

November 17, 2017

Dear Dr. Kirsten Thonicke,

5 Please find enclosed our revised manuscript entitled "Sensitivity of woody carbon stocks to bark investment strategy in Neotropical savannas and forests " by Trugman et al. (MS No.: bg-2017-336) for your consideration.

We are grateful for the suggestions by both the reviewers and by the editor. By addressing these concerns, we think that the manuscript has been substantially improved. Our detailed responses are given below. We look forward to your decision.

10

Thank you for your consideration.

Sincerely,

15 Anna Trugman (on behalf of all of the authors)

Response to the Editor:

Dear Anna,

20

Thank you for providing us with the detailed response to both reviews.

Reviewer 1, point 2: If you decide to move Figures 2 and 3 as suggested by the reviewer to the supplement, please make sure that you adequately describe the validation results in the main text including modeling error or similar, and refer to the
25 respective figures in the supplement.

We have opted to move one model validation figure (previously Fig. 2) to the SI (now Fig. S2) and have kept one in the main text. We include a description of the model validation and an extended discussion of possible sources of modeling error in the main text (L213-230, L346-353).

30

Reviewer 1, point 3: I find it very important to add a figure illustrating mortality as suggested by the reviewer.

35 We have added a new figure (Fig. S5) illustrating aboveground biomass mortality and a description of AGB growth by size class in the different model versions at different fire frequencies and have added an additional section in the text discussing how growth and mortality impact AGB dynamics (L254-263).

Reviewer 2, discussion on bark thickness of small trees. Please check your text in the discussion if you could add a sentence reflecting the discussion between you and the reviewer. I think it is also informative for the reader of the final manuscript.

40 We have added a sentence to the discussion on bark thickness of small trees to address Reviewer 2's comments (L251-263).

With these points considered in the final version of the manuscript, I think the manuscript could be then ready for publication.

45 Best wishes,
Kirsten.

Response to Reviewer 1:

50 General comments

In the age of anthropogenically forced climate change, developing a comprehensively predictive Earth System Model is an extremely high scientific priority. Trugman et al is a highly relevant study that aims to assess hypotheses regarding the trade-off between fire adaptation in the form of bark thickness and growth and survivorship. The hypotheses evaluated in this study are clearly articulated in the Introduction and described in the Methods such that replicating this experiment would be fairly straightforward. ED2 is an appropriate tool and the Methods are, in general, appropriately designed for exploring the hypotheses of this study. Importantly, the source code for the model, which documents the exact model structure and parameter values used in this study, is included with the Supplement Information, thus making the model itself transparent and the simulations reproducible. This study makes two important contributions: 1) (model development) it demonstrates the importance of including a fire-adapted trait in terrestrial biosphere models and 2) (ecological understanding) it illustrates the potential role bark thickness has in modulating coexistence of different life forms (grasses vs. trees) and aboveground C-stocks in fire-regulated ecosystems. I do, however, recommend that, before this manuscript is accepted for publication, the authors address the concerns listed below and make clarifications in the text where necessary.

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We thank Reviewer 1 for the positive feedback highlighting our manuscript's contributions to both model development and ecological understanding. Please find our detailed responses and corresponding manuscript revisions below.

65

Specific comments

1. The Methods need to be clearer (refer to lines 96-100, 144-146) about the two new tropical PFTs not being simulated
70 simultaneously. As written, the Methods left me with the impression that both PFTs were being run simultaneously and that
direct selection for one strategy over the other was part of the experiment (line 144-146). I had to read the namelist (ex.
ED2IN_fire_control_MAP1450_FR3_pen1) to verify that only the savanna tree or forest tree (apparently PFT #26 for both?)
was being run with the C4 grass (PFT #1?) in each simulation. This needs to be clear so that the reader can fully understand
how to interpret the ecological significance of the results.

75

We apologize for the confusion. The savanna, forest, and C4 grass PFTs were all run simultaneously for all model
experiments (3 PFTs total). We cleaned up the namelist files in the source code and include a readme file in the run folder
with instructions on how to generate the namelist for the different model experiments. We have also clarified that 3 PFTs
were used in the methods (L148) so that the reader can fully understand how to interpret the ecological significance of the
80 results.

