

Author responses to reviewer and editor comments for manuscript submission BG-2016-190 r2

Below we outline our responses to the comments from reviewers for our paper entitled: **“Challenges and opportunities in modelling savanna ecosystems.”** **We include the tracked changes manuscript at the end of this PDF.**

We thank all reviewers for their valuable feedback and insights. Both reviewers #1 and #2 provided only minor corrections, which we are largely in agreement with and have consequently adjusted the text of the paper to reflect this. Reviewer #3 has provided valuable and extensive commentary and insight on savanna ecology that is appreciated and along with recommendations from the editor we have substantially added a strong theoretical background to our review. We feel now that the paper is comprehensive and will appeal to a wider audience thanks to the reviewer’s suggestions. At the same time we use the introductory sections (1 and 2) to cover the nature of savanna and many of the features that differentiate them globally. This paper builds on previous work (this special issue: Whitley et al. (2016)) that highlighted a set of processes related to savanna dynamics that are currently deficient in TBMs. In this paper, we continue to focus our discussion on how these processes are currently misrepresented (or absent) in TBMs and offer recommendations on how they could be developed to improve the predictive capability of such models in simulating the turbulent fluxes of savannas.

We have primarily focused discussion on three dynamic processes: i) phenology, ii) root water uptake and iii) disturbance (particularly fire), which are the first-order controls on savanna water and carbon exchange and should therefore be critical areas of future model development. Reviewer #3 raises issues regarding the lack of discussion relating to ecological processes such as tree-grass demographics, canopy structure, pulse responses to rainfall, etc. However, they could be seen as emergent behaviour resulting from the dynamical processes highlighted in this paper, and an expanded discussion of these issues could distract from what we consider the primary deficiencies that TBMs currently face in simulating savanna ecosystems. Furthermore, not all TBMs have the capability (or goal) of simulating complex vegetation dynamics. This is not to say these ecological properties of savannas are not important, on the contrary we believe that TBMs need to be able to replicate these effects, but this would be a consequent step after the first order processes we have highlighted have been improved. Nevertheless, we have included most of reviewer #3’s suggestions. We also wish to stress that reviewer #3 has raised important issues ubiquitous within savanna ecology that could serve as a basis for future work and would serve as natural progression to what we have presented here.

Reviewer comments are numbered below, where we have answered each to the best of our ability and made the appropriate changes where necessary in our manuscript. Once again, we would like to thank the reviewers and the editor for taking the time to examine this work and provide valuable feedback.

L51: Remove “current-generation” as one might read this that previous generations were immune this challenge.

Author response: Done.

L60: Remove “,namely”

Author response: Done.

L67: Try “the effects”

Author response: Done.

L78: Something is off here as “and provide important in providing ecosystem services,…” makes no sense.

Author response: Has been corrected to: “... and **are** important in providing ecosystem services...”

L84: Try “creates”

Author response: “and create demographic ...” has been changed to “that create demographic...”

L88: The antecedent of “it” is unclear, use “fire” again here.

Author response: Done

L96: I think you want “confounding” here?

Author response: Done

L102: Try “the current generation of TBMs has...”

Author response: Done

L126: I think you “proceed” given that you use present tense throughout here.

Author response: Done

L184: Remove the first “region”

Author response: Done

L189: Replace “For the” with “As an”

Author response: Done

L190: Try “to emerge”

Author response: Done

L207: Replace “...occupy the top ranks among terrestrial biomes, together contributing c. 30%” with “...contribute c. 30%”

Author response: Done

L243: Try “are”

Author response: Done

L246: “until”? Until what?

Author response: Sentence is complete now: “...until *later in this paper.*”

L268: Try “are”

Author response: Done

L310: Try “partition” and “LAI.”

Author response: Done

L335: Remove comma after “advances”. Also, I must state that the paper needs a good final proofreading. I have pointed out several (albeit minor) issues but have certainly not caught all the comma issues, and sundry other language faux pas.

Author response: Done, and furthermore we have gone through the text again to identify other typos and grammatical issues.

L567: What is NATT? Maybe define in L560 above.

Author response: The acronym has now been correctly added after the definition given at the beginning of the paragraph.

L572: Regarding your “as they cannot capture. . .” comment. I would dispute this especially as you invoke the space for time argument above. FLUXNET can quite do the same thing.

Author response: The reviewer is quite correct, and we have qualified this statement to say: “as they cannot *completely* capture. . .”

L575: Citations are off.

Author response: Fixed

L591: I appreciate that the authors can’t solve all these data limitations. But the “such data may be critical” comment is an interesting one, especially in the context of rather dear excavation studies. I’d like more detail.

How many such excavation studies with what sampling design frame do you envision? That is, how do we move forward as a community to actually get the right data?

Author response: Root excavation studies as mentioned was only given here in a general sense as an example, however we see the reviewers point that such field campaigns are complex and expensive (in cost, time and labour), such that this warrants a further expansion of detail. We have therefore added the following lines to qualify our statement not just for root excavations, but also for all ecological trait information:

“We recommend that future EC studies, particularly along transects as mentioned above, should include intensive field campaigns that are targeted towards a more complete characterisation of the site. This would include key flux measurements (e.g. sapflow, stomatal conductance, leaf water potentials, deep soil water measurements, root excavations and the collection of plant trait data (e.g. leaf mass per area, capacitance, Rubisco activity, etc.) within the footprint of an EC tower. Collaborative research networks, such as TERN (Terrestrial Ecosystem Research Network), NEON (National Ecological Observatory Network) and SAEON (South African Environmental Observation Network) that have the resources and infrastructure to conduct such campaigns will be instrumental to meet these demands for more observational data.”

L603: In this section I would encourage the authors to cite some other developments here, e.g., ILAMB, that certainly hold promise to improve benchmarking. PALS is well and good but there is more afoot.

Author response: We agree with the reviewer and have incorporated mention of ILAMB and other model intercomparison projects (e.g. PILPS, C4MIP) into this part of the discussion.

L692: Might NEON be a good idea? I must say I’ve noted a rather Australian-centric view of the literature. That is not bad, particularly in an OzFLux special issue, but again there are other things afoot and this is a review paper. And savannas do not exist solely in Australia.

Author response: We have now included mention of NEON as well as SAEON at the end of Section 3.1 (see response to comment on L591)

L703: I am confused on the juxtaposition of long-term EC sites and fire return. A fire typically has adverse consequences for a FLUXNET installation. Are you advocating pre- and post-fire EC measurements?

Author response: Fire is a frequent occurrence in savanna and has a major impact on fluxes and we propose that savanna FLUXNET installations quantify the effects of fire as per Beringer et al. (2007) and as was mentioned in Section 2.3. In this regard we are advocating pre- and post-fire measurements, as this would allow TBMs (those that include the simulation of fire) to be tested on whether they have the capability to simulate the nonlinear response of the canopy (due to scorching and reduced surface albedo) during the post-fire recovery period.

My minor comments are:

Comment 1: I found the description of additional dataset (ancillary and remote sensing data) which can be used to test the ecological model a little bit unclear. However, this part can be easily improved by the authors by adding more details on the **variables** which can be extrapolated from these datasets at the end of the session on “Datasets to inform model development” (P18, L583).

Author response: We have now made reference to common model parameters that would benefit from the collection of specific environmental information. This text is quoted below as:

“Digital soil atlases also provide an excellent resource in parameterising simulated soil profiles (e.g. Isbell, 2002; Sanchez et al., 2009). However, the spatial resolution of these data products can be coarser than the operating resolution of many TBMs, such that site-level measurements should be used when possible. Excavation studies that quantify savanna tree root-systems (Chen et al., 2004) and soil-moisture probes installed at greater depths (> 2 m) are informative about the evolution of the soil-root zone over time (e.g. surface root density, root depth), and such data may be critical to understanding whether current root-water extraction schemes in TBMs are capable of simulating the dry season response of savanna tree species (Whitley et al., 2015). Finally, localised observations of plant traits such leaf-mass per area, leaf capacitance, tree height, etc. are needed to inform a better parameterisation of savanna specific PFTs (Cernusak et al., 2011). For example, specific leaf-level information such as Rubisco activity (V_{cmax}) and RuPB regeneration (J_{max}) for both C_3 and C_4 plants are critically needed to inform the Farquhar leaf photosynthesis models (Farquhar et al., 1980), while information on g_s and leaf water potential (Ψ_{leaf}) are important in parameterising the many stomatal conductance models used in TBMs (Ball et al., 1987; Medlyn et al., 2011; Williams et al., 1996). Leaf capacitance and water potential data are also critically important in characterising model sensitivity to drought (Williams et al., 2001), but this information is severely lacking for savannas.”

Comment 2: A short discussion on the scale mismatch between these datasets (including EC) and the model grid should be added in the “Model evaluation and benchmarking”.

Author response: We agree that the intention of almost all TBMs is to be run at the global scale does not match the scale at which validation occurs. Model evaluation of TBMs occurs at the ecosystem scale (a moderate resolution of ~ 1 km), commensurate with resolution of flux tower data and remotely sensed data products (e.g. Best et al., 2015; Blyth et al., 2010). Consequently, there is little scale mismatch between what is used to run (inputs) and validate (outputs) the models.

Specific comments

P5, L139: Please substitute “ecosystem types” with “ecoclimate regions”

Author response: Done

P7, L183: Please define the two acronyms: LSM and DGVM

Author response: Done

P9, L252: This should be section “3” and not section “2”. Please check and re-number, where needed, all sections

Author response: Done. All section numbering has been updated accordingly.

P9, L252: Please eliminate “:” and the end of the title

Author response: Done

P17, L524: Please eliminate “ground-based”

Author response: Done

P17, L531-534: This sentence is not very clear for people that don’t know very well how models and the eddy covariance system work. Please rephrase

Author response: We have changed the sentence in accordance with this request:

“Turbulent fluxes measured by EC systems that include net ecosystem exchange and latent and sensible heat are common model outputs, such that this information is commonly used to validate TBMs. Local meteorological forcing (e.g. short-wave irradiance; SW, air temperature, rainfall, etc.) that is concurrently measured with the turbulent fluxes by other instruments (rainfall and temperature gauges, radiation sensors, etc.) are common model inputs and are used to drive TBMs.”

P17, L534: I would like to use “ecosystem scale” instead of “spatial scale” to better give the idea of the spatial representativeness of EC data which are limited to the footprint area

Author response: Done

P17, L534: Please refer to Aubinet et al., 2012

Aubinet, M., Vesala, T., and Papale, D.: Eddy Covariance – A Practical Guide to Measurement and Data Analysis, Springer, ISBN: 978-94-007-2351-1, 2012

Author response: Done

P17, L535: Please add reference: Balzarolo et al., 2014; doi:10.5194/bg-11-2661-2014

Author response: Done

P18, L567: Please explain NATT^[1]_{SEP} P18, L583: Please revise this sentence, which is not very clear

Author response: Definition has now been inserted, and sentence now reads as:

“A recent model intercomparison study by Whitley et al. (2015) used turbulent flux observations sampled along the NATT to evaluate a set of six TBMs, and documented only poor to moderate performance for those savanna sites.”

P18, L573: Are you referring to long-term temporal predictions?

Author response: No, what we are alluding to in this sentence is that eddy-covariance systems may not have been running for long enough (i.e. the sampling period of the time-series) at a site to pick up any long-term structural changes (e.g. such as those caused by cyclones, or large fires). If a model is attempting to simulate a demographic shift in vegetation (i.e. the tree/grass ratio) then longer term datasets such as those from satellite would be more useful in validating this prediction.

P21, L680: Please refer to Fluxnet (Baldocchi et al., 2001)

Baldocchi, D. D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, J. W., Oechel, W., Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities, *B. Am. Meteorol. Soc.*, 82, 2415–2435, 2001.

Author response: Done

P22, L693: Please also refer to NEON (National Ecological Observatory Network)

Author response: Done

Figure 1: please add (a) and (b) in the figure and check the appropriate units to the y-axis (mean annual rainfall is correct in mm/month?)

Author response: Done, the units are correct but we have rescaled the values to be mm/year.

