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Challenges and opportunities in modelling savanna ecosystems

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Abstract

The savanna complex is a highly diverse global biome that occurs within the seasonally dry tropical to sub-tropical equatorial latitudes. Savannas are open-canopy environments that encompass a broad demographic continuum, often characterised by a dynamically changing dominance between C_3-tree and C_4-grass vegetation, where frequent environmental disturbances such as fire modulates the balance between ephemeral and perennial life forms. Climate change is projected to result in significant changes to the savanna floristic structure, with increases to woody biomass expected through CO_2 fertilisation in mesic savannas and increased tree mortality expected through increased rainfall interannual variability in xeric savannas. The complex interaction between vegetation and climate that occurs in savannas has traditionally challenged current-generation terrestrial biosphere models (TBMs), which aim to simulate the interaction between the atmosphere and the land-surface to predict responses of vegetation to changing in environmental forcing. In this review, we examine whether TBMs are able to adequately represent savanna dynamics and what implications potential deficiencies may have for climate change projection scenarios that rely on these models. We start by highlighting the defining characteristic traits and behaviours of savanna, how these differ across continents, and how this information is (or is not) represented in the structural framework of many TBMs. We highlight three dynamic processes that we believe directly affect the water-use and productivity of the savanna system, namely: phenology; root-water access; and fire dynamics. Following this, we discuss how these processes are represented in many current generation TBMs and whether they are suitable for simulating savanna dynamics. Finally, we give an overview of how eddy-covariance observations in combination with other data sources, can be used in model benchmarking and inter-comparison frameworks to diagnose the performance of TBMs in this environment and formulate roadmaps for future development. Our investigation reveals that many TBMs systematically misrepresent phenology, effects of fire and root-water access (if they are considered at all) and that these should be critical areas for future development. Furthermore, such processes must not be static (i.e. prescribed behaviour), but be capable of responding to the changing environmental conditions in order to emulate the dynamic behaviour of savannas. Without such developments, however, TBMs will have limited predictive capability in making the critical projections needed to understand how savannas will respond to future global change.

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1 Introduction

Savanna ecosystems are a diverse and complex biome covering approximately 15 to 20% of the global terrestrial surface (Scholes and Hall, 1996) and provide important in providing ecosystem services, that maintain biodiversity and support the majority of the global livestock (van der Werf et al., 2008). Savannas are characterised by a multifaceted strata of vegetation, where an open C_3-woody canopy of trees and shrubs overlies a continuous C_4-grass layer and occur in regions that experience a seasonal wet-dry climate, have low topographic relief and infertile soils (Scholes and Archer, 1997). Savanna vegetation structure (defined by the ratio of woody to herbaceous cover) is further modulated by disturbance events (predominantly fire) and create demographic bottlenecks, preventing canopy closure that results in an open, woody system (Scholes and Archer, 1997). Indeed, fire disturbance is a defining characteristic of savannas, particularly for mesic regions (mean annual precipitation; MAP > 650 mm), potentially holding the ecosystem in a 'meta-stable' state, such that if it were excluded this open C_3/C_4 system would likely shift to a closed C_3 forest or woodland (Bond et al., 2005; Sankaran et al., 2005). The role of fire in modulating vegetation structure allows savannas to occur across a broad demographic continuum, where the density of woody biomass is coupled to the annual amount of rainfall (Hutley et al., 2011; Lehmann et al., 2011). These environmental traits and behaviours therefore mark savannas as one of the most complex terrestrial biomes on the planet, and understanding the vegetation dynamics and underlying processes of this ecosystem type (especially in response to future global change) has proven a confronting task for the ecosystem modelling community (House et al., 2003; Scheiter and Higgins, 2007).

Terrestrial biosphere models (TBMs), which aim to predict ecosystem water and carbon transfer between the land-surface and the atmosphere (among other processes), have mostly underperformed for savanna ecosystems (Whitley et al., 2015). While the reasons for this are in some cases model-specific, a general question can be formed about whether the current generation of TBMs have the predictive capability to adequately simulate savanna dynamics and their response to future global change. Additionally, if such limitations do exist, are they a result of an incorrect parameterisation of physical parameters (e.g. root depth, maximum RuBisCO activity, sand and clay soil contents, etc.), the misunderstanding or absence of dynamic biophysical processes (e.g. phenology, root-water uptake, etc.), the challenge of simulating stochastic events linked to disturbance, or a combination of all three? Particular attributes that characterise savanna environments, such as frequent fire

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disturbance, the seasonality of available soil-water, and the annual recurrence of C_4 grasses (which except for grasslands are absent in other biomes) are not universally represented in most model frameworks. While some TBMs have been specifically designed with savanna dynamics in mind (Coughenour, 1992; Haverd et al., 2016; Scheiter and Higgins, 2009; Simioni et al., 2000), some are closer to modified agricultural models (Littleboy and Mckeon, 1997), with most TBMs attempting to capture savanna dynamics through calibration to the observed time-series and ad-hoc substitutions of missing processes (Whitley et al., 2015). Furthermore, little has been done to investigate why simulating savanna dynamics has fallen outside the scope and capability of many TBMs, such that these problems can be identified and used in on-going model development.

In this paper we review the current state of modelling for the savanna complex, with emphasis on how the dynamics and biophysical processes of the savanna ecosystem may challenge current-generation TBMs. We start with an overview of the global savanna complex and the many biomes that fall under this definition. Moreover, we discuss how the distinct characteristics, dynamics and regional differences among global savanna types may have implications for future global change. We then proceeded to outline how some of the defining physical processes of savanna are commonly misrepresented in TBMs and if these hamper the necessary predictive capability to answer questions on the future of this biome. Finally we conclude with a discussion on model evaluation and benchmarking for this ecosystem, where we argue that eddy flux measurements in combination with observations from multiple data sources (phenocams, remote-sensing products, inventory studies) are needed to give a complete assessment of whether simulated processes are representative of savanna dynamics.

2. The savanna biome

2.1 *Characteristics and global extent*

Savannas occur in the tropical to sub-tropical equatorial latitudes, occupying a significant portion of the terrestrial land-surface that experiences a seasonal wet-dry climate (Fig. 1). Savannas are therefore associated with many ecosystem types and have a global extent that covers 15.1 million km^2 (almost half) of the African continent (Menaut, 1983), 2.1 million km^2 of the Cerrado, Campos and Caatinga ecoregions in South America (Miranda et al., 1997), 1.9 million km^2 of the Australian tropical north

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(Fox et al., 2001), as well as parts of peninsular India, southeast Asia (Singh et al., 1985), California and the Iberian peninsula (Ryu et al., 2010a). Despite the large geographical distribution, the structure of vegetation in these regions has converged towards a similar formation of mixed C_3 trees and C_4 grasses. However, this similarity can only be considered from a purely qualitative standpoint, as the floristic structure is the result of independent but analogous selective pressures imposed by the expansion of C_4 grasses into these regions 6 to 7 Ma (Osborne and Beerling, 2006). In fact it is difficult to consider savannas as a singular biome, as in reality they are closer to a set of independent biomes that may be deflected from equilibrium with their climate due to a combination of resource limitation (soil-moisture and soil nutrients), growing conditions (temperature) and frequent disturbances (fire and herbivory) (Lehmann et al., 2014). Lehmann et al. (2011) quantified the different extents of savanna globally, showing that for each continent they occupy distinctly different climate spaces. For example, South American savannas are limited to a high but narrower range of MAP (~1000 to 2500 mm), while African and Australian savanna occur over lower but wider range of MAP (~250 to 2000 mm), and are further separated by strong differences in rainfall interannual variability and soil nutrient contents (Bond, 2008). Furthermore, Lehmann et al. (2014) shows that different interactions between vegetation, rainfall seasonality, fire and soil fertility occur on each continent and act as determinants of above-ground woody biomass for the ecosystem.

