Supplementary Material for

Quantifying the environmental limits to fire spread in grassy ecosystems.

Anabelle W. Cardoso*[1,2], Sally Archibald[2], William J. Bond[3], Corli Coetsee[4,5], Matthew Forrest[6], Navashni Govender[5,7], David Lehmann[8], Loïc Makaga[8], Nokukhanya Mpanza[4], Josué Edzang Ndong[8], Aurélie Flore Koumba Pambo[8], Tercia Strydom[4,9], David Tilman[10], Peter D. Wragg[11], A. Carla Staver[1]

[1]Ecology and Evolutionary Biology Department, Yale University, 165 Prospect Street, New Haven, Connecticut, 06511, USA.
[2]Centre for African Ecology, School of Animal, Plant, and Environmental Sciences, University of the Witwatersrand, 1 Jan Smuts Avenue, Braamfontein, 2000, Johannesburg, South Africa.
[3]Biological Sciences Department, University of Cape Town, Rondebosch, Cape Town, 7700, South Africa.
[4]Scientific Services Kruger National Park, South African National Parks, Skukuza, Private Bag x 402, South Africa.
[5]School of Natural Resource Management, Nelson Mandela University, George Campus, 6530, South Africa.
[6]Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, Frankfurt am Main, 60325, Germany.
[7]Conservation Management Kruger National Park, South African National Parks, Skukuza, Private Bag x 402, South Africa.
[8]Agence Nationale des Parcs Nationaux, Residence Royale, Quartier Kalikak, Libreville, BP 20379, Gabon.
[9]Soil, Crop and Climate Sciences Department, University of the Free State, Bloemfontein, 9300, South Africa.
[10]College of Biological Sciences, University of Minnesota, 1987 Upper Buford Circle, St. Paul, Minnesota, 55108, USA.
[11]Department of Forest Resources, University of Minnesota, 1530 Cleveland Ave N, St. Paul, Minnesota, 55108, USA.
*Corresponding author: Anabelle W. Cardoso
Please note that author order from Bond to Wragg has been alphabetized.

Email: anabellecardoso@gmail.com

ORCID: https://orcid.org/0000-0002-4327-7259

Author Contributions: AWC, SA, and ACS designed the study. AWC led the data analyses and manuscript writing. AWC, SA, WJB, CC, NG, DL, LM, NM, JEN, AFKP, TS, DT, PDW, ACS contributed data and/or assisted with data collection. SA and ACS designed and coded the infection model. AWC prepared the first manuscript draft with input from ACS and SA. All authors provided substantive manuscript feedback.

Competing Interest Statement: The authors have no competing interests.

Classification: Research article.

Keywords: fire thresholds, ecological modelling, percolation theory, savanna,

This PDF file includes:

Extended Methods
Supplementary figures 1-6
Supplementary table 1

Extended methods

Lopé National Park in Gabon (Lopé) (11.6°, -0.2°):

The northern part of Lopé where this study took place is a forest-savanna mosaic, with closed-canopy rainforest extending through the south of the park (1, 2). Mean annual rainfall is 1442mm (1984–2016), mean annual temperature is 24◦C (2003–2016), and mean annual humidity is 81% (2003–2016) (3). All fires in this study were lit between mid-July and mid-September 2019, the long dry season when fires normally occur. The fires were part of the normal fire management plan of the park, which tries to maximize fire intensity during burning as a way to maintain the savanna component of the mosaic, which would otherwise be lost to encroaching forest (4).

Prior to each fire, a 100x100m plot was walked along its length in 10 equally-spaced parallel transects. Grass biomass was recorded every 2m using a calibrated disc pasture meter (see Cardoso et al. (2018)). Biomass measurements exceeding 2 tons.ha-1 were classified as "flammable" (6), and the ρ for the plot determined as the proportion of "flammable" measurements. After the fire, plots were revisited, and the proportion burned determined by noting whether each biomass measurement location was within the fire scar or not.

