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Alternate grassland states are determined by palatability-flammability trade-offs

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Trends in Ecology and Evolution

Alternate grassland states are determined by palatability-flammability trade-offs

--Manuscript Draft--

Manuscript Number:	TREE-D-18-00264R1
Article Type:	Forum
Keywords:	grass; grazers; fire; grazing lawn; savanna; forest
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Order of Authors:	Gareth Hempson Sally Archibald Jason E. Donaldson Caroline E.R. Lehmann
Abstract:	Fire and mammalian grazers both consume grasses, and feedbacks between grass species, their functional traits and consumers have profound effects on grassy ecosystem structure worldwide, such that savanna and grassland states determined by fire or grazing can be considered alternate states. These parallel savanna-forest alternate states that likewise have myriad cascading ecosystem impacts.

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12 January 2019

Dear Dr Andrea Stephens,

Thank you for the opportunity to resubmit our manuscript 'Alternate grassland states are determined by palatability-flammability trade-offs' to Trends in Ecology & Evolution.

We have now addressed all of the concerns raised by the reviewers. While we have made a number of revisions to our manuscript, these are necessarily limited due to the word limit of the article. Our response to reviewers also includes a wide range of references that we are unable to include in the manuscript, which hopefully provides sufficient evidence to support our arguments where requested by the reviewers. Note that our response to your comments follow at the end of this letter.

Should our manuscript be accepted for publication, we would like to ask whether it is possible to list two corresponding authors – this has arisen because the University of Edinburgh is willing to pay open access fees should Dr Lehmann be listed as a corresponding author.

We have also unfortunately not been able to find time to produce a Figure360 video; it has simply just been a very busy time of year for us all – the grasses are now flowering and our main field season has started.

Yours sincerely,

A handwritten signature in black ink, appearing to read 'G. Hempson'.

Dr Gareth Hempson



Response to the Editor

As you can see from reading the referee reports were generally positive. Reviewer 1 comments on the lack of data etc (see their second main issue). I would like you to be clear what data are available, and if none/little, suggest the type of data that would be needed to test the ideas presented here.

We feel that there is a wealth of data supporting our arguments, and have provided a full response to Reviewer 1; this includes a substantial (although by no means comprehensive) set of references. Briefly, we'd contend that it is well established in the literature that there are positive feedbacks between grazers and grazing lawns, and between fire and fire-grasses (sometimes referred to as the grass-fire cycle). This is the first piece of evidence for alternate stable states – a positive feedback that maintains each state. Furthermore, the literature also includes a wide array of studies that explore the processes that lead to the formation and 'reversal' of these states – and shows that these follow different ecological pathways – this is evidence for hysteresis (discussed more fully below), which further supports our argument that these grass communities constitute alternate stable states. What has not been done, however, is to link up all this evidence in the way we have here.

That said, there remains much work to be done to understand the specifics of the general processes that we describe, and how these change across environments. This forms a core component of our current research – for example, frequent grazing does not always produce grazing lawns, it can also result in a switch to annual species and a loss of cover (see our response to Reviewer 1 re 'desertification'). Also, the generalist grass communities that lie between the grazing-lawn and fire-grass 'basins of attraction' vary across environmental gradients, such that the ecological pathways that characterise grazing-lawn to fire-grass transitions and vice versa are likely different under different environmental contexts. While these details are important, we would prefer not to distract from the description of the general patterns that we provide in our manuscript, keeping our primary focus on the communities where positive feedbacks clearly produce alternate stable states.

This also relates to Reviewer 2's point regarding exceptions - what would be an exception vs. a rejection of the hypotheses put forward?

Reviewer 2: Also as written, the manuscript does not consider exceptions to the ideas put down here: Are there no cases where short grass states occur in high productivity systems or tall grass in low productivity without invoking the mechanisms here.....and how do they differ from these systems.

Central to our arguments is that the grazing-lawn and fire-grass states that we describe here are dependent on positive feedbacks with grazing and fire respectively. Rejection of our hypothesis would occur if these states could persist without these consumers – there is clear evidence for these feedbacks (and the community dependence on them) under many conditions, so we're confident that our hypotheses have wide relevance. However, grasses are a hugely diverse and varied family, so there is clearly potential for exceptions (in the sense of community structure) to arise – reedbeds, for example, are a tall grass community that is not fire-dependent. Short statured grass communities also occur under highly productive conditions in temperate regions where growing seasons are short – there is simply inadequate time for fire-grass communities to develop (and then dry out sufficiently in the plant dormancy season for them to burn). Note however that grazer and fire feedbacks with grazing-lawn and fire-grass communities are in essence part of their definition – if they are not fire-dependent, then they are not fire-grasses (even though they may be structurally similar, e.g. reedbeds). Our purpose here then is to draw particular attention to two grass community types – both maintained by positive feedbacks with consumers – and that co-occur as alternate stable states in savannas and grasslands.

I would also like you to clarify in the text that there is a continuum, I agree with Reviewer 1 that the text suggests that the states are a dichotomy (or rather a tri-chotomy).

There is in some sense a continuum, but crucial evidence for alternate stable states is that each state forms a 'basin of attraction' – which is resilient – meaning that for a state shift to be initiated, a perturbation is required that is large enough to shift the state beyond the critical bifurcation point and into a transitional phase that may then be 'captured' by a new basin of attraction – i.e. an alternate stable state. An important feature of alternate stable states is hysteresis, a dependence on prior conditions that means that the trajectory between phases is different in different directions. Thus while there is a continuum between states in the sense that you can move back and forth between them, the ecological pathway, and the rate (and likelihood) of change in each direction is different – without this you simply have a gradual gradient (or continuum) of community turnover. We would thus prefer not to emphasise the term 'continuum' in the text, as we feel that it would undermine our efforts to present evidence for the existence of alternate stable states. Furthermore, it seems that Reviewer 1 may have misinterpreted parts of our manuscript, in the sense that they appear to feel that we consider grazing-lawn and fire-grass communities to not be part of savannas, or that we have somehow considered the savanna-forest comparison to be focussed on trees alone. Rather, we present a discussion of alternate grass community states that occur within savannas and grasslands, and then compare this to savanna-forest alternate stable states. **We have tried to clarify this in**

the text by modifying Figure 1 to indicate that the grass communities we discuss occur in the savanna biome, and then highlighting that it is the traits of grasses in mesic savannas that maintain fires, and hence are fundamental to shaping the savanna-forest boundary.

From an editorial perspective, I thought that the paper was very well written. I particularly liked the Figures and felt they supported the text well. As someone who does not work on grasslands nor stable states, I was unclear as to whether your framework applies to all grasslands globally or just to the African savanna? You don't mention grasslands elsewhere and all of your examples are African. A couple of extra words in the Abstract would clarify this (and if global, add a non-African reference or two).

Thank you. Our framework applies to grassy ecosystems globally that are able to support frequent fires and grazers – this spans all continents (excl. Antarctica of course), but not all latitudes (mainly due to growing season length constraints to fire-grasses at high latitudes, although this is an area of ongoing research). Africa, however, has been the location for much of the research on the dynamics we describe (intact large mammal grazer communities and many fire-prone ecosystems) – hence our bias towards African references. We have indicated that our framework applies globally by modifying the abstract to include ‘worldwide’ and replacing Bond & Keeley 2005 with Knapp et al. 1999, which is an example of bison lawns and fire-grass communities in Konza Prairie in North America. Note that D’Antonio & Vitousek 1992 discuss examples of positive feedbacks with fire-grasses across the globe – although this is largely in the form of consequences of invasions by African and South American fire-grasses.

In addition, please also pay particular attention to the following points:

*** Please follow our Instructions to Authors for the correct style for the reference list.**

We have checked through, and detected a few errors – hopefully all have been ironed out now; journal abbreviations are based on references in previous issues of Trends in Ecology & Evolution.