Differences in the magnitude and interaction of environmental effects have indicated savanna vegetation dynamics to be region-specific (Bond, 2008; Bowman and Prior, 2005; Lehmann et al., 2014; Lloyd et al., 2008; Scholes and Hall, 1996), such that there are marked differences in how regional flora (primarily woody species) coordinate their functional traits to operate within their respective climate space (Cernusak et al., 2011; Eamus, 1999). For example, major distinctions can be drawn between the savanna flora of Africa, Australia and South America. Canopies of the African and South American savanna regions are characterised by shallow rooted, deciduous woody species that follow a short-term growth strategy that maximises productivity while environmental conditions are favourable (Archibald and Scholes, 2007; Higgins et al., 2011). In contrast, the savanna canopies of northern Australia are dominated by deep rooted, evergreen *Eucalyptus* and *Corymbia* woody species that favour a long-term strategy of conservative growth that is insured against an unpredictable climate (Bowman and Prior, 2005; Eamus, 1999). Consequently, the functional traits that support deciduous, evergreen or annual strategies have a major impact on the water and carbon exchange

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of the system. For example, Australian mesic savanna tree canopies operate at almost constant rates of assimilation and transpiration all year round, due to their deep and extensive root system and ability to make adjustments to canopy leaf area in times of stress (O'Grady et al., 1999). These differences highlight quite importantly that savanna ecosystems cannot be simply reduced to a generalised plant functional types (PFT) applied globally in some LSM and DGVM frameworks. One alternative may be to define region region-specific PFTs to fully capture the distinctly different dynamics that are occurring across the ensemble of savanna biomes. A promising alternative approach of some recent models is to allow savanna composition to emerge from environmental selection from a mixture of PFTs or trait combinations, reflecting global diversity in savannah vegetation (e.g. Haverd et al., 2015; Scheiter and Higgins, 2009; Smith et al., 2001). For the example, the HAVANA model allows traits such tree and grass phenology, leaf-area, rooting depth and relative cover emerge from the meteorological variations and their effect on evolving ecosystem state (Haverd et al. 2015). Because traits define the response of the vegetation to climate, it is important that they are adequately represented in TBMs.

2.2 *The implications of climate change*

Projected global increases in both temperature and the variability of precipitation patterns as a result of anthropogenic climate change are expected to lead to significant changes in the structure and diversity of global terrestrial ecosystems (IPCC, 2013; Rogers and Beringer, 2016). This will make modelling under these transient conditions difficult, challenging TBMs in how they represent the response of the savanna ecosystem to structural shifts in vegetation through CO_2 fertilisation, increased rainfall seasonality, and changing fire dynamics.

Savannas may be susceptible to small perturbations in climate and could potentially shift towards alternate closed-forest or open-grassland states as a result (Scheiter and Higgins, 2009). The total carbon pool of some savannas can be considered as modest when compared with other ecosystems (e.g. rainforests). However, in terms of net primary productivity (NPP), tropical savannas and grasslands occupy the top ranks among terrestrial biomes, together contributing *c.* 30% of annual global NPP (Grace et al., 2006). A shift in the savanna state towards a more closed system, may lead to these regions becoming a substantially larger carbon sink (Higgins et al., 2010). Observations

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of increased woody vegetation cover (woody encroachment) in many semi-arid ecosystems and savannas worldwide over recent decades have been attributed to positive effects of increased atmospheric CO_2 on plant water-use effects (Donohue et al., 2009; Fensholt et al., 2012; Liu et al., 2015). Models suggest that such effects are predicted to continue in the future. CO_2 fertilisation is also expected to favour the more responsive C_3 vegetation, leading to the competitive exclusion of C_4 grasses via supressed grass growth and reduced fire impacts (Bond et al., 2005). Model projections by Scheiter and Higgins (2009), and Higgins and Scheiter (2012) suggest future range shifts of African savanna into more arid climates as a consequence of elevated CO_2, with concurrent transformation of current savanna habitats to forests under a stationary rainfall assumption. Recent evidence underscores the significant role of savannas in the global carbon cycle (Ahlström et al., 2015; Haverd et al., 2016; Poulter et al., 2014).

The response of savanna structure and function to changes in precipitation patterns is highly uncertain (Rogers and Beringer, 2016). Scheiter et al. (2014) investigated the effect of variable rainfall seasonality, projecting modest to large increases in above-ground biomass for savannas in northern Australia. The authors showed that woody biomass in this region increased despite significant changes to precipitation regimes, being predominantly driven by CO_2 fertilisation and rainfall seasonality determining the magnitude of the increase (Fig. 2) (Scheiter et al., 2014). However, some studies have indicated that while increased rainfall seasonality may have a small effect in mesic savanna systems, it may potentially act as an opposing effect to woody encroachment in semi-arid savanna systems (Fensham et al., 2009; Hiernaux et al., 2009). For example, Fensham et al. (2009) have shown significant tree mortality to occur as a result of drought in a semi-arid savannas in south-west Queensland, suggesting that severe water-stress may counteract the positive effect of CO_2 fertilisation on ecosystem carbon balance. Alternatively, forest dieback as a result of increased rainfall seasonality and more frequent drought occurrence may lead to an expansion of savanna distribution in some regions. For example, simulations of the Amazon basin have projected a possible conversion of rainforest to savanna in eastern Amazonia as a result of forest dieback induced by severe water stress and fire disturbance (Cox et al., 2004; Malhi et al., 2009).

Finally, fire can play a critical role in mediating the floristic structure of the savanna ecosystem, deflecting woody vegetation from its physiognomic potential with climate (Scholes and Archer, 1997). Increased warming and rainfall seasonality is expected to alter the interaction between climate, fire and savannas in the future (Beringer et al., 2014), however we leave discussion of savanna fire dynamics and the ability of TBMs to

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246 simulate this process until in the paper. Permanent shifts in the structure and
247 physiology of the savanna complex as a result of climate change is expected to have a
248 major impact on the exchange of water, energy and carbon that occurs in this system,
249 which in turn ultimately affects global biogeochemical cycling and climate (Beringer et
250 al., 2014; Pitman, 2003).

251

252 **2. The capability of models to simulate savanna ecosystems:**

253 The term '*terrestrial biosphere model*' refers to a variety of bottom-up modelling
254 approaches that simulate coupled dynamics of water, energy, carbon, and in some cases
255 nutrients in vegetation and soils. TBMs range from stand models, which simulate
256 specific ecosystems in high detail, up to dynamic global vegetation models (DGVMs),
257 which can simulate multiple ecosystems at a coarser level. Consequently, TBMs
258 collectively operate over different temporal and spatial scales and employ processes of
259 different scope in simulating ecosystem dynamics. However, common to all TBMs is that
260 they are governed by the same biophysical principles of energy and mass transfer that
261 determines the dynamics of plant life (Pitman, 2003). Consequently, the predictive
262 capability of different TBMs at determining the exchange of water, energy and carbon
263 between the surface and atmosphere should be convergent within a reasonable degree
264 of error (Abramowitz, 2012). However, model intercomparison and benchmarking
265 studies have shown that many TBMs are unable to meet reasonable levels of expected
266 performance as a result of a systematic misrepresentation of certain ecosystem
267 processes (Abramowitz et al., 2008; Best et al., 2015; Blyth et al., 2011; Mahecha et al.,
268 2010). The misrepresentations of ecosystem processes is particularly evident in
269 savannas, for which many TBMs have not been developed for, nor tested on (Baudena et
270 al., 2015; Whitley et al., 2015). Ecosystem processes critical to savannas, such as the
271 complex tree-grass phenology (either deciduous-annual, or evergreen-annual), seasonal
272 competition and access to belowground resources (soil moisture and nutrients) and
273 stochastic disturbance events (fire), are less prevalent in other ecosystems and are
274 therefore not well represented (or even missing) in many TBMs (House et al., 2003;
275 Whitley et al., 2015). Conventional TBMs still lack a lot of this capability and therefore
276 have limited application for biomes in the seasonally dry tropics, which in turn becomes
277 a large source of uncertainty in future global studies (Scheiter and Higgins, 2009).
278 However, we believe that incorporating key processes that drive savanna dynamics into
279 current-generation TBMs has great potential, considering that even small modifications

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can lead to large gains in performance (Whitley et al., 2011). Below, we have identified phenology, root-water uptake and fire disturbance as three critical processes in savannas that deserve special consideration in modern TBMs.