Ten to fifteen minutes before each fire, ten fuel moisture measurements were taken by clipping and weighing ten grass samples, which were then oven dried to constant weight and reweighed. Fuel moisture content was determined as the amount of water in the sample as a percentage of the dried weight. During burning, rate of spread of the fire front was measured using type-K thermocouples connected to data loggers (HOBO UX120 4-Channel Thermocouple Logger) that logged temperature every second. Thermocouples were positioned at 30cm, above ground level at each corner of a 1x1m square, with at least three such squares used in each fire. From this set-up, at least three triangles could be used in each fire to calculate rate of spread according to the method described by Simard et al. (1984). The point at which the fire front passed a

thermocouple was assumed to be when the temperature recorded by the thermocouple peaked. During burning, a portable weather station (Kestrel 5500L) was used to log ambient temperature, relative humidity, and wind speed and direction every 30s.

Hluhluwe-iMfolozi in South Africa (HiP) (-28.2°, 31.9°):

HiP covers a wide range of vegetation types, from semi-arid thorn savanna in the lowlands to a forest-savanna mosaic in the more mesic uplands (8). Mean annual across the park varies from 600 to 1000mm, mean annual temperature is around 25 °C and mean annual humidity is around 75% (8, 9). Fires in this data set were lit in the dry season (July to October 2002) to approximate the "natural" wildfire regime.

We sampled thirty plots at ten sites. Each plot was between 640 and 880 m2 and was divided into 2x2m grid cells. Grass biomass was measured at the center of the grid cell using a calibrated disc pasture meter and these values were used to infer the fuel connectivity (ρ) for each plot. After burning, each grid cell was recorded as unburnt (proportion burned=0), partially burned (proportion burned=0.1 to 0.5), or fully burned (proportion burned=0.5 to 1), and the average proportion burned for the entire plot was calculated (see (10) for a description of the plots).

Kruger National Park in South Africa (Kruger) (-24.0°, 31.6°):

Kruger is mostly savanna, with more mesic savanna in the south, more open grasslands in the middle, and woodier Colophospermum mopane dominated savanna in the north. Mean annual rainfall ranges from 737mm in Pretoriuskop (PKP) and 550mm in Skukuza (SKZ) in the south to 544mm MAP in Satara (SAT) and 496mm in Mopani (MOP) further northwards. Mean annual temperature is approximately around 27°C and mean annual humidity is around 63% (9). The majority of fires in Kruger were lit as part of the long-term ongoing Experimental Burn Plot project that aims to capture the effects of different burning regimes on vegetation (11). Since 1954, plots across a precipitation gradient approximately 7ha in size have been burned in one of twelve burn

treatments. These treatments spanned different burn seasons (late summer, autumn, late winter, after spring rains, and mid-summer) and fire frequencies (every 1, 2, 3, 4, 6, and 45 years). Each treatment is replicated four times at PKP, SKZ, SAT, and MOP. Generally, fires were lit during the hottest, driest times of the day (10am to 3pm).

Of the 1004 fires in Kruger, 965 occurred in the Experimental Burn Plots. Of these fires, 26 (5 in PKP, 5 in SKZ, 6 in SAT, and 10 in MOP) had detailed measurements collected using the same protocol as in Lopé. The remaining 939 Experimental Burn Plot fires (207 in PKP, 235 in SKZ, 302 in SAT, and 195 in MOP) had fuel moisture recorded as the mean of four samples, while temperature, humidity, and wind speed were recorded as one mean value during the burn. Rate of spread was estimated in two ways, either by measuring the time taken for the fire front to pass between two points of known distance apart, or as a function of the area burnt by the head fire, the mean length of the fire front, and the mean duration of the burn (details can be found in Govender et al., 2006).

In addition to the Experimental Burn Plot fires, a further 39 fires were applied as part of a landscape-level experiment in the Satara region of the park (see Donaldson et al., 2018, for more details). These fires were applied across two seasons (early in the burning season: April/May, late in the burning season: September/October). These fires were repeated in the same locations for four years, resulting in fires with a range of fuel moisture, weather conditions, and fuel connectivities (each year the connectivity of the landscape decreased as grazing kept the grass short). Prior to each fire, point-location data on grass height (fuel connectivity) were collected from transects placed systematically across the burn block. The same points were afterwards assessed for whether they burned or not (proportion burned). Fuel moisture was estimated as the mean of 4 grab-samples for each fire, using the same drying and weighing protocol as in Lopé. Fire behavior data were collected using a hand-held weather meter and quantifying rate of spread

as the time taken for the flame front to move a set distance (at least 3 measures per fire on the head fire).