2. I am not strongly convinced by the ecological importance of the results presented in Figures 2 and 3. In several panels it is
difficult to visually discern that the “bark” performed better than the “no bark” or what the differences, where present,
actually mean. For example, in all of the panels the IQR of the “no-bark” is tighter than the “bark”, and hence, is in better
85 agreement with the IQR of the observations. Or, for Fig 3a, I would not necessarily consider the “bark” to do a better job
“capturing” the observations relative to the “no-bark” just because the observations fell within the broad error range of the
bark-model predictions (line 224). Benchmarking new model capability is important, and I think these are obvious choices as
benchmarks. However, I am not sure what these benchmarks add to the central argument (and scientific contribution) of this
paper (e.g. as I take it, the central argument is: Abstract lines 23-25, Introduction line 6, Figures 5 and 6, Results lines 275-
90 276, Discussion line 280, 316-317, Conclusions lines 343-346). Consider moving Figures 2 and 3 to the Supplemental. Even
if model performance against the benchmarks in Figures 2 and 3 is weak, as I would contend, I do not view this as a major
problem for this paper because the emergent pattern in Figure 6 supports the “bark” hypothesis that this study seeks to
evaluate.

95 Your point is valid, and Reviewer 2 shared similar concerns. We have moved Figure 2 to the SI (now Fig. S2). We have kept
one validation figure in the main text because benchmarking new model capabilities is an important component to any
modeling paper. We also include an extended discussion of model validation weaknesses in the results (L213-230) and
discussion section on “limitations and future work” (L346-353).

100 3. In replacement of Figures 2 and 3 in the main text, it would be nice to see a figure of how the demographic rates that give rise to Figures 5 and 6 differ between “bark” and “no-bark”. Demography is the fundamental feature of the ED2 hypothesis, as explained in Moorcroft et al. 2001. Therefore, it would be informative to see how the internal dynamics of the model that are central to its hypothesis (i.e. predictions of demographic rates of growth, recruitment, mortality) are modified by inclusion of the bark strategy. In essence, this is the interesting ecology that ED2 and this study have great potential to
105 inform. Figure S1 is the only figure of demographic rates and it is an informative starting point, but by itself, it does not close-the-loop for explaining the patterns in Figures 5 and 6. It seems to me that a mortality figure would also be useful for helping to explain the interaction between the survivorship hypothesis (Eqn2) and the different growth rates.

Thank you for this helpful suggestion. We have added an additional figure (Fig. S5) to highlight the difference in AGB mortality by size classes in the different model versions at different fire frequencies and use this figure in the text to explain the interaction between the survivorship hypothesis and the different growth rates (L254-263).
110

4. The meaning of the variation in Figures 2 and 3 is unclear. I do not understand how time factors into these distributions. Presumably, the observations are based on census data that was collected at one point in time, July 2012 (line 182). How was
115 the model output sampled to generate the error estimate? If the errors are one spatial (or across individuals), one temporal then how do we compare the errors? Please clarify in the caption, text or both.

The range in the model output represents the range in simulated AGB or tree size over a 10-year period following a 35-year model spin up (L188-189). Variation in the observations is due to variation between plot biomass or in variation across
120 individuals within plots. Although the errors are not analogous, we intended to represent the range in model output resulting from growth and variable meteorological forcing over the 10-year time period. We clarified this further in the text and the captions (L194-198).

5. I suggest a stylistic revision regarding verb tense for sentences describing model predictions. Since the model is a
125 hypothesis, the verb tense should be in the present when speaking about model predictions. For example, at line 240 it says “predicted”, but it should read “predicts”. “The hypothesis predicts. . .” = “The model predicts. . .”

We revised the verb tense describing the model predictions according to your suggestion.

130 6. I suggest that the final sentence of the Abstract focus on the scientific contribution to ecology and not on model development. Model development speaks to a subset of ecologists. Since the Abstract may be the only thing many people read, the concluding sentence should be about the most important scientific contribution and speak to the broadest community you are trying to reach.

