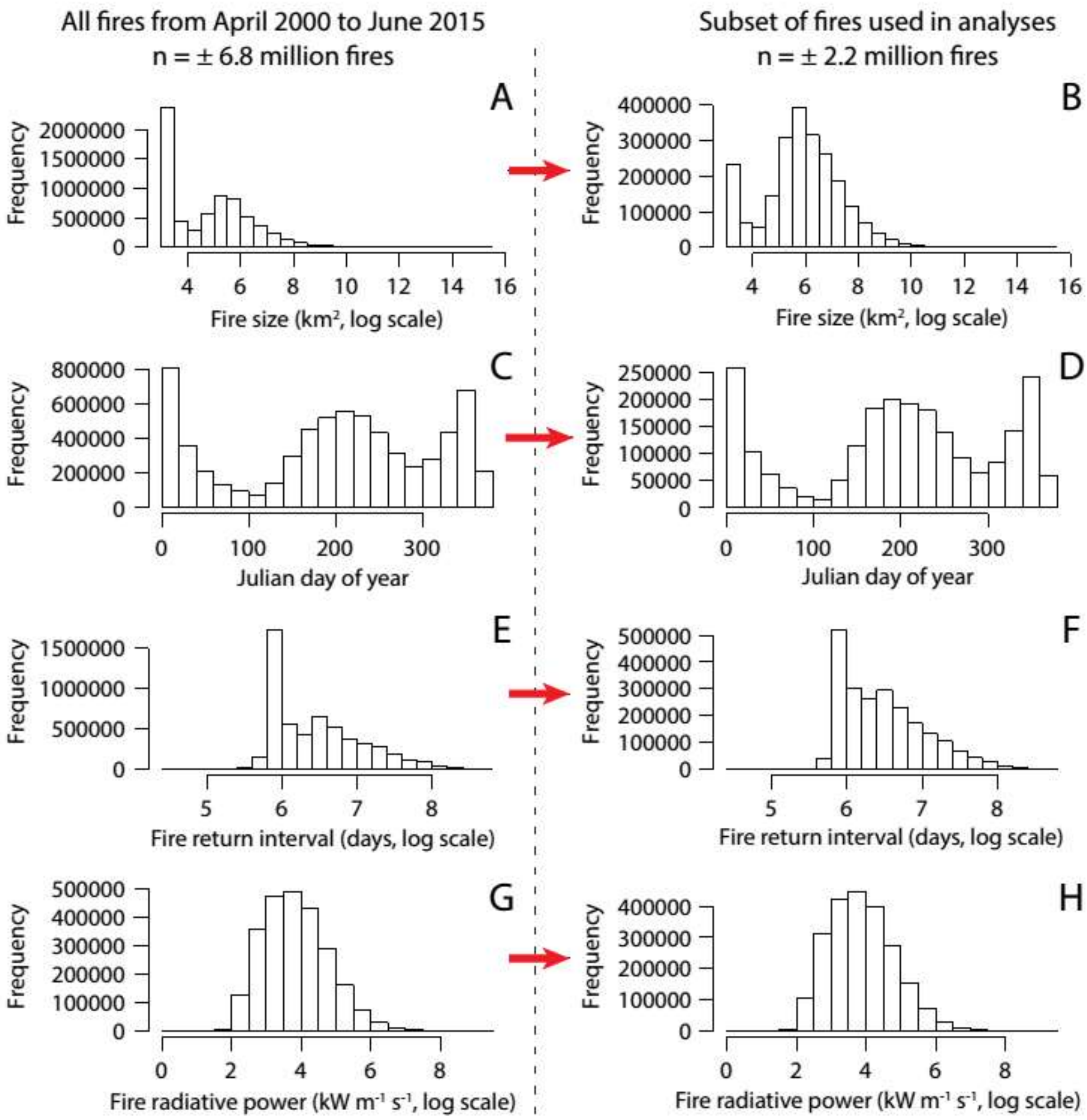

Figure A1. Fire attribute frequency distributions for the full data set (A, C, E & G) and for the subset of fires used in the analyses (B, D, F & H). Individual fires in the full data set required values for each of the four fire attributes in order to be included in the pyrodiversity analyses.