In addition to the fires described above, an additional set of ongoing long-term monitoring plots from Kruger were included in this study to evaluate patterns in fuel connectivity and proportion burned over space and time. These 533 "Veld Condition Assessment" plots (50 x 60m) were established in 1989 to monitor grass biomass and inform fire management across the park. Of the original sites, 363 have been continuously monitored since then (1989-2012, 2016-2018), with grass biomass being measured every 2m in four transect lines equally spaced along the plot (14). Over the same time period, Kruger has also kept detailed fire records from across the park. Historically, fire scars were drawn by hand and have subsequently been digitized, and more recently MODIS satellite-derived fire-scar mapping has been used (14). The proportion of sites that burned in any given year was strongly correlated with the proportion of Kruger that burned in that year (slope=1.1, intercept=0.0, adjusted R2=0.88, p<0.0001), indicating that the sites are a good representation of the ecosystem.

Cedar Creek Ecosystem Science Reserve, USA (Cedar Creek) (45.4°, -93.2°):
Cedar Creek is a tallgrass prairie oak savanna (15). Mean annual precipitation is ~775mm, mean annual temperature is around 8∘C, and mean annual humidity is around 75%, with strong temperature seasonality. For this work, we used a set of 158 out of 168 plots (9 x 9m squares) established in 1994 as part of the long-term Big Biodiversity ("BigBio") experiment (16); this experiment intensively manipulates herbaceous community species richness with outcomes for herbaceous biomass that are the basis for the canonical relationship between biodiversity and ecosystem function. Ten plots were excluded because they have permanent equipment established to warm plots as part of another experiment which obstructed estimates of burned area. As a matter of routine, all 168 of these plots are burned annually, after snowmelt but before the growing season begins in earnest, to clear biomass accumulated during the previous year

and to control possible woody encroachment into experimental plots. For this work, we observed fire behavior across plots in April 2014 to evaluate how biomass and therefore fuel cover variation (i.e., fuel continuity) translated into differences in fire behavior and burned area (i.e., proportion burned).

To control for probability of edge effects (since plots are small – 9 x 9 m – and each plot was lit along its edge via a propellant), subplots of 5 x 5m were established in the center of each BigBio plot. Fuel connectivity and proportion burned estimates were done by establishing a 0.5m grid (i.e., 11 x 11 sample points across the whole subplot) and evaluating the state of the vegetation that intersected the grid at each sample point. Before the fire, a sample point was scored as "flammable" if the intersection crossed grass and "not flammable" if it crossed bare ground. After the fire, the sample point was scored as "burnt" if the intersection crossed black/charred vegetation and "unburnt" if the intersection crossed green vegetation or bare ground. The grid was evaluated using photographs of each plot taken before and after each fire from a telescopic boom lift ~ 8m above the center of each plot, using a Canon Rebel T3i with Tamron 10-22mm lens set at 10mm, demarcating each plot corner with white paper plates for contrast. Because the BigBio experiment aims to eliminate previous season biomass before the next growing season, plots that do not burn completely are relit; however, for this work, post-burn plots were photographed after only the first burn and before reburning. Photographs were analyzed by two independent undergraduate research assistants (L. Ashbrook and M. Sagedahl) and when they differed by > 10%, reconciled by a third (A.C. Staver). We also collected ground-based estimates of flammable area at 21 subplots before burning and of burned area at 17 subplots after burning, to ground-truth the photographic scores. Overall, photo-based evaluations of burned area were closely predictive of field calibrations ($R^2 = 0.954$, $p < 0.001$, $n = 38$), with nearly as good validation across pre- ($R^2 = 0.885$, $p < 0.001$, $N = 21$) and post-burn plots ($R^2 = 0.928$, $p < 0.001$, $n = 17$).

All subplots were included in flammable vs. burned analyses except those where the large

majority of biomass (> 75%) was contributed by non-grass herbaceous species (i.e., forbs),

based on 2012 biomass estimates published elsewhere for the BigBio experiment. This

eliminated 92 plots for a total of 66 plots out of the original 158 sampled.

