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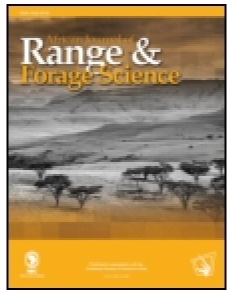

Could CO2-induced changes to C4 grass flammability aggravate savanna woody encroachment?

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Abstract:	Fire plays an important role in maintaining the savanna tree-grass balance by limiting the recruitment of heat-sensitive tree seedlings. However, fire behaviour may change under increasing CO_2 concentrations, due to altered flammability of the grassy layer. Here, we determined the effect of predicted future CO_2 concentrations, and how it interacts with water-availability, on grass flammability and traits influential to flammability, and uncovered the physiological mechanisms underpinning these responses. Using the widespread C_4 savanna grass, Themeda triandra, as a model, we found that improved water-use efficiency under elevated CO_2 (800ppm) resulted in a larger (greater aboveground biomass) but wetter (higher moisture content) grass fuel load, that cured at a slower rate under drought conditions. These changes were associated with increased time to ignition, reduced flaming times and predicted rate of spread. We modelled the effect of altered grass flammability on fire behaviour at a national level (South Africa), finding large-scale reductions in fire spread under elevated CO_2, mitigating the converse effects of predicted increases in aridity, and marginal increases in fireline intensity. CO_2-induced reductions in fire frequency, spread or intensity could have serious implications for savanna vegetation dynamics, possibly exacerbating the woody encroachment already seen in these ecosystems across the world

2. Introduction

In tropical savannas, fire is a highly frequent disturbance that is essential in maintaining the balance of the two life forms present – C_4 grasses and C_3 savanna trees (van Langevelde et al., 2003; Bond et al., 2005; Sankaran et al., 2005). Regular fire maintains an open canopy that allows shade-intolerant C_4 grasses to thrive by limiting the recruitment and maturation of savanna trees (Bond & Midgley, 2001). The grassy understory fuels fire in these ecosystems, and therefore, it is the flammability of the grass community that determines fire behavior (Bond and van Wilgen, 1996; Beckage et al., 2009; Prior et al., 2017). The key plant traits that determine savanna grass flammability are the amount of aboveground biomass and its moisture content (Simpson et al., 2016), as these dictate how much fuel is available and how easy it is to ignite and spread fire. However, both of these traits may be altered under increasing atmospheric CO_2 concentrations. Elevated CO_2 (eCO_2) can enhance C_4 grass productivity, through stimulating photosynthetic capacity (Wand et al., 1999) or by improving water relations in these seasonally-dry habitats (Quirk et al., 2019). Related to the improved water relations is the maintenance of higher biomass moisture contents into the dry season when savanna fire activity peaks. The effect of eCO_2 on savanna grass flammability is largely unknown (Manea et al., 2015), but is crucial in predicting how fire behavior may alter in the future, and thus the continued co-existence of trees and grasses in these ecosystems.

Plant flammability is a key determinant of fire activity worldwide (Bond and van Wilgen, 1996; Beckage et al., 2009; Prior et al., 2017). This is true for savannas where the strong influence of grass flammability on fire behavior is evidenced by striking examples of altered fire behavior alongside changes in the flammability of the grass layer (D'Antonio, 2000; Platt and Gottschalk, 2001; Davies and Nafus, 2012, Setterfield et al., 2013). Savanna grasses differ substantially in their flammability (Simpson et al., 2016). This inter-specific variation means that even within a landscape, spatial differences in grass community composition, and thus flammability, can mediate fire behavior. For example, changes in the flammability of the grass layer alone were responsible for fires becoming less intense on the approach to the interface between savanna and tropical forest in Gabon (Cardoso et al., 2018). Alternatively, having a similarly flammable grass layer can result in convergent fire regimes in savannas with drastically different climatic conditions (e.g. Longleaf pine savanna in the USA vs. Eucalypt savanna in Australia; Archibald et al., 2018).

The flammability of a plant depends on chemical and physical plant traits that together contribute to biomass ignitability (the ability to ignite and spread fire), sustainability (the time that combustion is maintained), and combustibility (burning intensity; Rothermel, 1972; van Wilgen et al., 2010; Pausas et al., 2017). Above-ground biomass drives combustibility and sustainability with high biomass species burning more intensely and for longer and producing high predicted fire spread rates (Simpson et al., 2016). Biomass moisture content determines how plant material absorbs heat energy, with high moisture levels translating into delayed ignition, lower combustion, and reduced rates of fire spread (Rothermel, 1972; Pyne, 1976). The moisture in a plant acts as a sink for heat energy, reducing the heat energy available for ignition (Chuvieco et al., 2004). For example, higher fuel moisture contents resulted in reduced combustion and lower rates of fire spread in savanna fire trials in South Africa (Govender et al., 2006). The contribution of these two grass traits to savanna fire behavior varies across rainfall gradients, with low-rainfall savanna fires being biomass (fuel) limited and high-rainfall savanna fires being limited by fuel moisture (Alvarado et al., 2019).

Rising atmospheric CO_2 has the potential to alter savanna grass flammability because it influences both the amount and the moisture content of biomass (Fig. 1). eCO_2 can directly affect grass productivity through the stimulation of photosynthetic capacity. C_4 grasses may show enhanced carbon assimilation under eCO_2 despite their carbon concentrating mechanism, and therefore a greater biomass production, although this response appears to be variable (Wand et al., 1999). Of greater importance however, is the indirect impact of CO_2-induced improved water relations on increased savanna grass biomass. eCO_2 reduces stomatal conductance (G_{st}) and transpiration, while allowing photosynthetic capacity to be maintained (i.e. enhanced water use efficiency (E), WUE; Atkin et al., 1999; Saralabai et al., 1997). High temperatures and irradiance levels, combined with seasonal rainfall, means that savanna grasses are susceptible to water limitation (Osborne and Sack, 2012). Therefore, improved water relations under eCO_2 allows the effects of water limitation to be delayed or reduced, and assimilation (and therefore growth) to be maintained for longer (Reyes-Fox et al., 2014). As well as increasing biomass, this may also result in higher fuel moisture contents, due to plant water potential being maintained higher for longer into the dry season. Experiments that have investigated the effects of eCO_2 on C_4 grasses have found evidence for both of these predicted changes. For example, Quirk, Bellasio and colleagues (2019) found that the C_4 savanna grass, *Eragrostis curvula*, had more aboveground biomass that also had higher relative water contents when grown under *e*CO_2. How increases in biomass quantity and moisture content under *e*CO_2 will interact to drive changes in grass flammability is unclear due to their opposing impacts.

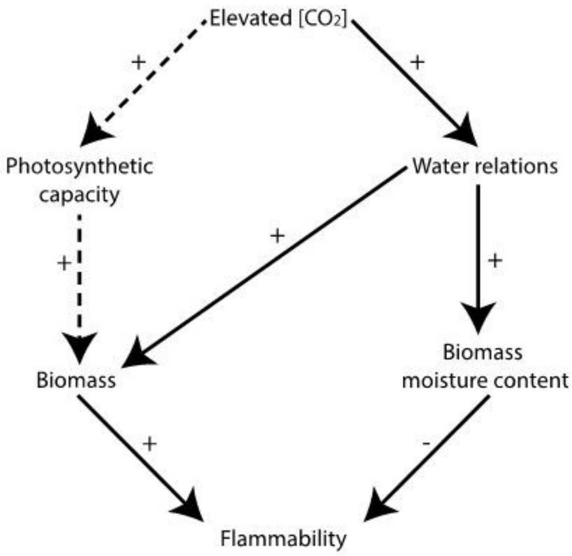


Figure 1. Potential impacts of elevated atmospheric CO_2 concentrations ([CO_2]) on savanna grass traits and flammability. Dashed lines represent smaller or less certain effects.

CO_2-induced changes to grass flammability could have significant impacts on savanna community composition and structure, particularly if grass flammability is reduced. Savannas have experienced a significant reduction in fire activity over the past few decades (Andela et al., 2017;) mostly due to increased fuel moisture levels (Zubkova et al., 2019), and this pattern could be further exacerbated through future reductions in grass flammability. Less frequent fire is both a cause and consequence of rapidly increasing tree densities in savannas: fewer fires allow more tree individuals to escape the 'fire trap' and establish (Smit et al., 2010), and more trees reduce fire activity by shading out the grass understory. This positive feedback may be intensified in the future by the CO_2-fertilisation of C_3 savanna trees (Bond and Midgley, 2000; Kgope et al., 2010). On the other hand, *e*CO_2 could increase grass flammability and fire activity, and so limit woody plant establishment via increased seedling mortality.

The aim of this study is to determine how savanna grass flammability is altered under *e*CO_2. Here we used plants of a typical C_4 grass species that is widespread in

South African savannas, *Themeda triandra*, grown under ambient and predicted future [CO_2], to test the impacts of *e*CO_2 on different flammability components and their underlying plant traits. Various authors have predicted increases in fire activity as the climate becomes warmer and drier (e.g. Flannigan et al., 2009; Fargeon et al., 2020; Smith et al., 2020), but these not do consider the effects of CO_2 on vegetation. To determine the role of water availability on an *e*CO_2 effect, plants were also subjected to either a well-watered or a water-limited treatment before traits and flammability measurements were taken. We also undertook a modelling exercise to see how flammability changes may impact on country-wide fire behaviour.

3. Materials and methods

3.1. Study species

Themeda triandra Forssk. (Poaceae, Panicoideae, Andropogoneae; hereafter simply referred to as *Themeda*) is one of the most widespread and ecologically dominant C_4 grass species in paleotropic savannas (Snyman et al., 2013; Dunning et al., 2017). This perennial, tussock-forming grass has a close association with recurrent fire: it is reliant on periodic burning to persist (Snyman et al., 2013) and is lost from a system when both fire and grazing are excluded (Danckwerts, 1993). It recovers rapidly after fire by resprouting from basal meristems (Bond et al., 2003; Morgan and Lunt, 1999) and has been shown to plastically adjust traits relating to post-fire recovery in order to maximise fitness under different fire regimes (Simpson et al., 2019).

In this study, *Themeda* plants were collected from a grassland site in the Eastern Cape of South Africa (coordinates: -33.278, 26.489). To simulate a typical field scenario in terms of biotic interactions and plant densities, three *Themeda* tussocks (each consisting of 8 tillers) were planted along with one seedling of the common C_3 savanna trees, *Vachellia karroo* Hayne., in large 25L plastic pots (31x40cm). *V. karroo* seedlings grown with the *Themeda* were all similar in size (2.5±0.4g). Only data from the focal species, *Themeda*, is discussed in this manuscript. Soil was obtained from a nearby savanna where both *Themeda* and *V. karroo* grow naturally (Fort Beaufort, Eastern Cape) classified as Loam soil and considered to be representative of local savanna soil nutrient and texture (19 / 8 / 70 % clay / silt / sand respectively).

3.2. Experimental conditions

The study plants were subjected to experimental conditions at the Rhodes University Elevated CO_2 Facility (RUECF; Grahamstown, Eastern Cape) from mid-growing season (December) until mid-dry season (June). This facility consists of 3m-diameter open-top chambers (OTCs) with clear-plastic sides (for a full description of the OTC construction; see Baso et al., 2021). CO_2 concentrations within 12 of the OTCs was set at one of two levels: ambient (400ppm) or elevated (800ppm; reflecting the Representative Concentration Pathway (RCP)-8.5 predictions for the turn of the 21st century; Pachauri et al., 2014). CO_2 concentrations were measured with open-path CO_2 analysers every second (GMP343, Vaisala, Finland), and maintained using a proportional–integral–derivative procedure to control injection of CO_2 (2873 proportional valve, Burkert, Germany). The OTCs were ventilated via a perforated, circular diffuser supplied by a 3-phase fan, positioned at the plant canopy level. The precision of the CO_2 treatment control within each OTC was good (>70% of measurements within 1 standard deviation of the target; details given in Table S1). Additional sensors were used to monitor solar energy (ES2, Delta-T Devices, Ltd.), rainfall (RG2 Rain gauge sensor, Delta-T Devices, Ltd). Environmental data for the experiment is summarized in Table S2. OTCs led to + 4°C increases in temperature, and this was not affected by CO_2 treatment.

In addition to the CO_2 treatment (n=30 for both CO_2 concentrations; spread across 12 OTCs), plants were also subjected to one of two different water-availability treatments to simulate savanna conditions in wet and dry seasons. Plants were either well-watered (daily watering) or exposed to a series of four-week drought cycles, separated by two-day watered recovery periods. Soil water content (5TM volumetric water content sensors, Decagon Devices, Pullman, WA) and soil water potential (MPS-6 soil water potential sensors, Decagon Devices) were monitored and recorded every five seconds in a subset of pots from both treatments to ensure watering treatments were conducted correctly (n=8 per treatment combination). Plants were grown under these conditions for 24 weeks during the growing season (December to June, ending at the beginning of the cold season). The first drought cycle was implemented after 8 weeks of growth to increase establishment success. After 24 weeks, the mean soil water content was 24 ± 5.6 and 9 ± 6.2% at the time of harvest for watered and drought treatments, respectively. Soil water content did not differ significantly between CO_2 treatment and are thus grouped for the average values presented.

3.2. Water and performance measurements

In order to determine a mechanism that could explain differences in plant traits and flammability at the end of the experiment, the growth and performance of *Themeda* plants were monitored during the treatments. Measures of photosynthetic activity and water relations, including both *ACi* curves and instantaneous gas exchange measurements, were examined by individually enclosing leaves of a subset of plants in the chamber of an infrared gas analyser (Li-Cor 6400, Li-Cor Biosciences, Lincoln, NE, USA). Leaf temperature and leaf-to-air vapour pressure deficit were kept below 1.5 kPa, block temperature was held constant at 30°C and photosynthetically active radiation at 1500 mol m^{-2} s^{-1}. Instantaneous measurements of carbon assimilation rate (*A*), G_{st}, *WUE* (A/G_{st}), and *E* were conducted on a subset of individuals (n=8) for all treatments. Leaf water potential (leafψ) was measured on a clipped leaf after gas exchange measurements using a Schölander pressure chamber. Gas exchange measures were taken at three time points through the experiment (8 weeks apart) each in the final week of a four-week drought cycle, with the final time point including leaf water potential measures.

3.3. Plant traits influential to flammability

After 24 weeks of growth under the experimental conditions, all tussocks from each pot were destructively harvested in order to measure traits influential to flammability. The two key traits (aboveground biomass quantity and moisture content) were measured on the harvested shoot biomass. Aboveground dry biomass (fuel load; in g) was measured after oven-drying the harvested shoot biomass at 60°C to a constant dry weight. Biomass moisture content (in g g^{-1}) was calculated by dividing the difference between fresh and dry shoot biomass by the dry shoot biomass. Another trait we thought would be influential to flammability and vegetation modelling (Scheiter et al., 2012) is leaf curing rate. This indicates the speed at which dry, dead biomass (that is highly flammable) accumulates. In order to measure leaf curing rate, and how it is affected by CO_2, the length of the cured section of leaves was measured twice weekly on the same six marked leaves per individual during the experiment, in both aCO_2 and eCO_2 treatments. Length of cured leaf was deemed a suitable measure of curing as we observed *Themeda* leaves to cure from the tip down rather than in a series of leaves. This was only done on plants in the drought treatment, as those in the watered treatment did not senesce. A curing rate (in mm day^{-1}) was determined from a linear relationship fitted to the length of the cured leaf section over time.

Two other grass traits important to flammability, although to a lesser extent than biomass quantity and moisture content, were also measured. The surface area to volume ratio (SA:V) of grass leaves influences flaming duration, with high values associated with low flaming duration (Simpson et al., 2016). Leaf SA:V was calculated on five leaves per individual by dividing leaf surface area (determined by scanning the leaves in a flat-bed scanner and using Image-J software to measure an area of pre-defined colour) by leaf volume. The latter was defined by multiplying leaf area by leaf thickness, which was measured using digital callipers (accurate to 0.01 mm) for five leaves and averaged. Biomass density, a measure of fuel load per unit volume, contributes to grass combustibility, such that plants with high biomass density combust most rapidly (Simpson et al 2016; Gao and Schwilk, 2018; Wigley et al., 2021). After wet biomass was recorded, biomass density (in g cm^{-1}) was measured as the vertical biomass distribution for each plant. For this, the relationship between the logged cumulative dry biomass and vertical height (vertical height intervals of 2, 10, 20 or 30 cm depending upon plant height) for each individual was determined. The biomass of each grass clump was separated into the described height intervals and weighed after oven-drying at 60°C. Linear models were fitted to the relationship between cumulative dry biomass and vertical height. The slope of this relationship was used as a proxy for biomass density, with higher values indicating more densely packed biomass.

3.3. Flammability measurements

Leaf-scale flammability was measured as the culmination of three components; ignitability (time to ignition), sustainability (amount of time that combustion is sustained), and combustibility (mass loss rate) (Anderson, 1970). Leaf-scale measurements were used as they have been found to be relatively good proxies of plant-scale flammability in savanna grasses (Simpson et al., 2016), despite these scales of flammability traits being decoupled in other plant groups (Alam et al., 2020). These three components were measured at the end of the experiment by exposing leaf subsets of 0.2g (±0.001 g) cut into 2 cm segments to temperatures of ≈ 400°C with a flame directed at a metal plate on which the leaves were placed. Flammability tests were carries out in a fume cupboard with a constant vertical wind speed of 0.2 m s^{-1} to ensure consistent conditions for all samples (Simpson et al, 2016). All samples ignited and burned. The temperature of the metal plate was monitored with a thermocouple and was maintained at 400 ± 30°C. Flaming tests were filmed at 25 frames s^{-1} and analysis of these videos allowed for the calculation of (i) Ignitability - time to ignition (the time from application to first flaming), (ii) Sustainability - flaming time (the time from ignition to extinction), and (iii) Combustibility (leaf mass divided by flaming time).