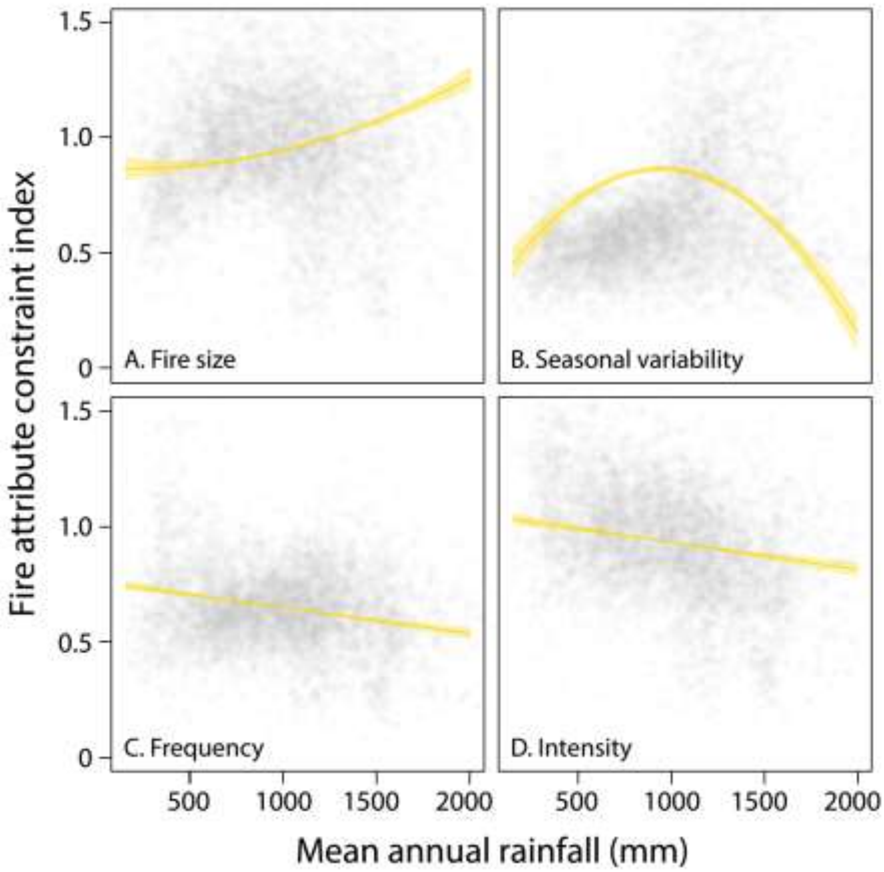

Figure A2. Fire attribute constraints on pyrodiversity in relation to mean annual rainfall: A) variation in fire size, B) variation in when fires occur within a year, C) variability in the length of time between fires, and D) the variation in fire intensity. Grey points represent the raw data, with median model predictions and the associated 95 % credible interval estimate range shown by the solid yellow line and shaded region respectively. Analyses were performed at 30 min spatial resolution. Model predictions account for spatial autocorrelation in the data, which is the primary reason for the apparent poor fit to the raw data in panels A and B.