2.1 Phenology

Phenology is an expression for the seasonal dynamics of structural vegetation properties of an ecosystem, defining its growing season and ultimately its productivity (Moore et al., 2016a). Here we limit our discussion to the phenology of leaf cover. In seasonally dry climates phenology is driven by soil-moisture availability and the length of the growing season for shallow rooting plants is determined by the seasonality of rainfall (Kanniah et al., 2010; Ma et al., 2013; Scholes and Archer, 1997). Plants respond differently to water availability, such that phenology is a function of the dominant species within the ecosystem. Deciduous trees and annual grasses are photosynthetically active during the wet season only and respectively senesce or become dormant or senesce at the beginning of the dry season, while evergreen trees may remain permanently active throughout the year, potentially responding to soil-moisture depletion by gradually reducing their canopy leaf area (Bowman and Prior, 2005). These dynamics are critically important, as they control the amount and seasonality of carbon-uptake and water-use. In TBMs, ecosystem phenology is typically represented in one of two ways. The first is via direct *prescription* of this information as an additional input to the model, where observations of leaf area index (LAI) (either in-situ measurements or satellite derived products) are used to express the change in ecosystem canopy cover over time (Whitley et al., 2011). The second is as a *prognostic* determination using a growth sub-module, where carbon allocation and leaf metabolic activity are simulated and dependent upon the time-varying conditions of temperature and soil-water availability (Scheiter and Higgins, 2009). Prescription of phenology from observed LAI dynamics requires an accurate determination of the separate tree and grass components from bulk ecosystem LAI to be feasible for savanna ecosystems (Whitley et al., 2011). In many cases, this separation is assumed to be static, ignoring the different seasonal changes in tree and grass cover over time (Scholes and Archer, 1997). In fact, no models that we are aware of dynamically partitions prescribed LAI Donohue et al. (2009) offers an *a priori* method that can determine separate tree and grass LAI signals. This method assumes that the high variability in the bulk signal is attributed to herbaceous vegetation, such that the remaining, less variable signal is attributed to

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314 woody vegetation (Fig. 3). A prescription of separate tree and grass LAI inputs was
315 found to be necessary for simulating water and carbon exchange for a mesic savanna
316 site in northern Australia (Whitley et al., 2011), and in determining a reduced error
317 estimate of the Australian continental water and carbon balance (Haverd et al., 2013) to
318 which savannas contribute significantly. The major drawback to prescribing LAI as a
319 model input is that the model's scope is limited to hindcast applications. Because this
320 information is supplied to the model, the floristic structure and its evolution over time is
321 fixed, and cannot respond to changing environmental conditions (e.g. shifts in
322 precipitation patterns) that are likely to have an impact on the tree-grass demography
323 (Ma et al., 2013). Consequently, a dynamic approach where savanna phenology is
324 explicitly simulated and dynamically responds to climate and disturbance offers a more
325 promising path forward.

326 Allocation-growth schemes allow models to express phenology in terms of the evolution
327 of carbon investment in leaf area over time, limited by the availability of resources for
328 growth (Haverd et al., 2016). These schemes effectively work by distributing assimilated
329 carbon (via net primary productivity; NPP) to the root, stem and leaf compartments of
330 the simulated plant, where allocation to the leaf is dependent on the plant being
331 metabolically active or dormant (Cramer et al., 2001). In some TBMs, allocation to these
332 compartments is a fixed ratio (set according to plant functional type) and metabolic leaf
333 activity is defined through a set of threshold bioclimatic indicators (e.g. photoperiod,
334 moisture availability and temperature) that determine whether conditions are
335 favourable for photosynthesis (Jolly et al., 2005). However, more recent advances, use
336 an alternative approach of dynamically guiding allocation towards the compartment
337 that most limits a plant's growth (Scheiter and Higgins, 2009) or dynamically optimising
338 daily allocation, to maximise long-term NPP and control the competitive balance
339 between trees and grasses (Haverd et al., 2016). The latter approach, based on
340 optimality theory (Raupach, 2005), is related to the approach followed by Schymanski et
341 al. (2009), who assumed that vegetation dynamically optimises its properties (root
342 system and foliage) to maximise its long-term net carbon profit. These approaches,
343 which assume a more dynamic coupling between allocation and phenology, allow plant
344 form and community structure to evolve in response to changes in resource availability
345 (light, water or carbon) over time, with phenology becoming an emergent property of
346 this process. Dynamic allocation schemes enable a TBM to answer questions regarding
347 how changing climate or elevated atmospheric CO_2 concentrations may alter structural

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348 properties of the ecosystem, and the resultant feedbacks on water, carbon and energy
349 cycling (Scheiter and Higgins, 2009; Schymanski et al., 2015).

350

351 *2.2 Root-water access and uptake*

352 The root zone is critically important in maintaining water and carbon fluxes, as it
353 defines an ecosystem's accessible belowground resources and vulnerability to
354 prolonged dry periods (De Kauwe et al., 2015). For seasonally dry climates (common for
355 savannas), productivity is primarily limited by dry season water-availability (Kanniah et
356 al., 2010), which is largely determined by the root zone water storage capacity and
357 hence rooting depth. Co-ordination of the whole soil-root-leaf-atmosphere pathway in
358 response to the highly seasonal climate is critical to the survival of savanna plants and is
359 intrinsically linked to their phenology. For example, deciduous and annual savanna
360 species have shallow root profiles (approx. 0.5 to 2 m) and highly conductive vascular
361 systems to maximise productivity during the wet season (February and Higgins, 2010).
362 In contrast, evergreen savanna species invest in highly regulated hydraulic architectures
363 and deep root systems (> 2 m) that can access deep soil water stores to maintain
364 continuous productivity throughout the dry season (Bowman and Prior, 2005). It is
365 therefore critically important that the specific root system and hydraulic architectures
366 of savanna species be adequately represented in models to simulate water and carbon
367 fluxes of this system.

368 Soil and plant hydraulic traits such as rooting depth and distribution, stem hydraulic
369 resistance, and sand and clay contents are typically represented as fixed parameters in
370 TBMs. Of these traits, the root profile acts as the first-order control on soil-water supply
371 and therefore determines the capability of a simulated plant to remain active through
372 rain-free periods (Eamus et al., 1999). The root profile within a soil column is generally
373 modelled as an exponentially declining of root-surface area with depth, the limit of
374 which extends to some prescribed level. Although some models are capable of
375 dynamically determining the size of the root profile as an emergent property of
376 productivity and climate (e.g. Haverd et al., 2016; Schymanski et al., 2009), more
377 typically, the maximum rooting depth is fixed at approximately 1.5 to 2.0 m (Whitley et
378 al., 2015). However, studies have shown that woody plants in semi-arid or seasonally
379 dry climates (particularly those in Australia) exhibit deep root systems to remain active
380 during prolonged dry periods (Duursma et al., 2011; Hutley et al., 2000; O'Grady et al.,

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1999). Numerous modelling studies have shown that a rooting profile of significant depth (> 2 m) is required to achieve good model-data agreement (Fisher et al., 2007; Haxeltine and Prentice, 1996; Schymanski et al., 2009; Whitley et al., 2011, 2015). While characterisation of the rooting depth in savanna modelling exercises may be seen as a matter of correct parameterisation rather than one of systematic process, its role as a first-order control on water supply in seasonally water-limited systems gives it significant weight in the overall determination of carbon uptake. Furthermore, long-term responses of rooting depth to climate change or elevated atmospheric CO_2 concentrations may substantially alter structure, resource use and carbon uptake of savanna ecosystems (Schymanski et al., 2015). Consequently, rooting depths that sufficiently represent either deciduous or evergreen tree species need to be considered when modelling savannas.