*** A solidus (/) can be ambiguous, therefore, please change ALL solidi to 'and', 'or', 'and/or' or '-' where appropriate.**

We have changed grazing-lawn – fire-grass/savanna – forest to “grazing-lawn savanna – fire-grass savanna – forest”

*** Please note that the figures should 'stand alone' and thus figure legends need to be explanatory rather than just descriptive.**

We have revised the legend for Figure 1 to now read:

Figure 1. Grazing-lawn vs. fire-grass and savanna vs. forest alternate stable states. The probability of occurrence of grazing-lawn savanna, fire-grass savanna and forest changes across a productivity gradient (middle panel). This is due to environmental limits on grazers, fire and biomass production (lower panel), that in turn shape the role that each can play as ecological drivers (top panel), primarily through modifying the light environment. At high productivity, forest can shade out fire-grass savanna, which in turn can shade out grazing-lawn savanna at mid-level productivity. On the other hand, positive feedbacks between grazers and grazing-lawn grasses, and fire and fire-grasses, can promote their expansion up the productivity gradient – until these consumers themselves become constrained by environmental limits. These dynamics give rise to alternate grazing-lawn vs. fire-grass alternate stable states in savannas, which share parallels with previously described savanna-forest alternate stable states.

We hope that the legend for Figure 1 is adequate – elaboration would increase overlap with the rest of the text in Box 1.

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Not applicable to this manuscript.

Response to reviewers

Thank you for your time and the valuable feedback that has helped to improve our manuscript. Our responses are structured as follows: reviewer comments in bold, our response in regular text, and changes to the manuscript highlighted in blue.

Reviewer #1:

In this article, the authors contrast traits, drivers, and state trajectories among four communities common in African ecosystems: grazing lawns vs. fire prone tallgrass swards and fire-prone savanna trees, and dense woodland forest. An argument is presented such that traits and relationships among fire and/or grazers regulate herbaceous ecosystem state (between grazer dominated versus fire-dominated). As presented the article is interesting and informative, and accessible to a broad audience. The authors are esteemed savanna ecologists with varying career stage (Hempson and Donaldson are future stars, while Archibald and Lehmann are established mid-career stars). While I am supportive of the general question of inquiry (understanding the drivers and consequences of ecosystem state transitions), I have several significant concerns detailed as follows.

I struggled with the comparison between grassland dominated states and woody dominated states largely because for most savannas, the short lawn grass community, tall grass community, and savanna tree community are often intermixed. Savannas are by definition an ecosystem type that includes stable grass-tree dynamics typically regulated by the interplay of grazers and fire. Grass communities and savanna trees are not discrete states, but rather species in these community types exist in a heterogeneous framework that well describes the tropical / subtropical savanna biome. As such, the comparison dichotomy presented here between lawn grass and tall grass OR savanna tree vs forest tree seems fixed and arbitrary.

Yes indeed – and we by no means wish to imply that there is a dichotomy between lawn and tall grass 'OR' savanna [tree] vs forest tree systems. Rather, our interest lies in first exploring the dynamics that maintain the various functionally distinct grass communities that occur within savannas (and grasslands); that these co-occur (giving rise to savanna heterogeneity) is central to our argument for the existence of alternate stable states. Thereafter, we contrast these grass community alternate stable states with previously described savanna-forest alternate stable states,

and which typically occur in more mesic, higher productivity systems. Here we wish to clarify that it is the grasses in these mesic savannas that are central to maintaining fire in the system, and hence the savanna-forest boundary. Rather than suggesting a dichotomy between fire-grass and savanna systems (or any other grassy/woody state), we instead wish to show that a particular grass functional community typifies mesic savannas, whose traits then underpin the savanna-forest alternate stable state phenomenon. We have attempted to illustrate this in Figure 1, where tall grass is shown as the ecological driver supporting fire and hence transitions from mesic savanna to the forest state. **To help clarify this, we have modified the legend and central panel of Figure 1 to now indicate that grazing-lawns and fire-grasses are savanna vegetation types.** Hopefully this now makes it clear that we do not consider grazing-lawns or fire-grass states as being distinct from savannas, but rather a component of savannas. For the rest, the distinctions between either grass community states, or biome-level states, are defined by positive feedbacks – and thus form well-defined basins of attraction.

The second main issue with the framework of this study is I know of no data in the literature to suggest these two communities (lawn grass vs. tallgrass swards) are alternative stable states [citations #4, 6 are not evidence of alternate stable states]. Looking through the guidelines for 'Forum' articles at TREE, unpublished data, simulations, and meta-analyses are not to be included in this article type. Given that there is not published data to support this argument (grass type alternative stable states) I don't see how publication in the current framework is viable.

Grazing-lawn and fire-grass communities are well documented in the literature, although 'fire-grass' is a name we've chosen to use here, given the lack of a single, widely utilised term. McNaughton's seminal work (McNaughton 1984) on grazing lawns sparked widespread interest into the processes/mechanisms involved in the formation and maintenance of lawns (e.g. Ruesch & McNaughton 1987, McNaughton et al. 1997, Hamilton & Frank 2001, Cromsigt & Olf 2008, Stock et al. 2010, Veldhuis et al. 2014, Donaldson et al. 2018); their grazing value is also widely recognised (e.g. Prins 1996, Cingolani et al. 2005, Verweij et al. 2006) although they appear surprisingly undervalued in a commercial rangeland context. Grazing lawns have also been identified in a wide array of contexts – e.g. bison (Knapp et al. 1999), prairie dog (Detling & Painter 1983) and goose lawns (Person et al. 2003) in North America, cattle (Bokdam & Gleichman 2001) and goose (van der Graaf et al. 2005) lawns in Europe, marsupial lawns in Tasmania (Leonard et al. 2010), native large mammal grazers in Nepal (Karki et al. 2000) and sheep lawns in South America (Cingolani et al.

2005). There is thus widespread recognition of the existence of lawns as a distinct grass community in a wide variety of landscapes, maintained by specific processes.

Fire-grasses occur worldwide, but are perhaps best known from Africa and South America. African fire-grasses have proved to be highly invasive elsewhere, with their spread enhanced by modification of the 'grass-fire cycle' (as prominently described by D'Antonio & Vitousek 1992). For example, the invasion of *Andropogon gayanus* in the Northern Territory, Australia, has led to the establishment of hot, annual fires, which has had negative effects on native species that are not adapted to this fire regime (Rossiter et al. 2003, Petty et al. 2007). Similarly, fire-grasses from Africa and South America have invaded Hawaii (Hughes et al. 1991, D'Antonio & Vitousek 1992), and African fire-grasses (e.g. *Hyparrhenia rufa*) have invaded the Americas (Williams & Baruch 2000), posing threats to forests (Janzen 1988). The existence of fire-grass communities – and the positive feedbacks that maintain them – are thus also widely documented. Our contribution here is to draw together these observations, while also recognising that many grass communities regularly experience intermediate levels of both fire and grazing and are characterised by distinct suites of grass functional types (i.e. not simply a mix of grazing-lawn and fire-grasses, although growth form plasticity means that there may be some species overlap [space limitations preclude a full discussion of these intermediate, generalist communities]).

Evidence for alternate stable states includes assessing whether positive feedbacks maintain each stable state – this is adequately documented in the literature. Furthermore, these states co-occur under the same environmental conditions. Additional evidence for alternate stable states is that they are not simply a gradual, smooth continuum, but that hysteresis has indeed manifested – i.e. the pathway of change between states is contingent not only on current conditions, but also on prior conditions. Accordingly, the initial condition is fundamental to determining what sort of perturbation is required to initiate a change (i.e. exceed the resilience of the state, moving the system passed a critical bifurcation point), and consequently, the likelihood of change and the rate of change once a large enough perturbation occurs. We contend that adequate evidence exists in the literature to propose that the type and magnitude of perturbation necessary to produce shifts from grazing-lawn to fire-grass states, or vice versa, exist in the literature, and that these pathways are different – i.e. the initial condition of whether you're starting in a grazing-lawn or fire-grass state is fundamental to determining the ecological pathway. Forum articles are restricted to 1200 words and 12 references; we are simply unable to fully expand on all these ideas – and properly reference them – within this article type.