Figure 2: it is not very clear the use of “2012” and “2011” in the legend. Please change or explain in the caption.

Author response: Done.

The reviewer points that we have omitted “some important theory and themes in savanna ecology, and misrepresents some of the broad geographic context of global savannas”. Given the previous aims we consciously did not attempt an ‘ecological’ review that could be a distraction from the main paper. However, given the opportunity to review the paper we have now provided a clear overview of the global savanna ecology and this has been included in the text. We have added considerable material and therefore do not include the specific changes below but rather show them changes and additions as track changes in the supplied manuscript.

Note: we have removed the listing of references for brevity, but can be referred to in the reviewers original commentary.

Comment 0: Regarding Root Water Uptake: This is a worthwhile focus for improvements of TBMs but the authors have a rather specific read on the relevant literature. A few key citations I’d recommend are below, offering expanded perspectives on how to proceed with improving root water uptake in TBMs. Key considerations go beyond just prescribing rooting depth but also: dynamic uptake in response to soil water availability in the vertical profile, adaptive adjustments of the root distributions in response to water availability over seasonal and multi-year timescales, hydraulic redistribution along pressure gradients and via roots, soil water limitation function limiting productivity and evapotranspiration and associated water demand and water potential along the root to leaf and atmosphere continuum. I, too, caution against weighting root water up- take by fine root distribution because many plants are able to sustain water uptake and transpiration from deep taproots that access the saturated zone or deep unsaturated zone water sources even when fine roots (all concentrated near the surface) are in very dry soil layers. Furthermore, plant capacitance (storage) is important for accurately representing plant water potential, especially when water supply is limited or when root-to-leaf transport resistances inhibit water delivery to the site of transpiration at the leaf.

Author response: We agree that other belowground processes the reviewer has mentioned are critical to simulating integrated representation of the soil-vegetation-atmospheric continuum (SVAC). Section 2.2 on root-water access and uptake does cover most of the processes the reviewer has mentioned, particularly dynamic uptake. We have also added a paragraph to capture the other dynamic ecological processes that could be important along with additional material as found in the track changes manuscript. It should be said that the aim of this section is to argue for a better representation of root water access in and around the rhizosphere, as this describes the supply end of the SVAC. Consequently it acts as a first order control for savanna water and carbon exchange in the dry season, which has not been modelled well in past studies. Hence we have specifically focused our discussion on this limitation, and that the modelling community could easily address this. Regarding plant capacitance, we agree that this is a critical parameter towards vegetation drought responses and have amended the second sentence of the first paragraph of Section 2.2 to reflect this.

“For seasonally dry climates (a fundamental characteristic of savanna ecoclimatic regions), productivity is primarily limited by dry season water-availability (Kanniah et al., 2010), which is largely determined by plant regulation of water transport (through leaf stomatal conductance and stem capacitance) and the root zone water

storage capacity and access (distribution of fine root biomass)."

Comment 1: A host of other processes of importance and interest in savannas are missed. For example, pulse response processes, stand-scale vegetation composition, plant-scale competitive interactions, stand-scale vegetation structure, landscape patterning of vegetation, nutrient cycling and interactions with herbivores, and more are all given little if any attention. Arguably many of those processes are important for representing savanna-atmosphere interactions, and for assessing savanna responses to global change factors. Given that this paper is intended to be a review of key processes that need to be considered to accurately model savanna ecological responses to global change factors, I would encourage additional discussion of these missed processes and their implications and importance for the stated aims.

Author response: We agree that these are important processes in savanna ecology, however and we have taken the opportunity to mention these throughout the manuscript. We also make a comment that the *stand-scale vegetation composition, plant-scale competitive interactions, stand-scale vegetation structure, etc.* can be seen as emergent properties of the three dynamic processes that our paper focuses on. Given that the discussion is focussed on the first order controls on savanna water and carbon exchange and how these are likely misrepresented (or absent) from modern TBMs we concentrate on how TBMs can better simulate savanna intra- and interspecies competition, canopy structure, etc. the 3 first-order dynamic processes as a priority..

Comment 2: Savanna ecologists would be underwhelmed by the three dynamic processes that are highlighted: phenology, root water uptake, and fire, given that these have long been the focus of their work going back many decades (e.g. Walter 1973). For example, the seminal work by Brian Walker (1981) is surprisingly absent from the present review even though this was foundational work identifying the importance of root zone separation and differential uptake zones for grass/herbaceous and woody PFTs in the savanna matrix. This was nicely tested in the Scholes and Walker (1993) book which is also missed. It is surprising that competitive interactions and differential resource access are not noted here, nor differential response of PFTs and species to single and multifactor drivers of CO₂, drought, warming, and increasing VPD. While I agree that the three features highlighted in the present paper are essential and yet poorly represented (if at all) in TBMs, such models will still not be up to the task of predicting responses to global changes without representation of a host of other factors.

Author response: We are fully aware of the decades of ecological research on the three dynamic processes that are highlighted in our review section; phenology, root water uptake, and fire, but these have been poorly captured in TBMs to date, and this is the focus of this paper. Our goal is not to provide a review of determinants of savanna structure and function but to target the failing of TBMs. However, we have also added material that points to the many other dynamic processes that could be influential.

Comment 3: Grazing and browsing are of central importance in many of the world's savannas, strongly influencing vegetation cover, loss of productivity and biomass, species composition, and affecting site fertility but this driver is hardly mentioned, receiving just one or two sentences. A bit more on this subject would seem warranted for such a review.

Author response: We certainly agree that grazing and browsing are one of many important factors that modulate the savanna structure and state. However, animals are not a modelled process in TBMs and this paper is focussed on simulated processes that control savanna water and carbon exchange. Nevertheless, we have added material in the background to global savannas.

Comment 4: Corresponding to the above, a nod to the alternate stable states literature is missing here, including Walker '81, Noy-Meir 1975, and others mentioned below.

Author response: We have now added a section describing these meta-stable systems into the main text.

Comment 5: Discussion of the global context and diversity of savanna attributes and strategies is lacking and in some ways misleading. Section 2.1, particularly Line 169+: The language here misrepresents the growth and longevity strategies of woody plants in Africa. Many of the woody species in at least southern Africa do indeed have deep roots but groundwater is deep (probably deeper than in much of Australia) so there is less potential to rely on near surface (<10 m) water sources. The Archibald and Scholes '97 paper does not mention roots once, and says nothing about strategies of water access. The Higgins '11 paper also offers little on root water uptake. Both of those papers do indeed discuss and quantitatively document phenological dynamics, but neither indicates that the full woody component of southern African savannas is deciduous (indeed *Acacia* sp. often retain leaves consistently through the dry season). However both represent only southern African ecosystems at best (really, Kruger Park). Yet this statement is as grandiose as generalizing from these studies to all African and South American savannas! That's stretching it a bit, no? A much broader literature must be invoked if the authors truly want to discuss geographic patterns of root water uptake, and diversity in savanna traits and properties. Furthermore, this must consider not just phenology but also water availability in the unsaturated and saturated zones, and not confuse mesic and arid savanna types. The present interpretation seems to conflate shallow groundwater availability or its absence with a difference in plant strategy. However, woody species of savannas around the world "favour a long-term strategy of conservative growth that is insured against an unpredictable climate", not just those in Australia. To include more on the global biogeography of savannas relevant to a modeling context I'd recommend some additional reading (and citation of) works in: Hill, Michael J. and Hanan, Niall P. eds (2011). *Ecosystem Function in Savannas: Measurement and Modeling at Landscape to Global Scales*. (CRC Press, Boca Raton, Florida) 559 pp.

Author response: We have now added material covering the global context and diversity of savanna

attributes and strategies found in the track changes document. We have also included citations from Bowman and Prior (2005), Lehmann et al. (2011, 2014) and Stevens et al. (2016) that support our argument that woody species among continents can be clustered as we have stated in the text. The Archibald and Scholes (1997) is a mistake and should be Scholes and Archer (1997), now corrected, while Higgins et al. (2011) has been removed given that it does not directly support our claims. We do agree that not all African woody species are shallow-rooted and have qualified the statement to read as:

“Canopies of the African and South American savanna regions are predominantly characterised by deciduous woody species that are in most cases (although not always) shallow-rooted and follow a short-term growth strategy that maximises productivity while environmental conditions are favourable”

We do not believe that expanding the discussion on global savanna attributes to cover every degree of separation of plant traits between and within continents benefits our argument on the 3 dynamics processes that we believe currently hamper TBM performance in savanna ecosystems. The primary point of this section is to highlight and provide context that these differences suggest that savannas cannot be lumped into some generalised group or plant functional type (PFT), but show clear distinctions. Rather, we argue that region specific PFTs will likely be required for good model performance in this ecosystem. However, this is not to say that the assignment of correct trait information is the answer to improved model performance in savannas, rather a better representation of phenology, root-water uptake and disturbance (fire) in TBMs is required to fill this gap.

Comment 6: The Pulse-Reserve paradigm in dryland ecology is noticeably absent from this review despite the well-known importance of rainfall pulses in organizing complex ecological and biophysical dynamics in water-limited environments. Many plant and ecosystem phenological dynamics are organized around rainfall pulses, including leaf-out and senescence, up- and down-regulation of productivity, respiration and decomposition bursts, reproduction and establishment events, and so forth. “Pulse” is not mentioned once in the current review.

Author response: We agree that the ecosystem response to rainfall pulses in arid climates is an important behaviour for TBMs to capture. We have now provided some references and links to the importance of pulse dynamics in the track changes version of the document. However, TBMs should have the capability to capture this response, and if not, it is likely not a missing mechanism per se, rather a lack of sensitivity. We have discussed issues related to this response in the sections on root-water uptake and phenology.

Comment 7: Section 3.1: Possibly also mention potential for additional measurements to inform root water uptake dynamics (maybe around L590): -experimental use of isotopes to trace root water uptake dynamics (see work of Todd Dawson’s lab for example). - standard field-measured sapflow and leaf gas exchange are surprisingly not mentioned but can be particularly useful when coupled with detailed soil moisture profile

measurements, where changes over time directly indicate the effects of water uptake. -weighing lysimeter studies, while very intensive, have also been used to detect whole plant uptake. -groundwater wells would also be enormously helpful and are so often missed in ecological and even hydrological studies in savannas (and other ecosystems), yet are critical for characterizing the availability and dynamics of deep water sources. - groundwater maps, where available, are low hanging fruit for incorporation into spatial applications of TBMs. - another key thing that is missing is detailed mapping of C3 and C4 vegetation types (grasses/herbaceous), and their separate phenologies. -remotely sensed surface temperature is another valuable constraint on ecosystem water status (I think Damian Bonal was working on this and published on it).

Author response: We have added many of the suggested edits. See the response to comment 1 of reviewer #2. In addition we have added the following into the section on “*Datasets to inform model development*”; Other useful approaches for elucidating how and where plants gain their water, include sap flow measurements (Zeppel et al., 2008), gas chambers (Hamel et al., 2015) and soil-plant-water experiments (Midwood et al., 1998). In addition, hydrogen and oxygen stable isotope ratios of water within plants provide new information on water sources, interactions between plant species and water use patterns under various conditions (see review by Yang et al. (2010)).

Comment 8: Conclusions go uncomfortably beyond what is supported in this paper and stray from the paper’s clear focus on how to improve TBM performance for savannas. For example:

“Projected higher temperatures and rainfall variability, potentially promoting more frequent fires, could favour C4 grasses in mesic savanna, while drier conditions are expected to increase tree mortality in semi-arid savanna. Conversely, increases to atmospheric CO2 are expected to favour C3 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.”

Author response: We have now deleted this text

Comment 9: Again, it is recommended that the authors expand the scope of highlights to also emphasize ecosystem structural and compositional dynamics that are of central importance to TBM processes: particularly differential resource acquisition (primarily water) and competitive interactions. E.g. around L694.. model and data efforts should also target those attributes of savannas. Perhaps the authors roll all of that into “phenology” but I’d argue that this is a mistake, where phenology is only one component of vegetation dynamics. The underlying competitive interactions, mortality and growth dynamics, and how these shift in response to a suite of climate, atmospheric compositional, soil fertility, land use and other global change factors could receive more attention in this review.