Directly coupled to the characterisation of the root-zone is the systematic process by which soil-water is extracted by the root system. The process of root-water uptake in TBMs has been simulated using numerous schemes. One approach assumes that the amount of extracted water by roots is a function of the root density distribution within the soil column and is expressed through an additional sink term to the Richard's equation, which represents the flow of water in an unsaturated soil (Wang et al., 2011). In such schemes, root-water uptake may be weighted by the distribution of fine-root biomass in the soil, such that soil-layers with the greatest density of fine-root biomass largely determine the soil-water status of the plant, its stomatal behaviour, and therefore its sensitivity to soil drying (Wang et al., 2011). The exponential decay function conventionally used to describe the root profile in most TBMs (an exception is Schymanski et al. 2009) can result in simulated stomatal behaviour that is heavily weighted towards the moisture content of the upper soil profile, making them highly sensitive to drought (De Kauwe et al., 2015). In reality, the active root distribution of savannas is not static, nor so limited, but responds dynamically to wherever water is available. For example, eucalypts occurring in Australian mesic savannas invest in 'dual-root' systems that are capable of switching their root activity between subsurface and subsoil respectively to access water continually during both wet and dry seasons (Chen et al., 2004). Alternative root-water uptake schemes do exist that describe a more dynamic response to long-term changes in soil conditions. One such scheme by Williams et al. (2001) considers root activity to change over time and be concentrated towards parts of the root zone where the plant can sustainably extract the maximal amount of available water. Consequently, this scheme effectively weights soil-water status over the

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distribution of fine-root biomass, such that simulated root-water uptake dynamically responds to the wetting and drying of the soil profile over time (Fig. 4). Another alternative approach by Schymanski et al. (2008) allows the root zone to dynamically adjust the vertical distribution of root biomass in the profile to balance canopy water demand while minimising structural costs of maintaining such a root system . These alternate schemes offer a more dynamic approach to modelling the hydraulic architecture of species occurring in savannas and other semi-arid ecosystems, and have demonstrated high predictive skill in these environments (Schymanski et al., 2008, 2009; Whitley et al., 2011). Therefore, given the distinct seasonality of savanna ecosystems, dynamic root-water extraction schemes are needed to simulate how the root zone responds to the evolution of soil-water supply over time.

2.3 Disturbance

Ecosystem structure and function in seasonally dry tropical systems such as savanna, is strongly shaped by environmental disturbance, such as persistent herbivory pressures, frequent low-impact fire events, and infrequent high-impact cyclones (Bond, 2008; Hutley and Beringer, 2011). Fires have a significant impact on land-surface exchange and vegetation structure and contribute to greenhouse gas emissions through the consumption of biomass (Beringer et al., 1995, 2014). Fire has the capacity to alter land-surface exchange fluxes through the removal of functional leaf area (reduced LAI) and the blackening of the surface (reduced albedo), temporarily reducing net carbon uptake (Beringer et al., 2003, 2007) and altering the atmospheric boundary layer to affect convective cloud formation and precipitation (Görgen et al., 2006; Lynch et al., 2007). Regarding vegetation structure, fire influences the competitive balance between tree and grass demographics, suppressing recruitment of woody saplings to adults, thereby deflecting the system from reaching canopy closure (Beringer et al., 2014; Higgins et al., 2000). Work by Bond et al. (2005) underlines the potential effect of removing fire from the savanna system, with substantial increases in woody biomass and major structural shifts towards closed forests. This is further supported by more empirical studies involving fire exclusion experiments and showing similar tendencies towards woody dominance (Bond and Van Wilgen, 1996; Scott et al., 2012). Given that future climate projections point to predict higher temperatures and less precipitation for sub-tropical regions (Rogers and Beringer, 2016) the representation of short- and long-term impacts of fire on savanna structure and function in TBMs may be important in understanding

Biogeosciences Discuss., doi:10.5194/bg-2016-190, 2016
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450 how savanna landscapes may respond to changes in fire frequency and intensity (Bond
451 et al., 2005).

452 Fire is commonly simulated as a stochastic process, with the probability of occurrence
453 increasing with the accumulation of litterfall and grass biomass (fuel loads), combined
454 with dry and windy environmental conditions that promote ignition (generally through
455 lightning) (Kelley et al., 2014). The simulated amount of biomass consumed after an
456 ignition event differs among models. Recent advances in simulating savanna fire
457 processes have led to more complete representations of the complex interaction
458 between fire and woody vegetation and how this shapes savanna structure. For
459 example, Scheiter and Higgins (2009) consider a 'topkill' probability that supresses
460 woody plant succession if fire intensity is of a critical magnitude determined by the
461 plant's fire-resisting functional traits (e.g. height, stem diameter, bark thickness). This
462 scheme allows fire to directly shape the savanna tree population through the dynamics
463 of woody establishment, resprouting and mortality. Additionally, Kelley et al. (2014)
464 have similarly considered how fire-resisting functional traits of woody vegetation alter
465 the fire dynamics of seasonally dry environments. It should be noted that both studies
466 do not consider anthropogenic ignition events, whereas recent work by Scheiter et al.
467 (2015) suggests that fire management can be simulated using fixed fire return intervals.

468 Many TBMs simulate fire as an instantaneous event through emissions and removal of
469 biomass, but may not consider the transient effects that fire has on land-surface after the
470 event has occurred. It has been demonstrated previously that these post-fire effects on
471 canopy surface mass and energy exchange can be significant, with fire indirectly
472 supressing productivity by *c.* 16% (+0.7 tC ha^{-1} yr^{-1}) (Fig. 5) (Beringer et al., 2007).
473 During this period, resprouting rather than climate drives productivity, with respiration
474 exceeding photosynthesis as a result of the regenerative cost of replacing damaged or
475 lost stems and leaf area (Cernusak et al., 2006). In fact many modelling analyses of
476 savannas dynamics have removed the post-fire periods completely from any assessment
477 of performance, such that evaluation has been limited to periods where the model is
478 considered to be 'fit for purpose' (Whitley et al., 2011, 2015). Fire is an integral part of
479 savanna dynamics; it is important to include fire events in the analysis of savanna
480 carbon and water fluxes or model performance. Furthermore, an accurate and robust
481 representation of fire effects on savanna ecosystems is needed to answer questions
482 about how savanna dynamics may change under future climate scenarios, as fire
483 regimes have significant impacts on the carbon balance of these systems (Beringer et al.,
484 2014).

Biogeosciences Discuss., doi:10.5194/bg-2016-190, 2016
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485 Other disturbance regimes such herbivory pressures and cyclones have limited to no
486 representation in models. The removal of aboveground biomass through grazing and
487 browsing, is commonly represented as a set fraction that is removed over time
488 according to the degree of local agricultural pressures, but has been represented
489 dynamically in some models (e.g. Pachzelt et al., 2015). Termite pressures have also
490 been shown to supress productivity (Hutley and Beringer, 2011), but this loss may be
491 too small to be considered as a significant consumer of biomass in TBMs. No models that
492 the authors are aware of simulate the effect of cyclones on vegetation dynamics in
493 tropical systems despite their impact on long-term ecosystem productivity. Cyclones are
494 infrequent but high impact disturbance events that occur in any mesic savanna that lies
495 close to the coastline, and can effectively 'restart' the savanna system through the mass
496 removal of woody biomass (Hutley et al., 2013). Hutley and Beringer (2011) have shown
497 that for an Australian mesic savanna, a bimodal distribution of the tree class sizes at the
498 site indicates two major recruitment events that corresponds with two of the last great
499 cyclones to occur in the region. Despite the immediate and significant loss of woody
500 biomass during those events, recovery was possible and pushed this site to a carbon
501 sink over many decades. Despite the impact that cyclones have on savanna structure it is
502 somewhat understated in the literature, possibly due to the integrated loss in
503 productivity over long-periods being small (Hutley et al., 2013). However, we believe
504 because cyclones modulate savanna structure so strongly, there is a need for such
505 dynamics to be considered in TBM frameworks, particularly for long-term projections
506 on productivity. While few models have the capability to simulate the full spectrum of
507 environmental disturbance effects on savanna ecosystems explicitly, the significant
508 modulating impact they have on savanna structure and function flags these processes as
509 a high priority in future model development.