- Bokdam, J., & Gleichman, J. M. (2000). Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied ecology*, 37(3), 415-431.
- Cingolani, A. M., Posse, G., & Collantes, M. B. (2005). Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology*, 42(1), 50-59.
- Cromsigt, J. P., & Olff, H. (2008). Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes. *Oikos*, 117(10), 1444-1452.
- D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics*, 23(1), 63-87.
- Detling, J. K., & Painter, E. L. (1983). Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. *Oecologia*, 57(1-2), 65-71.
- Donaldson, J. E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z., & Parr, C. L. (2018). Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*, 55(1), 225-235.
- Hamilton III, E. W., & Frank, D. A. (2001). Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology*, 82(9), 2397-2402.
- Hughes, F., Vitousek, P. M., & Tunison, T. (1991). Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. *Ecology*, 72(2), 743-747.
- Janzen, D. H. (1988). Tropical dry forests. *Biodiversity*, 130-137.
- Karki, J. B., Jhala, Y. V., & Khanna, P. P. (2000). Grazing Lawns in Terai Grasslands, Royal Bardia National Park, Nepal 1. *Biotropica*, 32(3), 423-429.
- Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C., & Towne, E. G. (1999). The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience*, 49(1), 39-50.
- McNaughton, S. J. (1984). Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist*, 124(6), 863-886.
- McNaughton, S. J., Banyikwa, F. F., & McNaughton, M. M. (1997). Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science*, 278(5344), 1798-1800.
- Person, B. T., Herzog, M. P., Ruess, R. W., Sederger, J. S., Anthony, R. M., & Babcock, C. A. (2003). Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. *Oecologia*, 135(4), 583-592.
- Petty, A. M., Werner, P. A., Lehmann, C. E., Riley, J. E., Banfai, D. S., & Elliott, L. P. (2007). Savanna responses to feral buffalo in Kakadu National Park, Australia. *Ecological Monographs*, 77(3), 441-463.
- Prins, H. H. T. (1996). Patch selection: predators and grazing by 'rule of thumb'. In *Ecology and Behaviour of the African Buffalo* (pp. 178-217). Springer, Dordrecht.
- Rossiter, N. A., Setterfield, S. A., Douglas, M. M., & Hutley, L. B. (2003). Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions*, 9(3), 169-176.
- Ruess, R. W., & McNaughton, S. J. (1987). Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos*, 101-110.

- Stock, W. D., Bond, W. J., & Van De Vijver, C. A. (2010). Herbivore and nutrient control of lawn and bunch grass distributions in a southern African savanna. *Plant Ecology*, 206(1), 15-27.
- van der Graaf, A. J., Stahl, J., & Bakker, J. P. (2005). Compensatory growth of *Festuca rubra* after grazing: can migratory herbivores increase their own harvest during staging?. *Functional Ecology*, 19(6), 961-969.
- Veldhuis, M. P., Howison, R. A., Fokkema, R. W., Tielens, E., & Olff, H. (2014). A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant–soil water balance. *Journal of Ecology*, 102(6), 1506-1517.
- Verweij, R., Verrelst, J., Loth, P. E., MA Heitkönig, I., & MH Brunsting, A. (2006). Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. *Oikos*, 114(1), 108-116.
- Williams, D. G., & Baruch, Z. (2000). African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological invasions*, 2(2), 123-140.

Other concerns:

The definitions of alternative stable states, hysteresis and regimes shifts in the first paragraph are unsatisfactory. There are fixed definitions for these terms. I would recommend the authors use the accepted terminology.

Without elaboration by the reviewer, it is hard to know what parts of our phrasing are unsatisfactory. We'd contend that while succinct, our usage of the terms conform to the widely accepted norms, and given the word limit of the article, providing comprehensive definitions for these terms would be at the expense of the focal points of our manuscript. Instead, we have looked to briefly introduce the core concepts around alternate stable states, and provide a key reference that discusses these in full (Scheffer & Carpenter 2003). Note that in Box 1 we expand on the first paragraph by discussing the evidence for grazing-lawn and fire-grass alternate stable states.

Given the reviewer's next comment, we have modified the last sentence of the first paragraph to read: 'This is evidence for hysteresis – an important property of alternate stable states – and means that initial conditions and lag effects shape how regime shifts occur [1].' [replacing: This is known as hysteresis – an important property of alternate stable states – meaning that initial conditions determine how regime shifts occur [1].]

- Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in ecology & evolution*, 18(12), 648-656.

In addition, I disagree with the assessment that initial conditions dictate how regime shifts occur. For most ecosystems, regime shifts are a byproduct of changes along a continuum of disturbance or resource change, not a simple reflection of the initial conditions.

Hysteresis is the phenomenon whereby prior conditions shape the trajectory of a particular process – i.e. there are lag effects. A consequence of this is that a shift from A to B follows a pathway different to that from B to A. To initiate a regime shift, a perturbation is required that is large enough to move the system out of the basin of attraction that maintains that state – the system then enters a transitional phase, and can then be ‘captured’ by a new basin of attraction (should an alternate state exist) – completing the regime shift. We by no means wish to assert that it is only the initial condition that shapes this process – however, because A to B and B to A are different, the initial condition is fundamental to setting the pathway that will be followed: the initial condition determines the type and size of perturbation that is necessary to escape the initial basin of attraction, and hence the likelihood of this occurring. Once the critical bifurcation point has been passed (i.e. the resilience that maintains a system within a basin of attraction has been exceeded), then the community/ecosystem trajectory will be influenced by environmental variation that moves it towards one or another new basin of attraction – or it could persist on a continuum where it simply responds to current conditions (i.e. without pronounced hysteresis).

To clarify that we do not intend to imply that hysteresis means that only initial conditions are relevant, we have modified the last sentence of the first paragraph to read: ‘This is evidence for hysteresis – an important property of alternate stable states – and means that initial conditions and lag effects shape how regime shifts occur [1].’ [replacing: This is known as hysteresis – an important property of alternate stable states – meaning that initial conditions determine how regime shifts occur [1].]

Some of the dichotomies between grass traits in the section "Traits and positive feedbacks" do not apply only to one grass community. For example, lawn grasses can have equivalently high rates of photosynthesis as sward grasses, and sward grasses are as susceptible to light limitation as lawn grasses. Light limitation for grasses is the primary driver of bush encroachment in many grassland ecosystems.

Yes indeed, but 1) we do not suggest that fire-grasses have higher photosynthetic rates than lawn-grasses, and 2) that woody species can shade out tall fire-grasses does not have particular bearing

on our discussion of grazing-lawn vs. fire-grass states, and is a central point in our discussion of the dynamics at the savanna-forest boundary.

With regard to photosynthetic rates, we indicate that fire-grasses have high photosynthetic rates which allows rapid regrowth – after *surviving* the fire. Lawn grasses, some of which may indeed have similarly high photosynthetic rates (Anderson et al. 2013 – although we would not consider the two bunch grasses they studied to be fire-grasses i.e. *Sporobolus pyramidalis* and *Panicum maximum*), would need to recruit into the region and then outcompete the rapidly regrowing fire-grasses. Equivalent photosynthetic rates would thus be more than enough for established fire-grasses to hold a competitive edge over newly recruited species. Nonetheless, it is worth noting that Ripley et al. (2015) show that the three species of Andropogonae (the typical fire-grass subfamily, with the study including *Hyparrhenia hirta*, a typical fire-grass) had higher photosynthetic rates than the species they studied in three other sub-families (although no lawn grasses were studied).

The reviewer is correct in pointing out that light limitation of grasses (with fire-grasses not being exempt) is an important process in bush encroachment – in mesic savannas, this encroachment would likely be by species typically associated with forest margins, which can ultimately lead to a shift to the forest state. In drier systems, bush encroachment is likely to lead to a dominance of woody shrubs (e.g. *Dichrostachys cinerea*), without a transition to forest – although thicket vegetation types may develop. These may represent alternate stable states if they are maintained by positive feedbacks, and as pointed out by Reviewer 2, more general principals may emerge through an examination of these and other vegetation types that co-occur with savannas. That trees can shade out fire grasses is consistent with our description of dynamics at the savanna-forest boundary.

Anderson, T. M., Kumordzi, B. B., Fokkema, W., Fox, H. V., & Oloff, H. (2013). Distinct physiological responses underlie defoliation tolerance in African lawn and bunch grasses. *International Journal of Plant Sciences*, 174(5), 769-778.