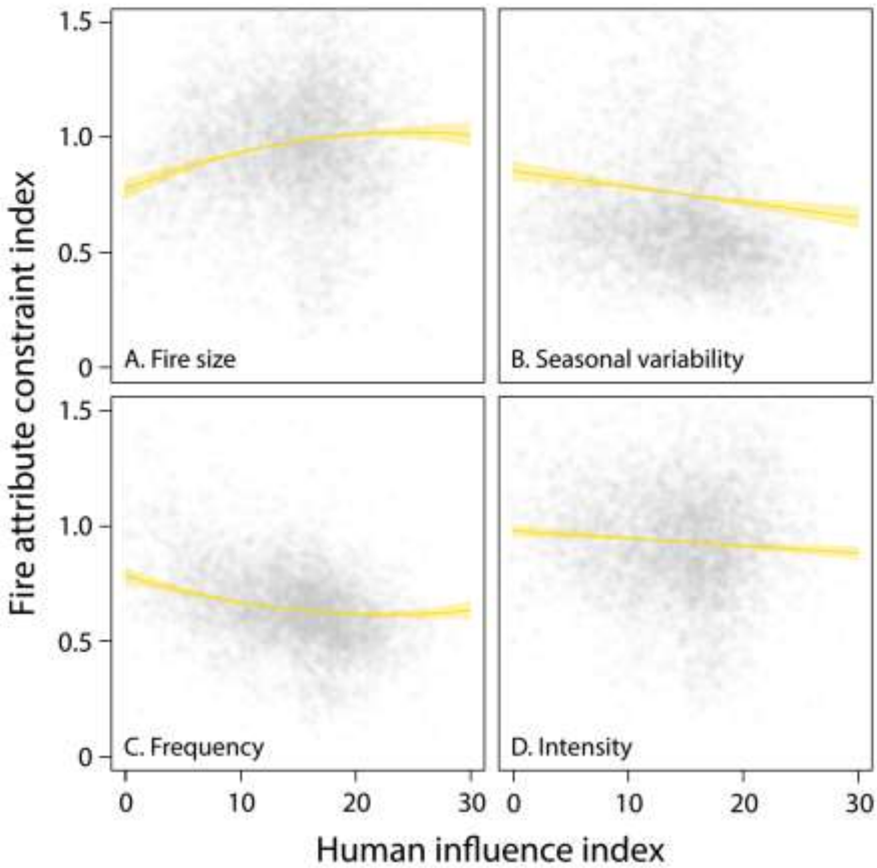

Figure A3. Fire attribute constraints on pyrodiversity in relation to the human influence index (Sanderson *et al*., 2002): A) variation in fire size, B) variation in when fires occur within a year, C) variability in the length of time between fires, and D) the variation in fire intensity. Grey points represent the raw data, with median model predictions and the associated 95 % credible interval estimate range shown by the solid yellow line and shaded region respectively. Analyses were performed at 30 min spatial resolution.

Supplementary tables

Table A1. Derivation of vegetation type classifications from White (1983) mapping units. Vegetation mapping units were grouped based on broad similarities in the physiognomy of the dominant plant groups.

Vegetation types	White (1983) mapping units
Caesalpinioid savanna	25, 26, 27, 28
Forest	1a, 2, 3, 4, 6, 8, 9, 77
Forest-grassland mosaic	11a, 12, 15, 16, 16a, 16b, 16c, 17, 19a, 19b, 20, 65, 66
Grassland	58, 59, 60, 61, 64, 75
Mixed savanna	22a, 24, 29a, 29b, 29c, 29d, 29e, 31, 32, 33, 35a, 35b, 35c, 36, 37, 38, 39, 40, 42, 43, 44, 45, 47, 48, 56, 62, 63
Shrubland	50, 51, 52, 53, 54a, 54b, 57a, 57b, 68b, 71, 74

Table A2. Median and 95 % credible intervals of parameter estimates for mean annual rainfall as a predictor of the constraint that different fire attributes (size, season, frequency and intensity) place on overall pyrodiversity, at 30 min spatial resolution. Mean annual rainfall (MAR; mm) was fitted as either a linear or quadratic effect; only the best model for each fire attribute is shown. Conditional autoregressive models were fitted in INLA and account for spatial autocorrelation within a Bayesian framework. ΔWAIC is provided based on difference in WAIC between full model and linear model (for fire size and fire season), and between linear and the null model (for fire frequency and fire intensity); values below -2 are usually considered to indicate strong support.

Fire attribute model	Model term	0.025 quantile	0.5 quantile	0.975 quantile	ΔWAIC
Fire size	Intercept	0.9386	0.9489	0.9592	-6.81
	MAR	0.0652	0.0800	0.0947	
	MAR ^{2}	0.0104	0.0201	0.0298	
Fire season	Intercept	0.8497	0.8665	0.8832	-442.9
	MAR	-0.0477	-0.0271	-0.0061	
	MAR ^{2}	-0.1256	-0.1095	-0.0932	
Fire frequency	Intercept	0.6466	0.6495	0.6523	-247.7
	MAR	-0.0559	-0.0460	-0.0361	
Fire intensity	Intercept	0.9287	0.9323	0.9360	248.8
	MAR	-0.0613	-0.0487	-0.0363	

Table A3. Median and 95 % credible intervals of parameter estimates for the human influence index (Sanderson *et al*., 2002) as a predictor of the constraint that different fire attributes (size, season, frequency and intensity) place on overall pyrodiversity, at 30 min spatial resolution. The human influence index (HII) was fitted as either a linear or quadratic effect; only the best model for each fire attribute is shown. Conditional autoregressive models were fitted in INLA and account for spatial autocorrelation within a Bayesian framework. ΔWAIC is provided based on difference in WAIC between full model and linear model (for fire size and fire frequency), and between linear and the null model (for fire season and fire intensity); values below -2 are usually considered to indicate strong support.

Fire attribute	Model term	0.025 quantile	0.5 quantile	0.975 quantile	ΔWAIC
Fire size	Intercept	0.9733	0.9807	0.9881	-1.72
	HII	0.0344	0.0451	0.0559	
	HII^2	-0.0175	-0.0115	-0.0056	
Fire season	Intercept	0.7521	0.7587	0.7653	82.5
	HII	-0.0526	-0.0361	-0.0195	
Fire frequency	Intercept	0.6344	0.6396	0.6449	0.77
	HII	-0.0368	-0.0289	-0.0211	
	HII^2	0.0053	0.0096	0.0139	
Fire intensity	Intercept	0.9284	0.9320	0.9357	43.84
	HII	-0.0272	-0.0172	-0.0071	