510

511 **3. Testing and developing models for application in savannas**

512 Given that there are strong indications that critical savanna processes are likely
513 misrepresented in current-generation TBMs, there is a clear need for further model
514 testing and evaluation to be conducted for this ecosystem. Savannas have been the
515 subject of improved research over the past two decades, resulting in a good and
516 evolving understanding of their complicated structure, function, and contribution to
517 global biogeochemical cycling (Higgins and Scheiter, 2012; Lehmann et al., 2014;
518 Sankaran et al., 2005; Scholes and Archer, 1997). Despite this, our increased

Biogeosciences Discuss., doi:10.5194/bg-2016-190, 2016
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519 understanding of savanna dynamics has not been properly translated into many modern
520 TBMs, with the effect of major deficiencies in modelling this ecosystem (Whitley et al.,
521 2015). Consequently, there is still a great necessity for continuous, consistent and
522 objective studies to test and develop how savanna dynamics are represented and
523 simulated. Below we highlight how datasets from multiple sources that include eddy
524 flux towers, satellites, and ground-based *in situ* studies can inform model development
525 and be used in evaluation and benchmarking studies.

526

527 *3.1 Datasets to inform model development*

528 Eddy-covariance (EC) systems that observe the instantaneous response of water, energy
529 and carbon exchange to variability in climate and the evolution of this response over
530 time provide crucial information on which to test and develop TBM application in
531 savanna ecosystems. Quantities measured by EC directly mirror the inputs and outputs
532 of TBMs, namely turbulent fluxes of water, heat and CO_2 observed in parallel with local
533 meteorological forcing (e.g. short-wave irradiance; SW, air temperature, rainfall, etc.) at
534 the same temporal and spatial scale. Consequently, these datasets offer an unparalleled
535 capability in diagnostic model evaluation (Abramowitz, 2012; Mahecha et al., 2010). The
536 use of EC datasets to evaluate TBMs and inform further development has been a long
537 running practice within the ecosystem modelling community, with particular success
538 being reported for some savanna studies in Australia (Haverd et al., 2013, 2016;
539 Schymanski et al., 2009; Whitley et al., 2011, 2015). Here we outline two opportunities
540 of using EC systems to assess model skill for savanna ecosystems are highlighted in
541 these studies.

542 The first of these addresses the problem of EC datasets representing the integrated sum
543 of turbulent fluxes for the entire system (i.e. soil, grass, shrubs and trees), and these are
544 not easily separated. Assessing model performance using bulk measurements does not
545 consider the separate responses of the functionally different C_3 tree and C_4 grass
546 components that respond differently to climate (Whitley et al., 2011, 2015). However, a
547 recent study by Moore et al. (2016b) has shown for a mesic savanna site in Australia
548 that separate observations of canopy and understorey fluxes can be determined by
549 using a 'dual tower' EC system that observes turbulent fluxes at reference points above
550 and beneath the canopy (Fig 6). Datasets such as this provide a valuable resource to
551 analyse the skill of separate model processes, i.e. simulation of tree and grass leaf gas-

Biogeosciences Discuss., doi:10.5194/bg-2016-190, 2016
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552 exchange, which tests the degree of model equifinality (Bevan and Freer, 2001) at
553 predicting the bulk ecosystem flux. A further collection of coupled over- and
554 understorey EC datasets is therefore critically needed to verify that simulated tree and
555 grass dynamics are correctly represented in TBMs.

556 The second opportunity addresses the issue of savanna landscape heterogeneity.
557 Savannas are not a homogeneous PFT, but rather a continuum of changing tree and
558 grass demographics that shift biogeographically with rainfall and other factors (Ma et
559 al., 2013). Ecological gradient studies, such as the Kalahari Transect (Scholes et al.,
560 2004) and North Australian Tropical Transect (Hutley et al., 2011), have shown
561 turbulent fluxes along a declining rainfall gradient to be strongly linked to structural
562 changes in vegetation (Beringer et al., 2011a, 2011b). In essence, the spatial response to
563 a systematic decline in rainfall represents the possible future temporal response to
564 changing climate, such that transects can be used to evaluate TBMs by their ability to
565 emulate the full spectrum of savanna behaviour rather than at just one point. A recent
566 model intercomparison study by Whitley et al. (2015) used turbulent flux observations
567 sampled along the NATT to evaluate a set of six TBMs, and documented only poor to
568 moderate performance being observed. Model evaluations studies that test model
569 predictive skill across both time and space are therefore crucial to projecting how
570 savannas dynamically respond to changing climate.

571 While EC systems provide valuable datasets on which to test and develop models, they
572 are unable to provide a complete evaluation, as they cannot capture long-term temporal
573 and spatial scale features (e.g. demographic structural shifts in vegetation), nor provide
574 detail on underlying ecosystem processes (e.g. root-water dynamics and carbon
575 allocation) (Abramowitz, 2012; Haverd et al., 2013; Keenan et al., 2012)(Abramowitz,
576 2012; Haverd et al., 2013). Additional sources of data and their collection are therefore
577 critical to informing how well models are representing the specific dynamics that unique
578 to savannas. Model inversion studies have shown EC datasets give significant constraint
579 to predictions of NPP, however extra ancillary data that is informative of other
580 underlying processes was required to further constrain uncertainty (Haverd et al., 2013;
581 Keenan et al., 2012). Here, we suggest how each of the three critical savanna processes
582 highlighted in this paper can potentially be tested in addition to EC datasets. Satellite
583 derived estimates of remotely sensed near-surface reflectance (Ma et al., 2013; Ryu et
584 al., 2010b) and digital imagery from 'PhenoCams' (Moore et al., 2016a; Sonnentag et al.,
585 2012), provide a good resource for testing simulated phenology, particularly the 'green-
586 up' and 'brown-down' phases. Additionally, Advanced Very High Resolution Radiometer

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587 (AVHRR) data can provide 'burnt area' maps that quantify the frequency of fire events,
588 which can inform the probability of occurrence in simulated fire-dynamics. Above- and
589 belowground carbon inventory studies (Chen et al., 2003; Kgope et al., 2010) provide
590 highly valuable sources information in how plants allocate their resources for growth,
591 which can test the efficacy of TBM allocation scheme. Excavation studies that quantify
592 savanna tree root-systems (Chen et al., 2004) and soil-moisture probes installed to
593 greater depths (> 2 m) are informative about the evolution of the soil-root zone over
594 time, and such data may be critical to understanding whether current root-water
595 extraction schemes in TBMs are capable of simulating the dry season response of
596 savanna tree species (Whitley et al., 2015). Finally, localised observations of plant traits
597 such leaf-mass per area, stomatal conductance, tree height, etc. are needed to inform a
598 better parameterisation of savanna specific PFTs (Cernusak et al., 2011). Given that
599 there are many interacting effects occurring in savannas, an integration of multiple data
600 sources is therefore necessary for a more complete evaluation of how well TBMs
601 perform in this environment.