Ripley, B., Visser, V., Christin, P. A., Archibald, S., Martin, T., & Osborne, C. (2015). Fire ecology of C3 and C4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology*, 96(10), 2679-2691.

On line 76, what do you mean by 'competitive demands of each system'?

For savannas, we are referring to the requirement for savanna trees to be able to complete their life cycle while exposed to fire at regular intervals (NB traits include: bark thickness, bud position in the

bark layer and resprouting), browsing and competition from grass are also important at some life stages. For forests, we are referring to the requirement for forest trees to be able to complete their life cycle under light-limited conditions in the seedling and sapling phases (NB traits: seed size, leaf area index, photosynthesis light response curves), and to exploit canopy gaps when they occur.

The text on line 79 states that fire grasses invest less belowground than savanna trees or grazing lawn grasses. What evidence exists for this statement? Sward grasses often have 2/3 of their total biomass allocated belowground, although this can vary by species and ecosystem type. In addition, grazing often results in greater growth allocation aboveground, to replace the tissue lost. If anything, I would expect the allocation of growth above:belowground to favor lawn grasses rather than sward grasses. Regardless, you must provide some evidence to support your claim.

We agree that fire-grasses can sometimes have large below-ground reserves. However, there are also stunning examples of very minimal below-ground investment (e.g. *Tristachia superba*). Ripley et al. (2015) also show the above:below-ground biomass ratio to be highest in the Andropogonae – the classic fire-grass subfamily (although not all species are fire-grasses); **we now cite this reference at the relevant point in the text.** Moreover, an unpublished meta-analysis by our students shows that the effect of grazing is not uniformly to decrease below-ground reserves, and we believe this depends strongly on the ecological strategy of the grasses involved. Thus, while we feel there is sufficient evidence to merit our phrasing in the manuscript of ‘likely with lower belowground investment’, we agree that this is a very important point to resolve, and are currently working on a large common garden experiment contrasting resource allocation in a range of fire- and grazer-adapted grasses. Note that the text in line 79 is intended to compare fire-grasses to grazing-lawn grasses, and forest trees to savanna trees.

The last portion of the manuscript (lines 131-134) does not flow from the rest of the manuscript, and does not have appropriate citations (such as Archibald and Hempson, Phil Roy Soc B 2016). As presented here, this is an odd ending to the manuscript and doesn't reflect the main premise of the article.

We have replaced this ending with one that now refers back to the central novelty of our manuscript, that grass and their traits play an important role in shaping ecosystem dynamics:

'What appears to be clear, however, is that grasses and their traits are fundamental to orchestrating dynamics in these consumer-controlled ecosystems.'

Box 1 notes that 'fire grasses are unpalatable'. This is certainly not a universal trait. Many of the world's grasslands are dominated by 'fire grasses' and support large guilds of native grazers as well as the cattle industry for many countries. Even in Southern Africa, many tall grasses are very palatable including *Chloris gayana*, *Digitaria eriantha*, *Diheteropogon amplexans*, *Enteropogon macrostachyus*, *Eragrostis curvula*, *Panicum maximum*, and *Themeda triandra* to name a few.

None of the grasses that are listed would be considered as classic fire-grasses – these are all fairly generalist species that have life histories that allow them to persist under both fire and grazing (and thus would typically occur in communities near the diagonal black line in the figure in Box 1). For example, *Digitaria eriantha* is what is termed an “increaser 1” species in South Africa, which means that it increases when ungrazed AND unburned. Also among the species listed, *Themeda triandra* is an interesting case in that it is hugely variable in growth form – indeed, it can persist in lawns with prostrate leaves and dwarfed inflorescences, while other tall, stemmy growth forms allow it to persist in frequently burned swards. Note that the trait plasticity of this species would conform to our general formulation – the dwarfed form would be more palatable because a bite would be composed largely of digestible leaf material, while the tall form would have lower palatability due to bites containing a greater proportion of stem material – which has to have a high C:N ratio to provide the structural support to remain upright. We contend that it is reasonable to generalise that the requirement for structural support – obtained via carbon dense stems – and that is necessary to effect the tall, upright, fire-grass growth form, reduces fire-grass palatability relative to lawn grasses where leaves – with lower C:N ratios – are primarily ingested. We have modified the text to read 'fire-grasses are relatively unpalatable'.

In the figure for Box 1 (Figure 1), I believe a more appropriate alternative stable state for over grazing is desertification (similar to the long body of evidence by Steve Archer).

We agree fully that frequent grazing can lead to the formation of grazing lawns under some conditions, and 'overgrazed' conditions in others, and have a manuscript in preparation that explores where this is the case. Where heavy grazing leads to desertification there may well be positive feedbacks that maintain the state, with hysteresis potentially also manifesting during

transitions between states. Understanding the conditions when each feedback operates (i.e. grazing-lawn vs. desertification) is important and worthy of further elaboration, but again, with 1200 words it is not possible.

I also disagree with the supposition that tall grass swards have reduced moisture while lawn grasses have higher moisture (no citations are provided to support this in the text). The higher albedo and higher litter layer in tallgrasses typically results in HIGHER soil moisture, while lawns typically have reduced moisture as a byproduct of lower albedo, higher sensible heat, and greater evaporative demand.

We believe this is a misunderstanding. Yes, the microclimate and associated soil moisture levels in tall grass swards tend to be cooler and moister than in lawns (Vaieretti et al. 2010, van der Plas et al. 2013, Veldhuis et al. 2014 – although we have some data demonstrating that this is not always the case and that there is seasonal variation). However, that was not the point we were making here. We were discussing vegetation moisture levels – and specifically with regard to when these communities are consumed. High fuel moisture reduces ignitability, flammability etc. – so fire grasses are consumed when they are dry. Lawns by contrast are preferentially grazed when they are growing and the leaves are thus moist and actively photosynthesising – and yes, this is contingent on adequate soil moisture. As we note in the manuscript, grazers do not make much use of lawns for forage in the dry season, because the low leaf biomass is not replaced, and they are thus forced onto taller dry season forage reserves. These are likely to be generalist grasses occurring in wetter parts of the landscape – such as *Themeda triandra* growing in seep zones that is used by wildebeest in Kruger (Yoganand & Owen-Smith 2014). Alternately – or when even these grasses are dry – grazers need to have adequate access to drinking water to support metabolic processes; this is particularly important when forage is dry.

Vaieretti, M.V., Cingolani, A.M., Harguindeguy, N.P., Gurrich, D.E., & Cabido, M. (2010). Does decomposition of standard materials differ among grassland patches maintained by livestock? *Austral Ecology*, 35(8), 935-943.

van der Plas, F., Zeinstra, P., Veldhuis, M., Fokkema, R., Tielens, E., Howison, R., & Olf, H. (2013). Responses of savanna lawn and bunch grasses to water limitation. *Plant ecology*, 214(9), 1157-1168.

Veldhuis, M. P., Howison, R. A., Fokkema, R. W., Tielens, E., & Olf, H. (2014). A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant–soil water balance. *Journal of Ecology*, 102(6), 1506-1517.

Yoganand, K., & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, 37(10), 969-982.

Reviewer #2:

General Comments

The authors articulate an interesting and novel contribution to the literature on alternate stable states, and I agree that while tall-grass and short-grass states have long been recognized as distinctive and associated with different disturbance regimes, they have not been conceptualised and placed in the alternate stable state literature as in this contribution, and the trade-off between flammability and palatability traits in the grasses in these alternate states is an excellent new insight from this paper.

Written as a short forum note and to articulate this concept, the draft and the figures are appropriate and do a good job of articulating this new idea. It should generate a lot of research and subsequent development.

The contrast with forest-savanna alternate states is useful because light environments and fire are likewise important in those transitions, just as they are drivers of the tall grass-short grass transition- However, one cannot help but wonder how the manuscript would develop or what insights it would lead to if these were placed in the context of a suite of other known alternate vegetations states (eg- forest-grassland, thicket-grassland, thicket-savanna), and whether some overarching general principles might emerge- however that would clearly be a different manuscript altogether and may dilute the key messages and system focus of this one- so this is more of a thought exercise than a critique.