135 We revised the abstract's final sentence to focus on the ecological significance of bark thickness strategy in regulating tree size demography, and the subsequent impacts on aboveground C-stocks in fire-regulated ecosystems and the coexistence of different functional groups (L27-29).

140 7. Line 46. "comes at a growth cost: thicker-bark. . .grows more slowly. . .". This sentence is written as if this the carbon-cost trade-off is conclusively known, but it is not; it is a hypothesis. Indeed it is a hypothesis evaluated in this study with the no-cost bark PFT. Consider rephrasing.

Rephrased to highlight the uncertainty in the cost of bark investment (L47).

145 8. Line 72. "We then tested whether two hypotheses were consistent with model simulations." This does not read correctly to me. The model is the hypothesis and the simulations reflect the hypothesis. So, it is hard for me to rationalize how a hypothesis is consistent with itself. Consider revising.

Rephrased (L73-74).

150 9. Section 2.1. The source of the model parameter values needs to be cited. The only obvious reference for parameter values is for the brevideciduous PFT at line 97. For example, it is not clear what version of ED2 is the basis for the photosynthesis parameterization used in this study.

155 We clarify that Xu et al. (2016) is the source of the all model parameterizations unless otherwise specified (L83-84).

10. Line 168. Please provide the definition of the dry season used in this study (<100 mm/month?). It would also be helpful to know what fraction of annual precipitation falls during the dry season.

160 We have included monthly estimates for dry season precipitation (L171).

11. Line 210. Could tuning model parameters unrelated to bark thickness correct the overestimation of the forest species?

Tuning model parameters such as the maximum rate of carboxylation could correct for the overestimation of forest species.

165 In this study we considered the hypothesis that the carbon tradeoff on bark investment alone was responsible for the differences in growth rate between savanna and forest species. We have added a line in the text to acknowledge this point (L218-219).

12. Line 235. “likely”. This is speculative. This can be known with this model. Addressing item 3 above should make this
170 known.

We have rephrased the text and added additional figures and text to illustrate how bark investment strategy, fire, and precipitation interact to influence AGB growth and mortality (Fig S5, L251-263).

175 13. In the model code, the namelist needs to have a description of what PFT 26 actually is. There are several PFTs listed up to number 17 in the namelist; but after that, it is not clear what 26 is or what the other tropical PFTs (numbers 2-4) are. The PFTs above 17 are given some notation in the source code (e.g. in ed_params.f90), but it is still not clear what exactly that notation means. A little more clarification about the notation throughout the code would be helpful.

180 We have cleaned up the source code and include descriptions of the full list of PFTs in ed_params.f90, as well as a readme file in the /run folder with directions for potential users.

Technical comments

185 1. Line 18. “ED2” Define acronym.

Corrected

2. Line 215. “Fig1a”. Wrong reference?

190

Corrected to Fig. 2a

3. Line 248. “comprised a substantial fraction of AGB were prevalent. . .” This does not read smoothly to me. Consider revising.

195

Rephrased

Response to Reviewer 2:

200 Bark thickness can protect trees against fire damage and mortality. This feature is particularly important for survival in fire driven ecosystems such as savannas. Most dynamic vegetation models do, however, not consider tree plant functional types

with variable bark thickness and hence with different levels of resistance against fire. In this study, bark thickness is considered in the ED2 vegetation model to describe fire survivorship and it is explored how the introduction of more fire tolerant trees influences vegetation dynamics in neotropical forests and savannas. The authors argue that including fire tolerant trees improves agreement with empirical data and that it can increase the areas where savannas can occur.

The manuscript investigates an interesting and important question and it may contribute to our understanding of the distribution of savannas and how we can better model savannas. The manuscript is generally well written and formulates hypotheses that are then tested by model simulations.

I have some comments concerning the results. Generally I think that statistical test should be conducted to quantify agreement with data and differences between model runs. I am for example not convinced that in Fig 2a, the "Bark" simulations are better than the "No Bark" simulations. Maximum dbh of with bark simulations is higher than in the no bark simulations but differences in means are not visible in the panel. Histograms for the dbh or height distribution might be more illustrative than box plots.