Supplementary Figures and Tables

Figure S1: Map of grassy ecosystem sites in this study. These included: Cedar Creek Ecosystem Science Reserve in the United States of America (775mm mean annual precipitation (MAP)), Lopé National Park in Gabon (1442mm MAP), Hluhluwe-iMfolozi National Park in South Africa (600-1000mm MAP), Kruger National Park in South Africa (**A**), and the sites inside Kruger (park outline shaded dark grey) (**B**) including Mopani (496mm MAP), Satara (544mm MAP), Skukuza (550mm MAP), and Pretoriouskop (737mm MAP).
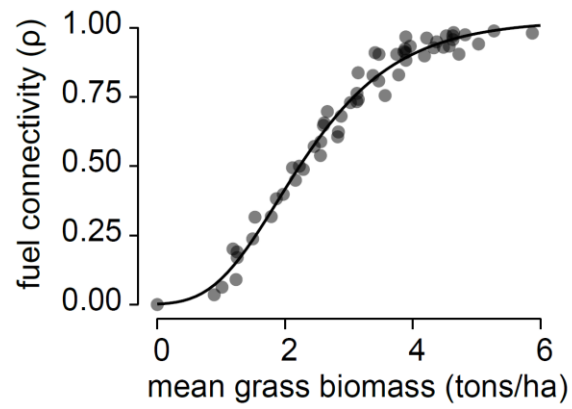
Figure S2: Fuel connectivity (ρ) increases with mean grass biomass (in 100m^2 plots). Line shows fitted Gompertz model, $\rho = 1.03 * e^{-6.42 * e^{-0.98 * mean\ grass\ biomass}}$, adjusted R^2=0.98, p<0.0001, n=57).