The relationship between plant-scale combustibility and plant biomass (with plant architecture intact) for *Themeda* has been previously established. Simpson et al (2016) burned whole tussocks of *Themeda* (obtained from the same site as this study) and quantified the strong linear relationship between maximum combustion rate and aboveground biomass (maximum combustion rate = 0.163 + 0.656*plant biomass; $P<0.001$, $n=7$, $R^2=0.84$). This relationship is based on partially-and fully-cured grass tussocks (as the relationship did not differ between them). We used this relationship to estimate maximum combustion rate for the whole grass tussocks in this study.

The fire spread rate (*ROS*), representative of community-scale flammability, was estimated from plant trait values from the experimental plants with Rothermel's (1972) surface fire spread model. Models were implemented using the ros() function in the Rothermel package (Vacchiano and Ascoli, 2014) in the R language and environment for statistical computing (R Core Team, 2021). Fire behaviour was simulated for each grass tussock through parameterization of the model with the following measured plant traits according to the methods of Simpson et al. (2016): Leaf SA:V (m^2 m^{-3}), fuel moisture content (%), fuel bed depth (cm – plant height), and fuel load (t ha^{-1} - total biomass divided by cover area for each tussock). Uniform weather and topography (site slope = 0%) were assumed for the simulation and all individuals were considered to be one-hour fuels. Dead fuel moisture of extinction was set at 60% for all simulations as this is the maximum possible value for one-hour fuels (Simpson *et al.*, 2016). Mid-flame wind speed was set at 3.6 km h^{-1} (mean wind speed in Grahamstown in July, the peak of the fire season; Simpson et al., 2016). A value of 8.8 kJ g^{-1} was used for fuel heat content (kJ kg^{-1} – effective heat of combustion) for all simulations based on the mean measured value for *Themeda* by Simpson *et al*. (2016).

We also estimated a landscape-scale measure of fireline intensity for *Themeda* based on traits under aCO_2 and eCO_2. Fire line intensity was predicted using the methods of Byram (1959). Fire line intensity (*FI*; in KJ m^{-2} s^{-1}) was calculated as I =

Hwr; where H = heat yield of the fuel (kJ g^{-1}; 8.8 kJ g^{-1} following Simpson et al., 2016), w = weight of available fuel (g m^{-2}), and r = *ROS* (ms^{-1}).

3.4. Predicting future fire behaviour in South Africa

To estimate the effects of CO_2-induced changes in grass flammability on fire behaviour over a larger scale, we estimated *ROS* (Rothermel, 1972) and predicted *FI* (Byram, 1959) under aCO_2 and eCO_2 for *Themeda* across South Africa for the month of July (i.e. the month of peak fire activity) based on a continuous ground cover of the widespread grass. This was done for South Africa due to the large portion of the country consisting of grassland and savannah biomes and the distribution of *Themeda* throughout the country. Although this is a simplistic approach, a general view on how CO_2-mediated changes to savanna grass flammability may change fire behaviour at a larger spatial scale is valuable. *ROS* and *FI* were modelled under 4 scenarios: (A) under current ambient conditions, (B) under RCP8.5 predictions of soil moisture changes, (C) under RCP8.5 predictions of soil moisture changes with the effects of eCO_2 on plant physiology and flammability incorporated, and (D) as in (C) but with the addition of an adjusted soil moisture scenario calculated according to measured experimental soil water savings associated with eCO_2. The countrywide version of the models were parameterised as done in 3.3 but with values for slope, wind speed and fuel moisture content varying spatially. A gridded dataset at a resolution of 5km was constructed for these variables. Slope values were calculated from the altitude values in the World Slope Model dataset using the terrain() function of package 'raster' (Hijmans et al., 2019). Gridded mean annual wind speed data was used from the Global Wind Atlas version 3.0 (Badger et al., 2019). Fuel moisture content in each grid cell was calculated for each CO_2 scenario (400 ppm or 800 ppm) using soil water content values based on either ambient or RCP8.5 projection scenarios for 2070 (RCP8.5 CCSM4, CM5A, CNRM-CM5, MIROC-ESM, and MPI-ESM-LR projections). The RCP8.5 CCSM4 projection is presented in the results and alternative projections are presented in the supplementary materials. Soil water content was calculated from measures of precipitation (CHELSA database, Karger et al., 2017), wilting points and field capacity (IGBP Global Soil Data Task, 2000) according to the methods described by Trabucco and Zomer, 2010). Soil moisture content was then converted into plant moisture content using linear relationships developed during the experiment between measured soil water content (%) and leaf moisture content (R^2 = 0.62 and 0.46 for 400 ppm and 800 ppm treatments, respectively; see Figure S.1). Adjusted soil water scenario used in (D) were adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving). This soil water saving was calculated from the change in measured soil water content over a 22 day period during the final 4 week drought cycle (8 soil sensors per treatment). Soil water savings were equal to the difference between the mean water loss at *a*CO_2 and at *e*CO_2, divided by that at *a*CO_2). The % difference was then used to add 24.08% of the value in each grid cell to the cell value. These gridded datasets were merged to the same extent and resolution using package 'raster' (Hijmans et al., 2019), before models were run for each grid cell for both aCO_2 and *e*CO_2.

3.5. Statistical analysis

The data obtained were analyzed using the R language and platform (R Core Team 2020). To determine the influence of the treatments (both CO_2 and water-availability) on *Themeda* traits and flammability, linear mixed-effects models were fitted using the nlme R package (Pinheiro et al., 2021). The fixed effects were the CO_2 treatment (either *a*CO_2 or *e*CO_2) and water treatment (watered or drought) and the OTC identifying number (1-12) was included as a random effect (to account for any differences arising from the position or functioning of the different OTCs). Statistics presented in the results show the effect of CO_2 treatment on individual groups. Principal component analyses (PCAs) were conducted using the FactoMineR R package (Lê et al., 2008) to display overall trait differences between plants grown at *a*CO_2 and *e*CO_2 under the two water-availability treatments. Separate PCAs were run for plant traits (leaf curing rate, biomass moisture, and biomass quantity) and flammability traits (time to ignition, sustainability, maximum combustion rate, *ROS*, and *FI*).

4. Results

4.1. Plant performance under *e*CO_2

G_{st} was similar in the two watering treatments at *a*CO_2, but under drought conditions, *e*CO_2 enhanced water savings and caused an average 30% reduction in G_{st}, although this effect was not significant ($T(6)=-0.7$, $p=0.53$). The lower G_{st} in combination with generally but non-significant higher photosynthetic rates (on average 52% higher; $T(8)=-1.04$, $p=0.33$) led to significant increases in *WUE* (Fig 2B; $T(8)=4.71$, $p<0.01$)

and less negative leafψ (Fig 2C; T(6)=1.81, p<0.01) in individuals exposed to drought. A knock-on effect of improved water relations under eCO_2 was a significant 58% reduction in leaf curing rates in grasses exposed to water limitation (Fig 2D; T(8)=-5.57, p<0.001).

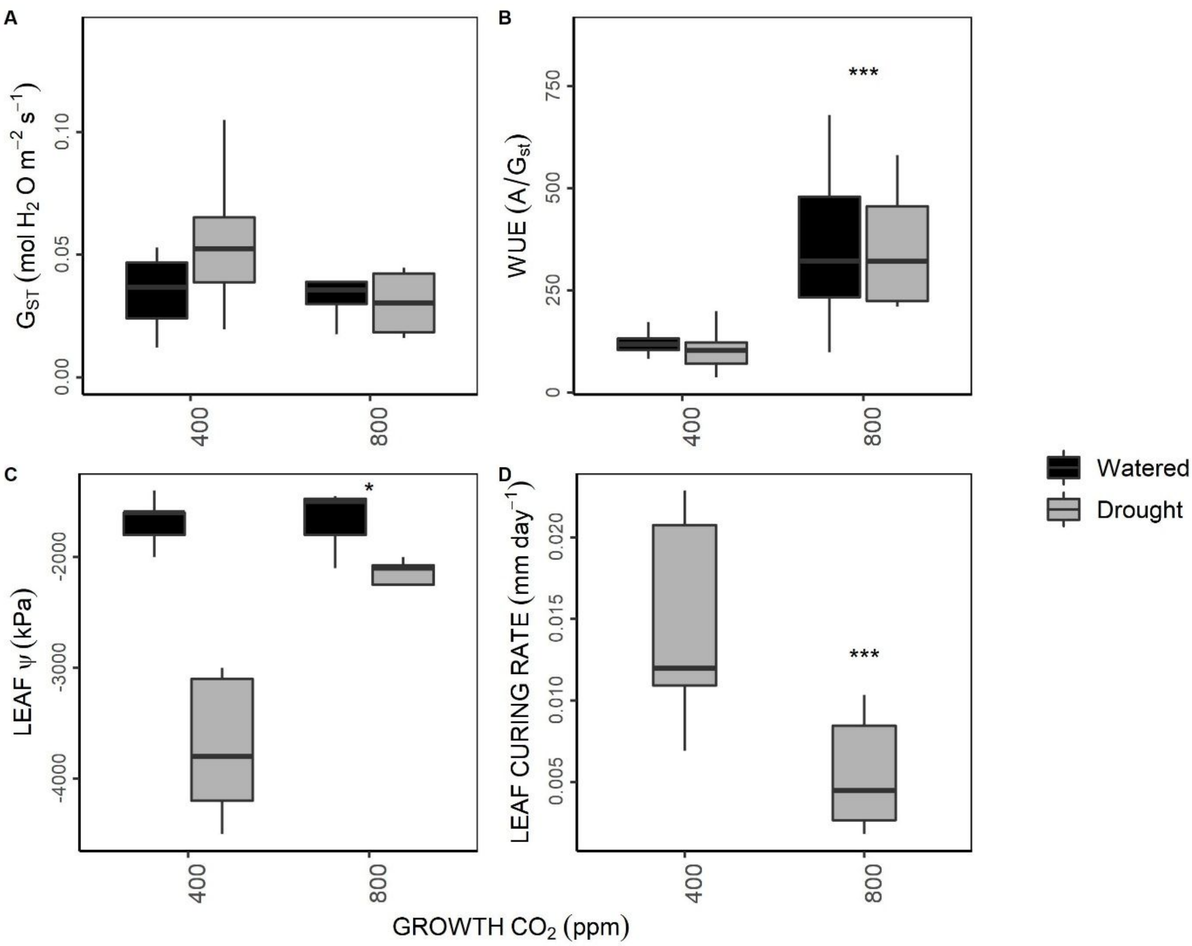


Figure 2. Stomatal conductance (G_{st}) [A], water use efficiency (*WUE*) [B], leaf water potential (leafψ) [C], and leaf curing rate [D] of individual *Themeda triandra* tussocks exposed to different CO_2 (400 or 800 ppm), water (watered or drought) treatments. Mean soil water content was 24 ± 5.6 and 9 ± 6.2% at the time the plants were harvested under the watered and drought treatments, respectively. Box plots show means, interquartile ranges and minimum/maximum values. * represents a significant effect of eCO_2 (p < 0.1; *, p < 0.05; ***, p < 0.001).

4.2. Plant flammability under eCO_2

Differential plant productivity and water relations under eCO_2 resulted in changes in traits influential to flammability. *Themeda* plants grown at eCO_2 had an average 14% higher aboveground biomass in watered conditions (T(8)=0.63, 0.54), and 38% higher under drought conditions (T(8)=2.48, p<0.05; Table 2). *e*CO_2 completely negated the adverse effects of drought to allow for similar levels of productivity when water was limited. *e*CO_2 had a significant effect on biomass moisture content in the drought treatment when soil moisture contents was low (<10%; Figure S.1). When soil moisture content is <10%, biomass moisture content is significantly higher under *e*CO_2 (33% under *a*CO_2 vs 47% *e*CO_2; T(8)=4.49, p<0.01). Biomass density and leaf SA:V were unaffected by CO_2 or water treatments (Table 2).

CO_2-induced changes in flammability traits had cascading effects on multiple aspects of flammability. At the leaf level, higher moisture contents under *e*CO_2 resulted in lower ignitabililty (a delay in ignition), with time to ignition increasing by 20% (T(8)=1.32, p<0.05) and 8% (T(8)=0.98, p=0.28) under well-watered and drought treatments respectively (Table 1). The length of time that flaming was sustained was generally, but not significantly, lower in grasses grown at *e*CO_2 (T(8)=-1.71, p=0.09 and T(8)=-1.42, p=0.16 in watered and drought treatments, respectively). Estimated maximum plant scale combustion rate was significantly higher with *e*CO_2 under drought conditions (T(8)=2.61, p<0.05).

When predicting fire behaviour, higher grass biomass moisture content overrode the effect of increased aboveground biomass at *e*CO_2 on fire behaviour, to generate lower predicted rates of fire spread and fire intensity (Table 1). Fire spread models parameterised with *Themeda* traits under the different treatments showed a 31% decline in predicted fire spread rate under well-watered conditions (T(8)=-1.76, p=0.43), and a 13% decline (T(8)=-2.75, p<0.01) under water-limitation. Similarly, there was a 12% decline in predicted fire line intensity under well-watered conditions (T(8)=-0.74, p=0.46), and a 4% decline under water-limitation (T(8)=-0.28, p=0.78).

Table 1. Fuel load per tussock, biomass moisture content, biomass density, leaf surface area:volume ratio, time to ignition, sustainability, combustibility, estimated maximum combustion rate, predicted rate of fire spread (*ROS*), and predicted fireline intensity (*FI*) of individual *Themeda* tussocks exposed to different CO_2 (400 or 800 ppm), and water (watered or drought) treatments (n=30 for each). Showing mean ± S.E. * represents a significant effect of *e*CO_2 (p < 0.1; *, p < 0.05; ***, p < 0.001).

Parameter	CO_2 (ppm)	Watered	Drought

2.1. Plant traits			
Fuel load per tussock (g)	**400**	15.37 ± 9.87	10.54 ± 5.1
	800	17.48 ± 6.55	16.98 ± 8.63 *
Biomass moisture content (%)	**400**	54.27 ± 24.01	50.15 ± 18.59
	800	56.28 ± 19.7	52.6 ± 19.15
Biomass moisture content when soil moisture content <10% (%)	**400**	-	32.53 ± 5.48
	800	-	47.0 ± 9.22 **
Biomass density (g cm^{-2})	**400**	1.64 ± 1.27	1.36 ± 0.74
	800	1.90 ± 0.83	1.70 ± 0.97
Leaf SA:V ratio	**400**	88.22 ± 34.97	89.85 ± 33.24
	800	84.14 ± 18.37	88.14 ± 31.70
2.2. Flammability measures			
Time to ignition (s)	**400**	2.47 ± 0.16	2.74 ± 1.43
	800	3 ± 0.17 *	2.98± 1.16
Sustainability (s)	**400**	65.47 ± 25.65	62.62 ± 28.05
	800	58.41 ± 24.71	57.31 ± 21.39
Combustibility (g s^{-1})	**400**	0.0036 ± 0.0014	0.0040 ± 0.0018
	800	0.0042 ± 0.002	0.0041 ± 0.0016
Estimated maximum combustion rate (gs^{-1})	**400**	10.33 ± 6.57	7.08 ± 3.35
	800	11.81 ± 4.35	11.30 ± 5.66 *
2.3. Fire behaviour			
ROS (m min^{-1})	**400**	2.44 ± 0.82	2.13 ± 0.78
	800	1.86 ± 0.93 *	1.88 ± 0.86 *
FI (KJ m^{-2} s^{-1})	**400**	77.9 ± 56.73	53.26 ± 32.76
	800	68.47 ± 50.47	51.18 ± 37.94

A principle components analysis (PCA) was used to examine the variance in traits associated with flammability according to CO_2 treatment. We discuss the PCA based on the droughted individuals here (so to include leaf curing rate in the analysis, which was only measured on droughted individuals); the PCA based on the well-watered individuals can be found in the supplementary information (Fig S.2). The first two principal components accounted for 88.35% (Fig. 3A) and 63.75% (Fig. 3B) of the total variance respectively. The PCA shows plant traits related to flammability to separate out according to CO_2 treatment (Fig. 3A). Knock-on effects of lower leaf curing rate were seen in the higher time to ignition and lower *ROS* at *e*CO_2 (Fig. 3B). The higher biomass quantity led to higher estimates of maximum combustion rate (*MCR*) and *FI* with *e*CO_2 (Fig. 3B). Table 2 shows the contribution of CO_2 treatment to leaf-scale flammability parameters used in Figure 3. CO_2 treatment significantly predicted leaf curing rate ($T(8)=-5.57$, $p<0.001$), biomass quantity ($T(8)=2.61$, $p<0.05$), estimated *MCR* ($T(8)=2.61$, $p<0.05$), and *ROS* ($T(8)=-1.89$, $p<0.05$).