We experimented with plotting model evaluations as histograms, however this did not prove to be more illustrative of the results. Comparing the below figure (analogous to the previous Fig. 2b, now Fig. S2b), the interquartile and median dbh value in the boxplots of Fig. S2b illustrates the distribution skew of tree size and is able to show this distribution in a more compact and easily comparable way. To address your concern, we extended our discussion of model validation and limitations (L213-230, L346-353).

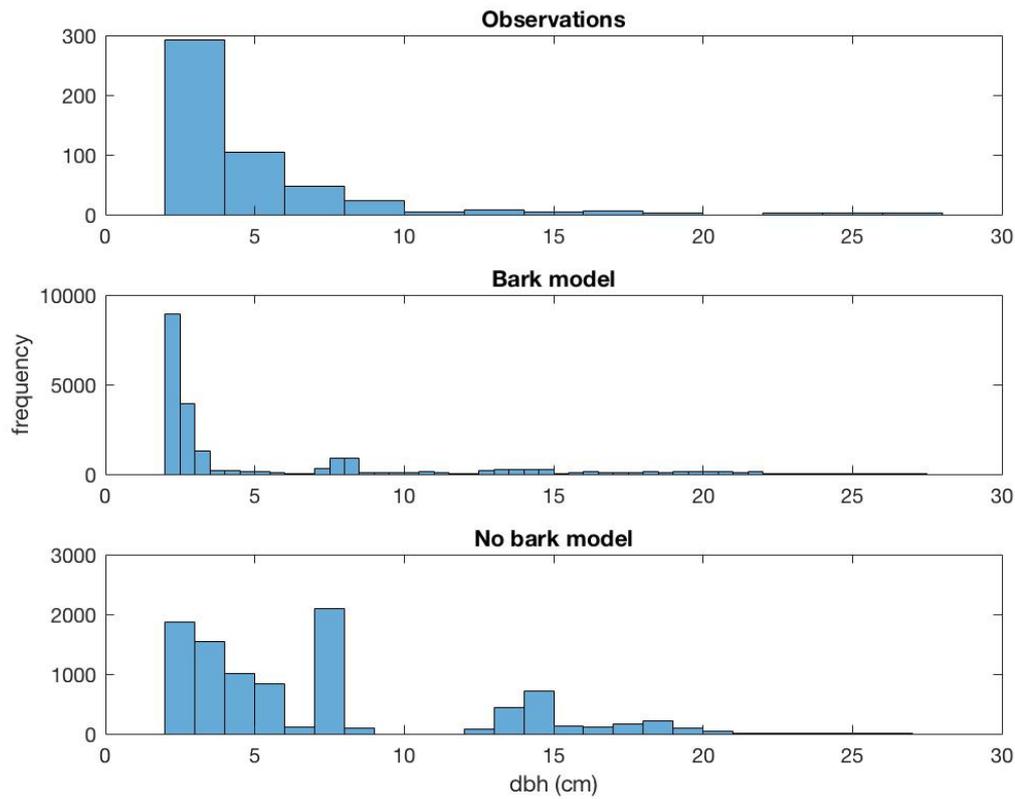


Fig. 4 suggests that there are more or less no small trees in with bark simulations while we often find many small trees in savannas due to the high re-sprouting rates. This biomass distribution suggests that re-sprouting and recruitment are not possible (resprouting is not included in the model and is identified as a limitation in the discussion) but I assume that it would strongly influence small tree numbers. I wonder how stable this vegetation state is: if simulations were continued and all tall trees die, would the simulated vegetation converge to a grassland without any trees because regrowth is not possible?

230 We edited and corrected several figures to better reflect what we did. First, as a clarification, the minimum tree size in the validation figures, Figure 4, and the corresponding SI figures should read $2\text{cm} < \text{dbh} < 8\text{cm}$, as we excluded trees smaller than 2cm dbh from our modeling results because trees smaller than 2cm were not surveyed in our observational comparisons. This change was made to all relevant figure captions and the methods section (L185).

235 The biomass fraction of small trees is not illustrative of the number frequency of small trees, as small tree biomass comprises a very small fraction compared to the large trees, so it is not necessarily the case that small trees are not present in the bark simulations. We have added an additional sentence to the discussion to further highlight this important point (L251-263).