602

603 *3.2 Model evaluation and benchmarking*

604 Multiple dynamic processes drive savanna structure and function, and an understanding
605 of the causes and reasons for why TBMs systematically misrepresent this ecosystem is
606 paramount to future development. Consequently, a complete diagnostic evaluation of
607 model performance in savanna ecosystems requires more than just simple model-model
608 and model-data comparisons where 'good performance' is determined from a score in a
609 given metric (e.g. a high correlation between observed and predicted values). Instead
610 evaluation should also consider parsimony, physical representativeness and 'out-of-
611 sample' capability of the model itself (Abramowitz et al., 2008). The Protocol for the
612 Analysis of Land-Surface models (PALS; http://www.pals.unsw.edu.au/) offers such a
613 formalism, using standardised experiments to benchmark TBMs in terms of how well
614 they should be expected to perform, based on their complexity and the information used
615 to drive them (Abramowitz, 2012). In brief, PALS uses a set of empirical benchmarks to
616 fulfil the role of an arbitrary TBM of increasing complexity by quantifying the amount of
617 information in the meteorological forcing useful to reproduce water, carbon and energy
618 exchange. This gives a point of reference to measure at what level of complexity a TBM
619 is performing, by comparison of the statistical performance between model and
620 benchmark (Best et al., 2015). For example, we can assess whether a sophisticated,

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state-of-the-art DGVM can outperform a simple linear regression against shortwave irradiance (SW) at predicting GPP. If the outcome of this test were negative, then this may suggest that the model does not capture the sensitivity of GPP to SW accurately, flagging it as a priority for investigation and development. The important distinction to make with the benchmarks is that they have no internal state variables such as soil moisture and temperature, nor any knowledge of vegetation or soil properties; they represent a purely instantaneous response to the meteorological forcing (Abramowitz et al., 2008). A direct application of this protocol was presented by Whitley et al. (2015) to assess the predictive capability of TBMs in savanna ecosystems by comparing model outputs to 3 simple empirical benchmarks. In this study the authors used 6 calibrated TBMs to predict ecosystem latent energy and GPP at five savanna sites along the NATT, and found that in almost all cases the LSMs could perform only as well as a multiple linear regression against SW, temperature and vapour pressure deficit (Fig 7). While an additional assessment of other outputs is required, the study highlighted that there are likely systematic misrepresentations of simulated phenology and root-water access in some of these models (Whitley et al., 2015). This is the first assessment of its kind for investigating how well savanna dynamics are captured by modern TBMs, and implies that without further development TBMs may have limited scope as investigative tools for future projections of savanna ecosystems.

4. Conclusion

There is a large degree of uncertainty as to what impact climate change may have on the structure and function of savanna ecosystems given their complex interaction with climate. Projected higher temperatures and rainfall variability, potentially promoting more frequent fires, could favour C_4 grasses in mesic savanna, while drier conditions are expected to increase tree mortality in semi-arid savanna. Conversely, increases to atmospheric CO_2 are expected to favour C_3 trees, reflecting woody encroachment that is already observed in many savannas globally (Donohue et al., 2009). Climate change therefore has the potential to alter the carbon balance, which may have major feedbacks on global climate and biogeochemical cycling. Because TBMs are the only interpreter of vegetation dynamics available to us that can reconcile the combination of effects induced by climate change, their predictive capability at representing savanna dynamics is of significant importance (Scheiter and Higgins, 2009). For TBMs to have the necessary skill required to simulate savannas under both present and future climate,

Biogeosciences Discuss., doi:10.5194/bg-2016-190, 2016
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model development must be concentrated towards more adequate representations of phenology, root-water uptake, and disturbance dynamics, notably fires. We outline our recommendations below in these areas:

(1) Phenology: A dynamic representation of how leaf area responds to seasonally changing environment conditions, such that it becomes an emergent property of the coupled dynamics of weather and ecosystem function.

(2) Root-water uptake: Rooting depth and root distribution profiles that represent the contrasting strategies of trees and seasonal grasses, including their temporal dynamics. Additionally, root-water extraction schemes that can dynamically respond to the wetting and drying of the soil over time, accessing soil-water from where it is sustainably available rather than where the highest density of root biomass occurs.

(3) Disturbances: The role of disturbance (ubiquitous to all savannas) in keeping savanna systems open needs to be accounted for in models. Models need to represent the dynamic processes that capture the effect of fire on savanna composition, particularly in suppressing woody growth. Additionally, recovery periods whether through fire (re-sprouting) or cyclones (re-establishment) should also be considered given the dynamic influence these events have on the long-term carbon balance of savannas.

In addition to the recommended areas for TBM development above, we also stress that any improvements made in the representation of the above processes must be followed with a more complete evaluation and benchmarking of TBMs that considers multiple data sources in order to better constrain model uncertainty. We have highlighted that EC systems provide an unparalleled source of data for testing the predictive capability of TBMs at simulating water and carbon exchange in savannas. The role of regional flux communities, such as the OzFlux network (Beringer et al., 2016), will be to advance applications of EC systems that target savanna characteristics specifically. Indeed, more studies are needed that measure overstorey and understorey turbulent fluxes (Moore et al., 2016b), given their ability to quantify the contribution of co-dominant tree and grass functional types. Additionally, a greater use of ecological transects as tools for model evaluation are needed to quantify the ability of TBMs to simulate savanna behaviour over changing floristic structure and climate (Hutley et al., 2011). However, additional ecological and physiological measurements are also needed to test modelled

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representations of root-zone water dynamics, carbon allocation and growth, phenology and the recovery of vegetation after major disturbance events (fire and cyclones); dynamic processes that cannot be verified by EC datasets alone. Facilities such as the Australian Super Site Network (Karan et al., 2016) run by the Terrestrial Ecosystem Research Network (TERN) will be critical to the collection of ecophysiological information that can inform how savanna dynamics are represented in TBMs.

Finally, we outline that future model experiments and inter-comparison studies that leverage EC and ecophysiological datasets should target each of the three previously mentioned processes individually. These may include rooting depth and water extraction experiments that test the sensitivity of TBMs to the dry season transition period, or fire management studies that investigate how the floristic structure in TBMs responds to variable fire frequency. Furthermore, such studies must also be conducted for savanna sites that have well-established datasets to test the processes in question. For example, we expect that any study that attempts to test or improve the representation of fire dynamics in TBMs is to be conducted at a site that has a long-running EC record (given the variable return time of fire events) and a full suite of concurrent ecophysiological measurements that quantifies the response of vegetation under post-fire recovery. Improving how savanna ecosystems are represented by TBMs will likely encompass the consideration of additional processes that have not been mentioned here. However, we believe that by identifying these processes as the cause for degraded model performance in this ecosystem, a roadmap for future development can be constructed that leverages the availability of rich datasets and current state-of-knowledge.

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727

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Biogeosciences Discuss., doi:10.5194/bg-2016-190, 2016
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Figure Captions:

Figure 1: Global maps of (a) mean annual temperature and (b) mean annual rainfall for the period 1901 to 2015, determined from the CRU TS v. 3.23 dataset (Harris et al., 2014). The dataset has been clipped to the eco-floristic regions that approximate the global extent of savannas using the following plant functional types: tropical moist deciduous forest, tropical dry forest, subtropical dry forest and tropical shrubland (Ruesch and Gibbs, 2008).

Figure 2: Predicted changes to aboveground biomass between 2012 and 2100 for the Australian savanna region following three scenarios of projected rainfall seasonality according to IPCC SRES A1B (IPCC, 2007). The simulations were conducted using an adaptive Dynamic Global Vegetation Model (aDGVM) shows predicted changes to (a) present day aboveground biomass, when (b) rainfall seasonality does not change, (c) rainfall seasonality increases, and (d) rainfall seasonality decreases. In all cases, the aboveground biomass of the Australian savanna region increases, with the magnitude of change determined by the degree of seasonality. Reprinted with permission from Scheiter et al. (2015).

Figure 3: Representation of how changes to (a) tree and grass phenology determines changes in (b) savanna gross primary productivity (GPP) for an Australian mesic savanna. Time-varying signals of tree and grass LAI (a) are determined from a MODIS bulk LAI product using the method of Donohue et al. (2009), and are prescribed as inputs to the Soil-Plant-Atmosphere (SPA) model to predict separate tree and grass GPP. Data and model outputs are from Whitley et al. (2015) (*this issue*).

Figure 4: Simulated differences in total ecosystem latent energy (LE) and the resultant evolution of soil moisture content through the soil profile over time for a mesic Australian savanna site. Simulations were conducted using two different terrestrial biosphere models (TBMs) that use different root-water extraction schemes. The top panel (a) shows outputs of savanna water flux using the Community Atmosphere Biosphere Land-surface Exchange (CABLE) model, where the density of the fine-root biomass weights soil-water extraction. The bottom panel (b) shows outputs of savanna water flux from the Soil-Plant-Atmosphere (SPA) model, where soil-water is dynamically extracted from where it sustainably available. Model outputs are from Whitley et al. (2015) (*this issue*).