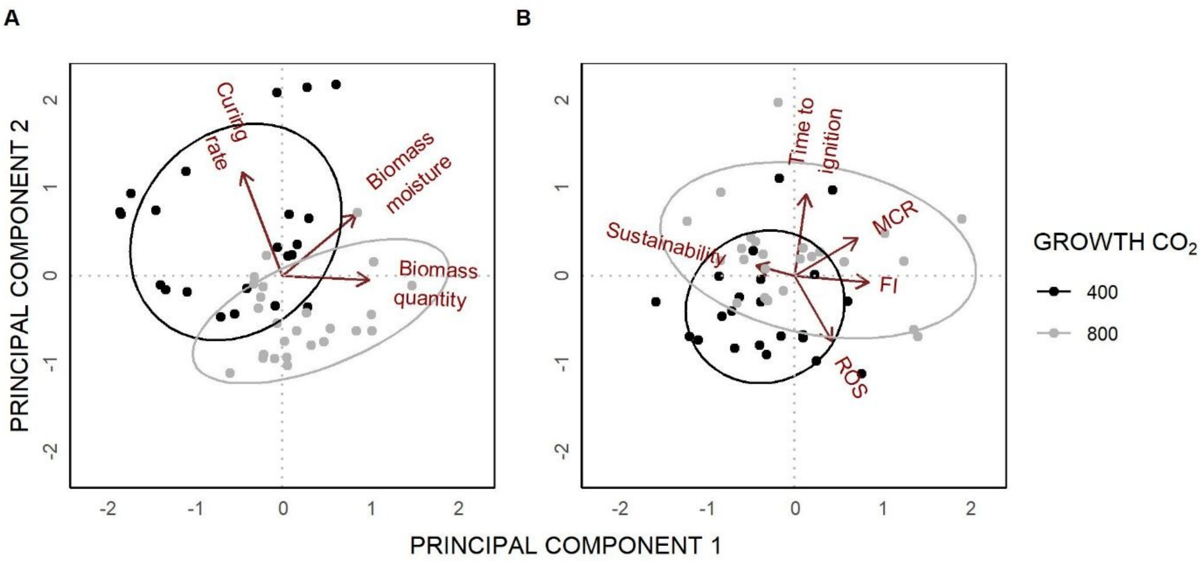


Figure 3. Principal components analysis of C_4 grass (*Themeda triandra*) traits associated with flammability: [A] leaf curing rate, biomass moisture, and biomass quantity. [B] sustainability, ignitability, maximum combustion rate (*MCR*), predicted rate of spread (*ROS*), and predicted fireline intensity (*FI*). All plants used in the PCA were exposed to drought.

Table 2. The contribution of CO_2 treatment to leaf-scale flammability parameters of C_4 grasses exposed to drought used in the principle component analysis in Fig. 3A (Leaf curing rate, biomass moisture, biomass quantity) and Fig. 3B (Time to ignition, sustainability, estimated maximum rate of combustion *MCR*, predicted rate of spread *ROS*, and predicted fireline intensity *FI*) as determined by linear mixed-effects models. Estimate values represent estimates of the slope, showing standard error (SE) and p values. * represents a significant effect of *e*CO_2 ($p < 0.1$; *, $p < 0.05$; ***, $p < 0.001$).

Model	**Parameter**	**Effect of CO_2 treatment**		
		Estimate	SE	P value

A. Plant traits	Leaf curing rate	-0.009	0.003	<0.001 **
	Biomass moisture	4.63	6.18	0.5
	Biomass quantity	6.45	2.47	<0.05 *
B. Flammability	Time to ignition	0.96	0.45	0.09
	Sustainability	-12.36	17.35	0.52
	MCR	4.24	1.63	<0.05 *
	ROS	-0.43	0.23	<0.05 *
	FI	24.26	13.96	0.15

4.3. Changes in fire behaviour under *e*CO_2 across South Africa

We predicted *ROS* (Fig. 4) and *FI* (Fig. 5) across South Africa for the month of July for a variety of climatic projection scenarios, based on a continuous ground cover of the widespread grass *Themeda*. Future soil moisture scenarios in Fig.4 and 5 are according to the RCP8.5 CNRM-CM5 projection. Alternative projections are presented in Fig. S3-10. We acknowledge that one species will not represent community level flammability, but instead this approach provides a basic estimation of a dominant species. When *ROS* is modelled for *Themeda* across South Africa at ambient environmental conditions, *ROS* is predicted to be higher in the more arid zones in the north-west of the country and lower along the coastal regions (Fig. 4A). Similar predictions are seen for *FI* (Fig. 5A). Accounting for predicted changes in soil water content by the year 2070 but excluding the effects of *e*CO_2 on the physiology and flammability of the grasses, our models predict *ROS* to increase in general across the country, with the most notable changes being seen in the western regions (Fig. 4B). *FI* changes are predicted to be more moderate than those of *ROS* and show increases only in the western regions of South Africa (Fig. 5B). Incorporating the effects of *e*CO_2 on the physiology and flammability of the grasses, we predict *ROS* to decrease relevant to ambient conditions (Fig. 4C) and *FI* (Fig. 5C) to increase slightly in certain areas along the west coast and central interior and to moderate the effects of reductions in soil water availability on *ROS* across much of the country. Further accounting for the effects of *e*CO_2, we predict both *ROS* and *FI* to decrease under an adjusted soil water scenario where soil water contents are adjusted according to experimentally measured soil water savings associated with *e*CO_2 (Fig. 4D and 5D).

We acknowledge that soil water savings would not be uniform across soil types but show that CO_2 associated soil water savings should be considered in predictions of future fire patterns.

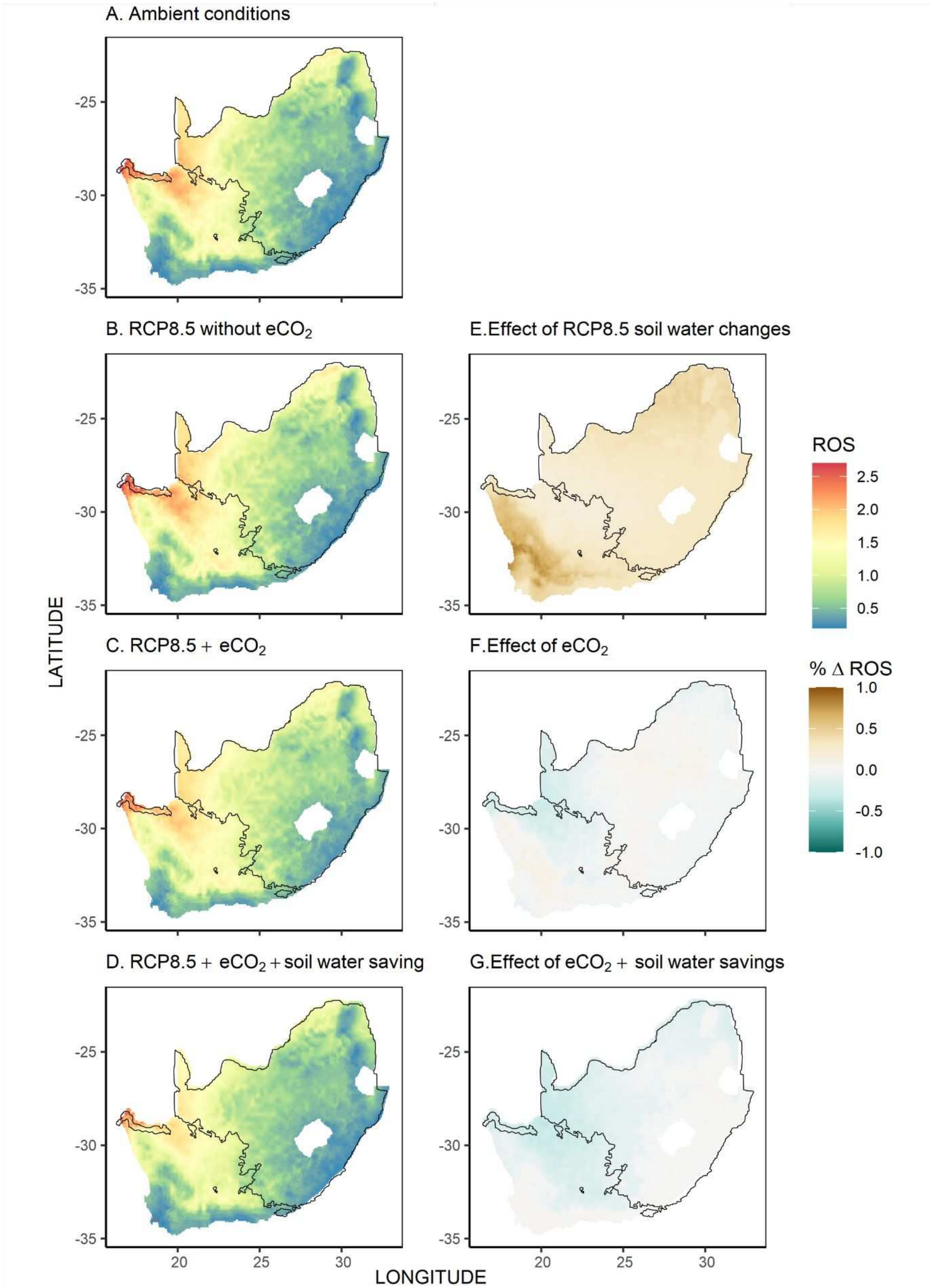
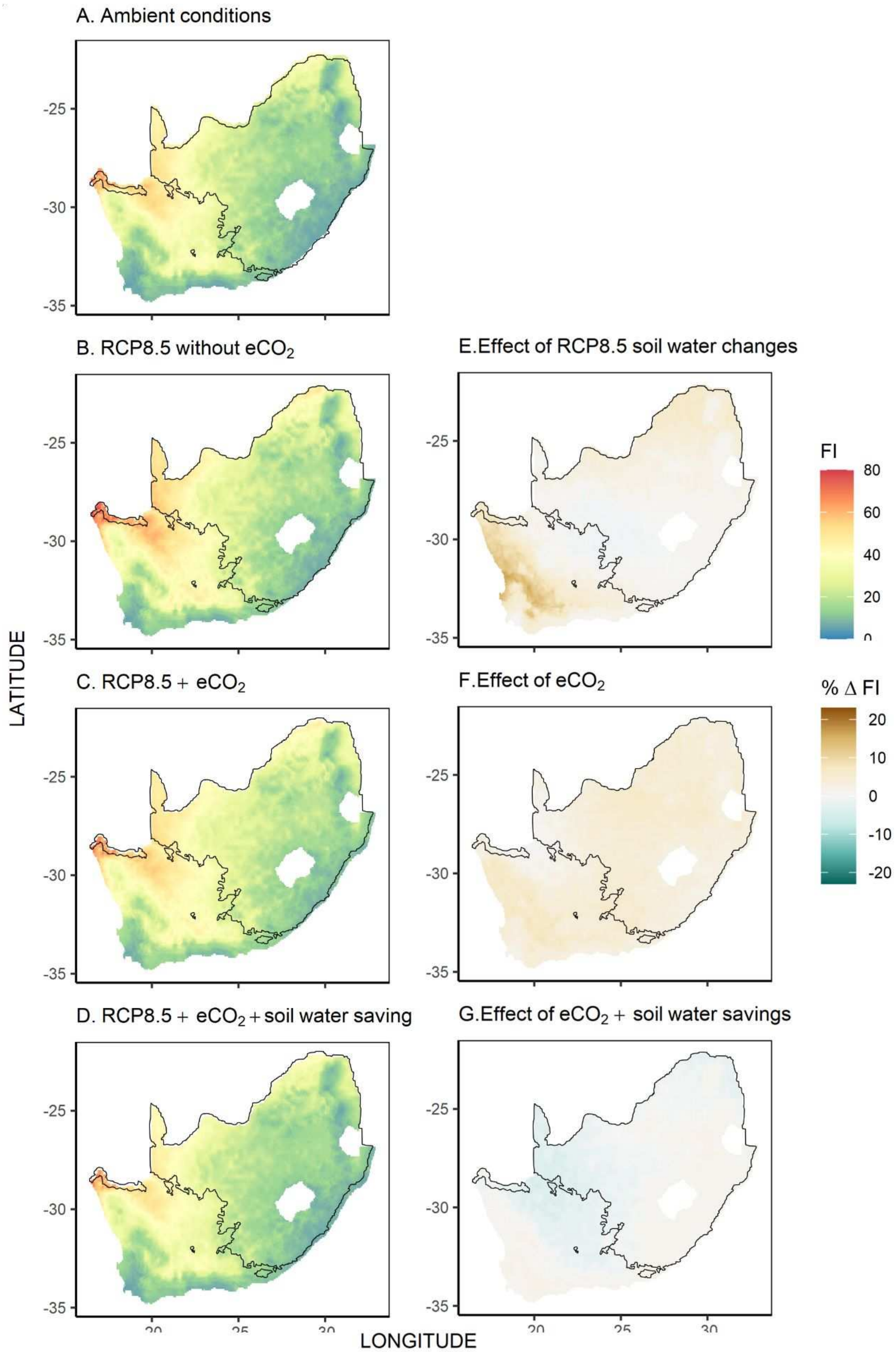


Figure 4. Rate of fire spread (*ROS*; m min^{-1}) (Rothermel, 1972) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil moisture conditions (for the year 2070 according to the RCP 8.5 CNRM-CM5

projection scenario) without the effects of eCO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of eCO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% lower soil water loss) associated with eCO_2 and with the effects of eCO_2 on plant physiology and flammability incorporated [D]. Predictions are based on the flammability of the widespread savanna grass, *Themeda triandra*, grown under aCO_2 (400ppm) and eCO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012). Plots using alternative projection scenarios are presented in Fig. S.3-S.6.



438

439 **Figure 5.** Fireline intensity (*FI*; KJ m^{-2} s^{-1}) (based on Byram's *FI*; Byram 1959) is
440 predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted
441 future soil moisture conditions (for the year 2070 according to the RCP 8.5 CNRM-

CM5 projection scenario) without the effects of *e*CO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of *e*CO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% lower soil water loss) associated with *e*CO_2 and with the effects of *e*CO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under *a*CO_2 (400ppm) and *e*CO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012). Plots using alternative projection scenarios are presented in Fig. S.7-S.10.

4. Discussion

Using the widespread, ecologically-dominant, C_4 savanna, *Themeda triandra*, as a model species, we determined the effect of predicted future CO_2 concentrations on flammability-influential traits and uncovered the physiological mechanisms underpinning these responses. By investigating the effects of water availability alongside CO_2 enrichment, we find a notable impact of *e*CO_2 on grass biomass quantity, moisture content and curing rates, with knock-on effects on flammability. Grasses took longer to ignite, sustained flaming for shorter times and spread fire at a lower rate on average when grown under *e*CO_2. We also modelled how these flammability effects might influence fire behaviour in South African grass-dominated ecosystems, and found much of this area would experience lower fire spread rates under *e*CO_2, but that future fireline intensity trends would be variable. These results suggest that future declines in grass flammability, and therefore fire activity, may benefit savanna trees at the expense of grasses, and contribute to the already-increasing trend of tree densities in savannas (Stevens et al., 2017).

Grass biomass was elevated under *e*CO_2, as has been found elsewhere for *Themeda*, and other C_4 savanna grass species (Wand et al., 1999 and references therein; Manea and Leishman 2019; Quirk et al., 2019). The mechanism responsible for this enhanced productivity is primarily due to improved water relations under *e*CO_2, as demonstrated by the larger biomass response in the drought treatment. We also found that the photosynthetic capacity of *Themeda* was improved at 800ppm CO_2, suggesting that the photosynthesis of this species is not carbon-saturated under aCO_2. This adds to a growing body of research that C_4 grasses can respond to eCO_2 through improved CO_2 assimilation rates (Wand et al., 1999). Better water relations under eCO_2 also had the effect of increasing leaf moisture content - *Themeda* plants were able to maintain higher biomass moisture contents across the range of soil moistures under eCO_2 (Fig. S1). This allowed plants to remain physiologically-active and productive for longer into dry-down, and delay the onset of leaf senescence.

As fire tends to show threshold behaviour, responding to biological and geophysical factors in non-linear ways (Archibald et al., 2017), even small changes in the flammability of a system can have large implications on fire characteristics (Cox and Durrett, 1988; Archibald et al., 2012). Therefore the modest CO_2-induced changes we see in grass flammability here, could result in considerable alterations to grass-fuelled fire regimes. The larger but wetter fuel load produced by *Themeda* plants under eCO_2 (particularly under water limitation) took longer to ignite, and burned at a faster rate once alight for a shorter period of time. In addition, eCO_2-grown plants also took longer to senesce, with grasses staying greener for longer under dry conditions. The only other paper that has investigated grass flammability under eCO_2, Manea et al., (2015), similarly found increased fuel loads in woodland understory grasses. Conversely, that study surprisingly found lower leaf moisture content under eCO_2, which the authors could not explain. A potential impact of the flammability changes found here is a reduction in fire occurrence under future CO_2 concentrations. If eCO_2 increases moisture biomass retention, more heat energy is required for ignition and fire spread (Trollope, 1978; Gill and Moore, 1996; Alessio *et al*., 2008; Plucinski and Anderson, 2008), resulting in fewer successful ignitions and smaller fires. As natural fire regimes largely coincide with the dry season in South African grass-dominated ecosystems, the slower curing rate of *Themeda* under eCO_2 may result in a delay in plants being sufficiently highly flammable to ignite and spread fire, and therefore the start of the fire season. Once alight however, the larger average *Themeda* biomass under eCO_2 resulted in higher estimated maximum combustion rates, although only significantly under water-limited conditions. This suggests that despite the higher moisture content of biomass under eCO_2, it should still combust equally or better than under ambient CO_2 levels, and that fire will continue to typically remove all aboveground grass biomass.

Future fire behaviour in grass-dominated systems is also determined by the ability of grasses to resprout after fire, and therefore recover aboveground biomass quickly to fuel subsequent fires, and the decomposition rate of grass biomass. Previous studies have found that the resprouting abilities of tropical grasses, including *Themeda*, are unaffected by *e*CO_2 (Kgope et al., 2010; Manea and Leishman., 2019), however grass decomposition may decline (Manea et al., 2015). Therefore, grass-driven changes in fire behaviour under *e*CO_2 are likely to result from changes in grass flammability alone, and not from changes in grass resprouting ability.