Author response: We refer back to our responses to comments 2 and 3, and maintain that what the reviewer is arguing for here is outside the scope of the paper’s aim. Differential resource acquisition, savanna structure

and composition could be seen as emergent properties of the 3 dynamic processes this paper is focussed on improving. Once these first-order processes are better represented, then a subsequent investigation could be conducted into savanna structure and composition. Representation of competitive interactions would require an entirely different level of model complexity, e.g. individual-based models, which is not the subject of this paper. Nevertheless, we do now acknowledge these in terms of future model development

“There is still great uncertainty in predicting the future of savanna biomes (Scheiter et al., 2015; Scheiter and Higgins, 2009) and improving how savanna ecosystems are represented by TBMs will likely encompass the consideration of additional processes that have not been mentioned here. This will no doubt include improved understanding of ecological theory that will lead to improvements in modelling ecosystem demographics and tree-grass interaction that will improve DGVMs.”

Some Details:

Why is root-water hyphenated? Do you mean ground-water or soil-water? Probably just drop the hyphen throughout.

Author response: We are referring to soil-water that is within the rhizosphere. The decision to hyphenate root-water is purely stylistic, following the style adopted in other topically related papers in the literature. We are happy to defer to the editor’s judgement on this.

Line 69+: not just “environmental conditions” but also biophysical and ecological conditions... that is, the ecosystem properties are themselves changing and this must be represented.

Author response: Done

Line 96: “confronting task” reword, unclear

Author response: Done

L100: “underperformed for savanna ecosystems” is too vague... what, specifically, lacks accuracy? “under” relative to what, other PFT or biome types, compared to data?

Author response: The term *underperformed* relates to statistical performance and refers to model error (difference between observation and prediction). This term is commonly used in the ecosystem modelling literature and references have been cited that go into this level of detail.

L105: “physical [and biological]”... most of these are not physical parameters.

Author response: We use the term physical in the context that they are not purely empirical or statistical; i.e. they are not arbitrary coefficients from a regression or polynomial equation.

References:

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Challenges and opportunities in modelling savanna ecosystems

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1 **Abstract**

2 The savanna complex is a highly diverse global biome that occurs within the seasonally
3 dry tropical to sub-tropical equatorial latitudes and are structurally and functionally
4 distinct from grasslands ~~or~~ and forests. Savannas are open-canopy environments that
5 encompass a broad demographic continuum, often characterised by a dynamically
6 changing dominance between C₃-tree and C₄-grass vegetation, where frequent
7 environmental disturbances such as fire modulates the balance between ephemeral and
8 perennial life forms. Climate change is projected to result in significant changes to the
9 savanna floristic structure, with increases to woody biomass expected through CO₂
10 fertilisation in mesic savannas and increased tree mortality expected through increased
11 rainfall interannual variability in xeric savannas. The complex interaction between
12 vegetation and climate that occurs in savannas has traditionally challenged ~~current-~~
13 ~~generation~~ terrestrial biosphere models (TBMs), which aim to simulate the interaction
14 between the atmosphere and the land-surface to predict responses of vegetation to
15 changing in environmental forcing. In this review, we examine whether TBMs are able to
16 adequately represent savanna dynamics and what implications potential deficiencies
17 may have for climate change projection scenarios that rely on these models. We start by
18 highlighting the defining characteristic traits and behaviours of savannas, how these
19 differ across continents, and how this information is (or is not) represented in the
20 structural framework of many TBMs. We highlight three dynamic processes that we
21 believe directly affect the water-use and productivity of the savanna system, ~~namely:~~
22 phenology; root-water access; and fire dynamics. Following this, we discuss how these
23 processes are represented in many current generation TBMs and whether they are
24 suitable for simulating savanna dynamics. Finally, we give an overview of how eddy-
25 covariance observations in combination with other data sources, can be used in model
26 benchmarking and inter-comparison frameworks to diagnose the performance of TBMs
27 in this environment and formulate roadmaps for future development. Our investigation
28 reveals that many TBMs systematically misrepresent phenology, the effects of fire and
29 root-water access (if they are considered at all) and that these should be critical areas
30 for future development. Furthermore, such processes must not be static (i.e. prescribed
31 behaviour), but be capable of responding to the changing environmental conditions in
32 order to emulate the dynamic behaviour of savannas. Without such developments,
33 however, TBMs will have limited predictive capability in making the critical projections
34 needed to understand how savannas will respond to future global change.

35 .

36 1 Introduction

37 Savanna ecosystems are a diverse and complex biome covering approximately 15 to
38 20% of the global terrestrial surface (Scholes and Hall, 1996) and ~~provide~~ are important
39 in providing ecosystem services, that maintain biodiversity and support the majority of
40 the global livestock (Van Der Werf et al., 2008). Savannas are characterised by a
41 multifaceted strata of vegetation, where an open C₃-woody canopy of trees and shrubs
42 overlies a continuous C₄-grass ~~layer~~ understorey and occur in regions that experience a
43 seasonal wet-dry climate, have low topographic relief and infertile soils (Scholes and
44 Archer, 1997). For simplicity, in this paper all woody plants are referred ~~referred to as~~
45 trees while grasses include all the herbaceous vegetation. Savanna vegetation structure
46 (defined by the ratio of woody to herbaceous cover) is further modulated by disturbance
47 events (predominantly fire) ~~and that~~ create demographic bottlenecks, preventing
48 canopy closure that results in an open, woody system (Scholes and Archer, 1997).
49 Indeed, fire disturbance is a defining characteristic of savannas, particularly for mesic
50 regions (mean annual precipitation [~~MAP~~] > 650 mm), potentially holding the
51 ecosystem in a 'meta-stable' state, such that if ~~it~~ fire were excluded this open C₃/C₄
52 system would likely shift to a closed C₃ forest or woodland (Bond et al., 2005; Sankaran
53 et al., 2005b). The role of fire in modulating vegetation structure allows savannas to
54 occur across a broad demographic continuum, where the density of woody biomass is
55 coupled to the annual amount of rainfall (Hutley et al., 2011; Lehmann et al., 2011).
56 These environmental traits and behaviours therefore mark savannas as one of the most
57 complex terrestrial biomes on the planet, and understanding the vegetation dynamics
58 and underlying processes of this ecosystem type (especially in response to future global
59 change) has proven a challenging task for the ecosystem modelling community (House et
60 al., 2003; Scheiter et al., 2013; Scheiter and Higgins, 2007) ~~(House et al., 2003; Scheiter~~
61 ~~and Higgins, 2007)~~.

62 Terrestrial biosphere models (TBMs), ~~which~~ aim to predict ecosystem water and carbon
63 transfer between the land-surface and the atmosphere (among other processes) and,
64 have mostly underperformed for savanna ecosystems (Whitley et al., 2016). While the
65 reasons for this are in some cases model-specific, a general question can be formed
66 about whether the current generation of TBMs ~~have~~ hasve the predictive capability to
67 adequately simulate savanna dynamics and their response to future global change.
68 Additionally, if ~~such~~ limitations do exist, are they a result of an incorrect
69 parameterisation of physical parameters (e.g. root depth, maximum RuBisCO activity,
70 sand and clay soil contents, etc.), the misunderstanding or absence of dynamic

71 biophysical processes (e.g. phenology, root-water uptake, [impacts of fire](#) etc.), the
72 challenge of simulating stochastic events linked to disturbance, or a combination of ~~all~~
73 ~~three~~[these](#)? Particular attributes that characterise savanna environments, such as
74 frequent fire disturbance, the [highly](#) seasonality of available soil-water, and the annual
75 recurrence of C₄ grasses (which except for grasslands are absent in other biomes) are
76 not universally represented in most model frameworks. While some TBMs have been
77 specifically designed with savanna dynamics in mind (Coughenour, 1992; Haverd et al.,
78 2016; Scheiter and Higgins, 2009; Simioni et al., 2000), some are ~~closer to~~[simply](#)
79 modified agricultural models (Littleboy and Mckean, 1997), with most TBMs attempting
80 to capture savanna dynamics through calibration to ~~the~~ observed time-series [data](#) and
81 ad-hoc substitutions of missing processes (Whitley et al., 2016). Furthermore, little has
82 been done to investigate why simulating savanna dynamics has fallen outside the scope
83 and capability of many TBMs, such that these problems can be identified and used in on-
84 going model development.

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

99

100 **2. The savanna biome**

101 2.1 *Characteristics and global extent*

102 [At a global scale, biome distributions typically conform to climatic and soil](#)
103 [envelopes and current and future distributions are predictable based on climate and](#)

ecosystem physiology. However, savannas occur in climatic zones that also support grasslands and forests (Bond 2005, Lehmann et al. 2011), a characteristic that poses major challenges for TBMs and Dynamic Global Vegetation Models (DGVMs). Savannas occur across 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 are the second largest tropical ecosystem after rainforests with a global extent of 15.1 million km², which comprises almost half of the African continent (Menaut, 1983), 2.1 million km² of the Cerrado, Campos and Caatinga ecoregions in South America (Miranda et al., 1997), 1.9 million km² of the Australian tropical north (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).

While the structure of vegetation in these regions has converged towards a formation of mixed C₃ trees and C₄ grasses, the extensive geographical range gives rise to a wide range of physiognomies and functional attributes with multiple interacting factors such as seasonality of climate, hydrology, herbivory, fire regime, soil properties and human influences (Walter, 1973; Walter and Burnett, 1971). A range of savanna types results with a tree-grass ratio varying from near tree-less grasslands to open forest savanna of high tree cover (Torello-Raventos et al., 2013) (Torello-Raventos et al. (2013)). These savanna assemblages can shift to grassland or forest in response to changes in fire regime, grazing and browsing pressure as well as changing levels of atmospheric CO₂ increases with climate change (Franco et al., 2014) (Franco et al., 2014) and modelling this structural and functional diversity is challenging (Moncrieff et al., 2016b) (Moncrieff et al. 2016). Lehmann et al. (2011) (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 savannas occur over lower but wider range of MAP (~250 to 2000 mm), and are further separated by strong differences in rainfall interannual rainfall 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.

2.2 Conceptual models of tree and grass co-existence

139 Savannas consist of two co-existing but contrasting life forms: tree and grasses. These
140 life forms can be considered as mutually exclusive given their differing fire responses,
141 and shade tolerances as well as their competitive interactions, with grasses
142 outcompeting trees for water and ~~nutirents~~nutrients when they occupy the same soil
143 horizons (Bond, 2008) (~~Bond 2008~~). Ecological theory would suggest exclusion of one or
144 the other and not the coexistence that is a defining characteristic of savanna (Sankaran
145 et al., 2004) (~~Sankaran et al. 2004~~). Over the last five decades numerous mechanisms
146 have been proposed to understand tree-grass coexistence (Bond, 2008; Lehmann et al.,
147 2011; Lehmann and Parr, 2016; Ratnam et al., 2011; Scholes and Archer, 1997; Walter
148 and Burnett, 1971) (~~Walter et al., 1971; Scholes and Archer, 1997; van Langerveld et al.,~~
149 2003; Bond et al., 2008; Ratnam et al., 2011; Lehmann et al., 2011; Lehmann and Parr,
150 2016). Contrasting conceptual models have been largely supported by empirical
151 evidence, but no single model has emerged that provides a generic mechanism
152 explaining coexistence across the three continents of the tropical savanna biome, Africa,
153 South America and Australia (Lehmann et al., 2014) (~~Lehmann et al., 2014~~). ~~MEcological~~
154 models can be broadly classified into two categories; 1) competition-based models that
155 feature spatial and temporal separation of resource usage by trees and grasses that
156 minimises interspecific competition enabling the persistence of both lifeforms and, 2)
157 demographic-based models where mixtures are maintained by disturbance that results
158 in bottlenecks in tree recruitment and/or limitations to tree growth that enables grass
159 ~~persistance~~persistence.