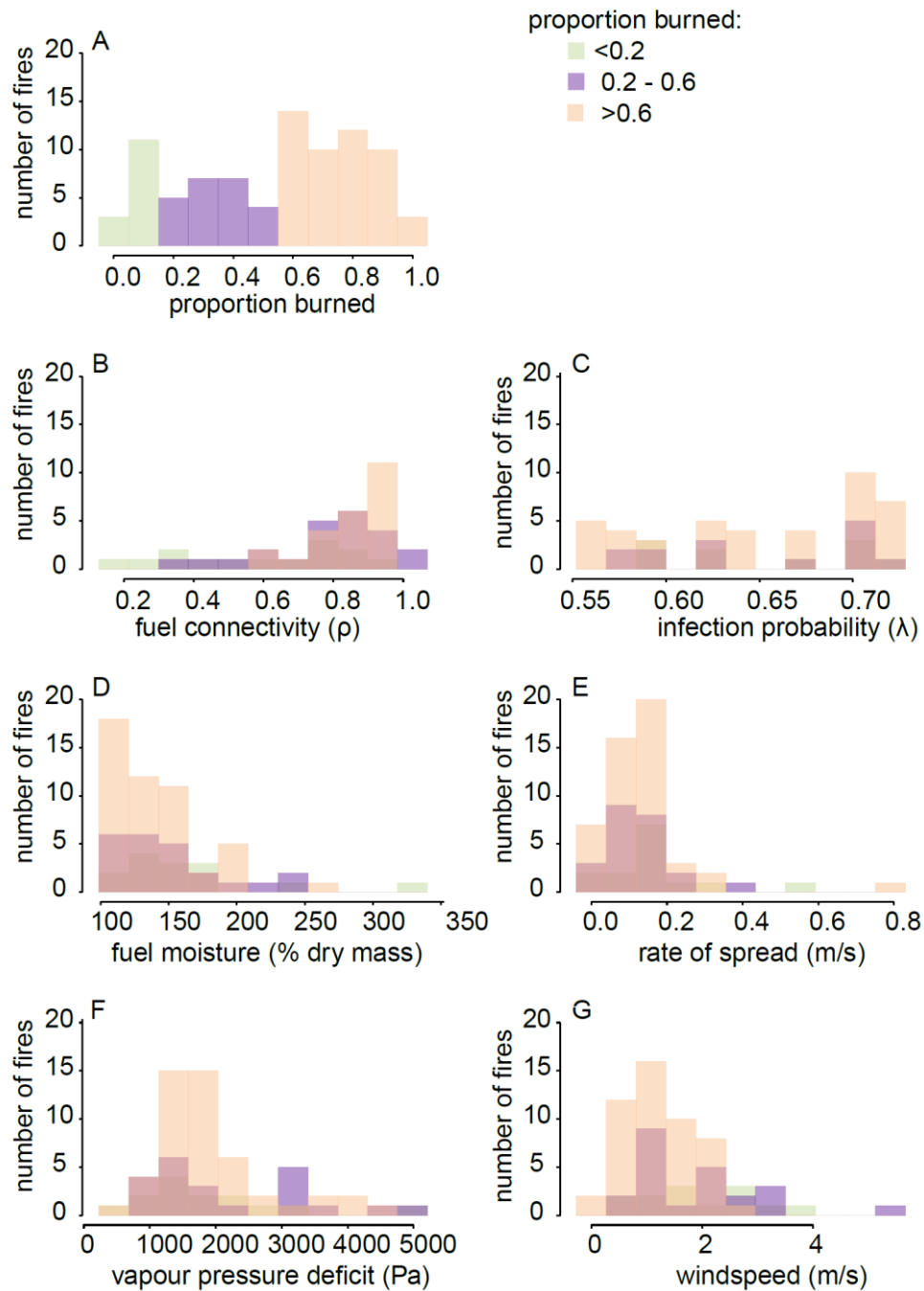**Figure S3:** All fires with fuel moisture content >100% (n=86), showing the differences between fires that had a burned area less than 0.2, between 0.2 and 0.6, and more than 0.6 (**A**), in terms of fuel connectivity (ρ) (**B**), infection probability (λ) (**C**), fuel moisture content (**D**), rate of spread (**E**), vapor pressure deficit (**E**), and wind speed (**F**).
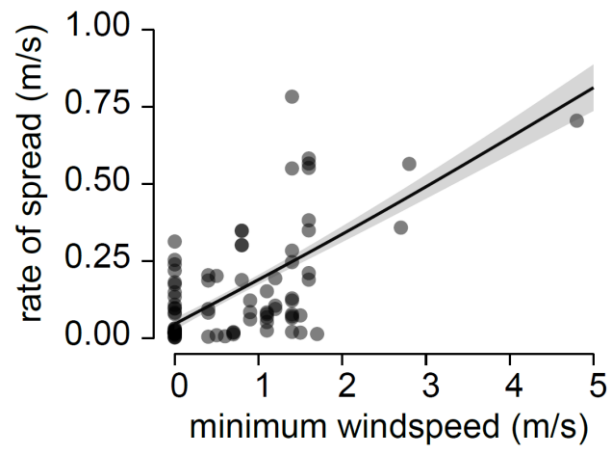
Figure S4: The relationship between rate of spread of the fire front as measured using thermocouples placed in a triangular setup and minimum measured wind speed during the same period. Line shows fitted linear model, $rate\ of\ spread\ =\ 0.04\ +\ 0.15*wind\ speed$, adjusted R^2=0.49, p<0.0001.
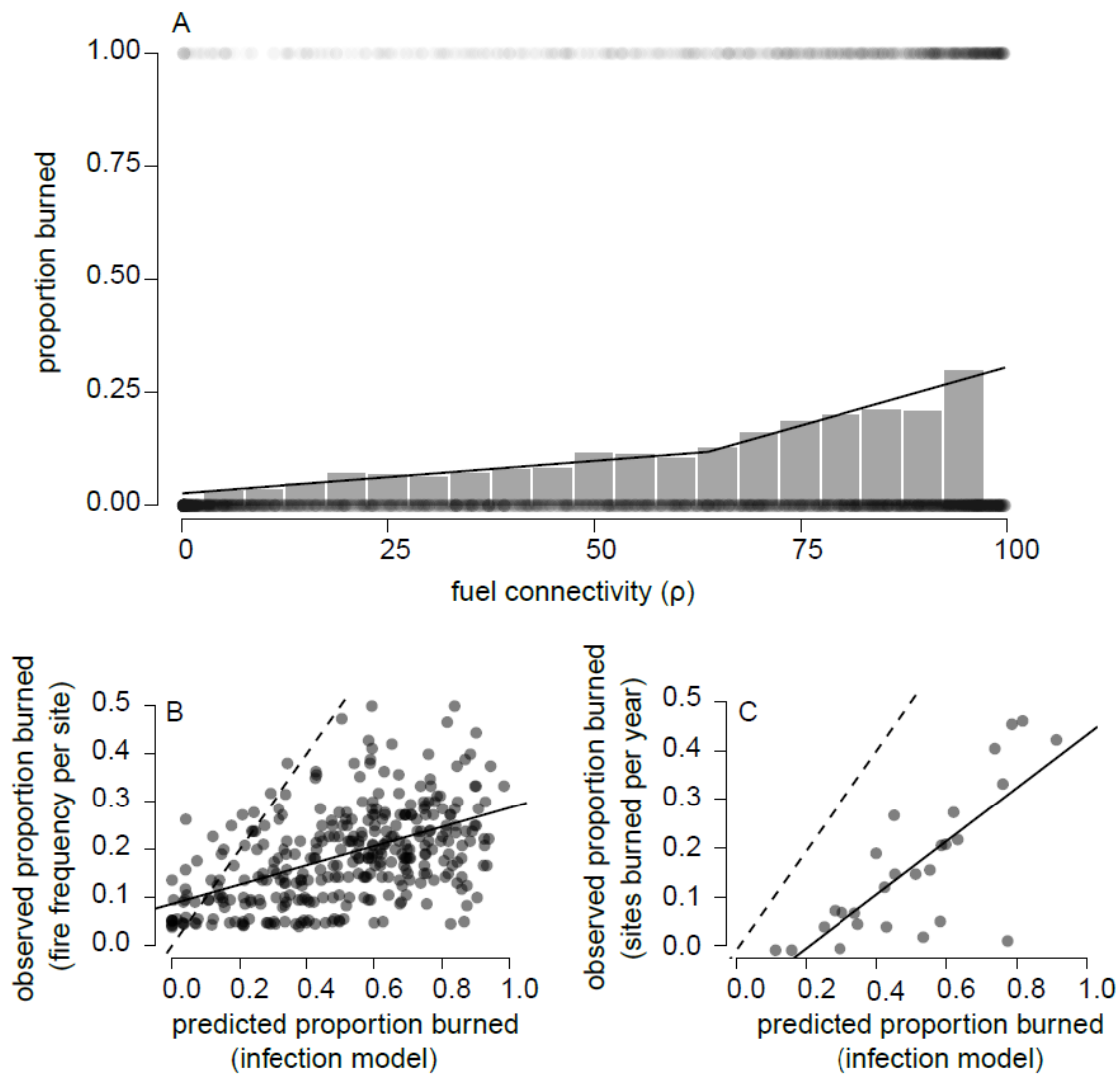
Figure S5: Using data from long-term monitoring sites in Kruger National Park, South Africa we show how the observed probability of a site burning in any one year changes with changes in the measured fuel connectivity (ρ) at that site (points show individual sites in individual years, bars show binned mean probability of burning, and line shows the two linear model fitted to the bars when ρ is < 0.64, then probability of burning = 0.03 + 0.001*(ρ /100); and when ρ is > 0.64, then probability of burning = -0.23 + 0.005*(ρ /100); adjusted