Yes, there is clearly an intriguing broader set of relations across the various vegetation states spanning the environmental gradient from arid savanna to forests. Bush encroachment and thicket formations likely have similar principles underlying their dynamics with the grass layer; there are likely to be very interesting parallels and differences between woody plant functional types and the various grass life histories. Light competition is an interesting avenue to explore – however, herbivory (i.e. browsing) may play a less prominent role, because of the lack of any obvious positive feedbacks between browsers and woody vegetation (although shrubs?).

Also as written, the manuscript does not consider exceptions to the ideas put down here: Are there no cases where short grass states occur in high productivity systems or tall grass in low productivity without invoking the mechanisms here.....and how do they differ from these systems. Again it may be a space constraint but such considerations might generally add more nuance to the paper, especially since it is a conceptual contribution.

Central to our arguments is that the grazing-lawn and fire-grass states that we describe here are dependent on positive feedbacks with grazing and fire respectively. Rejection of our hypothesis would occur if these states could persist without these consumers – there is clear evidence for these feedbacks (and the community dependence on them) under many conditions, so we're confident that our hypotheses have wide relevance. However, grasses are a hugely diverse and varied family, so there is clearly potential for exceptions (in the sense of community structure) to arise – reedbeds, for example, are a tall grass community that is not fire-dependent. Short statured grass communities also occur under highly productive conditions in temperate regions where growing seasons are short – there is simply inadequate time for fire-grass communities to develop (and then dry out sufficiently in the plant dormancy season for them to burn). Note however that grazer and fire feedbacks with grazing-lawn and fire-grass communities are in essence part of their definition – if they are not fire-dependent, then they are not fire-grasses (even though they may be structurally similar, e.g. reedbeds). While we agree that discussing these structurally similar grass communities would add more nuance to the manuscript, this would require removing content on – and possibly distract from – our main focus of drawing attention to the grazing-lawn and fire-grass alternate states.

Comments on the text

Line 27: Hysteresis- the idea that the system trajectory is determined by initial conditions- does not follow from the previous sentence about how the likelihoods and rates of transitions between the two alternate states are different- this does not immediately invoke hysteresis does it? Maybe change text here to not have it implied from the previous line.

We contend that where hysteresis is in effect, the difference in perturbation required to initiate a state shift means that the likelihood, rate and ecological pathway of a transition differs for shifts from A to B or vice versa. In response to this comment and those from Reviewer 1, we have modified

this sentence to read 'This is evidence for hysteresis – an important property of alternate stable states – and means that initial conditions and lag effects shape how regime shifts occur [1].' This retains the emphasis on the importance of the initial condition (which we feel is fundamental), but notes that current conditions can also produce lag effects contributing to hysteresis and the ecological pathway that is followed.

Line 40: replace 'the amount of fire and grazers' with 'whether a system is fire-or-grazer driven'

Done

Line 43- Please delete innumerable, too dramatic and unlikely to be correct

Done

Line 48: Replace 'overtopped' with 'shaded out'?

Done

Lines 52-54: I understand that stem is protected because grazers are primarily consuming the foliage which is dense and nutrient rich, and grows in the direction of bites, while the stem is lateral. How are the buds protected? And aren't all roots protected, whether it is a fire-grass or a graze-grass. Please clarify.

Grass buds (meristematic tissues) occur at a variety of positions within the plant – including at the apex of the culm, the leaf collar, the nodes, and the crown. A prostrate culm means that the apical meristem is often positioned below grazing depth – in contrast to an upright culm that is always exposed. More importantly in this context though, is that the leaf collar and nodes are also protected – the leaf has two components: a sheath that wraps around the stem, and originates at the node, and the blade (i.e. the main photosynthetic tissue that is free of the stem) that originates at the leaf collar (also against the stem and thus below grazing height). In a grazing lawn, the leaf blade tips that stick up into the reach of grazers are thus the oldest parts of the leaf – with new leaf blade tissue being produced at the collar – grazers thus tend to continually remove older, less efficient leaf tissues, promoting greater light intensities on younger tissues near the leaf collar meristems. In upright grasses (including fire-grasses), all these tissues are accessible to grazers.

Roots are protected in the sense that grazers are unable to grip onto the stem and thus uproot the plant – in contrast to some upright grasses. Consequently, there are a variety of rooting strategies – and breaking strategies (i.e. relative strength of rooting vs. culms) – that upright grass growth forms may adopt to protect their roots. Because fire-grasses are unlikely to be grazed, we do not expect these traits to be well-developed in this group of grasses – however, we are currently embarking on extensive field research to quantify these traits across a wide array of grasses and environments.

Also is it that grazing lawns grow unchecked by grazing or is it that grazing promotes grazing lawns by maintaining the required light levels- it is a matter of words, but one implies growth despite grazing and other growth enhanced by grazing.

We prefer to retain the wording ‘unchecked’ – with the associated implication of growth despite grazing, rather than a phrasing that would imply enhanced growth. This is because while enhanced growth appears to occur in some contexts, we suspect that this is not always the case. In particular, it is not clear what the point of reference should be. Without grazing, the lawn would self-shade and growth would decline – so simply by preventing self-shading, grazers should maintain higher lawn productivity than if not grazed; however, whether this growth can be enhanced relative to normal when light is not limiting is not always clear. Mechanisms by which growth may indeed be enhanced is through stimulation of soil microbe activity via an increase in soil exudates caused by grazing (Hamilton & Frank 2001) – however, the nutrients that these microbes provide may not always be limiting. Similarly, the dung and urine inputs from grazers being present may ‘fertilise’ the lawn – but again, if these are not limiting resources, then growth may not necessarily be enhanced. We thus prefer to retain the more conservative wording that restricts the implied effect to prevention of self-shading.

Hamilton III, E. W., & Frank, D. A. (2001). Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology*, 82(9), 2397-2402.

Line 56: Should this say 'Fire-grasses outcompete other grasses by changing their light environments'- which you then go on to explain in the following text. This is marginal, but the sentence reads oddly on the first read, and one wonders whether it means to say that that fire grasses dominate in high light environments or what exactly.....

We have changed 'dominating' to 'appropriating' – this better describes the intended mechanism, i.e. that fire-grasses shade out shorter growth forms.

Lines 83- 85: You describe what happens to grass production as productivity decreases- What happens to forest as productivity decreases?

We appreciate the close reading of our manuscript – this is indeed a component of the manuscript that we decided to cut so as to conform to the word limit. This is because the description is quite wordy – it mirrors that of grasses, however, in that as productivity decreases, trees remain vulnerable to consumers for longer (i.e. they take longer to progress through the consumer zone/height range in which fire and herbivores are able to consume them) – the longer this period, the lower the probability of a consumer remaining absent (Hoffman et al. 2012 – Fig. 3b shows this beautifully). Direct competition from grasses is also a problem – and the canopy closure required to shade-out grasses can also be prevented by tree-tree competition for resources. Nonetheless, dry forests do occur, and understanding the biogeography of these vegetation types is of much interest to us.

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C., Lau, O. L., Haridasan, M. & Franco, A. C. (2012). Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology letters*, 15(7), 759-768.

Line 106- '.....rely on taller grass reserves outside....': But the taller grasses also dry out in the dry season, which is why they form good fire fuel at the end of the dry season- So perhaps need to add something here? Is it that they dry out slower or that because they are tall, they provide the bulk (but low quality) needed to get herbivores across the dry season? Again just a small clarification.

Yes indeed – but from a grazer's perspective, the main problem with lawns drying out is not the lack of leaf moisture, but the lack of regrowth. Once grazing-lawns go dormant in the dry season they provide very little forage for grazers, who are thus forced to use taller grasses. As noted in response to Reviewer 1, taller grasses in wetter parts of the landscape and that remain green for longer are often utilised first (e.g. wildebeest in Kruger make small migrations from lawn areas to access *Themeda triandra* growing in seep zones during the dry season – Yoganand & Owen-Smith 2014). However, grazers can survive on dry grasses so long as they have access to drinking water to support metabolic processes (although the protein content of dry grasses is of relevance – hence the terms sweetveld vs. sourveld used in southern Africa).