240 Most analyses investigate vegetation in response to variable frequency while timing or intensity are not considered. Yet, these variables strongly influence vegetation responses to fire.

We include variable fire intensity/probability of mortality dependent on grass biomass (L133-140) in the model simulations. Further analysis on variable intensity would be an excellent avenue for study in future work.

245 It is stated in l. 60 that "DGVMs are still unable to fully capture global savanna extent". It would be very interesting to see how the updated model version influences the savanna distribution at larger spatial scales both in comparison to the original model version and to other DGVMs. I think this is not the scope of this study, nonetheless this point could be mentioned in the discussion.

250 We updated the discussion to emphasize the potential for bark investment strategy to improve model projections of savanna extent at broader spatial scales (L342).

Further comments:

255 l. 53: "Slower growth rates result in a population of smaller trees with relatively thinner bark" I would argue that bark thickness is not relevant for small trees anyway because they are in the flame zone and damaged by each fire. The capacity to regrow after fire might be more important. Bark thickness is mainly important for tall trees that managed to escape flame height.

260 Bark thickness could be relevant to smaller trees in that it could slow growth and prolonged the period during which trees are more susceptible to fire, depending on environmental conditions. Additionally, bark thickness might influence the threshold at which a tree could be considered large enough to no longer be susceptible to fire. We have added a line to the discussion to highlight this point (L313-315).

265 l. 62: suggest to reword to "carbon storage in the tropics" l. 106:

We reworded according to your suggestion

Please check table, I can't find definition of beta in Table 1.

270

We removed the reference to Table 1, as beta is defined in the main text (L108-112). We apologize for this stray reference from a previous draft.

l. 195: I suggest to make clear that the tree MAP levels are sites along the rainfall gradient.

275

We specify that MAP levels are sites along a rainfall gradient (L202-204).

l. 217: Fig 2a instead of 1a?

280 Corrected

l. 521: Fig 3 shows biomass but the caption says "woody carbon". Please check text for consistency.

Corrected

285

Fig 5: I suggest to replace the current color legend with a legend showing color and the associated fire return interval. Also I suggest to use a consistent notation: fire interval or fire frequency.

We consistently use fire frequency throughout the text. In the case of Figure 5, we think it makes most intuitive sense to refer to the return interval with longer return intervals corresponding to less frequent fire.

290

Sensitivity of woody carbon stocks to bark investment strategy in Neotropical

295 savannas and forests

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Abstract. Fire frequencies are changing in Neotropical savannas and forests as a result of forest fragmentation and increasing drought. Such changes in fire regime and climate are hypothesized to ~~decrease the stability~~destabilize of tropical carbon storage, but there has been little consideration of the widespread variability in tree fire tolerance strategies. To test how aboveground carbon stocks change with fire frequency and ~~community_~~composition of plants with different fire tolerance strategies, we update the Ecosystem Demography model 2 (ED2) ~~ED2 model~~ with (i) a fire survivorship module based on tree bark thickness (a key fire-tolerance trait across woody plants in savannas and forests), and (ii) plant functional types representative of trees in the region. With these updates, the model is better able to predict how fire frequency affects population demography and aboveground woody carbon. Simulations illustrate that the high survival rate of thick-barked, large trees reduces carbon losses with increasing fire frequency, with high investment in bark being particularly important in reducing losses in the wettest sites. Additionally, in landscapes that frequently burn, bark investment can broaden the range of climate and fire conditions under which savannas occur by reducing the range of conditions leading to either complete tree loss or complete grass loss. These results highlight that ~~woody biomass carbon stocks in the tropics~~tropical vegetation dynamics depend not only on rainfall and changing fire frequencies, but also on tree fire survival strategy. Further, our results indicate that fire survival strategy is fundamentally important in_ regulating tree size demography in ecosystems exposed to fire, regulat~~frequency~~which increases the preservation of aboveground carbon _stocks and the coexistence of different plant functional groups.~~Incorporation of a bark investment strategy in vegetation models holds promise for improving predictions of landscape level carbon dynamics and savanna distribution, particularly in the context of global climate change.~~