R^2=0.97, p<0.0001) (**A**). **B**) Shows the data in **FIG. 5A** compared to model predictions for the proportion burned, with the solid line showing the fitted linear model (slope=0.54, intercept=-0.1, adjusted R^2=0.58, p<0.0001). **C**) Shows the data in **FIG. 5B** compared to model predictions for the proportion burned, with the solid line showing the fitted linear model (slope=0.20, intercept=0.09, adjusted R^2=0.24, p<0.0001). All dotted lines show the relationship y = x which represents the perfect correlation between observed and predicted data.
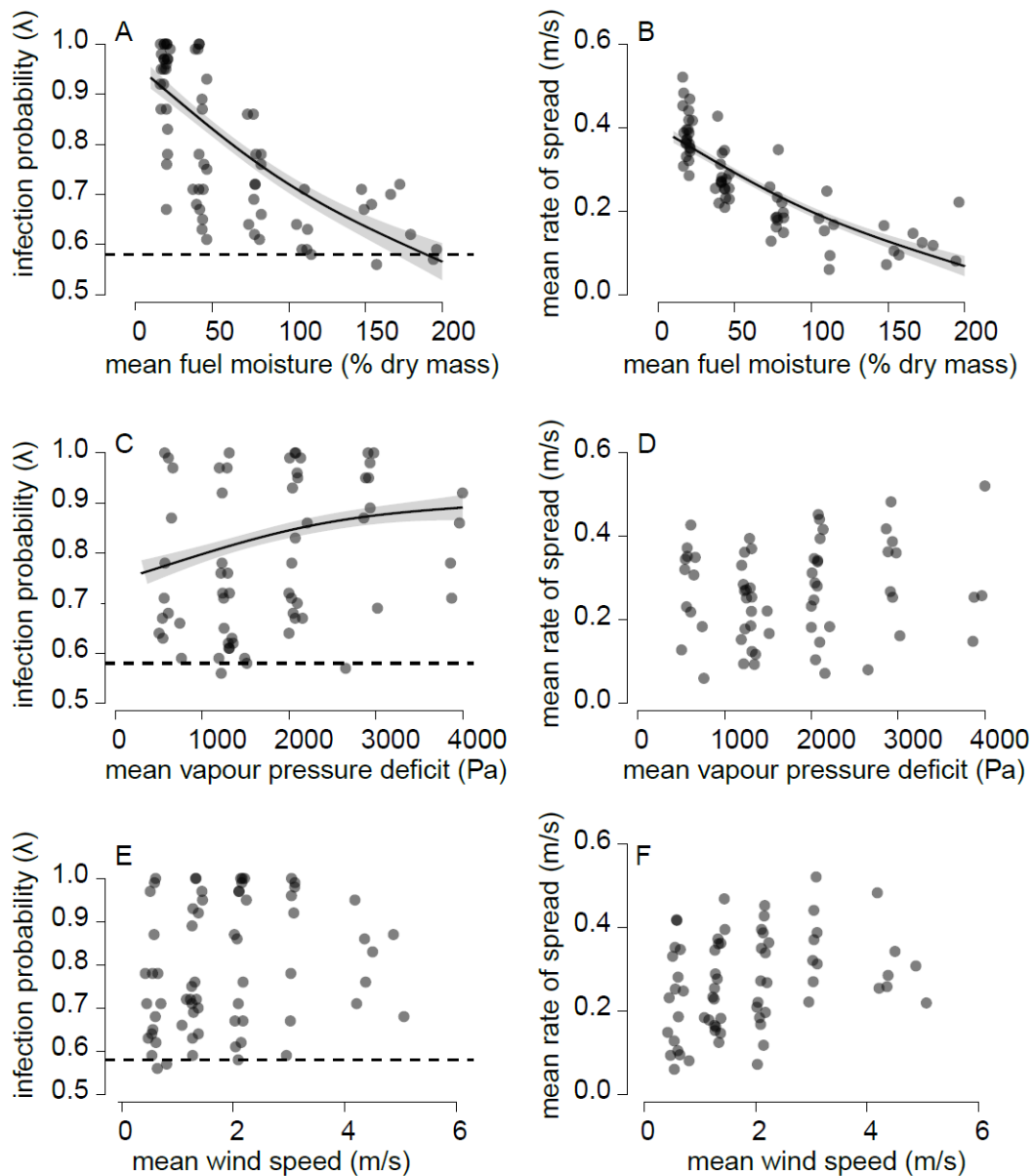
Figure S6: Estimated fire infection probability (λ) and rate of spread of the fire front decrease with increased fuel moisture (**A**, **B**), increase with vapor pressure deficit (**C**, **D**), and are not related to wind speed (**E**, **F**). Curves show the fitted generalized additive model (GAM), and curves are only plotted when significant, with standard errors of fits shaded in grey (**Table S1**). Curves shown were fitted when the other two variables were held at a constant median value (fuel moisture= 43%, vapor pressure deficit=2004 Pa, wind speed=1.4 m/s). In A, C and E, dashed lines show the minimum infection probability (λ=0.58) in observed "threshold fires" (those with burned area between 0.2 and 0.6) below which fire cannot successfully spread.