Figure 5: The nonlinear response of net ecosystem productivity (NEP) as the canopy

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regenerates after a fire event in 2003 at an Australian mesic savanna site. Fire disturbance of a sufficient intensity suppresses productivity, pushing the savanna state from sink to source over a period of 70 days at this site, as the rate of respiration exceeds the rate of assimilation due to resprouting costs. Empirical models created using an artificial neural network (NN) describe the 'UnBurnt' and 'Burnt' canopy NEP responses over the same period, and their difference estimates the loss of canopy productivity as a consequence of fire. Reprinted with permission from Beringer et al. (2007).

Figure 6: Smoothed (10-day running mean) time-series of understorey (red), overstorey (green) and total ecosystem (red) gross primary productivity (GPP) for a mesic savanna site in northern Australia. Rainfall is represented as black bars. Negative and positive signs represent the savanna state as a carbon source or sink respectively, and orange arrows depict the occurrence of fire events. Data products for total ecosystem and understorey GPP are inferred from observations of net ecosystem exchange using eddy-covariance towers at heights of 23 m and 5 m respectively. Overstorey GPP is determined as the difference between the ecosystem and the understorey. Reprinted with permission from Moore et al. (2016b) (*this issue*).

Figure 7: Rank plot showing the average performance of 6 terrestrial biosphere models (TBMs) across the North Australian Tropical Transect (NATT). The closer a model's rank is to 1 the better its performance is at predicting latent energy (LE) and gross primary productivity (GPP). Empirical benchmarks representing increasing levels of complexity (emp1 < emp2 < emp3) are represented as grey lines, and coloured lines denote each model. The lines have no scientific value and are used for visual purposes only. Benchmarking and model evaluation data are from Whitley et al. (2015) (*this issue*).

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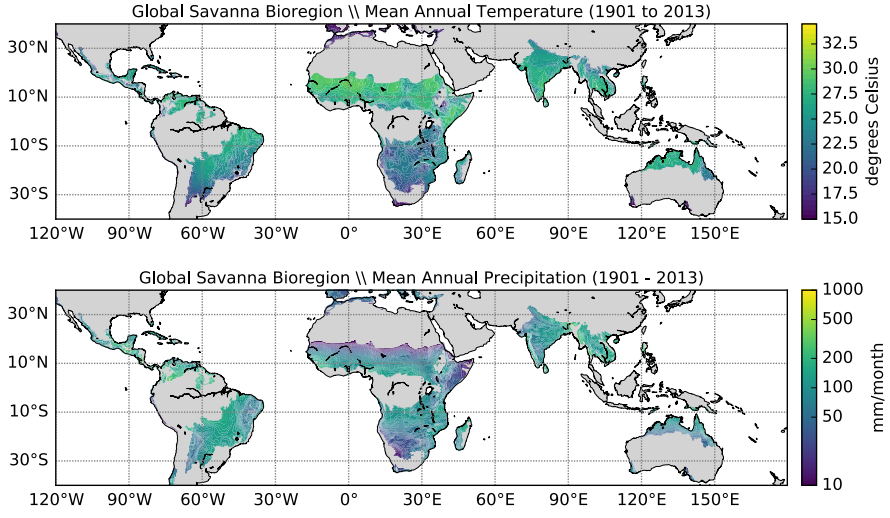

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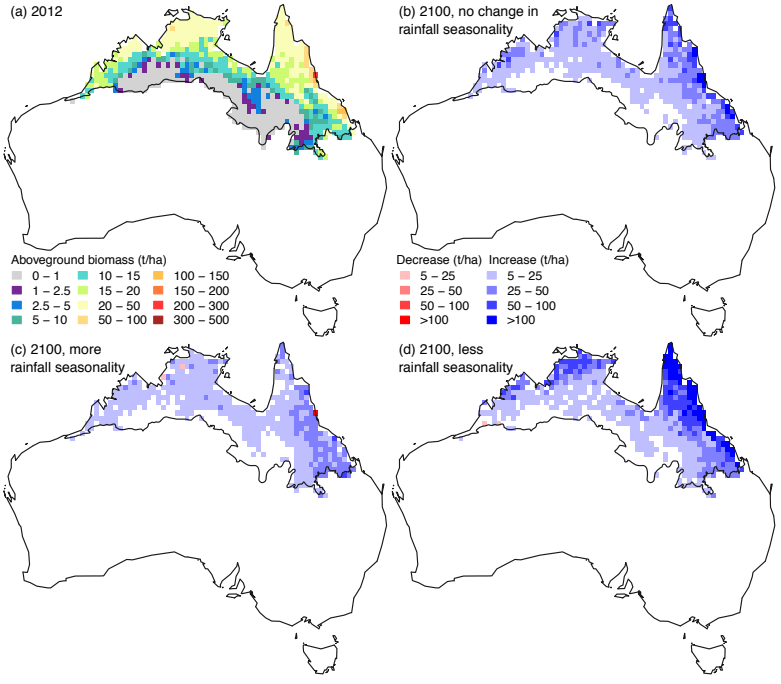

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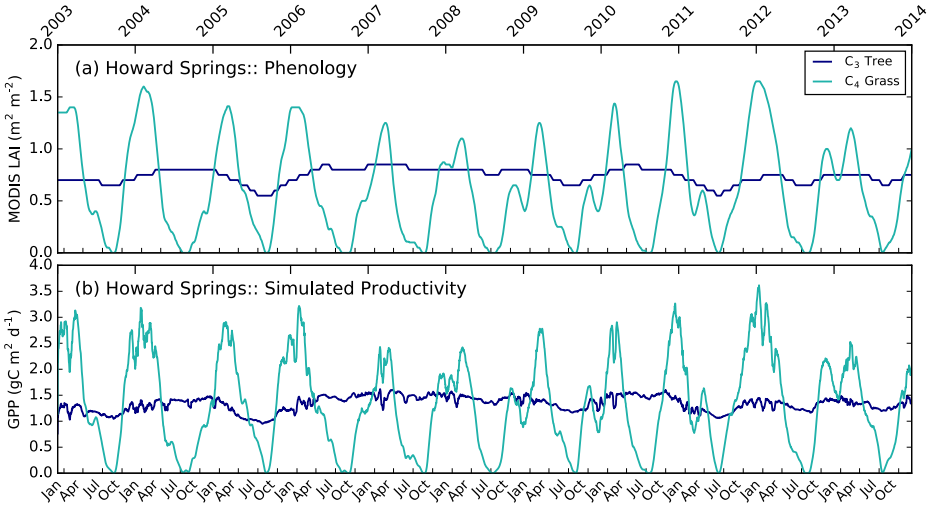