160 Root-niche separation models suggest there is a spatial separation of tree and grass root
161 systems that minimises competition, with grasses exploiting upper soil horizons and
162 trees developing deeper root systems; (i.e. Walter's two-layer hypothesis (Walter and
163 Burnett, 1971)) (~~Walter et al. 1971~~). Trees rely on excess moisture (and nutrient)
164 draining from surface horizons to deeper soil layers. Phenological separation models
165 invoke differences in the timing of growth between trees and grasses. Leaf canopy
166 development and growth in many savanna trees occurs prior to the onset of the wet
167 season, often before grasses have germinated or initiated leaf development. As a result,
168 trees can have exclusive access to resources at the beginning of the growing season, with
169 grasses more competitive during the growing season proper. Given their deeper root
170 systems, tree growth persists longer into the dry season, providing an additional period
171 of resource acquisition at a time when grasses may be senescing. However, grasses are
172 better able to exploit pulses of resources such as ~~sufaces~~surface soil ~~mositure~~moisture
173 and ~~nitrgen~~nitrogen following short-term rainfall events, particularly

174 ~~improtrantimportant preoesses~~processes regulating semi-arid savanna ~~(Scholes &~~
175 ~~Walker 1993)~~(Chesson et al., 2004). These spatial and temporal separation of resource
176 usage is thought to minimise competition, enabling co-existence. Other competition
177 models suggest that tree density becomes self-limiting at a threshold of available
178 ~~mositure~~moisture and/or nutrient and are thus unable to completely exclude grasses.
179 These models assume high rainfall years favour tree growth and recruitment, with poor
180 years favouring grasses and high interannual variability of rainfall maintaining a
181 relatively stable equilibrium of trees and grasses over time (Hutley and Setterfield,
182 2008)~~(Hutley and Setterfield, 2008)~~.

183 In many savannas, root distribution is spatially separated with mature trees exploiting
184 deeper soil horizons as the competitive root-niche separation model predicts. In semi-
185 arid savannas investment in deep root systems ~~could result in tree water stress~~may
186 ~~seem counter-intuitive~~, as rainfall events tend to be sporadic and small in nature, with
187 little deep drainage. In this case, surface roots are more effective at exploiting moisture
188 and mineralised nutrients following these discrete events and shallow rooted grasses
189 tend to have a faster growth response than trees to these pulse events (Jenerette et al.,
190 2008; Nielsen and Ball, 2015). ~~Despite the large geographical distribution, the structure~~
191 ~~of vegetation in these regions has converged towards a similar formation of mixed C₃~~
192 ~~trees and C₄ grasses. However, this similarity can only be considered from a purely~~
193 ~~qualitative standpoint, as the floristic structure is the result of independent but~~
194 ~~analogous selective pressures imposed by the expansion of C₄ grasses into these regions~~
195 ~~6 to 7 Ma (Osborne and Beerling, 2006). In fact it is difficult to consider savannas as a~~
196 ~~singular biome, as in reality they are closer to a set of independent biomes that may be~~
197 ~~deflected from equilibrium with their climate due to a combination of resource~~
198 ~~limitation (soil moisture and soil nutrients), growing conditions (temperature) and~~
199 ~~frequent disturbances (fire and herbivory) (Lehmann et al., 2014).~~

200 Differences in the magnitude and interaction of environmental effects have indicated
201 savanna vegetation dynamics to be region-specific (Bond, 2008; Bowman and Prior,
202 2005; Lehmann et al., 2014; Lloyd et al., 2008; Scholes and Hall, 1996) ~~(Bowman and~~
203 ~~Prior, 2005; Lehmann et al., 2014; Lloyd et al., 2008; Scholes and Hall, 1996)~~, such that
204 there are marked differences in how regional flora (primarily woody species)
205 ~~coordinate their~~have evolved functional traits to operate within their respective climate
206 space (Cernusak et al., 2011; Eamus, 1999). For example, major distinctions can be
207 drawn between the savanna flora of Africa, Australia and South America. Canopies of the
208 African and South American savanna regions are predominantly characterised by

209 ~~shallow rooted, by~~ deciduous woody species that are in most cases (although not
210 always) shallow-rooted and follow a short-term growth strategy that maximises
211 productivity while environmental conditions are favourable (Bowman and Prior, 2005;
212 Lehmann et al., 2011; Scholes and Archer, 1997; Stevens et al., 2017). In contrast, the
213 mesic savanna canopies of northern Australia are dominated by deep rooted, evergreen
214 *Eucalyptus* and *Corymbia* woody species that favour a long-term strategy of conservative
215 growth that is insured against an unpredictable climate (Bowman and Prior, 2005;
216 Eamus et al., 1999, 2001) ~~(Bowman and Prior, 2005; Eamus et al., 1999; 2001).~~
217 Consequently, the functional traits that support deciduous, evergreen or annual
218 strategies have a major impact on the water and carbon exchange of the ecosystem. For
219 example, Australian mesic savanna tree canopies operate at almost constant rates of
220 assimilation and transpiration all year round, due to their deep and extensive root
221 system and ability to make adjustments to canopy leaf area in times of stress (O'Grady et
222 al., 1999). In these savannas, root competition between both trees and grass roots in
223 upper soil layers is apparent, contrary to predictions of niche-separation models
224 ~~and that would predict that~~ tree and grass competition for water and nutrients would be
225 intense. This system serves as an example of where both root-niche and phenological
226 separation is occurring (Bond, 2008) ~~(Bond, 2008) and These differences~~ highlights
227 quite importantly the fact that savanna ecosystems cannot be simply reduced to ~~a~~
228 generalised plant functional types (PFT) and applied globally in some land-surface
229 model (LSM) and dynamic global vegetation model (DGVM) frameworks (Moncrieff et
230 al., 2016a). One alternative may be to define ~~region~~ region-specific PFTs to fully capture
231 the distinctly different dynamics that are occurring across the ensemble of savanna
232 biomes.

233 As an alternative conceptual model of tree-grass co-existence, savannas can be viewed
234 as meta-stable ecosystems, where a range of stable states is possible but the ecosystem
235 can be deflected from an equilibrium with climate and soil due to a combination of
236 frequent disturbances (fire and herbivory), resource limitation (soil-moisture and soil
237 nutrients) and growing conditions, in particular temperature (Lehmann et al., 2014)
238 ~~(Lehmann et al., 2014)~~. In this paradigm, demographic-based models suggest that
239 ~~moisture~~ moisture and nutrient partitioning is not the sole driver of co-
240 ~~existence~~ existence and that determinants of tree demographics and recruitment
241 processes ultimately set tree - grass ratios. Fire, herbivory and climatic variability are
242 fundamental drivers of tree recruitment and growth, with high levels of disturbance
243 resulting in demographic bottlenecks that constrain recruitment and/or growth of

244 [woody components and grass persistence results. At high rainfall sites, in the absence of](#)
245 [disturbance, the ecosystem tends towards forest. High levels of disturbance, particularly](#)
246 [fire and herbivory, can push the ecosystem towards a more open canopy or grassland;](#)
247 [this ecosystem trajectory is more likely at low rainfall sites.](#)

248 [The inherent complexity in savanna function is evident when savanna structure is](#)
249 [correlated with the most significant environmental determinants. Sankaran et al.](#)
250 [\(2005a\). Sankaran et al. \(2005\) examined the relationship between tree cover and mean](#)
251 [annual rainfall with a large scatter of tree cover observed at any given rainfall for](#)
252 [African savannas. Rainfall set an upper limit of savanna tree cover, with cover below this](#)
253 [due to the interaction of other determinants such as herbivory, site](#)
254 [characteristics \(drainage, nutrient availability,](#)
255 [temperature\) and fire frequency reducing tree cover and biomass below the maximum](#)
256 [possible for a given rainfall. Lehmann et al. \(2011, 2014\) took this analysis](#)
257 [further and examined 'savanna-limiting' mechanisms across tropical Africa, Australia](#)
258 [and South America. Their analysis suggested that tropical landscapes consist of](#)
259 [mosaics of closed-canopy forest, savanna and grasslands suggesting that the limits](#)
260 [of savanna is not simply determined by climate and soils alone. Over the entire range of](#)
261 [environmental conditions in which savannas occur, some fraction of the land surface is](#)
262 ['not-savanna' \(Lehmann et al., 2011\) suggesting that savannas](#)
263 [are not necessarily a stable state ecosystem and disturbance is required to enable tree](#)
264 [and grass co-existence.](#)

265 [It is likely that savanna structure and function results from the interaction of all](#)
266 [processes described above, providing complexity for TBMs, particularly DGVMs that](#)
267 [seek to predict current and future distributions of grassland-savanna-forest](#)
268 [transitions driven by future climatic and/or anthropogenic factors](#)
269 [\(Scheiter et al., 2013, 2015\). Including both competition and](#)
270 [disturbance processes into models can yield more realistic results for a broad range of](#)
271 [rainfall regimes. Competition for moisture between trees and grasses is a](#)
272 [significant factor in maintaining savannas in semi-arid regions whereas](#)
273 [disturbance processes that limits tree cover becoming more important in higher](#)
274 [rainfall savanna regions. \(Accatino et al., 2010\).](#)

275 A promising alternative approach of some recent models is to allow savanna
276 composition to emerge from environmental selection from a mixture of PFTs or trait
277 combinations, reflecting global diversity in savanna vegetation (e.g. Haverd et al., 2015;

278 Scheiter and Higgins, 2009; [Scheiter et al., 2013](#); Smith et al., 2001). ~~For the~~ As an
279 example, the HAVANA model allows traits such as tree and grass phenology, leaf-area,
280 rooting depth and relative cover to emerge from ~~incident the~~ meteorological variations
281 and their effect on the evolving ecosystem state (Haverd et al. 2015). Because traits
282 define the response of the vegetation to climate, it is important that they are themselves
283 adequately represented in TBMs.

284

285 2.2 *The implications of climate change*

286 Projected global increases in both temperature and the variability of precipitation
287 patterns as a result of anthropogenic climate change are expected to lead to significant
288 changes in the structure and diversity of global terrestrial ecosystems (IPCC, 2013;
289 Wilks Rogers and Beringer, 2017). This will make modelling [ecosystem distributions](#)
290 [and biogeochemical fluxes](#) under these transient conditions difficult, challenging TBMs
291 in how they represent the response of the savanna ecosystem to structural shifts in
292 vegetation through CO₂ fertilisation, increased rainfall seasonality, [changes in VPD](#) and
293 changing fire dynamics (Beringer et al., 2015).

294 Savannas may be susceptible to small perturbations in climate and could potentially
295 shift towards alternate closed-forest or open-grassland states as a result (Scheiter and
296 Higgins, 2009). The total carbon pool of some savannas can be considered as modest
297 when compared with other ecosystems (e.g. rainforests) (Kilinc and Beringer, 2007).
298 However, in terms of net primary productivity (NPP), tropical savannas and grasslands
299 ~~occupy the top ranks among terrestrial biomes, together contributing~~ make up a
300 significant proportion, contributing -c. 30% of annual global NPP (Grace et al., 2006). A
301 shift in the savanna state towards a more closed system, may lead to these regions
302 becoming a substantially larger carbon sink (Higgins et al., 2010). Observations of
303 increased woody vegetation cover (woody encroachment) in many semi-arid
304 ecosystems and savannas worldwide over recent decades have been attributed to
305 positive effects of increased atmospheric CO₂ on plant water-use effects (Donohue et al.,
306 2009; Fensholt et al., 2012; Liu et al., 2015). Models suggest that such effects are
307 predicted to continue in the future. CO₂ fertilisation is also expected to favour the more
308 responsive C₃ vegetation, leading to the competitive exclusion of C₄ grasses via
309 suppressed grass growth and reduced fire impacts (Bond et al., 2005). Model projections
310 by Scheiter and Higgins (Scheiter and Higgins, 2009), and Higgins and Scheiter (Higgins

311 and Scheiter, 2012) suggest future range shifts of African savanna into more arid
312 climates as a consequence of elevated CO₂, with concurrent transformation of current
313 savanna habitats to forests under a stationary rainfall assumption. Recent evidence
314 underscores the significant role of savannas in the global carbon cycle (Ahlström et al.,
315 2015; Haverd et al., 2016; Poulter et al., 2014).