We predicted landscape-scale fire behaviour across South African grass-dominated ecosystems based on *Themeda* trait data grown under different CO_2 treatments and on predicted changes in soil water availability. This simplistic approach resulted in the prediction that the rate of fire spread will increase over much of the country's grasslands and savannas as soil water availability declines, but that the effects of *e*CO_2 on plant physiology and flammability in *Themeda* will mitigate this effect (and even reverse this trend in some areas). Greater increases in biomass moisture content under these conditions, due to enhanced water use efficiency, drives these patterns, and suggests that *e*CO_2 may cause fire in low-rainfall savannas to be increasingly fuel-moisture limited (Alvarado et al., 2019). We took our predictions of the effects of *e*CO_2 on fire behaviour one step further by adjusting soil moisture scenarios by mean soil water savings measured during our experiments. Soil water savings led to further declines in predicted rate of spread. We predict fireline intensity to increase both with predicted declines in soil moisture and with the slightly heightened biomass accumulation associated with *e*CO_2. This effect was, however, reduced by *e*CO_2-associated soil water savings. These fire behavior models only use one fuel – *Themeda* – and therefore do not account for variation in fuels, which would include many herbaceous and woody plant species. Another caveat to this approach is that differences in soil fertility are not accounted for, which can mediate plant CO_2-responses (Reich et al., 2014). However, community-level flammability tends to be driven by the most flammable species present (van Altena et al., 2012; de Magalhães and Schwilk, 2012; Wyse et al., 2018), and grassy ecosystems are typically dominated by a few key species (Edwards et al., 2010). By using a highly flammable and widely-dominant species here, we can gain some insight into future changes in grass-fuelled fire behaviour. We only consider CO_2-induced changes to fire behaviour in South Africa here. However, when the extent of grass fuelled fires is considered (>80% of annual burnt area is grassy; van der Werf et al., 2006), changes in the flammability of grass communities could have considerable impacts upon fire regimes at a global scale. The simplistic approach of our models mean they are not suitable for strict prediction of fire behaviour but do shed light on the short falls of current fire modeling efforts and highlight the importance of CO_2 effects on both plant physiology and water relations as well as associated soil water savings.

Changes in fire regime, caused by increasing CO_2 concentrations, may directly impact on the grass communities that fuel fire. Fire regimes may act as a selection pressure or an ecological filter for certain traits associated with persistence in fire-prone landscapes (Keeley et al., 2011). For grasses, traits related to survival through fire and recovery afterwards, via resprouting or from seed, are linked to fire frequency (Forrestel et al., 2014). For example, less frequent fire is associated with more resprouting grass species and fewer seeder species (Simpson et al., 2021). Therefore, changes in fire frequency may result in altered grass communities in terms of the traits present. Similarly, grass lineages are strongly sorted along fire-frequency gradients, with some lineages having a low tolerance of fire and others being reliant on fire for survival (Uys et al., 2004; Visser et al. 2012; Lehmann et al., 2019). However, savanna grasses, including *Themeda*, are plastic in their fire-related traits (Simpson et al., 2019), and so may be able to tolerate fire-frequency changes and prevent associated alterations in grass community composition. Fire intensity appears to be less important than fire frequency in influencing grass traits (Uys et al., 2004; Peláez et al., 2013; Simpson et al., 2021), and so CO_2-induced changes in fire intensity are less likely to impact on grass communities in terms of the traits and species present.

Indirect effects of altered fire regime under eCO_2, mediated by changes in relative competitive ability of savanna trees and grasses, are much more likely to alter grass communities than direct effects. Studies in African savannas show that fire reduces woody biomass (Trapnell, 1959; van Wyk, 1971; Bond *et al*., 2005), or at least alters woody pant demographics, by causing either top-kill or mortality to individuals in vulnerable, small size classes (Higgins et al., 2007). Therefore, reductions in fire frequency lowers mortality in fire-sensitive tree species and allows more individuals to escape the 'fire trap' and reach maturity (Bond and Midgley, 2001; Smit et al., 2010). Increases in savanna tree abundance would decrease C_4 grass biomass due to heightened competition and shading (Angassa, 2005; Ratajczak et al., 2012), and therefore decreases fuel for fire. This positive feedback loop can ultimately lead to fire becoming rare or absent, once a certain tree-cover threshold is reached and the grass layer is too small and discontinuous to spread fire. In southern Africa, this threshold is ~40% tree cover, above which, burnt area declines rapidly (Archibald et al., 2009). Therefore *e*CO_2-induced changes to grass flammability, and fire behaviour, may contribute to altered savanna dynamics that threaten the existence of this biome.

6. Conclusions

This research sheds light on an understudied aspect of fire in a changing climate. Future changes in atmospheric CO_2 are predicted to alter grass flammability with serious implications for savanna vegetation dynamics. Improved water relations and productivity together resulted in a larger but wetter grass fuel load that took longer to ignite and spread fire at a lower rate. The relative influence of fuel moisture versus biomass appears to vary spatially, but with the effects of moisture changes being more important in general. We suggest that fire will be less frequent but possibly more intense at future CO_2 levels, although predicted changes in fireline intensity are marginal. We highlight the importance of including the effects of *e*CO_2 on both plant physiology and associated soil moisture savings in fire modelling. At a large spatial scale, reductions in fire spread may result in smaller fires and reduced fire frequency in grass-dominated systems. Therefore *e*CO_2-induced changes in grass flammability and fire frequency will likely exacerbate the trend in woody thickening of savannas into the future.

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Supplementary materials

Table S.1. % of the time where measured [CO_2] was within the standard deviation (SD), within 50 ppm, and within 100 ppm of the target [CO_2].

Target CO_2 (ppm)	% within S.D.	% within 50 ppm	% within 100 ppm
400	72.82	92.85	99.66
800	70.89	38.42	66.09

Table S.2. Environmental data for the experimental period in the open-top chambers. Data relating to temperature, relative humidity, precipitation, solar inclination, azimuth, elevation, hour angle, declination, and air mass experienced during the experimental period are shown.

Environmental variable	Mean	Minimum	Maximum
Temperature (°C)	19.25	0	42.92
Relative Humidity (%)	77.93	5.12	100.00
Daily precipitation (mm)	0.87		
Monthly precipitation (mm)	18.53		
Total accumulated precipitation (mm)	111.2		
Solar inclination (W/m²)	663.6		
Solar azimuth (°)	179.96		
Solar elevation (°)	4.94		
Solar hour angle (°)	-0.0002		
Solar declination (°)	-0.12		
Solar air mass	5.42		

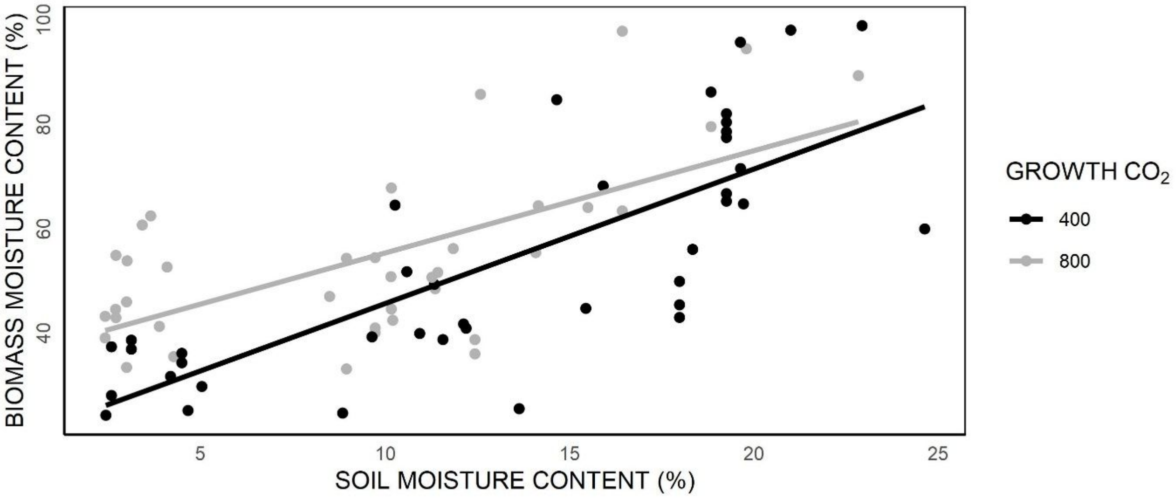


Figure S.1. The relationship between biomass moisture content and soil moisture content for *Themeda triandra* grasses exposed to different CO_2 (400 or 800 ppm) treatments. 400ppm: y=257.74x+19.789, R^2=0.60, p<0.001. 800ppm: y=218.83x+32.474, R^2=0.46, p<0.001.

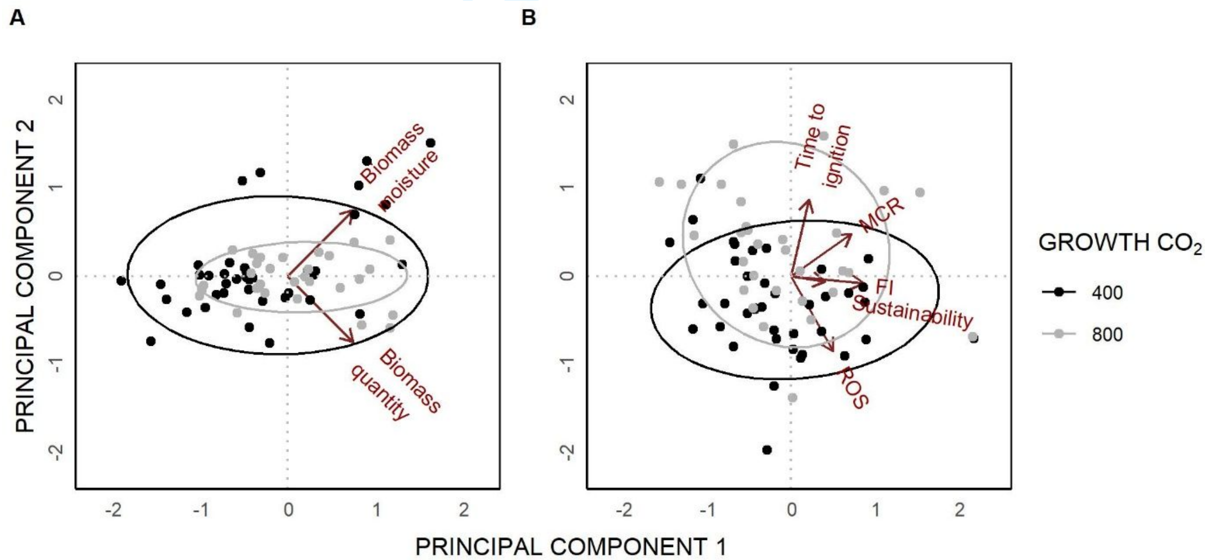


Figure S.2. Principal components analysis of C_4 grass (*Themeda triandra*) traits associated with flammability: [A] biomass moisture, and biomass quantity. [B] sustainability, ignitability, maximum combustion rate (*MCR*), predicted rate of spread (*ROS*), and predicted fireline intensity (*FI*). All plants used in the PCA were well watered.

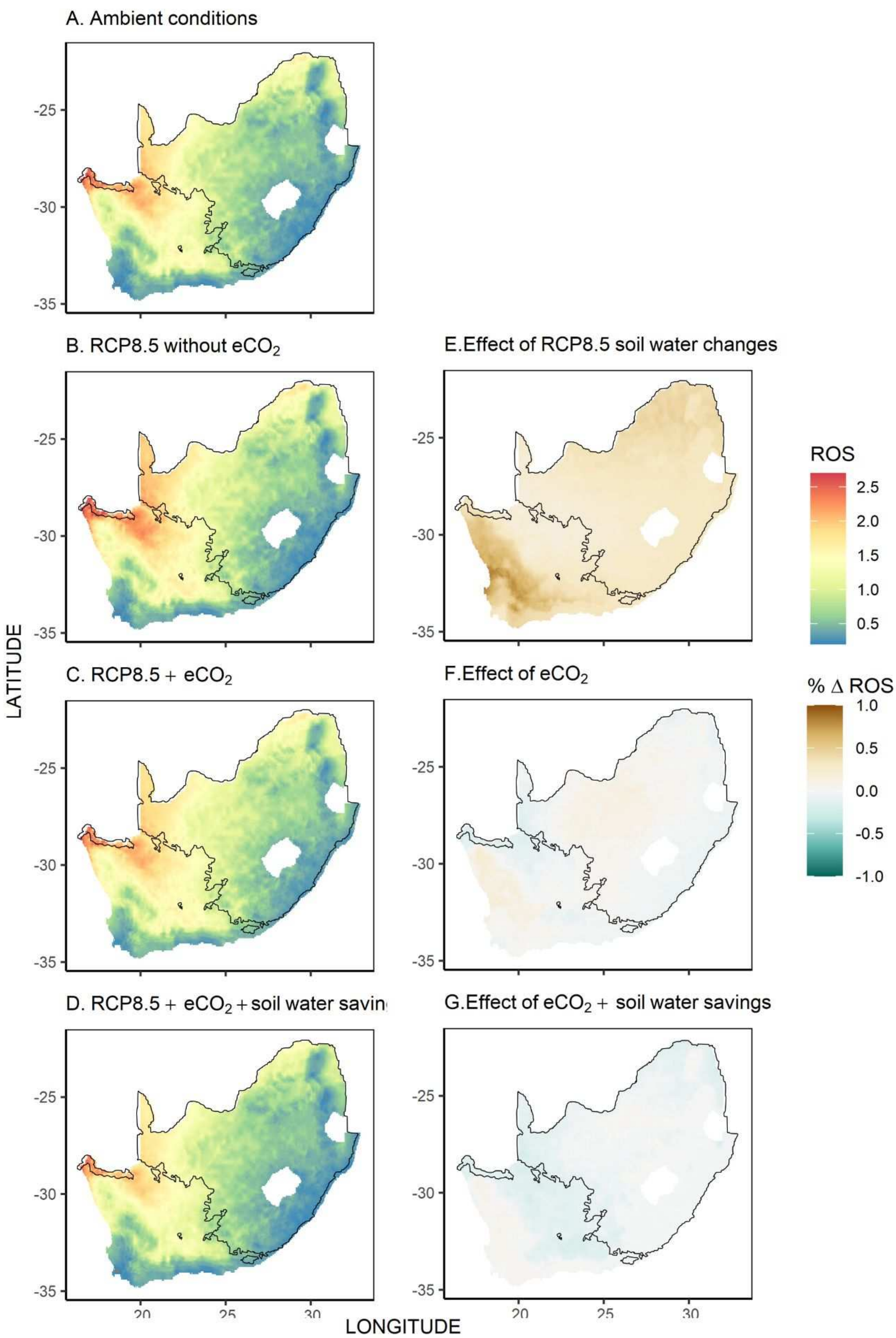


Figure S.3. Rate of fire spread (*ROS*; m min^{-1}) (Rothermel, 1972) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil

moisture conditions (for the year 2070 according to the RCP 8.5 CCSM4 projection scenario) without the effects of eCO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of eCO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving) associated with eCO_2 and with the effects of eCO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under aCO_2 (400ppm) and eCO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012).

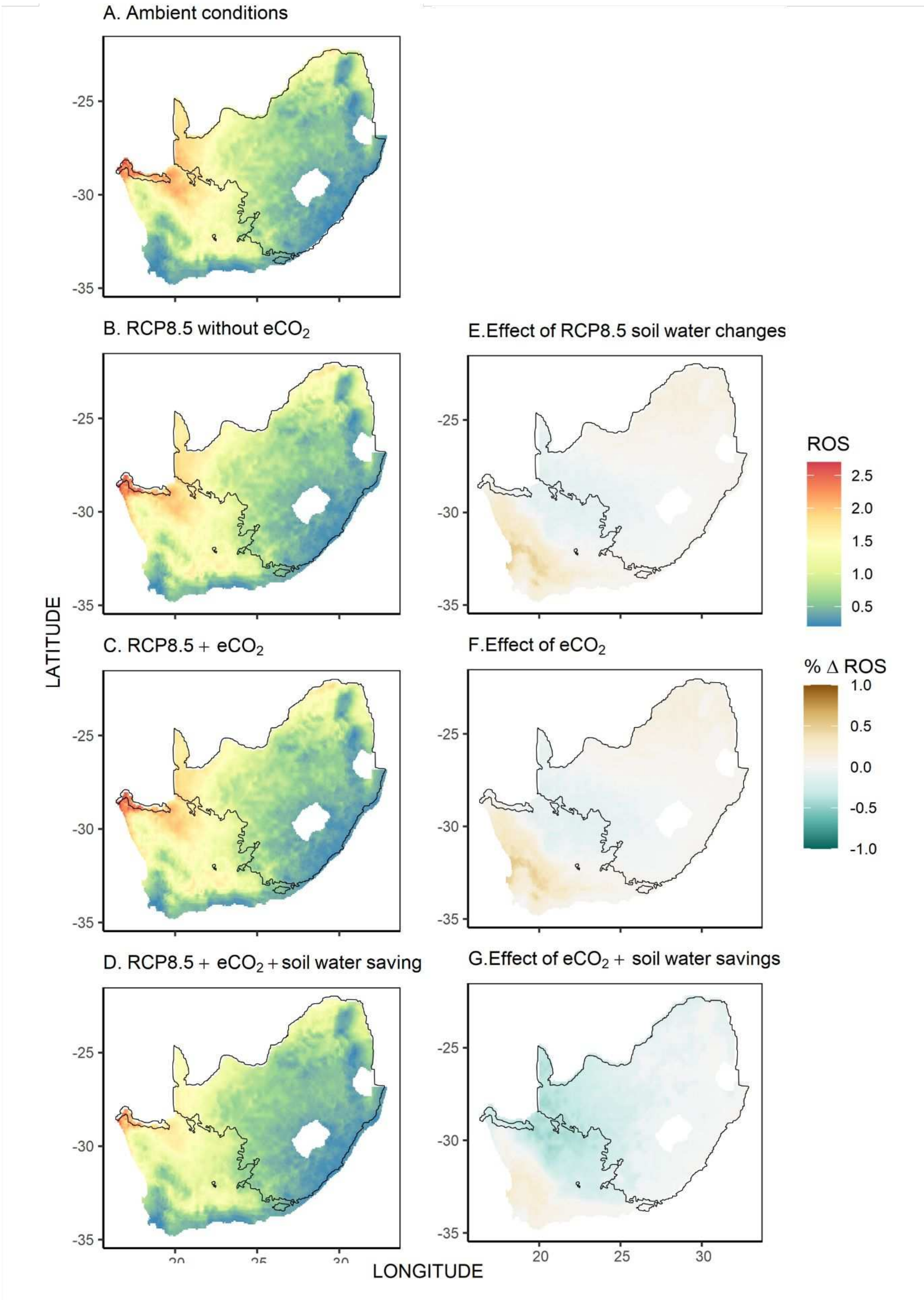


Figure S.4. Rate of fire spread (*ROS*; m min^{-1}) (Rothermel, 1972) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil moisture conditions (for the year 2070 according to the RCP 8.5 CM5A projection scenario) without the effects of *e*CO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of *e*CO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving) associated with *e*CO_2 and with the effects of *e*CO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under *a*CO_2 (400ppm) and *e*CO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012).