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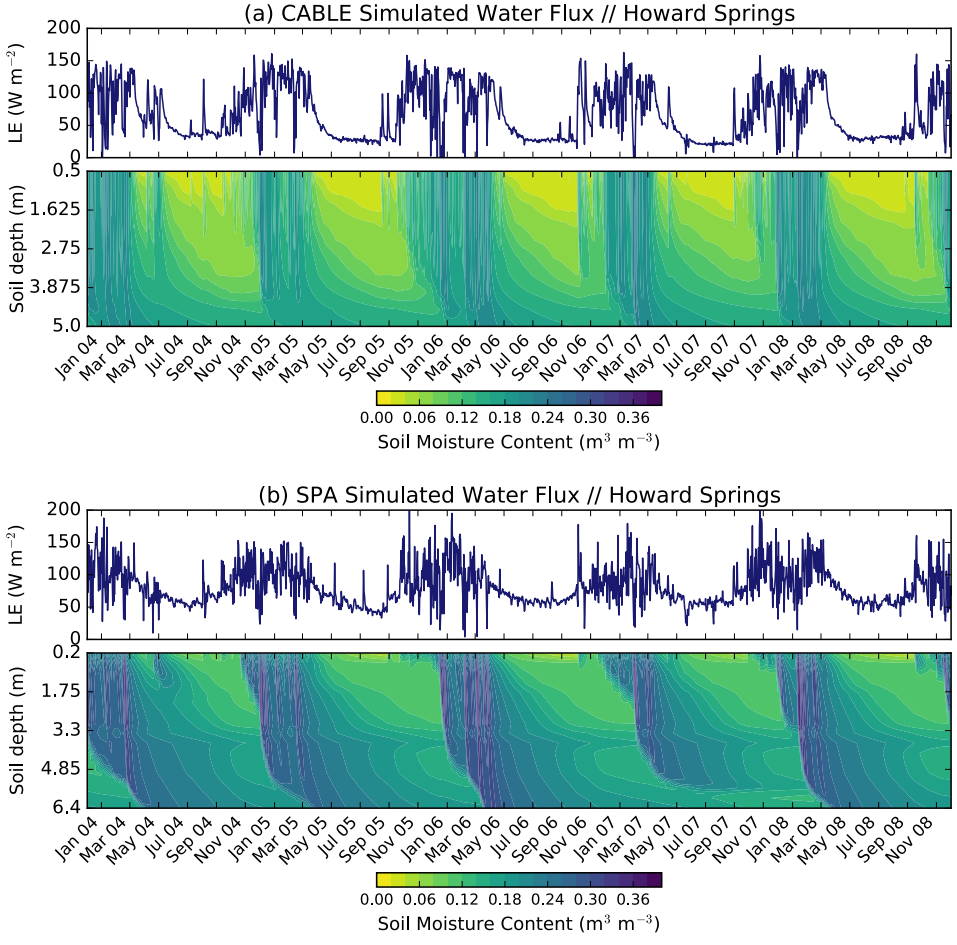

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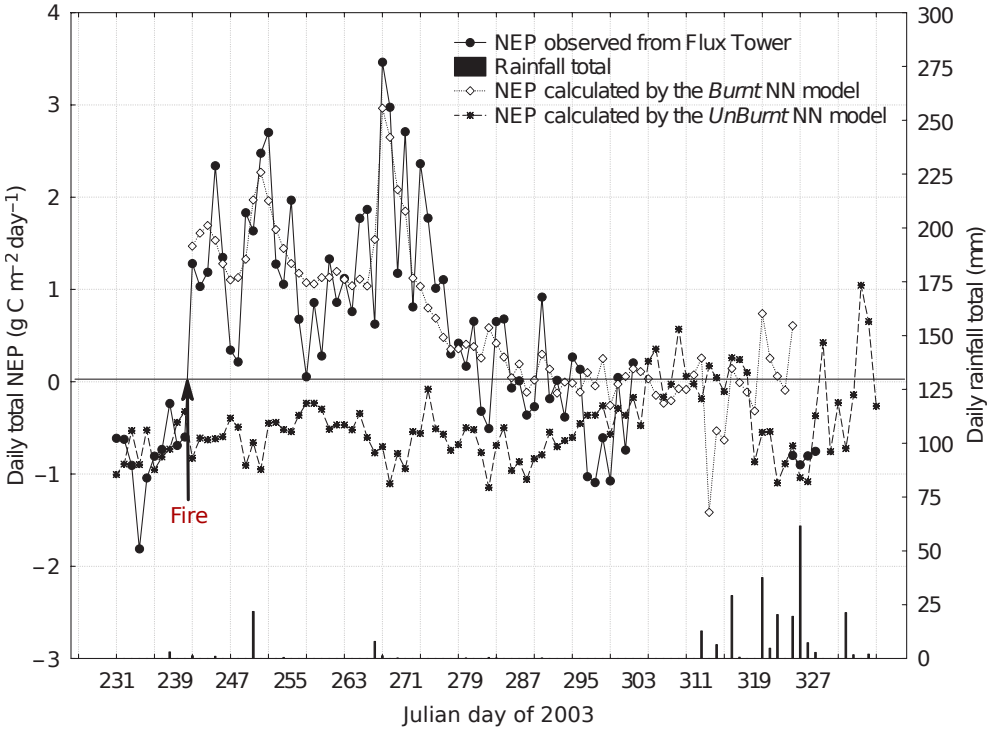

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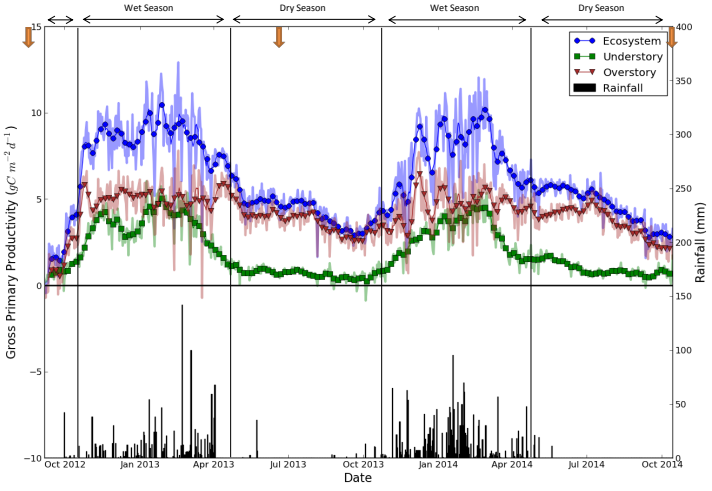

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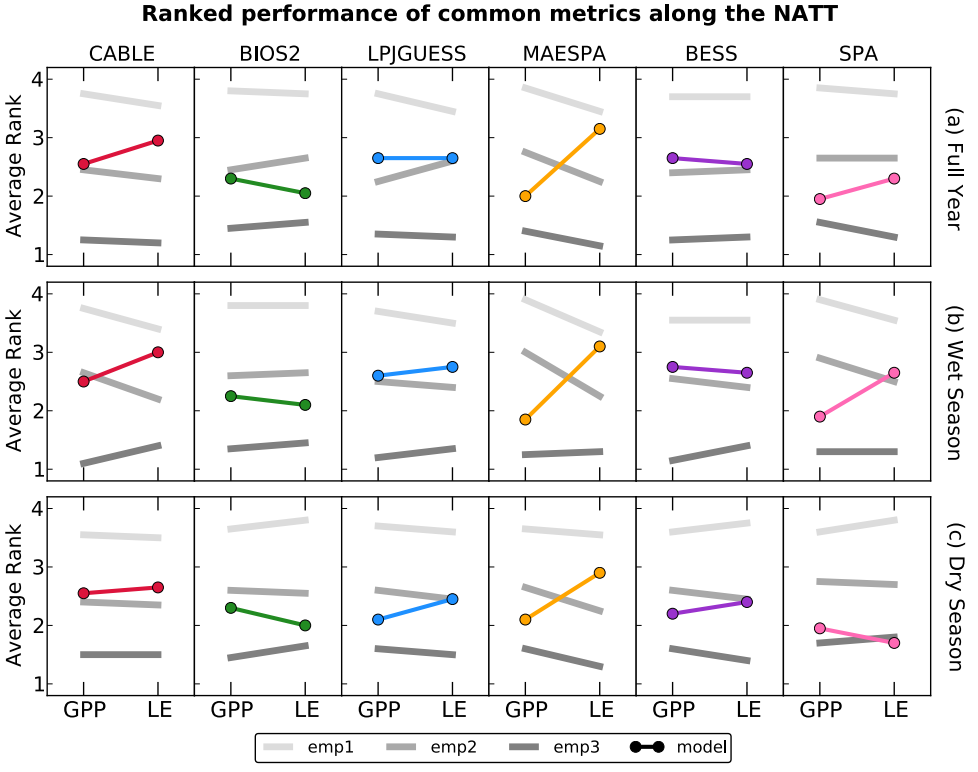

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