316 The response of savanna structure and function to changes in precipitation patterns is
317 highly uncertain (Wilks Rogers and Beringer, 2017). Scheiter et al. (2015) investigated
318 the effect of variable rainfall seasonality, projecting modest to large increases in above-
319 ground biomass for savannas in northern Australia. The authors showed that woody
320 biomass in this region increased despite significant changes to precipitation regimes,
321 being predominantly driven by CO₂ fertilisation and rainfall seasonality determining the
322 magnitude of the increase (Fig. 2) (Scheiter et al., 2015). However, some studies have
323 indicated that while increased rainfall seasonality may have a small effect in mesic
324 savanna systems, it may potentially act as an opposing effect to woody encroachment in
325 semi-arid savanna systems (Fensham et al., 2009; Hiernaux et al., 2009). For example,
326 Fensham et al. (Fensham et al., 2009) have shown significant tree mortality to occur as a
327 result of drought in a semi-arid savannas in south-west Queensland, suggesting that
328 severe water-stress may counteract the positive effect of CO₂ fertilisation on ecosystem
329 carbon balance. Alternatively, forest dieback as a result of increased rainfall seasonality
330 and more frequent drought occurrence may lead to an expansion of savanna distribution
331 in some regions. For example, simulations of the Amazon basin have projected a
332 possible conversion of rainforest to savanna in eastern Amazonia as a result of forest
333 dieback induced by severe water stress and fire disturbance (Cox et al., 2004; Malhi et
334 al., 2009).

335 ~~Finally, fire can play a critical role in mediating the floristic structure of the savanna~~
336 ~~ecosystem, deflecting woody vegetation from its physiognomic potential with climate~~
337 ~~(Scholes and Archer, 1997).~~ Increased warming and ~~changes to~~ rainfall seasonality ~~is are~~
338 expected to alter the interaction between climate, fire and savannas in the future
339 (Beringer et al., 2015), however, we leave discussion of savanna fire dynamics and the
340 ability of TBMs to simulate this process until ~~later~~ in ~~this~~ paper. Permanent shifts in the
341 structure and physiology of the savanna complex as a result of climate change is
342 expected to have a major impact on the exchange of water, energy and carbon that
343 occurs in this system, which in turn ultimately affects global biogeochemical cycling and
344 climate (Beringer et al., 2015; Pitman, 2003).

345

346 **23. The capability of models to simulate savanna ecosystems:**

347 The term '*terrestrial biosphere model*' refers to a variety of bottom-up modelling
348 approaches that simulate coupled dynamics of water, energy, carbon, and in some cases
349 nutrients in vegetation and soils. TBMs range from stand models, which simulate
350 specific ecosystems in high detail, up to ~~dynamic global vegetation models (DGVMs)~~,
351 which can simulate ecosystem composition, biogeochemical processes and
352 energy exchange and the spatial distribution of multiple ecosystems at a
353 ~~coarser level~~ regional to global scales. Consequently, TBMs collectively operate over
354 different temporal and spatial scales and employ processes of different scope in
355 simulating ecosystem dynamics. However, common to all TBMs ~~is~~ are that they are
356 governed by the same biophysical principles of energy and mass transfer that
357 determines the dynamics of plant life (Pitman, 2003). Consequently, the predictive
358 capability of different TBMs at determining the exchange of water, energy and carbon
359 between the surface and atmosphere should be convergent within a reasonable degree
360 of error (Abramowitz, 2012). However, model intercomparison and benchmarking
361 studies have shown that many TBMs are unable to meet reasonable levels of expected
362 performance as a result of a systematic misrepresentation of certain key ecosystem
363 processes. (Abramowitz et al., 2008; Best et al., 2015; Blyth et al., 2011; Mahecha et al.,
364 2010).

365 The misrepresentations of ecosystem processes is particularly evident in savannas, for
366 which many TBMs have not been developed for, nor tested on (Baudena et al., 2015;
367 Cramer et al., 2001; Whitley et al., 2016). Seasonal competition and access to
368 belowground resources (soil moisture and nutrients), impacts of browsing and grazing,
369 and stochastic disturbance events (fire), are less prevalent in other ecosystems and are
370 therefore not well represented (or even missing) in many TBMs (House et al., 2003;
371 Whitley et al., 2016). Other stochastic events common in savanna
372 environments are precipitation pulses that in semi-arid savanna, drive production and
373 respiration processes (Huxman et al., 2004; Williams et al., 2009). High spatial and
374 temporal variability of these pulse events, coupled with the differential
375 responses of tree and grasses complicates application of TBMs in savannas.
376 Precipitation pulses are particularly significant in semi-arid ecosystems and
377 pulse size determines the relative response of ecosystem respiration (Re) and gross
378 primary production (GPP), with large events driving high rates of Re that precedes

379 [any response in GPP and the ecosystem may switch to source of CO₂ to the atmosphere](#)
380 [for a period post event \(Huxman et al., 2004\). The annual C balance can be](#)
381 ~~determined~~[determined by the frequency, magnitude and duration of pulse events](#)
382 (Cleverly et al., 2013) ~~(Cleveley et al. 2013).~~

383 Conventional TBMs still lack ~~a lot of~~ this capability [and tend to underestimate Re and](#)
384 [overestimate Ra in semi-arid regions](#) (Mitchell et al., 2011) ~~(Mitchell et al., 2011)~~ and
385 therefore have limited application for biomes in the seasonally dry tropics, which in turn
386 becomes a large source of uncertainty in future global studies (Scheiter and Higgins,
387 2009). However, we believe that incorporating key processes that drive savanna
388 dynamics into current-generation TBMs has great potential, considering that even small
389 modifications can lead to large gains in performance ([Feddes et al., 2001](#); Whitley et al.,
390 2011). ~~It is clear from the above background and discussion that the ecological~~
391 ~~processes in savannas are numerous, detailed, complex and important as they can all~~
392 ~~have differential responses to environmental drivers. We suggest that most of the~~
393 ~~detailed ecological processes become emergent properties within model frameworks.~~
394 ~~Therefore we do not attempt to capture everything but Below, rather~~ we have identified
395 phenology, root-water uptake and fire disturbance as three critical processes in
396 savannas that deserve special consideration in modern TBMs [as explained below](#).

397 ~~23.1~~ Phenology

398 Phenology is an expression ~~for of~~ the seasonal dynamics of [the](#) structural vegetation
399 properties ~~of an ecosystem that define their, defining its~~ growing season and ultimately
400 ~~its-their~~ productivity (Moore et al., 2016a). Here we limit our discussion to the
401 phenology of leaf cover. In seasonally dry climates phenology is driven by soil-moisture
402 availability, and the length of the growing season for shallow rooting plants is
403 determined by the seasonality of rainfall (Kanniah et al., 2010; Ma et al., 2013; Scholes
404 and Archer, 1997). Plants respond differently to water availability, such that phenology
405 is a function of the dominant species within the ecosystem. Deciduous trees and annual
406 grasses are photosynthetically active during the wet season only and respectively
407 senesce or become dormant ~~or senesce~~ at the beginning of the dry season, while
408 evergreen trees may remain permanently active throughout the year, potentially
409 responding to soil-moisture depletion by gradually reducing their canopy leaf area
410 (Bowman and Prior, 2005). These dynamics are critically important, as they control the
411 amount and seasonality of carbon-uptake and water-use. In TBMs, ecosystem phenology
412 is typically represented in one of two ways. The first is via direct *prescription* of this

413 information as an additional input to the model, where observations of leaf area index
414 (LAI) (either in-situ measurements or satellite derived products) are used to express the
415 change in ecosystem canopy cover over time (Whitley et al., 2011). The second is as a
416 *prognostic* determination using a growth sub-module, where carbon allocation and leaf
417 metabolic activity are simulated and dependent upon the time-varying conditions of
418 temperature and soil-water availability (Scheiter and Higgins, 2009). Prescription of
419 phenology from observed LAI dynamics requires an accurate determination of the
420 separate tree and grass components from bulk ecosystem LAI to be feasible for savanna
421 ecosystems (Whitley et al., 2011). In many cases, this separation is assumed to be static,
422 ignoring the different seasonal changes in tree and grass cover over time (Scholes and
423 Archer, 1997). In fact, no models that we are aware of dynamically partition ~~prescribed~~
424 LAI as it is prescribed. Donohue et al. (Donohue et al., 2009) offers an *a priori* method
425 that can determine separate tree and grass LAI signals. This method assumes that the
426 high variability in the bulk signal is attributed to herbaceous vegetation, such that the
427 remaining, less variable signal is attributed to woody vegetation (Fig. 3). A prescription
428 of separate tree and grass LAI inputs was found to be necessary for simulating water
429 and carbon exchange for a mesic savanna site in northern Australia (Whitley et al.,
430 2011), and in determining a reduced error estimate of the Australian continental water
431 and carbon balance (Haverd et al., 2013) to which savannas contribute significantly. The
432 major drawback to prescribing LAI as a model input is that the model's scope is limited
433 to hindcast applications. Because this information is supplied to the model, the floristic
434 structure and its evolution over time is fixed, and cannot respond to changing
435 environmental conditions (e.g. shifts in precipitation patterns) that are likely to have an
436 impact on the tree-grass demography (Ma et al., 2013). Consequently, a dynamic
437 approach where savanna phenology is explicitly simulated and dynamically responds to
438 climate and disturbance offers a more promising path forward.

439 Allocation-growth schemes allow models to express phenology in terms of the evolution
440 of carbon investment in leaf area over time, limited by the availability of resources for
441 growth (Haverd et al., 2016). These schemes effectively work by distributing assimilated
442 carbon (via net primary productivity; NPP) to the root, stem and leaf compartments of
443 the simulated plant, where allocation to the leaf is dependent on the plant being
444 metabolically active or dormant (Cramer et al., 2001). In some TBMs, allocation to these
445 compartments is a fixed ratio (set according to plant functional type) and metabolic leaf
446 activity is defined through a set of threshold bioclimatic indicators (e.g. photoperiod,
447 moisture availability and temperature) that determine whether conditions are

448 favourable for photosynthesis (Jolly et al., 2005). However, more recent advances, use
449 an alternative approach of dynamically guiding allocation towards the compartment
450 that most limits a plant's growth (Scheiter and Higgins, 2009) or dynamically optimising
451 daily allocation, to maximise long-term NPP and control the competitive balance
452 between trees and grasses (Haverd et al., 2016). The latter approach, based on
453 optimality theory (Raupach, 2005), is related to the approach followed by Schymanski et
454 al. (2009), who assumed that vegetation dynamically optimises its properties (root
455 system and foliage) to maximise its long-term net carbon profit. These approaches,
456 which assume a more dynamic coupling between allocation and phenology, allow plant
457 form and community structure to evolve in response to changes in resource availability
458 (light, water or carbon) over time, with phenology becoming an emergent property of
459 this process. Dynamic allocation schemes enable a TBM to answer questions regarding
460 how changing climate or elevated atmospheric CO₂ concentrations may alter structural
461 properties of the ecosystem, and the resultant feedbacks on water, carbon and energy
462 cycling (Scheiter and Higgins, 2009; Schymanski et al., 2015).

463

464 23.2 Root-water access and uptake

465 The root zone is critically important in maintaining water and carbon fluxes, as it
466 defines an ecosystem's accessible belowground resources and vulnerability to
467 prolonged dry periods (De Kauwe et al., 2015). [Savannas occurs in For](#) seasonally dry
468 climates ~~and (common for savannas), where~~ productivity is primarily limited by dry
469 season water-availability. (Kanniah et al., 2010, 2011, 2012) ~~(Kanniah et al., 2010),~~
470 which is largely determined by [plant regulation of water transport \(through leaf](#)
471 [stomatal conductance and stem capacitance\)](#) and the root zone water storage capacity
472 ~~and access and hence (-rooting distribution of fine root biomass depth)~~ (Eamus et al.,
473 2002). Co-ordination of the whole soil-root-leaf-atmosphere pathway in response to the
474 highly seasonal climate is critical to the survival of savanna plants and is intrinsically
475 linked to their phenology. [Partitioning of root water uptake is a key component of](#)
476 [competition models describing tree-grass co-existence](#) ~~existence as described above.~~ For
477 example, deciduous and annual savanna species have shallow root profiles (approx. 0.5
478 to 2 m) and highly conductive vascular systems to maximise productivity during the wet
479 season (February and Higgins, 2010). In contrast, evergreen savanna species invest in
480 highly regulated hydraulic architectures and deep root systems (> 2 m) that can access
481 deep soil water stores to maintain continuous productivity throughout the dry season

482 (Bowman and Prior, 2005). It is therefore critically important that the specific root
483 system and hydraulic architectures of savanna species be adequately represented in
484 models to simulate water and carbon fluxes of this system.