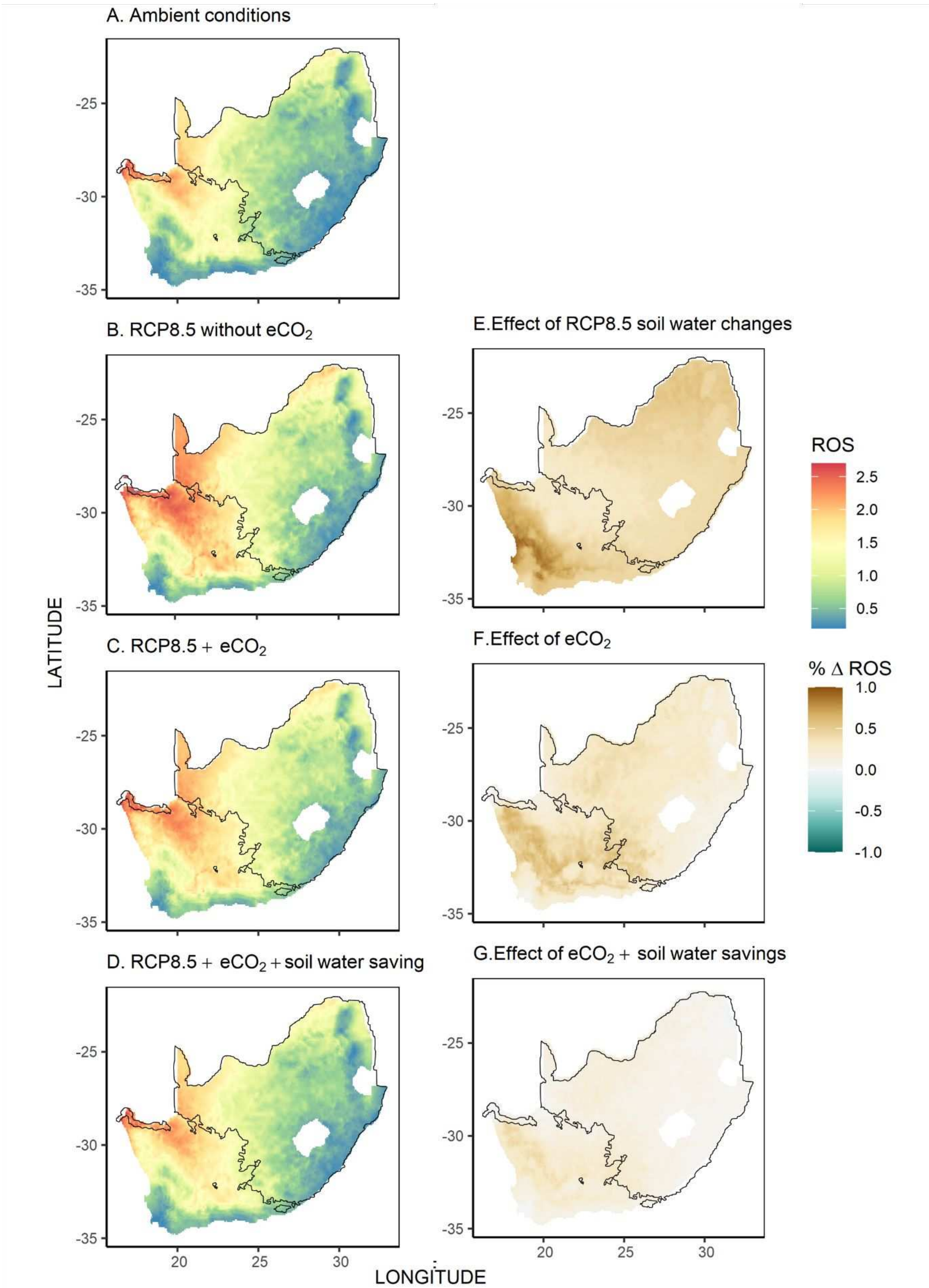


Figure S.5. Rate of fire spread (*ROS*; m min^{-1}) (Rothermel, 1972) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil

moisture conditions (for the year 2070 according to the RCP 8.5 MIROC-ESM projection scenario) without the effects of *e*CO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of *e*CO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving) associated with *e*CO_2 and with the effects of *e*CO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under *a*CO_2 (400ppm) and *e*CO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012).

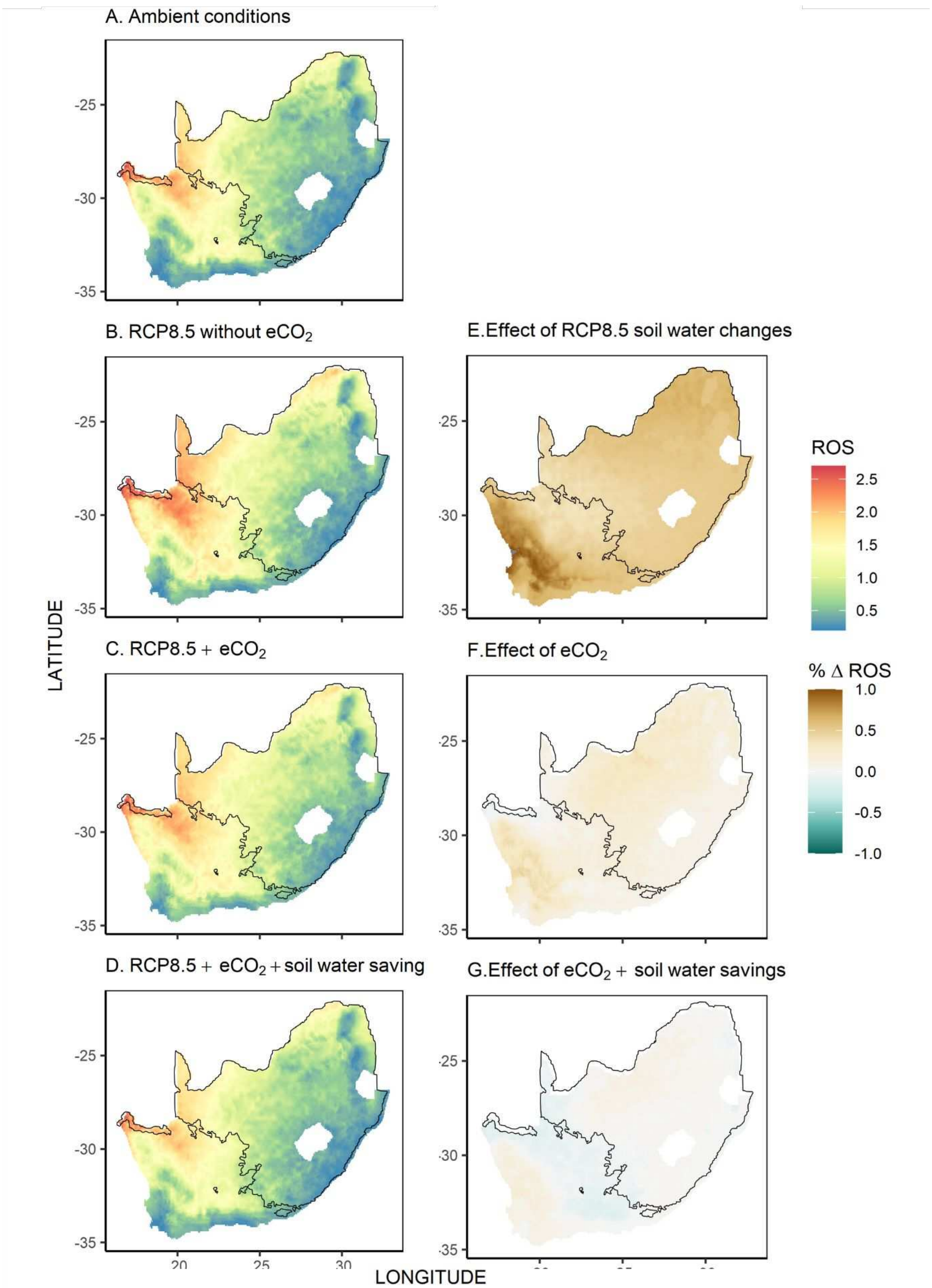


Figure S.6. Rate of fire spread (*ROS*; m min^{-1}) (Rothermel, 1972) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil

moisture conditions (for the year 2070 according to the RCP 8.5 MPI-ESM-LR projection scenario) without the effects of eCO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of eCO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving) associated with eCO_2 and with the effects of eCO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under aCO_2 (400ppm) and eCO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012).

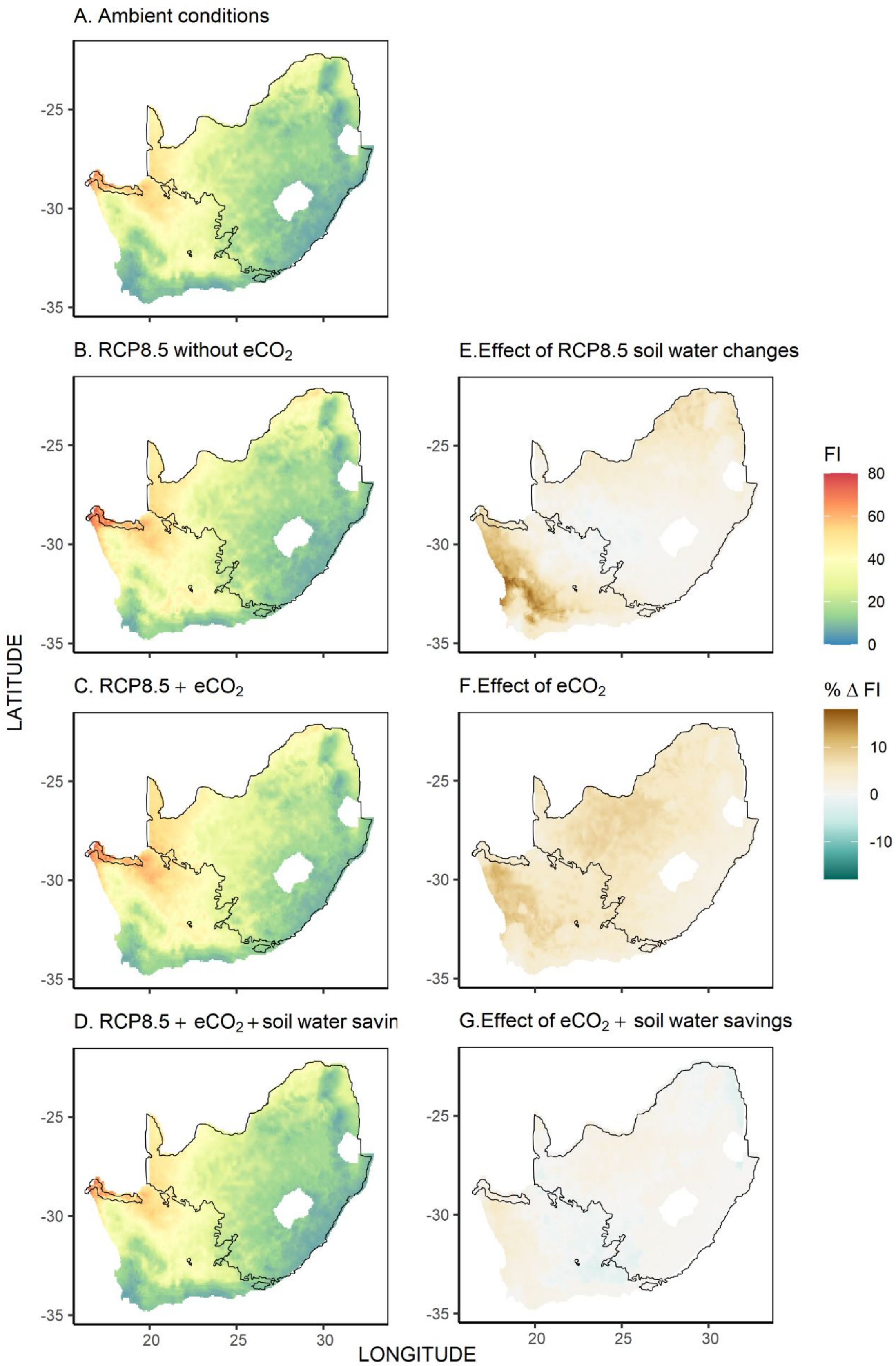


Figure S.7. Fireline intensity (*FI*; KJ m^{-2} s^{-1}) (based on Byram's *FI*; Byram 1959) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil moisture conditions (for the year 2070 according to the RCP 8.5 CCSM4 projection scenario) without the effects of eCO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of eCO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving) associated with eCO_2 and with the effects of eCO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under aCO_2 (400ppm) and eCO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012).

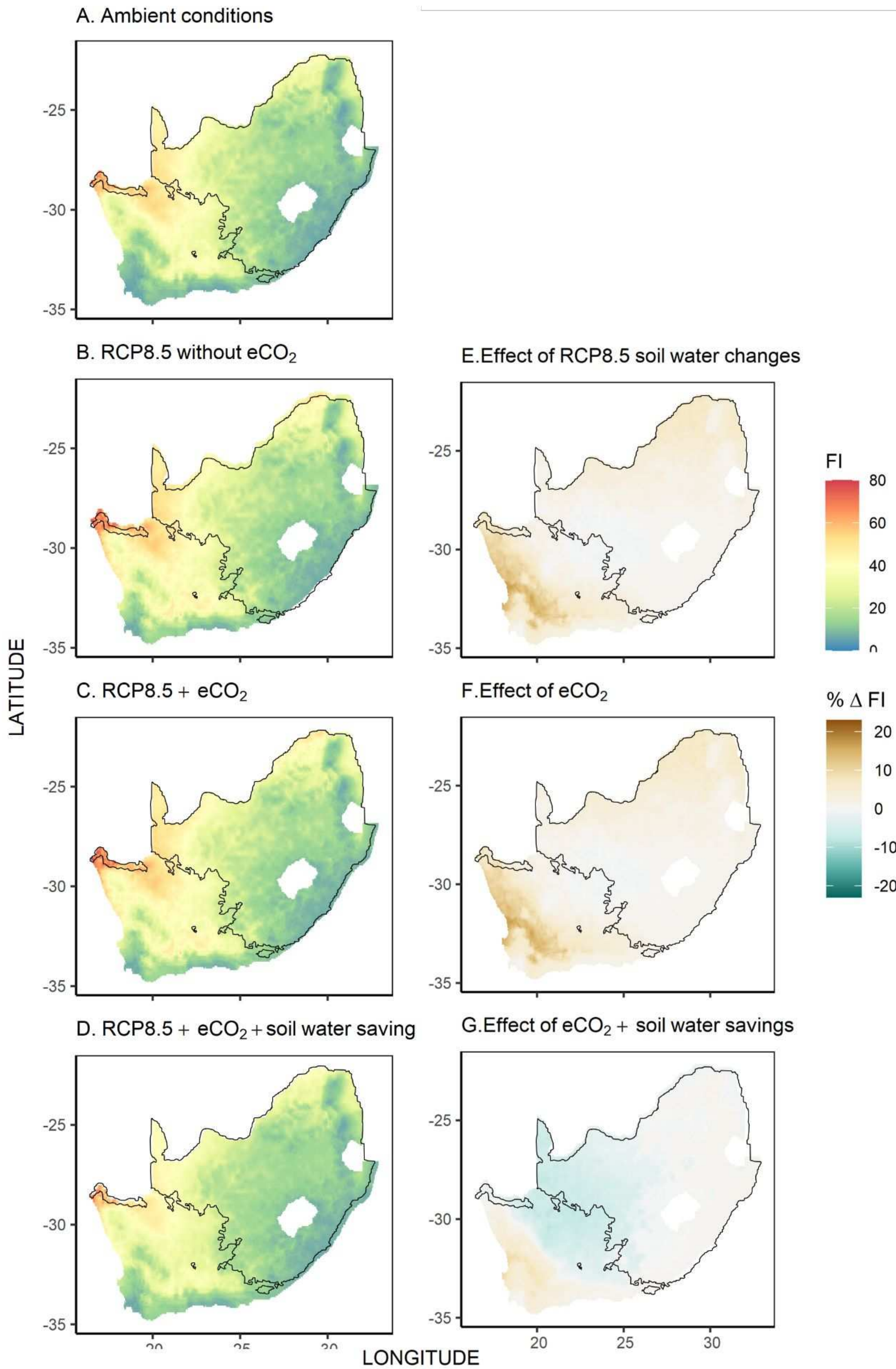


Figure S.8. Fireline intensity (*FI*; KJ m^{-2} s^{-1}) (based on Byram's *FI*; Byram 1959) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil moisture conditions (for the year 2070 according to the RCP 8.5 CM5A projection scenario) without the effects of *e*CO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of *e*CO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving) associated with *e*CO_2 and with the effects of *e*CO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under *a*CO_2 (400ppm) and *e*CO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012).