Table S1: Summary of fitted generalized additive models (GAMs). Each *n* represents a binned group of fires, grouped according to their mean fuel moisture (0-32%, 32-64%, 64-96%, 96-128%, >128%), vapor pressure deficit (0-850Pa, 850-1700Pa, 1700-2550Pa, 2550-3400Pa, >3400Pa), and wind speed (0-0.88m/s, 0.88-1.76m/s, 1.76-2.64m/s, 2.64-3.52m/s, >3.52m/s). An *infection probability* (λ) was fitted to each group of fires. Groups with fewer than 3 fires were excluded. All smooths were fitted using restricted maximum likelihood (REML), thin plate splines, a smoothing parameter of 0.6, and 3 knots (confirmed to be sufficient as k-index > 1 in all cases). Variables with a significant explanatory power (p<0.05) are marked with *.

λ ~ s(mean fuel moisture) + s(mean vapor pressure deficit) + s(mean wind speed) *n=68, adjusted R^2=0.60*			
	Estimated degrees of freedom	F	p value
Mean fuel moisture	1.2	40	<0.0001 *
Mean vapor pressure deficit	1.3	6	<0.001 *
Mean wind speed	1.2	1	0.12
mean rate of spread ~ s(mean fuel moisture) + s(mean vapor pressure deficit) + s(mean wind speed) *n=68, adjusted R^2=0.70*			
	Estimated degrees of freedom	F	p value
Mean fuel moisture	1.2	66	<0.0001*
Mean vapor pressure deficit	1.3	2	0.11
Mean wind speed	1.2	1	0.28