To provide more clarity, we have modified the text as follows: **'...grazers in seasonal environments rely on taller grass reserves outside of grazing-lawns to meet their intake requirements'**

Yoganand, K., & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, 37(10), 969-982.

Line 118-120: I really like that prediction, all else being equal I suppose though.

Thank you – yes, with all else being equal... so perhaps only in the simulation models.

Line 128: the 40% threshold comes out of the blue- And sounds like something globally applicable- please remove- or explain something related to it here

40% has been deleted

Line 131-134: Hmm...this concluding sentence focuses on losses of grazers while changing fire regimes are also widely reported, also with major consequences. Seems a bit odd to leave it with just the grazer message.

We have replaced this ending with one that now refers back to the central novelty of our manuscript, that grass and their traits play an important role in shaping ecosystem dynamics:

'What appears to be clear, however, is that grasses and their traits are fundamental to orchestrating dynamics in these consumer-controlled ecosystems.'

1 **Alternate grassland states are determined by palatability-flammability trade-offs**

2

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14

15 Keywords: grass, grazers, fire, grazing lawn, savanna, forest

16 Abstract

17

18 **Fire and mammalian grazers both consume grasses, and feedbacks between grass**
19 **species, their functional traits and consumers have profound effects on grassy**
20 **~~ecosystem~~land structure worldwide, such that savanna and grassland states determined**
21 **by fire or grazing can be considered alternate states. These parallel savanna-forest**
22 **alternate states that likewise have a myriad of cascading ecosystem impacts.**

23

24 Positive feedbacks can maintain ecosystems in alternate states where their structure and
25 function conform to a stable, yet dynamic, ecological regime [1]. Savanna-forest mosaics
26 provide a well-known example of alternate stable states [2], and, because the mechanisms
27 that cause shifts from savanna to forest ~~shifts~~ and *vice versa* are different, the likelihood, rate
28 and ecological pathway of transitions are different in each direction. This is known evidence
29 for hysteresis – an important property of alternate stable states – and means that initial
30 conditions ~~determine and lag effects shape~~ how regime shifts occur [1].

31

32 Grassy ecosystems also have alternate stable states (Box 1). Within grasses (Poaceae), a
33 family of over 11,000 species, there are numerous life history strategies [3] – yet two
34 strategies stand out for their remarkable ability to drive the ‘consumer regime’ in parts of a
35 grassland or savanna landscape towards a fire- or grazer-dominated state. On the one hand,
36 there are grasses with trait combinations that make them highly flammable but which also
37 increase their dominance under frequent burning [4]; these ‘fire-grasses’ are important to
38 maintaining the savanna-forest boundary [5]. On the other hand, ‘grazing-lawn’ grasses are
39 highly palatable and thus sought after by grazers, but the proliferation of these grasses is
40 promoted by regular grazing [6]. These positive feedbacks make it possible for shifts in grass

41 community composition to profoundly affect the ecosystem at large: whether a system is fire-
42 or grazer-driven ~~the amount of fire and grazers~~ has implications for soil carbon, nutrient
43 cycling, plant community composition, biodiversity, and habitat structure – among
44 ~~innumerable~~ other cascading effects [4,7,8].

45

46 *Traits and positive feedbacks*

47

48 Light competition underpins the dynamic in grazing-lawn or fire-grass community states.
49 Grazing-lawn grasses are short-statured, often laterally spreading, and vulnerable to being
50 overtopped-shaded out by the invasion of tall grasses [6,7,8]. Regular grazing is essential to
51 maintain high light-levels. Grazing-lawns are attractive to grazers because bites consist
52 mostly of densely packed leaf material (i.e. with low C:N ratios and high moisture), which
53 allows for efficient intake of nutritious forage while avoiding low quality stem material – and
54 therein lies the trick: by protecting stem material, roots and buds, grazing-lawns continue
55 growing largely unchecked by grazing, and are fierce competitors for space and resources
56 when light is not limiting [6,8].

57

58 Fire-grasses outcompete other grasses by dominating-appropriating the light environment [4].
59 Their tall, upright stature requires high C:N ratios providing structural support, and this,
60 along with high tannin levels, slows decomposition rates and results in the accumulation of
61 dead biomass [3,9]. Dead biomass obstructs light at ground-level while accumulation of a
62 low moisture dense fuel-bed supports frequent fire [10]. Fire-grasses are well equipped to
63 survive frequent fires with meristems insulated by layered leaf sheaths and a densely packed
64 plant base. To complete this feedback loop, fire-grasses have rapid post-fire regrowth
65 facilitated by high photosynthetic rates, providing little opportunity for other grasses to

66 establish [10]. While fire-grass and grazing-lawn feedbacks have long been established [4,6],
67 their opposing nature and implications for alternate stable states have not been elaborated.

68

69 *Contrasting grazing-lawn vs. fire-grass and savanna vs. forest alternate stable states*

70

71 The dynamics of grazing-lawn vs. fire-grass alternate states share many properties with
72 savanna vs. forest alternate states (Figure 1) despite fundamental differences in how each is
73 formulated. Grazing-lawn vs. fire-grass states are underpinned by trait differences within the
74 same plant life form, with each state dependent on positive feedbacks with a consumer (i.e.
75 grazing vs. fire). By contrast, savanna vs. forest states represent a shift from a tree-grass
76 mixture maintained by fire, to a tree-dominated, resource-limited system (i.e. light
77 competition) [5]. Unsurprisingly, savanna and forest trees require markedly different traits to
78 meet the competitive demands of each system [5].

79

80 Fire-grasses and forest trees are both the taller vegetation state, strong competitors for light,
81 and with likely lower belowground investment [10]. Accordingly, these vegetation states tend
82 to dominate under more productive conditions, but are able to expand into grazing-lawns or
83 savanna should grazers or fire be absent for long enough [2,7]. However, resource limitation
84 is likely to constrain how far down the productivity gradient these life history strategies
85 remain dominant. As productivity decreases, grass biomass production decreases, such that
86 fire frequency declines because fuel loads are insufficient for frequent fire, disrupting the
87 fire–grass feedback.

88

89 By contrast, grazing-lawn and savanna vegetation states dominate under less productive
90 conditions, and depend on grazers and fire respectively to maintain an open light environment

91 [2,6]. Opportunities to expand into fire-grass communities or forests occur during brief
92 windows when these taller vegetation types become palatable or flammable: fire-grasses are
93 palatable when regrowing after being burned, and forests become flammable during droughts
94 or unusually hot, dry, windy weather conditions. As productivity increases, grazing-lawns
95 require more frequent grazing ~~– and savannas require more frequent~~ ~~and fires – are required~~
96 ~~for grazing lawns and savannas in order~~ to persist. However, ~~but~~-associated shifts in forage
97 and fuel properties ultimately constrain how far up the productivity gradient each can occur:
98 grazer populations become limited by declining grass quality outside of grazing-lawns (see
99 below; F₂ in Figure I) [8], and fire is excluded in wet regions because fuels remain green and
100 are never dry enough to burn [11].

101

102 *Implications of spatial and temporal constraints on fire vs. grazers*

103

104 Fire and grazers are subject to different spatial and temporal constraints, which has
105 implications for the extent and configuration of ecosystem states in a landscape. For example,
106 ~~while the ability of~~ grazers can simply walk through ~~to traverse~~ unsuitable habitats, fires can
107 be halted by ~~is in contrast to the~~ fuel continuity barriers such as ~~to fire spread, which can be~~
108 ~~stopped by~~ roads, and indeed, short-grazed grasses. However, unlike fires, grazers need to
109 survive year-round. Consequently, when grasses stop growing in the dry season, grazers in
110 seasonal environments rely on taller grass reserves outside of grazing-lawns to meet their
111 intake requirements [8], ~~and g~~ Grazer populations thus can be limited by grass quality and
112 quantity outside of grazing-lawns (see above).