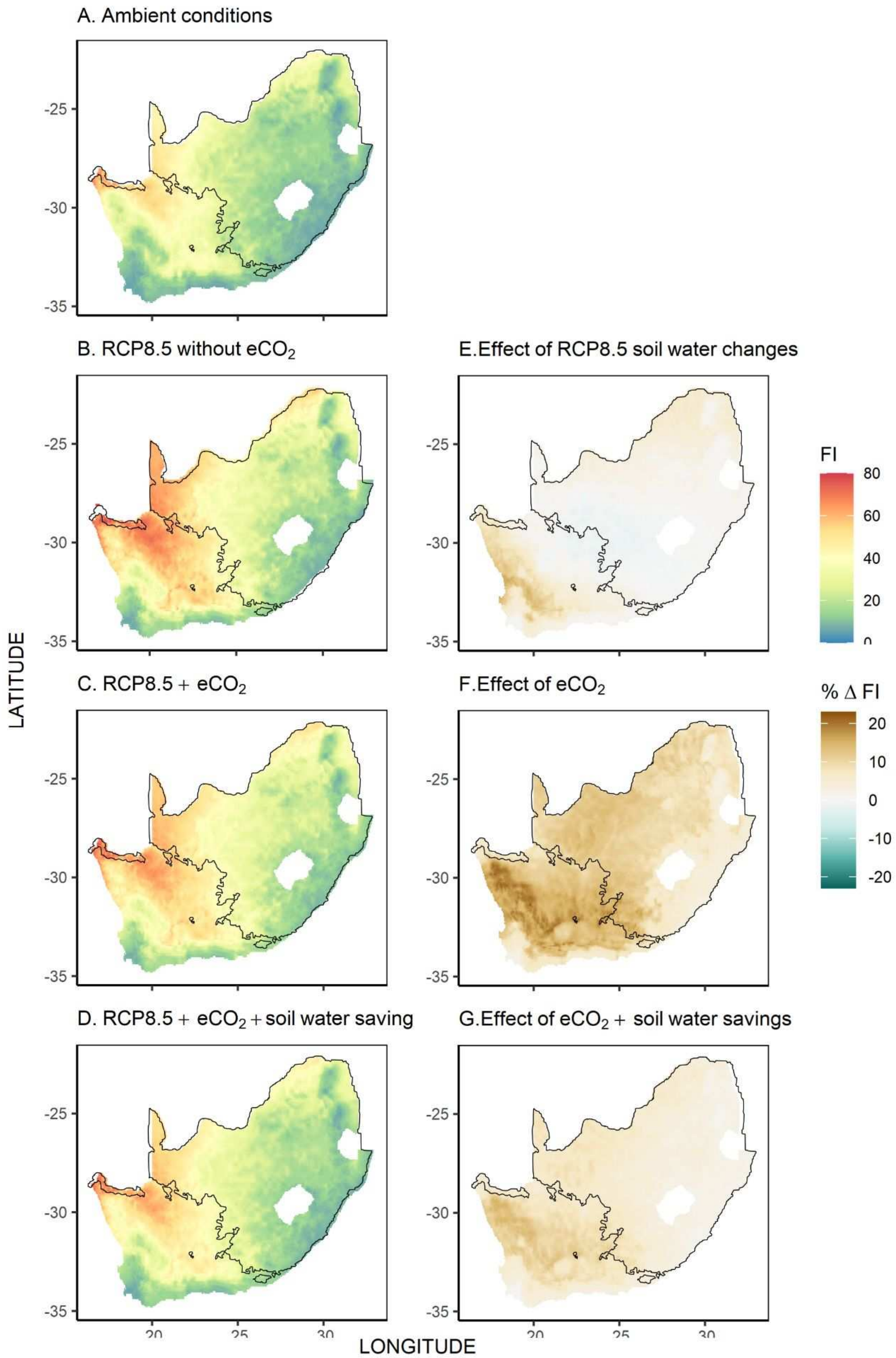


Figure S.9. Fireline intensity (*FI*; KJ m^{-2} s^{-1}) (based on Byram's *FI*; Byram 1959) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil moisture conditions (for the year 2070 according to the RCP 8.5 MIROC-

ESM projection scenario) without the effects of eCO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of eCO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving) associated with eCO_2 and with the effects of eCO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under aCO_2 (400ppm) and eCO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012).

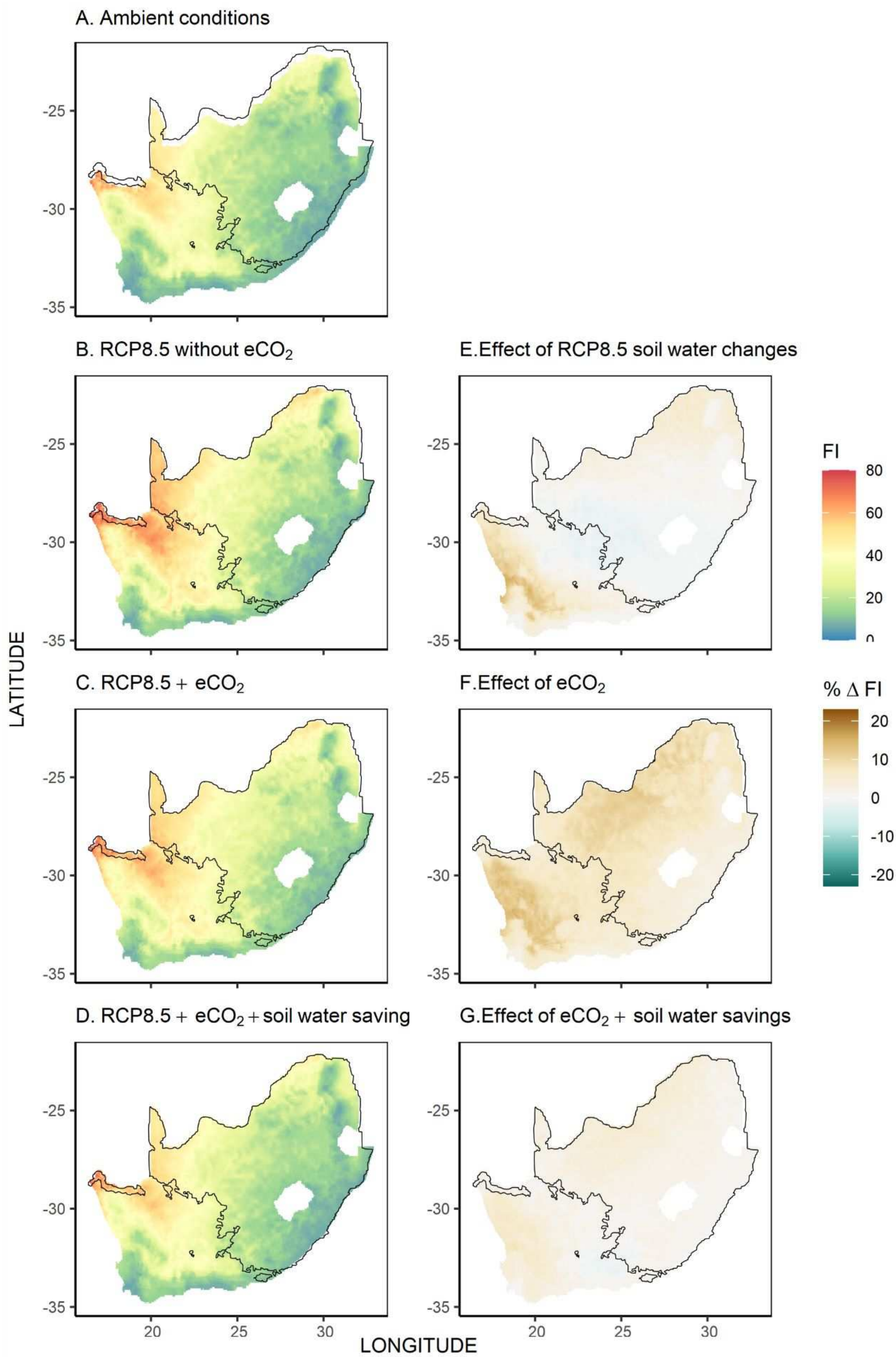
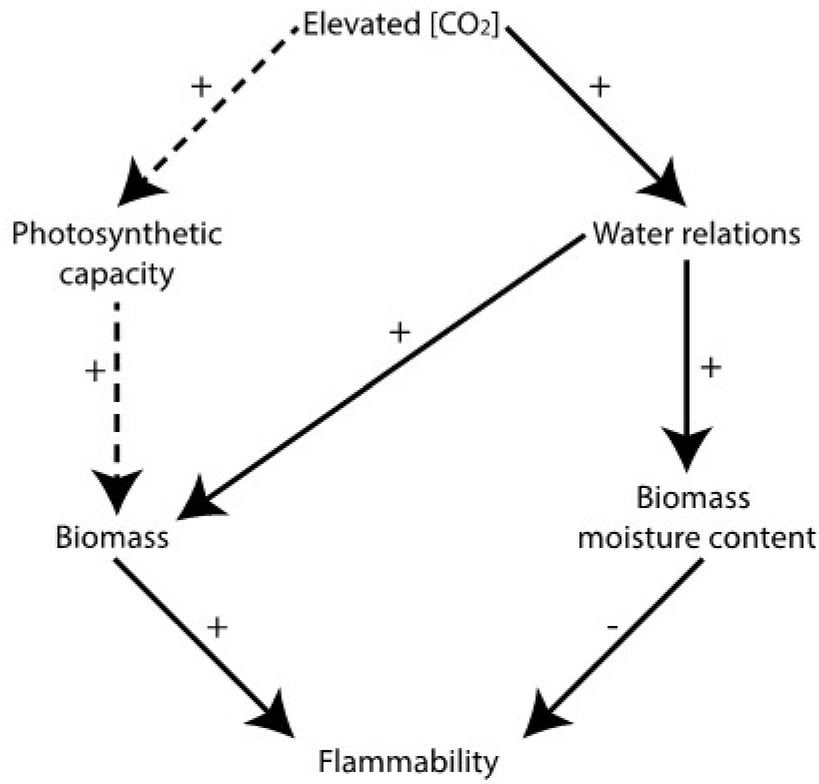


Figure S.10. Fireline intensity (*FI*; KJ m^{-2} s^{-1}) (based on Byram's *FI*; Byram 1959) is predicted for *Themeda triandra* grasses under ambient conditions [A], under predicted future soil moisture conditions (for the year 2070 according to the RCP 8.5 MPI-ESM-

LR projection scenario) without the effects of eCO_2 on plant physiology and flammability [B], under predicted future soil moisture conditions with the effects of eCO_2 on plant physiology and flammability incorporated, and under predicted future soil moisture conditions adjusted according to experimentally determined soil water savings (24.08 ± 4.26% soil water saving) associated with eCO_2 and with the effects of eCO_2 on plant physiology and flammability incorporated [D]. Predictions are based only on the flammability of the widespread savanna grass, *Themeda triandra*, grown under aCO_2 (400ppm) and eCO_2 (800ppm). The area outlined in black represents that currently classified as savanna or grassland biomes (South African National Biodiversity Institute, 2012).



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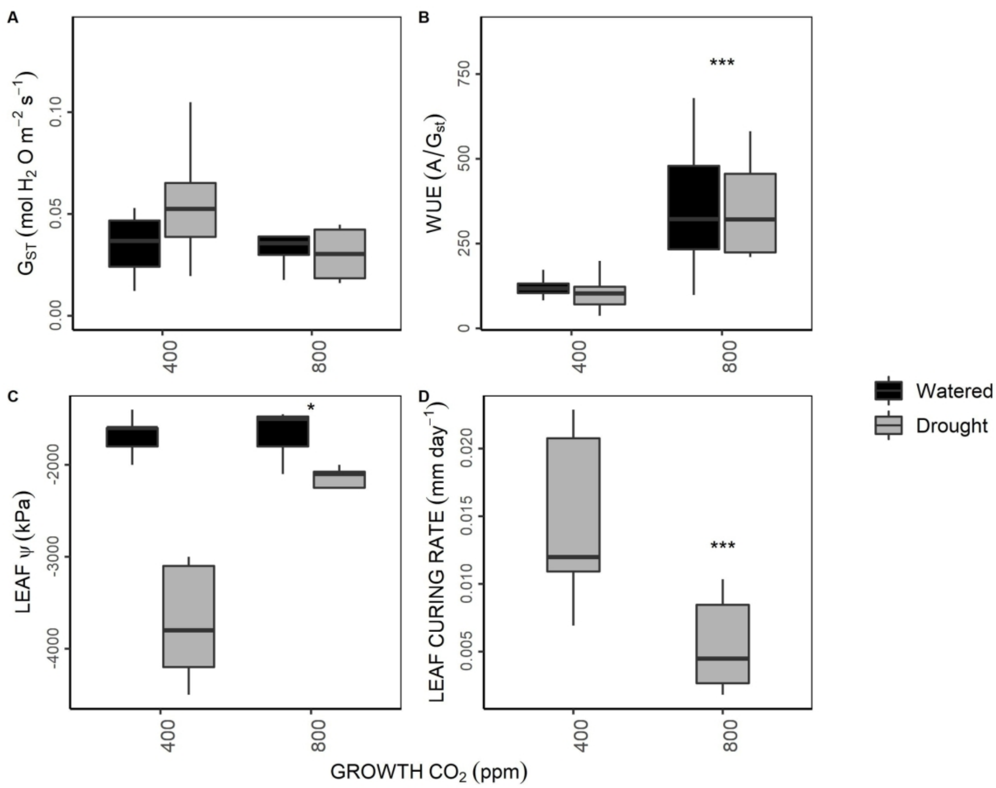

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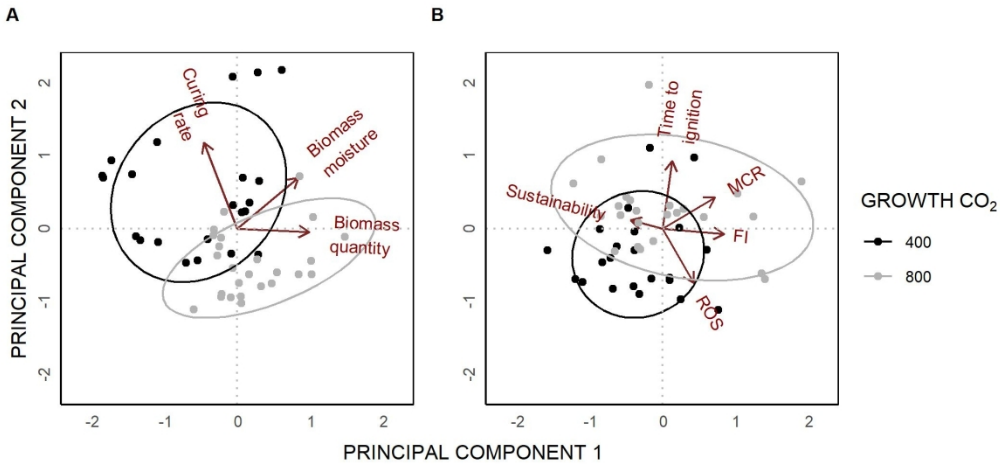

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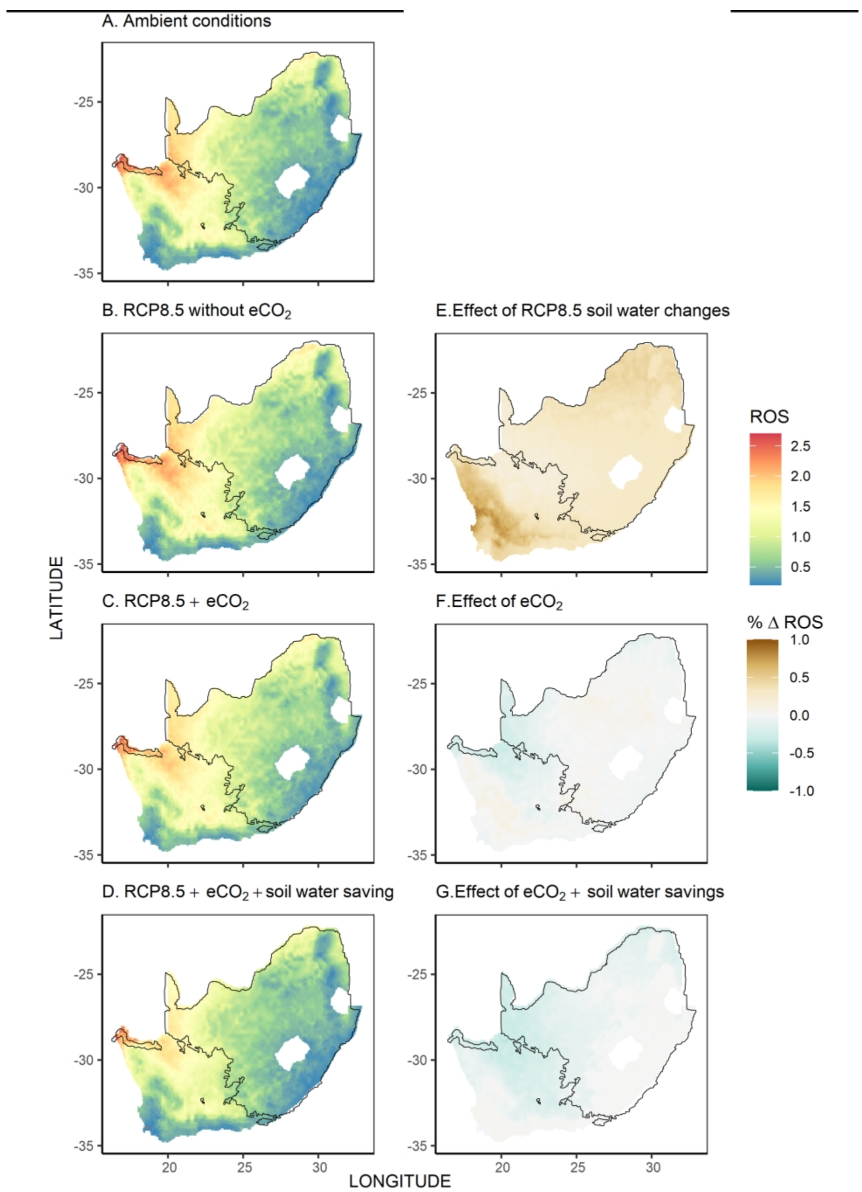