485 Soil and plant hydraulic traits such as rooting depth and distribution, stem hydraulic
486 resistance, and sand and clay contents are typically represented as fixed parameters in
487 TBMs. Of these traits, the root profile acts as the first-order control on soil-water supply
488 and therefore determines the capability of a simulated plant to remain active through
489 rain-free periods (Eamus et al., 1999). The root profile within a soil column is generally
490 modelled as an exponentially declining ~~of~~ root-surface area with depth, the limit of
491 which extends to some prescribed level. Although some models are capable of
492 dynamically determining the size of the root profile as an emergent property of
493 productivity and climate (e.g. Haverd et al., 2016; Schymanski et al., 2009), more
494 typically, the maximum rooting depth is fixed at approximately 1.5 to 2.0 m (Whitley et
495 al., 2016). However, studies have shown that woody plants in semi-arid or seasonally
496 dry climates (particularly those in Australia) exhibit deep root systems to remain active
497 during prolonged dry periods (Duursma et al., 2011; Hutley et al., 2000; O'Grady et al.,
498 1999). Numerous modelling studies have shown that a rooting profile of significant
499 depth (> 2 m) is required to achieve good model-data agreement (Fisher et al., 2007;
500 Haxeltine and Prentice, 1996; Schymanski et al., 2009; Whitley et al., 2016, 2011). While
501 characterisation of the rooting depth in savanna modelling exercises may be seen as a
502 matter of correct parameterisation rather than one of systematic process, its role as a
503 first-order control on water supply in seasonally water-limited systems gives it
504 significant weight in the overall determination of carbon uptake. Furthermore, long-
505 term responses of rooting depth to climate change or elevated atmospheric CO₂
506 concentrations may substantially alter structure, resource use and carbon uptake of
507 savanna ecosystems (Schymanski et al., 2015). Consequently, rooting depths that
508 sufficiently represent either deciduous or evergreen tree species need to be considered
509 when modelling savannas.

510 Directly coupled to the characterisation of the root-zone is the systematic process by
511 which soil-water is extracted by the root system. The process of root-water uptake in
512 TBMs has been simulated using numerous schemes. One approach assumes that the
513 amount of extracted water by roots is a function of the root density distribution within
514 the soil column and is expressed through an additional sink term to the Richard's
515 equation, which represents the flow of water in an unsaturated soil (Wang et al., 2011).
516 In such schemes, root-water uptake may be weighted by the distribution of fine-root

517 biomass in the soil, such that soil-layers with the greatest density of fine-root biomass
518 largely determine the soil-water status of the plant, its stomatal behaviour, and
519 therefore its sensitivity to soil drying (Wang et al., 2011). The exponential decay
520 function conventionally used to describe the root profile in most TBMs (an exception is
521 Schymanski et al. 2009) can result in simulated stomatal behaviour that is heavily
522 weighted towards the moisture content of the upper soil profile, making them highly
523 sensitive to drought (De Kauwe et al., 2015). In reality, the active root distribution of
524 savannas is not static, nor so limited, but responds dynamically to wherever water is
525 available. For example, eucalypts occurring in Australian mesic savannas invest in 'dual-
526 root' systems that are capable of switching their root activity between subsurface and
527 subsoil respectively to access water continually during both wet and dry seasons (Chen
528 et al., 2004). Alternative root-water uptake schemes do exist that describe a more
529 dynamic response to long-term changes in soil conditions. One such scheme by Williams
530 et al. (2001) considers root activity to change over time and be concentrated towards
531 parts of the root zone where the plant can sustainably extract the maximal amount of
532 available water. Consequently, this scheme effectively weights soil-water status over the
533 distribution of fine-root biomass, such that simulated root-water uptake dynamically
534 responds to the wetting and drying of the soil profile over time (Fig. 4). Another
535 alternative approach by Schymanski et al. (Schymanski et al., 2008) allows the root zone
536 to dynamically adjust the vertical distribution of root biomass in the profile to balance
537 canopy water demand while minimising structural costs of maintaining such a root
538 system . These alternate schemes offer a more dynamic approach to modelling the
539 hydraulic architecture of species occurring in savannas and other semi-arid ecosystems,
540 and have demonstrated high predictive skill in these environments (Schymanski et al.,
541 2008, 2009; Whitley et al., 2011). Therefore, given the distinct seasonality of savanna
542 ecosystems, dynamic root-water extraction schemes are needed to simulate how the
543 root zone responds to the evolution of soil-water supply over time.

544 In should be noted that the above discussion on root-water uptake is one based on
545 relatively simple model processes, however, savanna ecosystems have much more
546 complex interactions across the soil-root-stem-leaf-atmosphere continuum. Additional
547 processes such as adaptive changes in root architecture across seasonal and interannual
548 timescales, rhizosphere-root interactions, hydraulic redistribution, plant stem water
549 storage and limitations on leaf function due to water demand across soil-root-stem-leaf-
550 atmosphere continuum (Lai and Katul, 2000; Steudle, 2000; Vrugt et al., 2001) may also
551 be important in simulating root water uptake.

552 23.3 Disturbance

553 Ecosystem structure and function in seasonally dry tropical systems such as savanna, is
554 strongly shaped by environmental disturbance, such as persistent herbivory pressures,
555 frequent low-impact fire events, and infrequent high-impact cyclones (Bond, 2008;
556 Hutley and Beringer, 2011) all determining that shape tree demographics. Fires have a
557 significant impact on land-surface exchange and vegetation structure and contribute to
558 greenhouse gas emissions through the consumption of biomass (Beringer et al., 1995,
559 2015). Fire has the capacity to alter land-surface exchange fluxes through the removal of
560 functional leaf area (reduced LAI) and the blackening of the surface (reduced albedo),
561 temporarily reducing net carbon uptake (Beringer et al., 2003, 2007) and altering the
562 atmospheric boundary layer to affect convective cloud formation and precipitation
563 (Görngen et al., 2006; Lynch et al., 2007). Regarding vegetation structure, fire influences
564 the competitive balance between tree and grass demographics, suppressing recruitment
565 of woody saplings to adults, thereby deflecting the system from reaching canopy closure
566 (Beringer et al., 2015; Higgins et al., 2000). Work by Bond et al. (Bond et al., 2005)
567 underlines the potential effect of removing fire from the savanna system, with
568 substantial increases in woody biomass and major structural shifts towards closed
569 forests. This is further supported by more empirical studies involving fire exclusion
570 experiments and showing similar tendencies towards woody dominance (Bond and Van
571 Wilgen, 1996; Scott et al., 2012). Given that future climate projections point to predict
572 higher temperatures and less precipitation for sub-tropical regions (Wilks Rogers and
573 Beringer, 2017) the representation of short- and long-term impacts of fire on savanna
574 structure and function in TBMs may be important in understanding how savanna
575 landscapes may respond to changes in fire frequency and intensity (Bond et al., 2005).

576 Fire is commonly simulated as a stochastic process, with the probability of occurrence
577 increasing with the accumulation of litterfall and grass biomass (fuel loads), combined
578 with dry and windy environmental conditions that promote ignition (generally through
579 lightning) (Kelley et al., 2014). The simulated amount of biomass consumed after an
580 ignition event differs among models. Recent advances in simulating savanna fire
581 processes have led to more complete representations of the complex interaction
582 between fire and woody vegetation and how this shapes savanna structure. For
583 example, Scheiter and Higgins (2009) consider a 'topkill' probability that suppresses
584 woody plant succession if fire intensity is of a critical magnitude determined by the
585 plant's fire-resisting functional traits (e.g. height, stem diameter, bark thickness). This
586 scheme allows fire to directly shape the savanna tree population through the dynamics

587 of woody establishment, resprouting and mortality. Additionally, Kelley et al. (2014)
588 have similarly considered how fire-resisting functional traits of woody vegetation alter
589 the fire dynamics of seasonally dry environments. It should be noted that both studies
590 do not consider anthropogenic ignition events, whereas recent work by Scheiter et al.
591 (Scheiter et al., 2015) suggests that fire management can be simulated using fixed fire
592 return intervals.

593 Many TBMs simulate fire as an instantaneous event through emissions and removal of
594 biomass, but may not consider the transient effects that fire has on land-surface after the
595 event has occurred. It has been demonstrated previously that these post-fire effects on
596 canopy surface mass and energy exchange can be significant, with fire indirectly
597 suppressing productivity by *c.* 16% (+0.7 tC ha⁻¹ yr⁻¹) (Fig. 5) (Beringer et al., 2007).
598 During this period, resprouting rather than climate drives productivity, with respiration
599 exceeding photosynthesis as a result of the regenerative cost of replacing damaged or
600 lost stems and leaf area (Cernusak et al., 2006). In fact many modelling analyses of
601 savannas dynamics have removed the post-fire periods completely from any assessment
602 of performance, such that evaluation has been limited to periods where the model is
603 considered to be 'fit for purpose' (Whitley et al., 2016, 2011). Fire is an integral part of
604 savanna dynamics; it is important to include fire events in the analysis of savanna
605 carbon and water fluxes or model performance. Furthermore, an accurate and robust
606 representation of fire effects on savanna ecosystems is needed to answer questions
607 about how savanna dynamics may change under future climate scenarios, as fire
608 regimes have significant impacts on the carbon balance of these systems (Beringer et al.,
609 2015).

610 Other disturbance ~~processes regimes~~ such herbivory pressures and [impact of cyclones](#)
611 have limited to no representation in models. The removal of aboveground biomass
612 through grazing and browsing, is commonly represented as a set fraction [of cover or](#)
613 ~~productivity~~ [productivity](#) that is removed over time according to the degree of local
614 agricultural pressures, but has been represented dynamically in some models (e.g.
615 Pachzelt et al., 2015). [Grazing and browsing are of central importance in many of the](#)
616 [world's savannas and like fire, strongly influences cover and productivity](#) (Bond and
617 Keeley, 2005). [The importance of herbivory as a determinant varies between savanna](#)
618 [regions, and appears to largely reflect the abundance of large herbivores present. In](#)
619 [parts of Africa, woody vegetation density has sometimes been reduced by large](#)
620 [herbivores, for example uprooting of trees by elephants when browsing](#) (Asner et al.,
621 2016; Laws, 1970). ~~(Laws, 1970; Levick et al., 2016). Impact on savanna structure and~~

622 ~~function via consumption of biomass, seed predation, trampling of understory, and the~~
623 ~~pushing over and killing of trees and shrubs.~~

624 ~~Bond and Keeley (2005)~~~~Bond and Keeley (2005)~~ suggested that browsing is analogous
625 to fire as once saplings escape a flame or browsing height, they are beyond the reach of
626 most mammal herbivores. Invertebrates are also significant herbivores, particularly
627 grasshoppers, caterpillars, ants and termites. Mammal herbivores are typically
628 categorized as grazers, browsers or mixed feeders, who can vary their diet depending on
629 food availability. Large herbivores can lead to changes in species composition, woody
630 vegetation density and soil structure. Browsers such as giraffes can reduce woody
631 seedling and sapling growth thereby keeping them within a fire-sensitive heights for
632 decades. ~~Reductions~~Reductions in grass biomass following grazing leads to a reduction
633 of fuel and thus fire frequency and intensity, enhancing the survival of saplings and adult
634 tress (Bond, 2008)~~(Bond, 2008)~~. Fire also affects herbivory as herbivores may
635 ~~favor~~favoured post-fire vegetation regrowth.