113

114 These differences have consequences for the proportion of landscape that can be maintained
115 in a fire- or grazer-determined state. When conditions are conducive to fire, and if barriers to

116 spread are few, fire can convert entire landscapes into a fire-grass state [4]. However, the
117 maximum proportion of grazing-lawn is contingent upon adequate dry season resources to
118 support grazers [8]. These grazing-lawns can be configured as small, isolated patches near
119 water or on nutrient hotspots like termite mounds, or coalesced into large areas that offer
120 additional benefits such as improved predator detectability [8]. The extreme scenario occurs
121 where grazers undertake long distance migrations between dry and wet season ranges,
122 allowing for the formation of vast grazing-lawns e.g. the ~~vast~~ short-grass plains of the
123 Serengeti, which support over a million wildebeest in the wet season, and almost none in the
124 main dry season [12]. Seasonality should thus be an important predictor of lawn extent in an
125 ecosystem, with a greater proportion of lawn possible in less seasonal systems, or where
126 animals can migrate to track grass phenology.

127

128 In the savanna-forest literature, spatial barriers to fire spread have been discussed at two
129 scales: at local scale the forest boundary prevents fire spread if tree density is high enough to
130 reduce surface fuel flammability, while at landscape scale, fire is excluded when forest (non-
131 flammable) patches are extensive enough to prevent fire percolation through the landscape
132 [2,5]. Similarly, at local scale grazing-lawns have traits that make them non-flammable, while
133 at landscape scale grazers can effectively switch-off fire once grazing-lawn extent exceeds
134 the ~~40%~~ threshold to fire spread [12]. Enhancing our mechanistic understanding of the
135 distribution of ecosystem states along the grazing-lawn savanna – fire-grass /savanna – forest
136 continuum will require elaboration of the feedbacks to fire and grazer population size at both
137 scales. What appears to be clear, however, is that grasses and their traits are fundamental to
138 orchestrating dynamics in these consumer-controlled ecosystems. ~~Our understanding of the~~
139 ~~consequences of global megafaunal extinctions is ever increasing, but these insights from~~
140 ~~African ecosystems point to the profound extent to which a unique biodiversity has been lost~~

141 ~~and biological processes altered, and in turn those at risk due to continued extirpation of~~
142 ~~megafauna.~~

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144

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153

154 References

155

156 1. Scheffer, M. and Carpenter, S.R. (2003) Catastrophic regime shifts in ecosystems: linking

157 theory to observation. *Trends Ecol. Evol.* 18, 648–656

158 2. Staver, A.C. et al. (2011) Tree cover in sub-Saharan Africa: rainfall and fire constrain

159 forest and savanna as alternative stable states. *Ecology* 92, 1063–1072

160 3. Linder, H.P. et al. (2018) Global grass (Poaceae) success underpinned by traits facilitating

161 colonization, persistence and habitat transformation. *Biol. Rev. Camb. Philos. Soc.* 93,

162 1125–1144

163 4. D'Antonio, C.M. and Vitousek, P.M. (1992) Biological invasions by exotic grasses, the

164 grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87

165 5. Oliveras, I. and Malhi, Y. (2016) Many shades of green: the dynamic tropical forest–

166 savannah transition zones. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 371, DOI:

167 10.1098/rstb.2015.0308

- 168 6. McNaughton, S.J. (1984) Grazing lawns: animals in herds, plant form, and
169 coevolution. *Am. Nat.* 124, 863–886
- 170 7. ~~Bond, W. J. and Keeley, J.E. (2005) Fire as a global ‘herbivore’: the ecology and~~
171 ~~evolution of flammable ecosystems. *Trends Ecol. Evol.* 20, 387–394~~Knapp, A.K. et al.
172 (1999) The keystone role of bison in North American tallgrass prairie: Bison increase
173 habitat heterogeneity and alter a broad array of plant, community, and ecosystem
174 processes. *Bioscience.* 49, 39–50
- 175 8. Hempson, G.P. et al. (2015) Ecology of grazing lawns in Africa. *Biol. Rev. Camb. Philos.*
176 *Soc.* 90, 979–994
- 177 9. Simpson, K.J. et al. (2016) Determinants of flammability in savanna grass species. *J.*
178 *Ecol.* 104, 138–148
- 179 10. Ripley, B. et al. (2015) Fire ecology of C3 and C4 grasses depends on evolutionary
180 history and frequency of burning but not photosynthetic type. *Ecology* 96, 2679–2691
- 181 11. Krawchuk, M.A. and Moritz, M.A. (2011) Constraints on global fire activity vary across
182 a resource gradient. *Ecology* 92, 121–132
- 183 12. Holdo, R.M. et al. (2009) Grazers, browsers, and fire influence the extent and spatial
184 pattern of tree cover in the Serengeti. *Ecol. Appl.* 19, 95–109

Box 1: Alternate stable states in grassland communities

Grass biomass increases with productivity (Figure I; black diagonal), but departures occur when positive feedbacks with fire or grazing entrain communities into tall stature fire-grass (orange line) [4] or low stature grazing-lawn (green line) [6] states. These positive feedbacks arise because the grass traits that ‘attract’ fire or grazers are associated with traits that also promote competitive ability under these different consumer regimes. This confers stability to each state, with their resilience enhanced by the opposing nature of the traits that attract fire vs. grazers: fire-grasses are relatively unpalatable, and grazing-lawns are non-flammable. However, critical bifurcations occur when productivity changes – at F_1 , grass fuel continuity becomes too patchy to carry fires, and at F_2 , grazer populations decline due to the low quality of dry season reserves outside of lawns. External factors can also precipitate transitions by reducing the amount of fire (e.g. fire suppression) or grazers (e.g. poaching or disease). Hysteresis occurs due to the different mechanisms that drive state transitions: fire-grasses shade out grazing-lawn grasses, while trampling or concentrated post-fire grazing can allow grazing-lawn species to invade the fire-grass state. Transitions from grazing-lawn to fire-grass states (orange dotted lines) occur fastest at high productivity, while the slower, more stochastic fire-grass to grazing-lawn transitions (green dotted lines) are perhaps most likely at intermediate productivity, where grazers are abundant but the rate of reversion to the fire-grass state is moderate.