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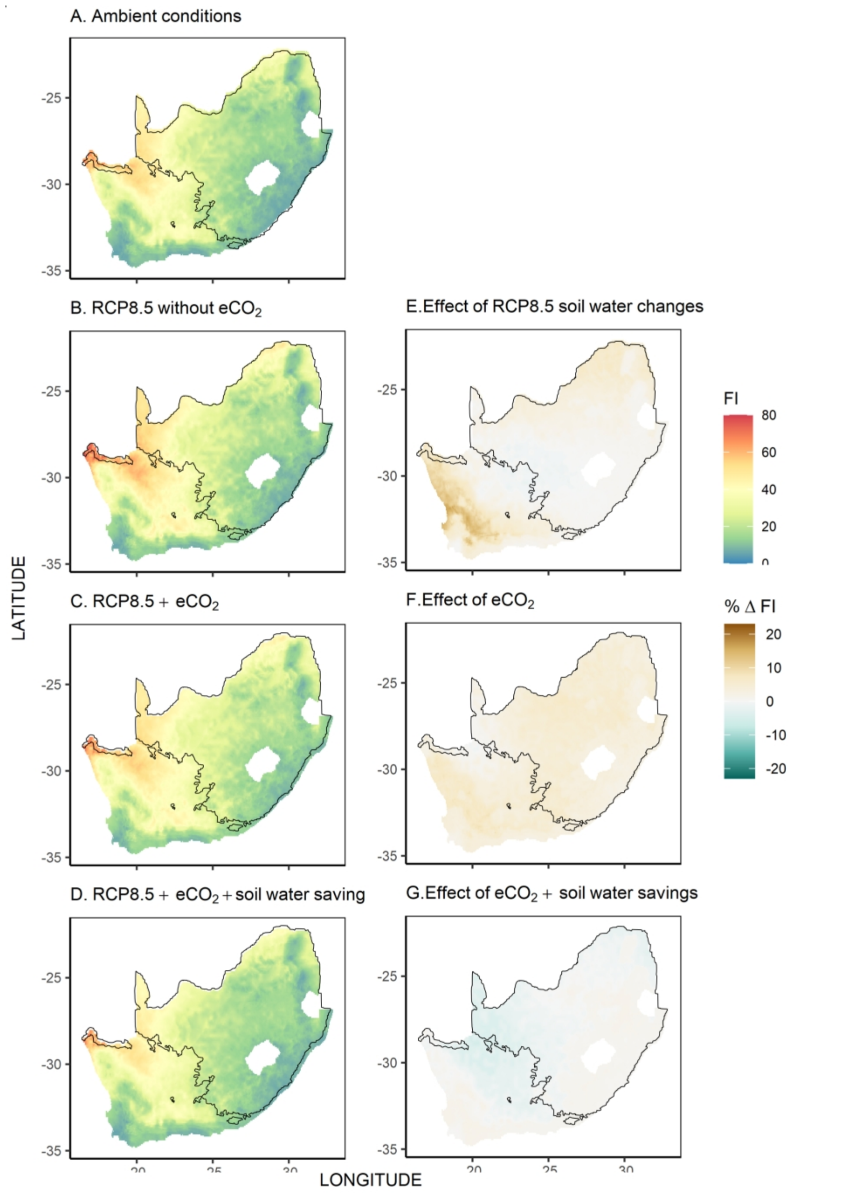

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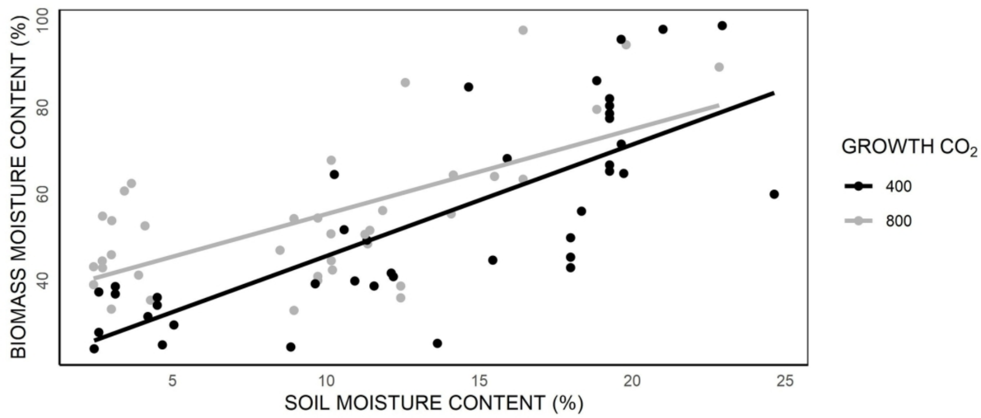
Parameter	CO_2 (ppm)	Watered	Drought
2.1. Plant traits			
Fuel load per tussock (g)	**400**	15.37 ± 9.87	10.54 ± 5.1
	800	17.48 ± 6.55	16.98 ± 8.63 *
Biomass moisture content (%)	**400**	54.27 ± 24.01	50.15 ± 18.59
	800	56.28 ± 19.7	52.6 ± 19.15
Biomass moisture content when soil moisture content <10% (%)	**400**	-	32.53 ± 5.48
	800	-	47.0 ± 9.22 **
Biomass density (g cm^{-2})	**400**	1.64 ± 1.27	1.36 ± 0.74
	800	1.90 ± 0.83	1.70 ± 0.97
Leaf SA:V ratio	**400**	88.22 ± 34.97	89.85 ± 33.24
	800	84.14 ± 18.37	88.14 ± 31.70
2.2. Flammability measures			
Time to ignition (s)	**400**	2.47 ± 0.16	2.74 ± 1.43
	800	3 ± 0.17 *	2.98± 1.16
Sustainability (s)	**400**	65.47 ± 25.65	62.62 ± 28.05
	800	58.41 ± 24.71	57.31 ± 21.39
Combustibility (g s^{-1})	**400**	0.0036 ± 0.0014	0.0040 ± 0.0018
	800	0.0042 ± 0.002	0.0041 ± 0.0016
Estimated maximum combustion rate (gs^{-1})	**400**	10.33 ± 6.57	7.08 ± 3.35
	800	11.81 ± 4.35	11.30 ± 5.66 *
2.3. Fire behaviour			
ROS (m min^{-1})	**400**	2.44 ± 0.82	2.13 ± 0.78
	800	1.86 ± 0.93 *	1.88 ± 0.86 *
FI (KJ m^{-2} s^{-1})	**400**	77.9 ± 56.73	53.26 ± 32.76
	800	68.47 ± 50.47	51.18 ± 37.94

Model	Parameter	Effect of CO_2 treatment		
		Estimate	SE	P value
A. Plant traits	Leaf curing rate	-0.009	0.003	<0.001 **
	Biomass moisture	4.63	6.18	0.5
	Biomass quantity	6.45	2.47	<0.05 *
B. Flammability	Time to ignition	0.96	0.45	0.09
	Sustainability	-12.36	17.35	0.52
	MCR	4.24	1.63	<0.05 *
	ROS	-0.43	0.23	<0.05 *
	FI	24.26	13.96	0.15



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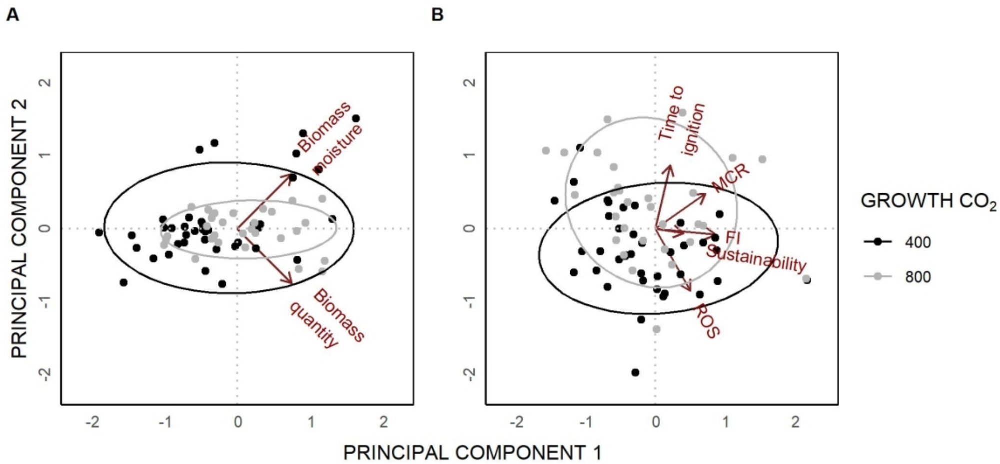

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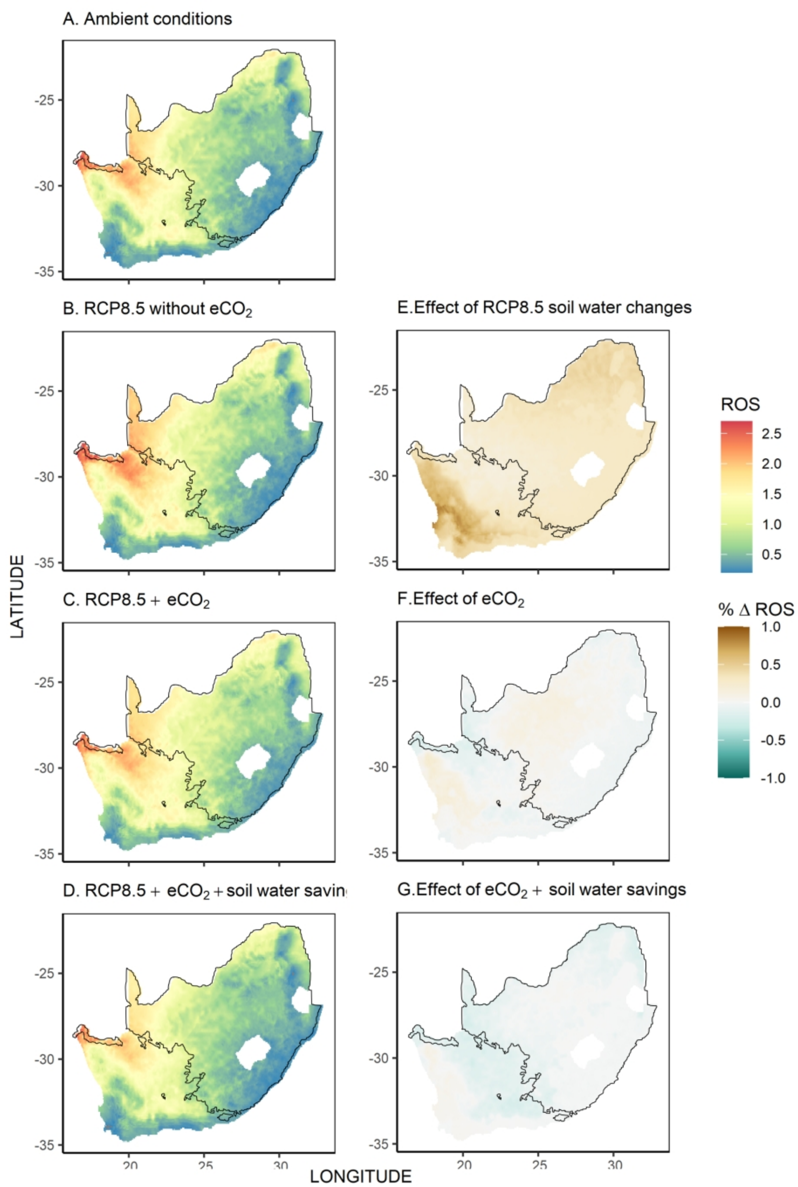

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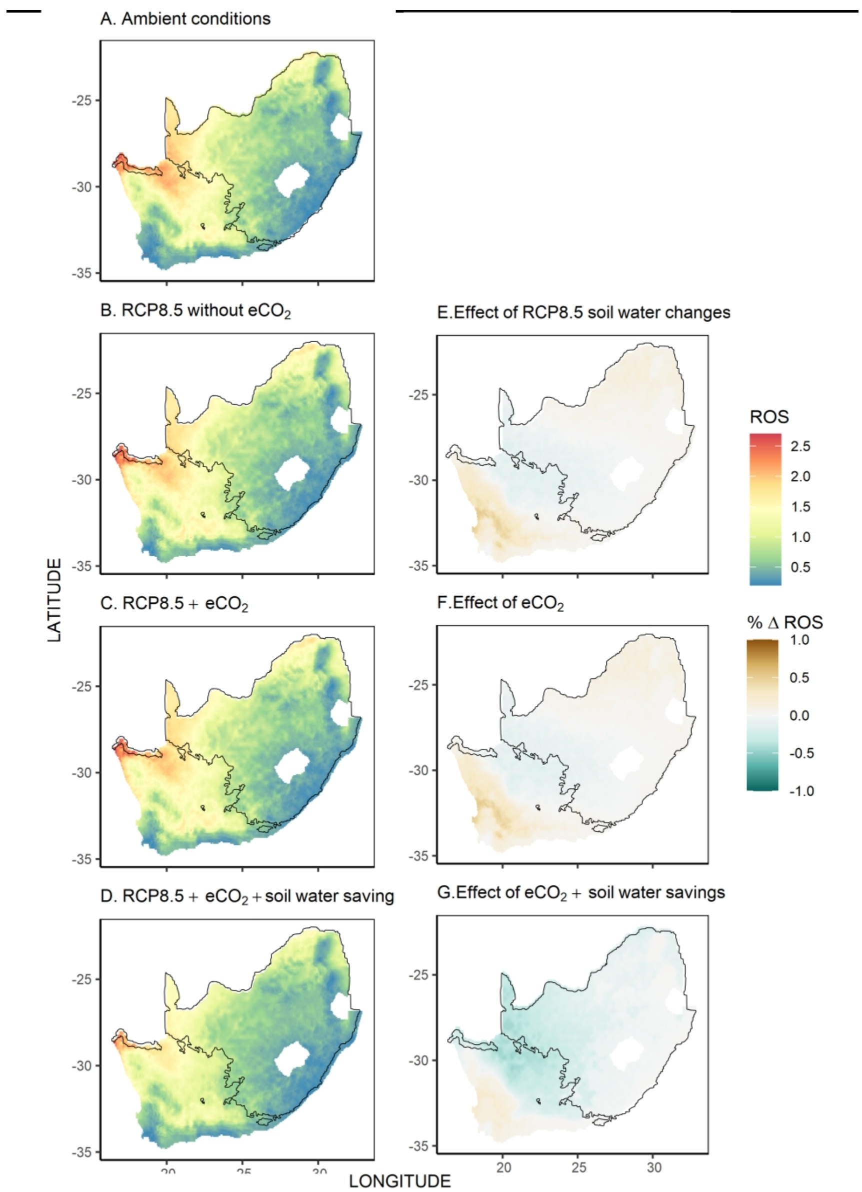

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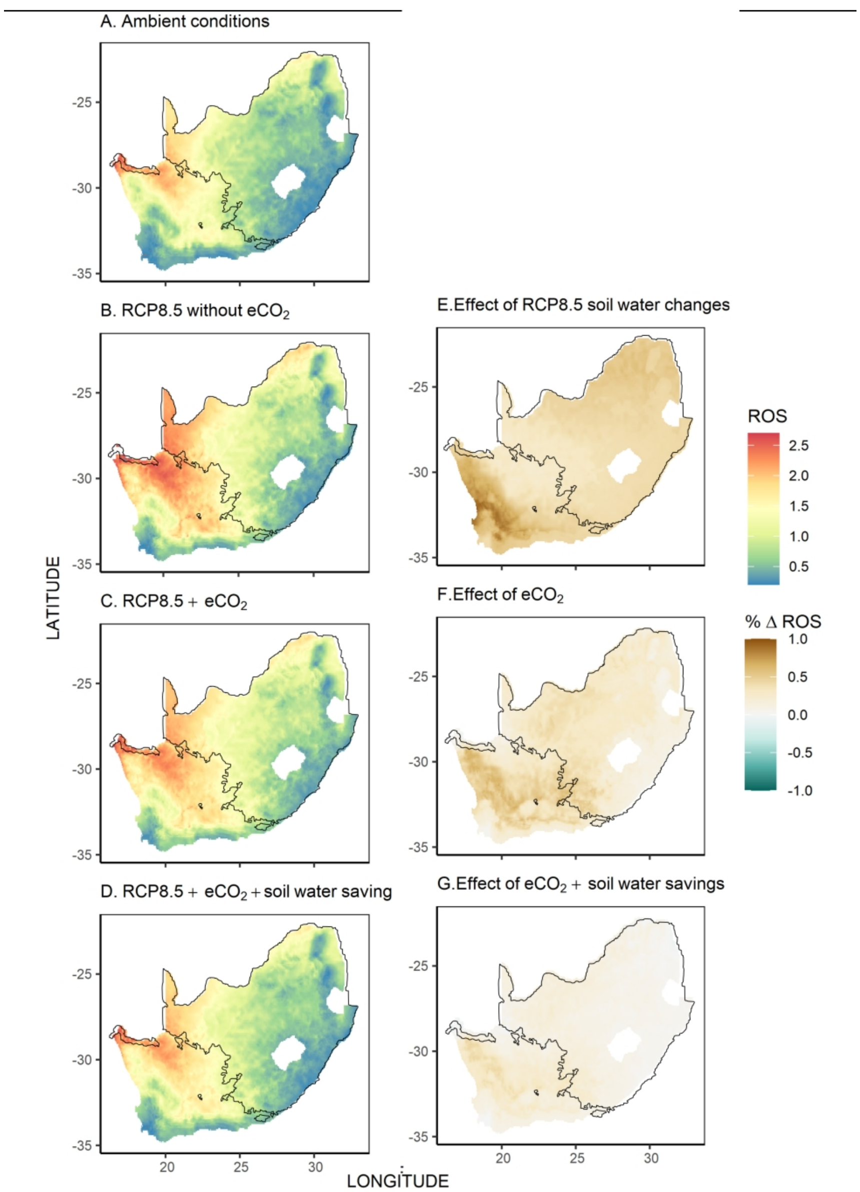