636 Termite pressures have also been shown to suppress productivity (Hutley and Beringer,
637 2011), but this loss may be too small to be considered as a significant consumer of
638 biomass in TBMs. No models that the authors are aware of simulate the effect of
639 cyclones on vegetation dynamics in tropical systems despite their impact on long-term
640 ecosystem ~~structure and~~ productivity. Cyclones are infrequent but high impact
641 disturbance events that occur in any mesic savanna that lies close to the coastline, and
642 can effectively 'restart' the savanna system through the mass removal of woody biomass
643 (Hutley et al., 2013). Hutley and Beringer (2011) have shown that for an Australian
644 mesic savanna, a bimodal distribution of the tree class sizes at the site indicates two
645 major recruitment events that corresponds with two of the last great cyclones to occur
646 in the region. Despite the immediate and significant loss of woody biomass during those
647 events, recovery was possible and pushed this site to a carbon sink over many decades.
648 Despite the impact that cyclones have on savanna structure it is somewhat understated
649 in the literature, possibly due to the integrated loss in productivity over long-periods
650 being small (Hutley et al., 2013) ~~as well as the difficulty in simulating cyclone frequency~~
651 ~~and intensity across the landscape at present or in the future~~. However, we believe
652 because cyclones modulate savanna structure so strongly, there is a need ~~for such~~
653 ~~dynamics~~them to be considered in TBM frameworks, particularly for long-term
654 projections on productivity. While few models have the capability to simulate the full
655 spectrum of environmental disturbance effects on savanna ecosystems explicitly, the

656 significant modulating impact they have on savanna structure and function flags these
657 processes as a high priority in future model development.

658

659 **34. Testing and developing models for application in savannas**

660 Given that there are strong indications that critical savanna processes are likely
661 misrepresented in current-generation TBMs, there is a clear need for further model
662 testing and evaluation to be conducted for this ecosystem. Savannas have been the
663 subject of improved research over the past two decades, resulting in a good and
664 evolving understanding of their complicated structure, function, and contribution to
665 global biogeochemical cycling (Higgins and Scheiter, 2012; Lehmann et al., 2014;
666 Sankaran et al., 2005b; Scholes and Archer, 1997). Despite this, our increased
667 understanding of savanna dynamics has not been properly translated into many modern
668 TBMs, with the effect of major deficiencies in modelling this ecosystem (Whitley et al.,
669 2016). Consequently, there is still a great necessity for continuous, consistent and
670 objective studies to test and develop how savanna dynamics are represented and
671 simulated. Below we highlight how datasets from multiple sources that include eddy
672 flux towers, satellites, and ~~ground-based~~ *in situ* studies can inform model development
673 and be used in evaluation and benchmarking studies.

674

675 *34.1 Datasets to inform model development*

676 Eddy-covariance (EC) systems that observe the instantaneous response of water, energy
677 and carbon exchange to variability in climate and the evolution of this response over
678 time provide crucial information on which to test and develop TBM application in
679 savanna ecosystems (Beringer et al., 2016a, 2016b). Turbulent fluxes measured by EC
680 systems that include net ecosystem exchange and latent and sensible heat are common
681 model outputs, such that this information is commonly used to validate TBMs. Local
682 meteorological forcing (e.g. short-wave irradiance; SW, air temperature, rainfall, etc.)
683 that is concurrently measured with the turbulent fluxes by other instruments (rainfall
684 and temperature gauges, radiation sensors, etc.) are common model inputs and are used
685 to drive TBMs. Additionally, both turbulent fluxes and meteorological forcing are
686 measured at Quantities measured by EC directly mirror the inputs and outputs of TBMs,
687 namely turbulent fluxes of water, heat and CO₂ observed in parallel with local

688 meteorological forcing (e.g. short wave irradiance; SW, air temperature, rainfall, etc.) at
689 the same temporal and spatial-ecosystem scale at which TBMs are commonly run
690 (Aubinet et al., 2012). Consequently, these datasets offer an unparalleled capability in
691 diagnostic model evaluation (Abramowitz, 2012; Balzarolo et al., 2014; Mahecha et al.,
692 2010). The use of EC datasets to evaluate TBMs and inform further development has
693 been a long running practice within the ecosystem modelling community, with
694 particular success being reported for some savanna studies in Australia (Barrett et al.,
695 2005; Haverd et al., 2013, 2016, Schymanski et al., 2007, 2009, Whitley et al., 2016,
696 2011) (~~Haverd et al., 2013, 2016; Schymanski et al., 2009; Whitley et al., 2016, 2011~~).
697 Here we outline two opportunities of using EC systems into ~~assessing~~ model skill for
698 savanna ecosystems ~~are highlighted in these studies~~.

699 The first of these addresses the problem ~~of that~~ EC datasets representing the integrated
700 sum of turbulent fluxes for the entire system (i.e. soil, grass, shrubs and trees) ~~that, and~~
701 ~~these~~ are not easily separated. Assessing model performance using bulk measurements
702 does not consider the separate responses of the functionally different C₃ tree and C₄
703 grass components that respond differently to climate (Whitley et al., 2016, 2011).
704 However, a recent study by Moore et al. (Moore et al., 2016b) has shown for a mesic
705 savanna site in Australia that separate observations of canopy and understorey fluxes
706 can be determined by using a 'dual tower' EC system that observes turbulent fluxes at
707 reference points above and beneath the canopy (Fig 6). Datasets such as this provide a
708 valuable resource to analyse the skill of separate model processes, i.e. simulation of tree
709 and grass leaf gas-exchange, ~~which and tests~~ the degree of model equifinality (Bevan
710 and Freer, 2001) at predicting the bulk ecosystem flux. A further collection of coupled
711 over- and understorey EC datasets is therefore critically needed to verify that simulated
712 tree and grass dynamics are correctly represented in TBMs.

713 The second opportunity addresses the issue of savanna landscape heterogeneity.
714 Savannas are not a homogeneous PFT, but rather a continuum of changing tree and
715 grass demographics that shift biogeographically with rainfall and other factors (Ma et
716 al., 2013). Ecological gradient studies, such as the Kalahari Transect (Scholes et al.,
717 2004) and North Australian Tropical Transect (NATT) (Hutley et al., 2011), have shown
718 turbulent fluxes along a declining rainfall gradient to be strongly linked to structural
719 changes in vegetation (Beringer et al., 2011a, 2011b). In essence, the spatial response to
720 a systematic ~~decline changes~~ in rainfall (or other resources or disturbance intensities)
721 represents the possible future temporal response to changing climate, such that
722 transects can be used to evaluate TBMs by their ability to emulate the full spectrum of

723 savanna behaviour rather than at just one point. A recent model intercomparison study
724 by Whitley et al. (2015) used turbulent flux observations sampled along the NATT to
725 evaluate a set of six TBMs, and documented only poor to moderate performance being
726 observed for those savanna sites. Model evaluations studies that test model predictive
727 skill across both time and space are therefore crucial to projecting how savannas
728 dynamically respond to changing climate.

729 While EC systems provide valuable datasets on which to test and develop models, they
730 are unable to provide a complete evaluation, as they cannot completely capture long-
731 term temporal and spatial scale features (e.g. demographic structural shifts in
732 vegetation), nor provide detail on underlying ecosystem processes (e.g. root-water
733 dynamics and carbon allocation) (Abramowitz, 2012; Haverd et al., 2013; Keenan et al.,
734 2012) ~~(Abramowitz, 2012; Haverd et al., 2013)~~. Additional sources of data and their
735 collection are therefore critical to informing how well models are representing the
736 specific dynamics that unique to savannas. Model inversion studies have shown EC
737 datasets give significant constraint to predictions of NPP, however extra ancillary data
738 that is informative of other underlying processes was required to further constrain
739 uncertainty (Haverd et al., 2013; Keenan et al., 2012). Here, we suggest how each of the
740 three critical savanna processes highlighted in this paper can potentially be tested in
741 addition to EC datasets. Satellite derived estimates of remotely sensed near-surface
742 reflectance (Ma et al., 2013; Ryu et al., 2010b) and digital imagery from 'PhenoCams'
743 (Moore et al., 2016a; Sonnentag et al., 2012), provide a good resource for testing
744 simulated phenology, particularly the 'green-up' and 'brown-down' phases. Additionally,
745 Advanced Very High Resolution Radiometer (AVHRR) data can provide 'burnt area'
746 maps that quantify the frequency of fire events, which can inform the probability of
747 occurrence in simulated fire-dynamics. Above- and belowground carbon inventory
748 studies (Chen et al., 2003; Kgope et al., 2010) provide highly valuable sources of
749 information in how plants allocate their resources for growth, which can test the efficacy
750 of TBM allocation scheme. Digital soil maps also provide an excellent resource in
751 parameterising simulated soil profiles (e.g. Isbell, 2002; Sanchez et al., 2009). However
752 the spatial resolution of these data products can be coarser than operating resolution of
753 many TBMs, such that site-level measurements should be used when possible.
754 Excavation studies that quantify savanna tree root-systems (Chen et al., 2004) and soil-
755 moisture probes installed to greater depths (> 2 m) are informative about the evolution
756 of the soil-root zone over time (e.g. surface root density, root depth), and such data may
757 be critical to understanding whether current root-water extraction schemes in TBMs are

758 capable of simulating the dry season response of savanna tree species (Whitley et al.,
759 2016). Other useful approaches for elucidating how and where plants gain their water,
760 include sap flow measurements (Zeppel et al., 2008), gas chambers (Hamel et al., 2015)
761 and soil-plant-water experiments (Midwood et al., 1998). In additional, hydrogen and
762 oxygen stable isotope ratios of water within plants provide new information on water
763 sources, interactions between plant species and water use patterns under various
764 conditions (see review by Yang et al. (2010)).

765 Finally, localised observations of plant traits such leaf-mass per area, stomatal
766 conductance (g_s), tree height, etc. are needed to inform a better parameterisation of
767 savanna specific PFTs (Cernusak et al., 2011). For example, specific leaf-level
768 information such as Rubisco activity (V_{cmax}) and RuPB regeneration (J_{max}) for both C_3 and
769 C_4 plants are critically needed to inform the Farquhar leaf photosynthesis models
770 (Farquhar et al., 1980), while information on g_s and leaf water potential (Ψ_{leaf}) are
771 important in parameterising the many stomatal conductance models used in TBMs (Ball
772 et al., 1987; Medlyn et al., 2011; Williams et al., 1996). Leaf capacitance and water
773 potential data are also critically important in characterising model sensitivity to drought
774 (Williams et al., 2001), but this information is severely lacking for savannas.

775 Given that there are many interacting effects occurring in savannas, an integration of
776 multiple data sources is therefore necessary for a more complete evaluation of how well
777 TBMs perform in this environment. We recommend that future EC studies, particularly
778 along transects as mentioned above, should include intensive field campaigns that are
779 targeted towards a more complete characterisation of the site. This would include root
780 excavations and the collection of plant trait measurements that sample such data within
781 the footprint of an EC tower. Collaborative research networks, such as those of TERN
782 (Terrestrial Ecosystem Research Network), NEON (National Ecological Observatory
783 Network) and SAEON (South African Environmental Observation Network) that have
784 the resources and infrastructure to conduct such campaigns will be needed to meet
785 these demands for more observational data.