187 Figure legends

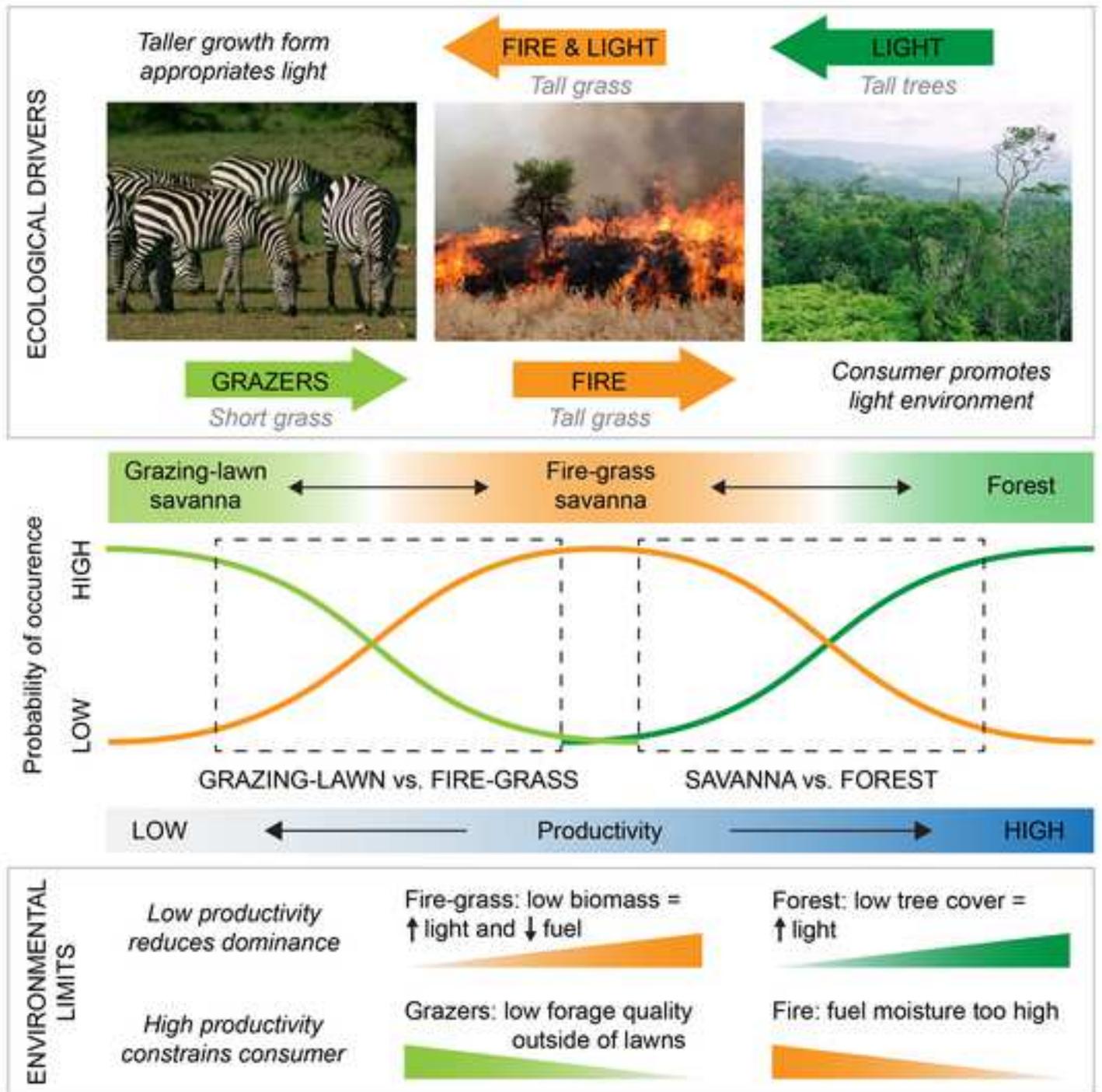
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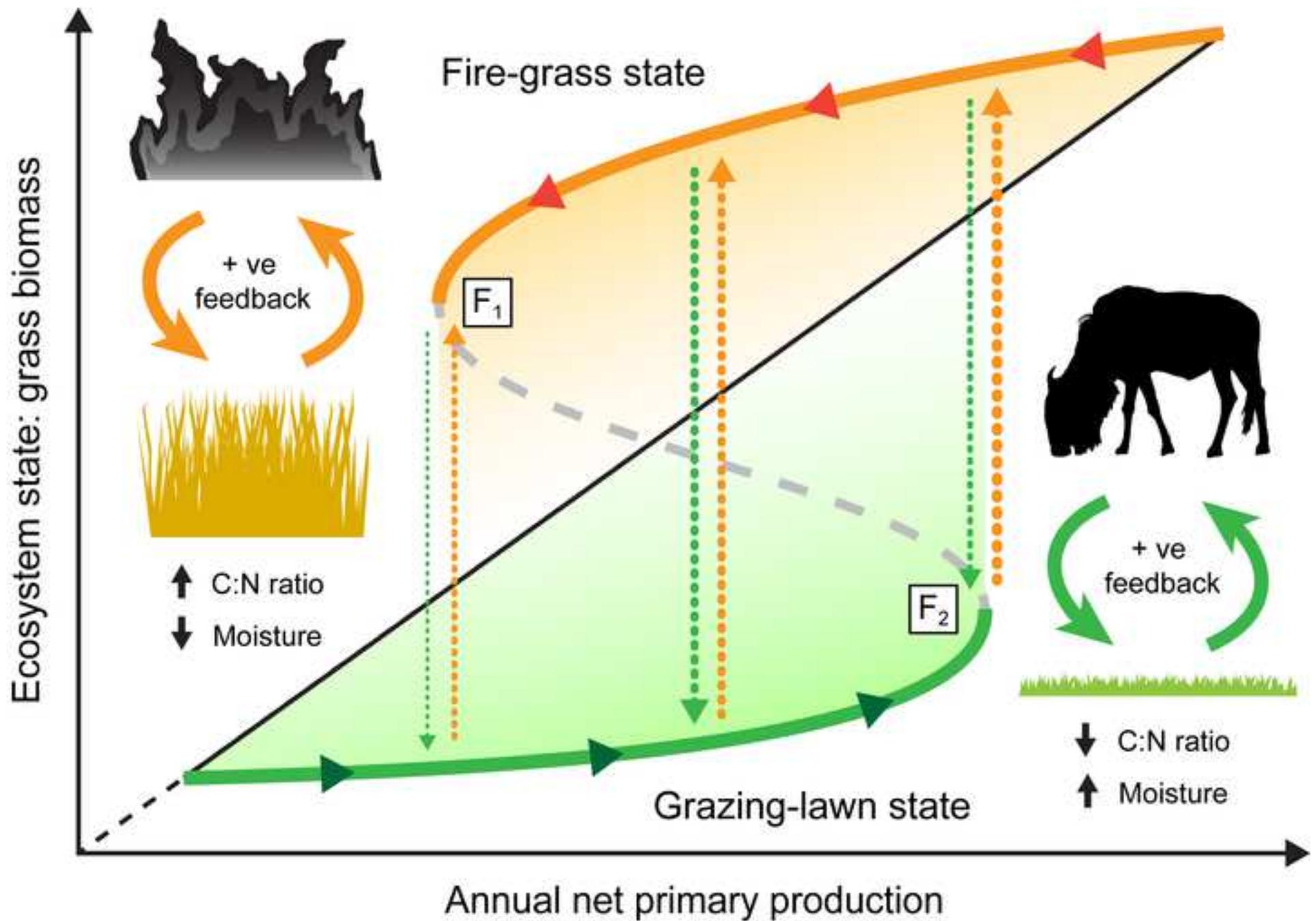
189 **Figure 1. Grazing-lawn vs. fire-grass and savanna vs. forest alternate stable states.** The
190 probability of occurrence of grazing-lawn savanna, fire-grass savanna and forest changes
191 across a productivity gradient (middle panel). This is due to environmental limits on grazers,
192 fire and biomass production (lower panel), that in turn shape the role that each can play as
193 ecological drivers (top panel), primarily through modifying the light environment. At high
194 productivity, forest can shade out fire-grass savanna, which in turn can shade out grazing-
195 lawn savanna at mid-level productivity. On the other hand, positive feedbacks between
196 grazers and grazing-lawn grasses, and fire and fire-grasses, can promote their expansion up
197 the productivity gradient – until these consumers themselves become constrained by
198 environmental limits. These dynamics give rise to alternate grazing-lawn vs. fire-grass
199 alternate stable states in savannas, which share parallels with previously described savanna-
200 forest alternate stable states.~~The probability of alternate states in both grazing-lawn vs. fire-~~
201 ~~grass and savanna vs. forest ecosystems changes across a productivity gradient. Fire-grass~~
202 ~~and forest states dominate higher up the productivity gradient, and being taller, are better~~
203 ~~light competitors than the grazing-lawn and savanna states respectively. On the other hand,~~
204 ~~grazing-lawn and savanna states both require a positive feedback with a consumer—i.e.~~
205 ~~grazers and fire respectively—for them to be maintained and potentially expand up the~~
206 ~~productivity gradient. Note that at even lower productivity, grazing-lawns gradually transition~~
207 ~~into different grass community states that are not discussed here.~~

208

209 **Figure I. Alternate grassland states.** Conceptual diagram of alternate fire-grass (orange
210 solid line) and grazing-lawn (green solid line) stable states along a productivity gradient.
211 Each state is stabilised by positive feedbacks (solid orange and green arrows) with fire and

212 grazers respectively, a dynamic underpinned by opposing C:N ratios and leaf moisture traits
213 amongst others. Transitions between states (dotted lines) occur when shifts in rainfall exceed
214 critical bifurcation points at F_1 or F_2 , or when external factors precipitate changes. Shading
215 represents grasses with higher palatability (green) or flammability (orange) respectively. The
216 black diagonal line represents the general linear increase in grass biomass with annual net
217 primary production.



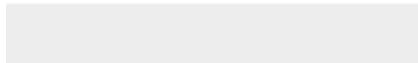




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Original Figure File

Figure 1 - Grass alternate states revised.ai





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Figure I - Box 1 - Grass alternate states.ai