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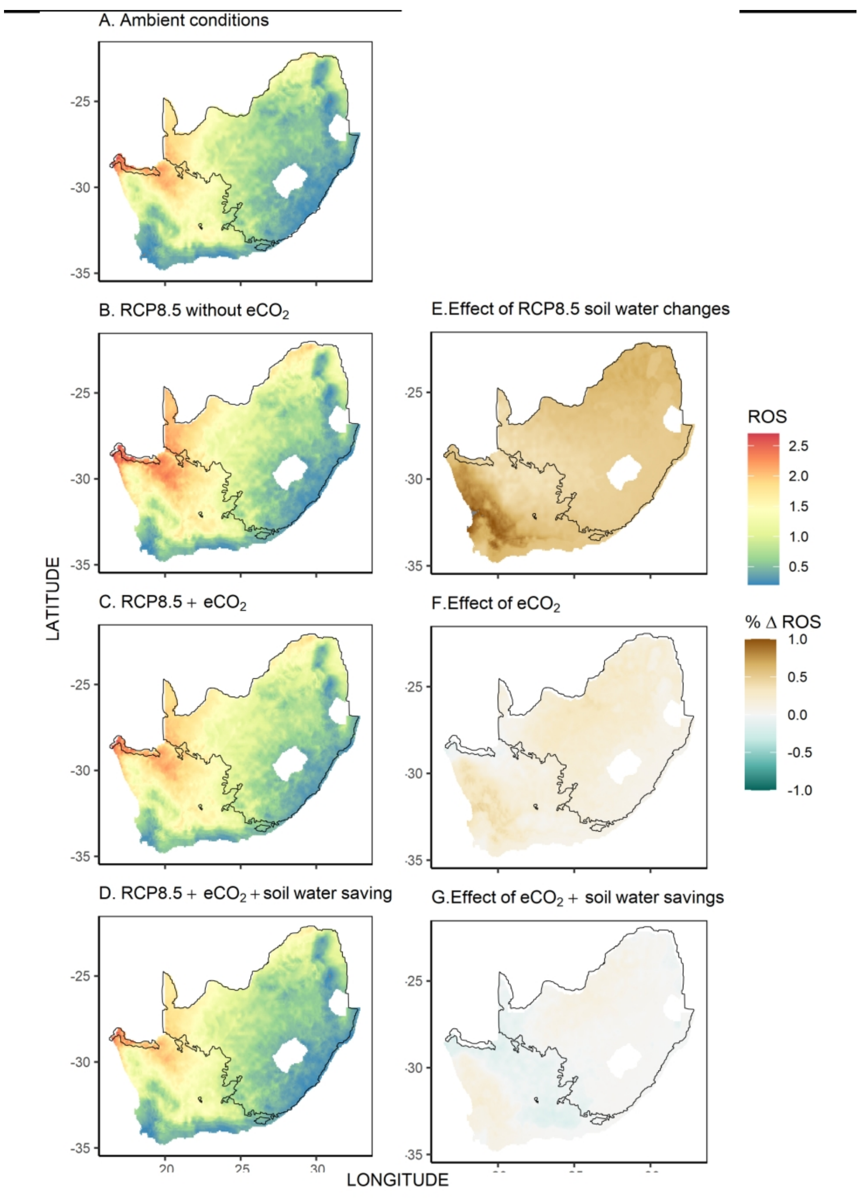

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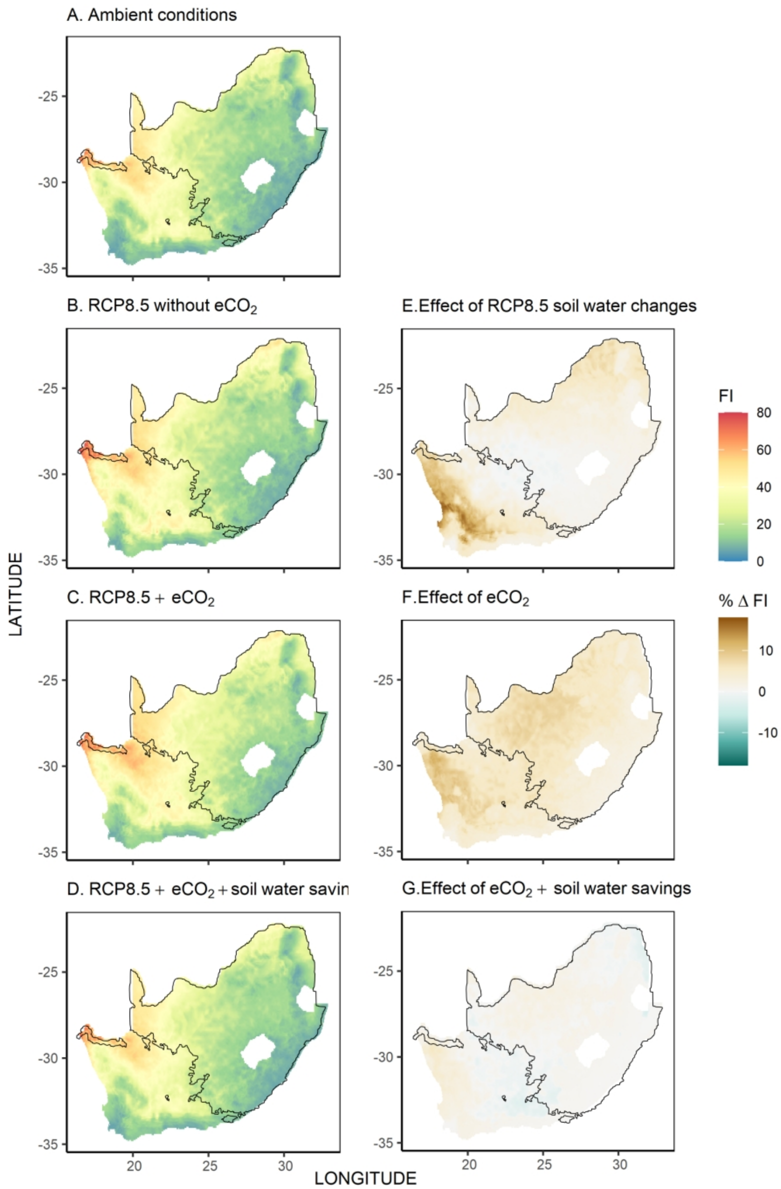

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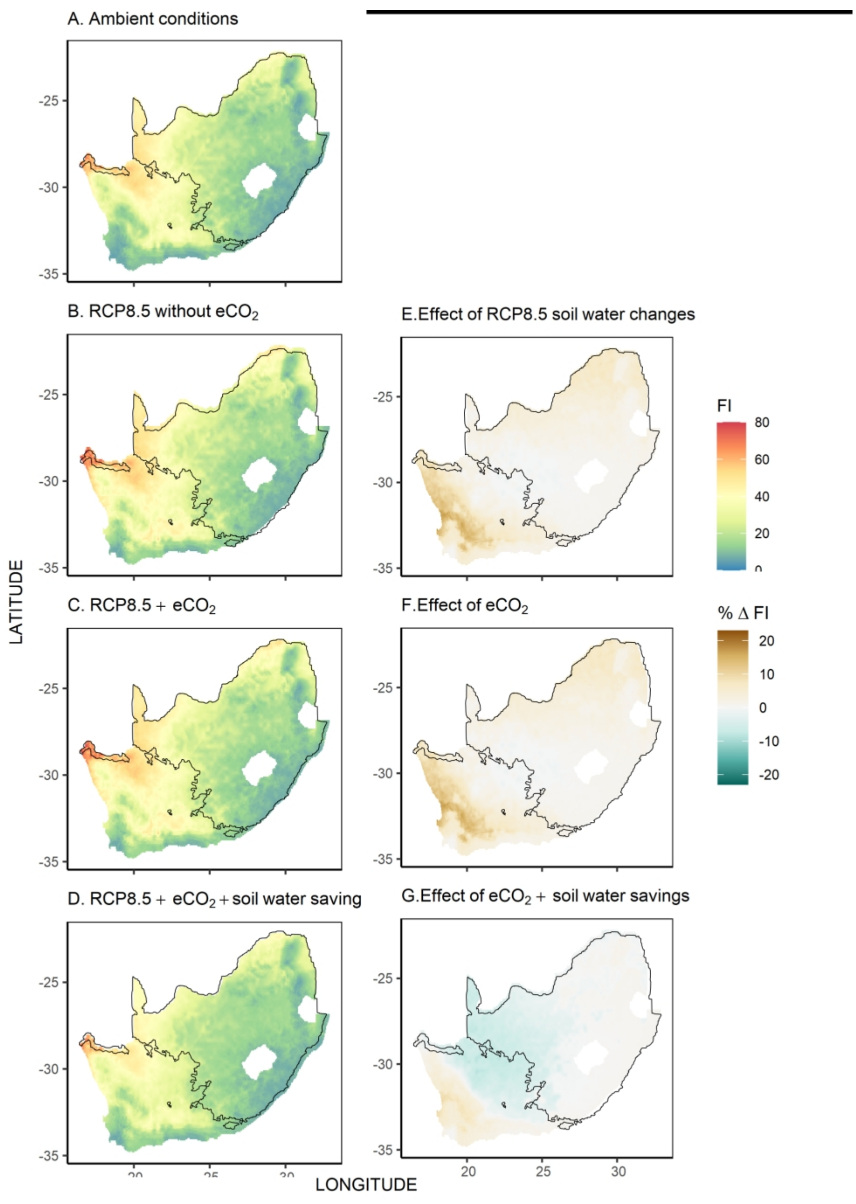

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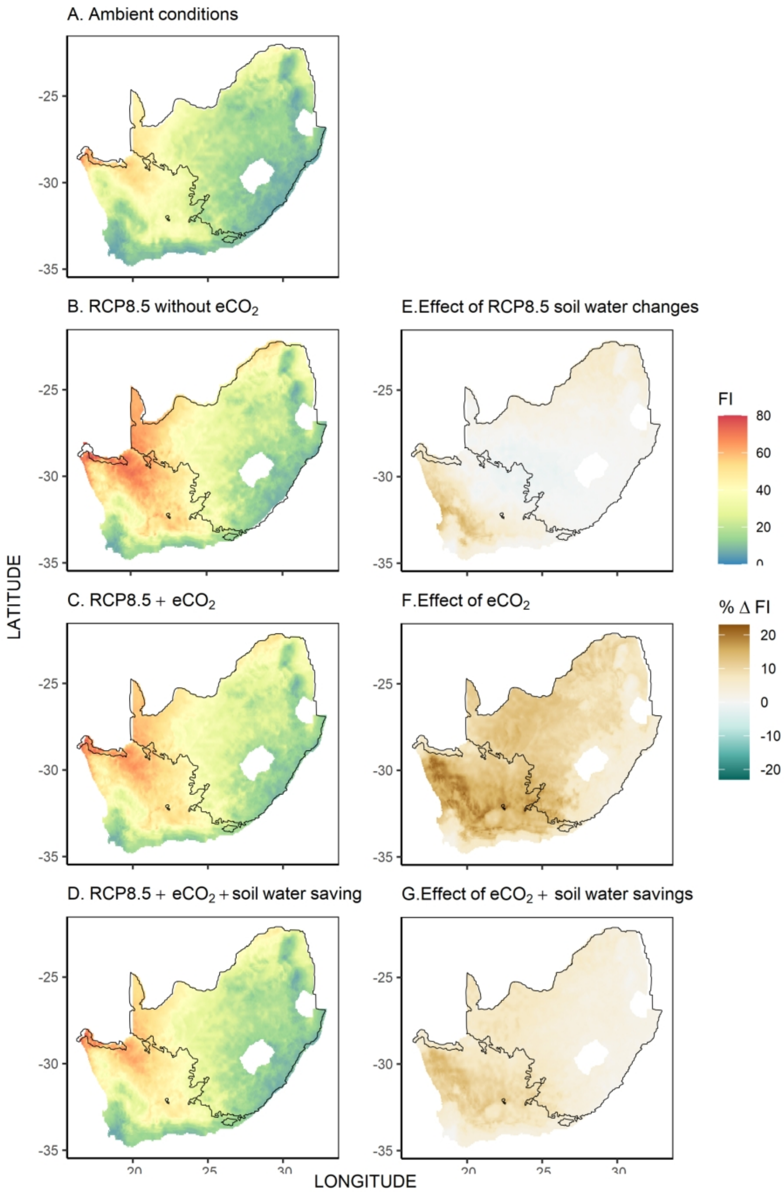
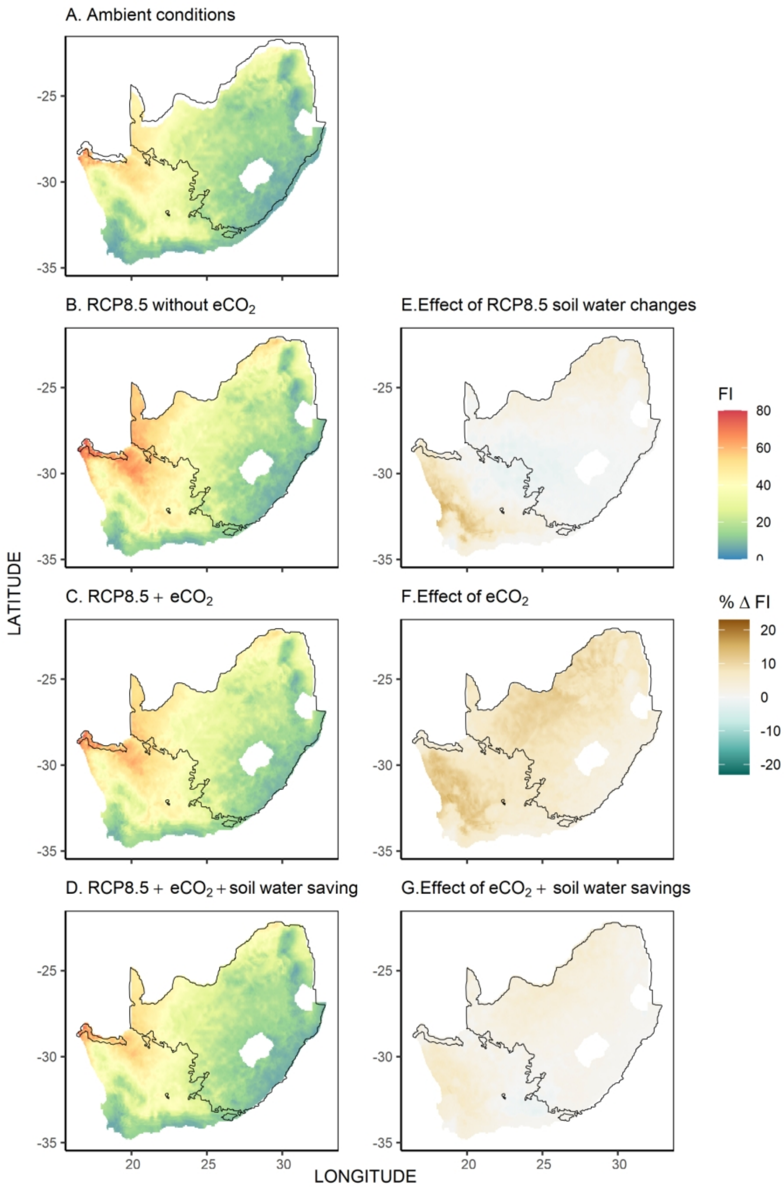


446x627mm (130 x 130 DPI)



446x627mm (130 x 130 DPI)

Target CO_2 (ppm)	% within S.D.	% within 50 ppm	% within 100 ppm
400	72.82	92.85	99.66
800	70.89	38.42	66.09

Environmental variable	Mean	Minimum	Maximum
Temperature (°C)	19.25	0	42.92
Relative Humidity (%)	77.93	5.12	100.00
Daily precipitation (mm)	0.87		
Monthly precipitation (mm)	18.53		
Total accumulated precipitation (mm)	111.2		
Solar inclination (W/m^2)	663.6		
Solar azimuth (°)	179.96		
Solar elevation (°)	4.94		
Solar hour angle (°)	-0.0002		
Solar declination (°)	-0.12		
Solar air mass	5.42		