786

787 *34.2 Model evaluation and benchmarking*

788 Multiple dynamic processes drive savanna structure and function, and an understanding
789 of the causes and reasons for why TBMs systematically misrepresent this ecosystem is
790 paramount to future development. Consequently, a complete diagnostic evaluation of

791 model performance in savanna ecosystems requires more than just simple model-model
792 and model-data comparisons where 'good performance' is determined from a score in a
793 given metric (e.g. a high correlation between observed and predicted values). Instead
794 evaluation should also consider parsimony, physical representativeness and 'out-of-
795 sample' capability of the model itself (Abramowitz et al., 2008). A holistic evaluation of
796 the biophysical, biogeochemical and ecological processes represented in TBMs has
797 therefore been the aim of many international model intercomparison projects, with
798 some notable examples being the Project for the Intercomparison of Land surface
799 Parameterization Schemes (PILPS) (Pitman, 2003) and the Coupled Carbon Cycle
800 Climate Model Intercomparison Project (C4MIP) (Friedlingstein et al., 2006). Most
801 recently the International Land Model Benchmarking Project (ILAMB) has been
802 established to holistically assess the major components of TBMs, through a model-data
803 comparison framework that utilises standardised benchmarking and performance
804 metrics to identify critical model deficiencies and guide future development (Luo et al.,
805 2012). A major goal of ILAMB is to support the development of open-source software
806 that can facilitate such a benchmarking framework by the international modelling
807 community. The Protocol for the Analysis of Land-Surface models (PALS;
808 <http://www.pals.unsw.edu.au/>) ~~has been recently developed to offers such a~~meet the
809 formalism outlined by ILAMB, using standardised experiments to benchmark TBMs in
810 terms of how well they should be expected to perform, based on their complexity and
811 the information used to drive them (Abramowitz, 2012). In brief, PALS uses a set of
812 empirical benchmarks to fulfil the role of an arbitrary TBM of increasing complexity by
813 quantifying the amount of information in the meteorological forcing useful to reproduce
814 water, carbon and energy exchange. This gives a point of reference to measure at what
815 level of complexity a TBM is performing, by comparison of the statistical performance
816 between model and benchmark (Best et al., 2015). For example, we can assess whether
817 a sophisticated, state-of-the-art DGVM can outperform a simple linear regression against
818 shortwave irradiance (SW) at predicting GPP. If the outcome of this test were negative,
819 then this may suggest that the model does not capture the sensitivity of GPP to SW
820 accurately, flagging it as a priority for investigation and development. The important
821 distinction to make with the benchmarks is that they have no internal state variables
822 such as soil moisture and temperature, nor any knowledge of vegetation or soil
823 properties; they represent a purely instantaneous response to the meteorological
824 forcing (Abramowitz et al., 2008). The protocol of PALS meets the four criteria outlined
825 by ILAMB that objectively, effectively and reliably measure the underlying processes of a
826 TBM to improve its predictive skill (Luo et al., 2012). A direct application of this protocol

827 was presented [in a model intercomparison study](#) by Whitley et al. (Whitley et al., 2015),
828 ~~to where they assessed~~ the predictive capability of TBMs in savanna ecosystems by
829 comparing model outputs to 3 simple empirical benchmarks. In this study the authors
830 used 6 calibrated TBMs to predict ecosystem latent energy and GPP at five savanna sites
831 along the NATT, and found that in almost all cases the LSMs could perform only as well
832 as a multiple linear regression against SW, temperature and vapour pressure deficit (Fig
833 7). While an additional assessment of other outputs is required, the study highlighted
834 that there are likely systematic misrepresentations of simulated phenology and root-
835 water access in some of these models (Whitley et al., 2016). This is the first assessment
836 of its kind for investigating how well savanna dynamics are captured by modern TBMs,
837 and implies that without further development TBMs may have limited scope as
838 investigative tools for future projections of savanna ecosystems.

839

840 **4.5. Conclusion**

841 There is a large degree of uncertainty as to what impact climate change may have on the
842 structure and function of savanna ecosystems given their complex interaction with
843 climate. ~~Projected higher temperatures and rainfall variability, potentially promoting
844 more frequent fires, could favour C₄ grasses in mesic savanna, while drier conditions are
845 expected to increase tree mortality in semi-arid savanna. Conversely, increases to
846 atmospheric CO₂ are expected to favour C₃ trees, reflecting woody encroachment that is
847 already observed in many savannas globally (Donohue et al., 2009). Climate change
848 therefore has the potential to alter the carbon balance, which may have major feedbacks
849 on global climate and biogeochemical cycling.~~ Because TBMs are the only interpreter of
850 vegetation dynamics available to us that can reconcile the combination of effects
851 induced by climate change, their predictive capability at representing savanna dynamics
852 is of significant importance (Scheiter and Higgins, 2009). For TBMs to have the
853 necessary skill required to simulate savannas under both present and future climate,
854 model development must be concentrated towards more adequate representations of
855 phenology, root-water uptake, and disturbance dynamics, notably fires. We outline our
856 recommendations below in these areas:

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

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

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

873 In addition to the recommended areas for TBM development above, we also stress that
874 any improvements made in the representation of the above processes must be followed
875 with a more complete evaluation and benchmarking of TBMs that considers multiple
876 data sources in order to better constrain model uncertainty. We have highlighted that
877 EC systems provide an unparalleled source of data for testing the predictive capability of
878 TBMs at simulating water and carbon exchange in savannas. The role of regional flux
879 communities, such as the OzFlux network (Baldocchi et al., 2001; Beringer et al., 2016a),
880 will be to advance applications of EC systems that target savanna characteristics
881 specifically. Indeed, more studies are needed that measure overstorey and understorey
882 turbulent fluxes (Moore et al., 2016b), given their ability to quantify the contribution of
883 co-dominant tree and grass functional types. Additionally, a greater use of ecological
884 transects as tools for model evaluation are needed to quantify the ability of TBMs to
885 simulate savanna behaviour over changing floristic structure and climate (Hutley et al.,
886 2011). However, additional ecological and physiological measurements are also needed
887 to test modelled representations of root-zone water dynamics, carbon allocation and
888 growth, phenology and the recovery of vegetation after major disturbance events (fire
889 and cyclones); dynamic processes that cannot be verified by EC datasets alone. Facilities
890 such as the Australian Super Site Network (Karan et al., 2016) run by the Terrestrial
891 Ecosystem Research Network (TERN) will be critical to the collection of
892 ecophysiological information that can inform how savanna dynamics are represented in
893 TBMs.

894 Finally, we outline that future model experiments and inter-comparison studies that
895 leverage EC and ecophysiological datasets should target each of the three previously
896 mentioned processes individually. These may include rooting depth and water
897 extraction experiments that test the sensitivity of TBMs to the dry season transition
898 period, or fire management studies that investigate how the floristic structure in TBMs
899 responds to variable fire frequency. Furthermore, such studies must also be conducted
900 for savanna sites that have well-established datasets to test the processes in question.
901 For example, we expect that any study that attempts to test or improve the
902 representation of fire dynamics in TBMs is to be conducted at a site that has a long-
903 running EC record (given the variable return time of fire events) and a full suite of
904 concurrent ecophysiological measurements that quantifies the response of vegetation
905 under post-fire recovery.

906

907 [Current remote sensing observations suggest tree cover is increasing and grassland-](#)
908 [savanna-forest boundaries are changing](#) (Bond, 2008) ~~(Bond 2008,)~~ and these changes
909 [can have large feedbacks to the earth-atmosphere system](#) (Liu et al., 2015) ~~(Liu et al.~~
910 [2015\). \[There is still great uncertainty in predicting the future of savanna biomes\]\(#\)
911 \(Scheiter et al., 2015; Scheiter and Higgins, 2009\) ~~\(Scheiter and Higgins, 2009; Scheiter~~
912 \[et al. 2015\\) and ~~im~~ improving how savanna ecosystems are represented by TBMs will
913 likely encompass the consideration of additional processes that have not been
914 mentioned here. \\[This will no doubt include improved understanding of ecological\\]\\(#\\)
915 \\[theory that will lead to improvements in modelling ecosystem demographics and tree-\\]\\(#\\)
916 \\[grass interaction that will improve DGVMs\\]\\(#\\). However, we believe that by identifying
917 these processes as the cause for degraded model performance in this ecosystem, a
918 roadmap for future development can be constructed that leverages the availability of
919 rich datasets and current state-of-knowledge.\]\(#\)](#)

920

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936

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1468 **Figure Captions:**

1469 **Figure 1:** Global maps of (a) mean annual temperature and (b) mean annual rainfall for
1470 the period 1901 to 2015, determined from the CRU TS v. 3.23 dataset (Harris et al.,
1471 2014). The dataset has been clipped to the eco-floristic regions that approximate the
1472 global extent of savannas using the following plant functional types: tropical moist
1473 deciduous forest, tropical dry forest, subtropical dry forest and tropical shrubland
1474 (Ruesch and Gibbs, 2008).

1475 **Figure 2:** Predicted changes to aboveground biomass ~~between over the period~~ 2012
1476 ~~and to~~ 2100 for the Australian savanna region following three scenarios of projected
1477 rainfall seasonality according to IPCC SRES A1B (IPCC, 2007). The simulations were
1478 conducted using an adaptive Dynamic Global Vegetation Model (aDGVM) ~~shows and~~
1479 ~~predicted predicts how changes to~~ (a) present day (2012) aboveground biomass
1480 ~~changes~~, when (b) rainfall seasonality does not change, (c) rainfall seasonality increases,
1481 and (d) rainfall seasonality decreases over the forecast period. In all cases, the
1482 aboveground biomass of the Australian savanna region increases, with the magnitude of
1483 change determined by the degree of seasonality. Reprinted with permission from
1484 Scheiter et al. (2015).

1485 **Figure 3:** Representation of how changes to (a) tree and grass phenology determines
1486 changes in (b) savanna gross primary productivity (GPP) for an Australian mesic
1487 savanna. Time-varying signals of tree and grass LAI (a) are determined from a MODIS
1488 bulk LAI product using the method of Donohue et al. (Donohue et al., 2009), and are
1489 prescribed as inputs to the Soil-Plant-Atmosphere (SPA) model to predict separate tree
1490 and grass GPP. Data and model outputs are from Whitley et al. (Whitley et al., 2016)
1491 ~~(Whitley et al., 2015)~~ (*this issue*).

1492 **Figure 4:** Simulated differences in total ecosystem latent energy (LE) and the resultant
1493 evolution of soil moisture content through the soil profile over time for a mesic
1494 Australian savanna site. Simulations were conducted using two different terrestrial
1495 biosphere models (TBMs) that use different root-water extraction schemes. The top
1496 panel (a) shows outputs of savanna water flux using the Community Atmosphere
1497 Biosphere Land-surface Exchange (CABLE) model, where the density of the fine-root
1498 biomass weights soil-water extraction. The bottom panel (b) shows outputs of savanna
1499 water flux from the Soil-Plant-Atmosphere (SPA) model, where soil-water is

1500 dynamically extracted from where it sustainably available. Model outputs are from
1501 Whitley et al. (Whitley et al., 2015) (*this issue*).

1502 **Figure 5:** The nonlinear response of net ecosystem productivity (NEP) as the canopy
1503 regenerates after a fire event in 2003 at an Australian mesic savanna site. Fire
1504 disturbance of a sufficient intensity suppresses productivity, pushing the savanna state
1505 from sink to source over a period of 70 days at this site, as the rate of respiration
1506 exceeds the rate of assimilation due to resprouting costs. Empirical models created
1507 using an artificial neural network (NN) describe the 'UnBurnt' and 'Burnt' canopy NEP
1508 responses over the same period, and their difference estimates the loss of canopy
1509 productivity as a consequence of fire. Reprinted with permission from Beringer et al.
1510 (Beringer et al., 2007).

1511 **Figure 6:** Smoothed (10-day running mean) time-series of understorey (red),
1512 overstorey (green) and total ecosystem (red) gross primary productivity (GPP) for a
1513 mesic savanna site in northern Australia. Rainfall is represented as black bars. Negative
1514 and positive signs represent the savanna state as a carbon source or sink respectively,
1515 and orange arrows depict the occurrence of fire events. Data products for total
1516 ecosystem and understorey GPP are inferred from observations of net ecosystem
1517 exchange using eddy-covariance towers at heights of 23 m and 5 m respectively.
1518 Overstorey GPP is determined as the difference between the ecosystem and the
1519 understorey. Reprinted with permission from Moore et al. (Moore et al., 2016b) (*this*
1520 *issue*).

1521 **Figure 7:** Rank plot showing the average performance of 6 terrestrial biosphere models
1522 (TBMs) across the North Australian Tropical Transect (NATT). The closer a model's rank
1523 is to 1 the better its performance is at predicting latent energy (LE) and gross primary
1524 productivity (GPP). Empirical benchmarks representing increasing levels of complexity
1525 (emp1 < emp2 < emp3) are represented as grey lines, and coloured lines denote each
1526 model. The lines have no scientific value and are used for visual purposes only.
1527 Benchmarking and model evaluation data are from Whitley et al. (Whitley et al., 2015)
1528 (*this issue*).