References

1. J. P. van de Weghe, Les Parcs Nationaux du Gabon: Lopé, Waka et Monts Birougou (ANPN and WCS Gabon, 2011).
2. F. White, "The vegetation of Africa: A descriptive memoir to accompany the Vegetation Map of Africa" (1983).
3. C. E. Tutin, et al., Lopé Weather Dataset. DataSTORRE (2019).
4. K. J. Jeffery, L. Korte, F. Palla, L. J. T. White, K. a Abernethy, Fire Management in a Changing Landscape : a case study from Lopé National Park. Parks 20, 35–48 (2014).
5. A. W. Cardoso, et al., Grass Species Flammability, Not Biomass, Drives Changes in Fire Behavior at Tropical Forest-Savanna Transitions. Front. For. Glob. Chang. 1, 6 (2018).
6. W. S. W. Trollope, L. A. Trollope, D. C. Hartnett, "Fire behaviour a key factor in the fire ecology of African grasslands and savannas" in Forest Fire Research & Wildland Fire Safety, (Millpress, 2002), pp. 2–14.
7. A. J. Simard, J. E. Eenigenburg, K. B. Adams, Ro. L. Nissen Jr, A. G. Deacon, A general procedure for sampling and analyzing wildland fire spread. For. Sci. 30, 51–64 (1984).
8. J. P. G. M. Cromsigt, S. Archibald, N. Owen-Smith, "Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story" in Conserving Africa's Mega-Diversity in the Anthropocene, (2018).
9. WorldWeatherOnline.com, Historical Average Weather (2020) (July 20, 2020).
10. T. Charles-Dominique, G. F. Midgley, K. W. Tomlinson, W. J. Bond, Steal the light: shade vs fire adapted vegetation in forest-savanna mosaics. New Phytol. (2018) https:/doi.org/10.1111/nph.15117.
11. R. Biggs, H. C. Biggs, T. T. Dunne, N. Govender, A. L. F. Potgieter, Experimental burn plot trial in the Kruger National Park: history, experimental design and suggestions for data analysis. Koedoe 46 (2003).
12. N. Govender, W. S. W. Trollope, B. W. Van Wilgen, The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. J. Appl. Ecol. 43, 748–758 (2006).
13. J. E. Donaldson, et al., Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. J. Appl. Ecol. 55, 225–235 (2018).
14. A. C. Staver, J. Botha, L. Hedin, Soils and fire jointly determine vegetation structure in an African savanna. New Phytol. 216, 1151–1160 (2017).
15. P. D. Wragg, T. Mielke, D. Tilman, Forbs, grasses, and grassland fire behaviour. J. Ecol. 106, 1–19 (2018).
16. D. Tilman, et al., The Influence of Functional Diversity and Composition on Ecosystem Processes. Science (80-.). 277, 1300–1303 (1997).