1 Introduction

Tropical savannas and forests are important components of the land carbon sink (Pan et al., 2011; Liu et al., 2015; Ahlström et al., 2015). However, their ability to continue sequestering carbon is uncertain (Malhi et al., 2008), due in part to the impact of projected increases in drought frequency and changes in fire regime on woody carbon stocks (Brando et al., 2014). Globally, tropical forests, savannas, and grasslands comprise ~60% of total terrestrial gross primary productivity (Beer et al., 2010), but are also responsible for over 65% of global carbon emissions stemming from fire and deforestation (van der Werf et al., 2010; van der Werf et al., 2009). The balance between biological carbon uptake through photosynthesis and carbon emissions from respiration and biomass burning determine whether tropical savannas and forests are a net carbon sink or source.

Fire is critical in defining the vegetation structure and distribution of tropical savannas and forests (Bond et al., 2005; Hoffmann et al., 2012a; Staver et al., 2011b). A positive feedback between flammable grass presence and tree fire mortality in open canopies has been identified as an important mechanism in maintaining savanna regions (Archibald et al., 2009; Hoffmann et al., 2012b; Staver et al., 2011a). Some trees can persist, despite high fire frequencies in many savannas, because they invest heavily in building thick bark (Pellegrini et al., 2017a). Thick bark insulates the xylem and phloem from fire damage, increasing the probability of tree fire survival (Brando et al., 2012; Hoffmann et al., 2012a), and potentially decreasing ecosystem carbon vulnerability to increasing fire frequency with global climate change (Pellegrini et al., 2016b). However, this increase in bark investment may come at a growth cost as: thicker-barked savanna species grow more slowly than thinner-barked forest species under similar growing conditions (Hoffmann et al., 2012a; Rossatto et al., 2009). Though many savanna trees have growth strategies that employ thick bark as a fire survival mechanism, species vary greatly in their investment in bark (Pausas, 2015; Pellegrini et al., 2017a; Rosell, 2016).

Climate, particularly precipitation, has the potential to interact with fire frequency and tree growth strategy (Brando et al., 2014). In locations with low precipitation, tree growth rates are much slower than in locations with high precipitation (Baker et al., 2003). Slower growth rates result in a population of smaller trees with relatively thinner bark than their larger counterparts, making their stems more vulnerable to fire. it more difficult for trees to grow and survive in high fire frequency regimes in dry regions. In addition to climate, physiology can play a role because some trees grow more rapidly than others due to differences in maximum photosynthetic capacity or specific leaf area (Rossatto et al., 2009). Tree growth rate is critical for determining the ability of trees to recover from fire, and consequently the fire frequency necessary to maintain savanna.

Simulating savanna vegetation dynamics is notoriously difficult. However, progress has recently been made in identifying some key mechanisms needed to stabilize savannas in dynamic global vegetation models (DGVMs) (Scheiter and Higgins, 2009; Lehsten et al., 2016; Baudena et al., 2015; Higgins et al., 2000; Haverd et al., 2013; Lasslop et al., 2016).

360 Despite recent progress, DVGMs are still unable to fully capture global savanna extent as emergent features, generally over-
predicting the [scope extent](#) of either grasslands or tropical forests (Lasslop et al., 2016). This makes it difficult to quantify
the impacts of projected climate change on [carbon storage in the tropics](#) ~~sal carbon storage~~ because both carbon storage
capacity and the resistance of ecosystem carbon to changes in precipitation and fire regime vary across tropical biomes.
Additional mechanisms observed to be important for maintaining tree-grass coexistence in empirical studies, such as
variability in tree fire survival strategy (Hoffmann et al., 2012a), are underrepresented in models (Haverd et al., 2013;
Lehsten et al., 2016). As a result, the implications of including variability in tree fire survival strategy are relatively untested,
365 providing one useful avenue to improve modelling of savanna-forest dynamics.

To better understand the sensitivity of tropical carbon storage to changes in rainfall regime and fire frequency, we
updated the Ecosystem Demography model 2 (ED2) to include distinct tropical savanna and forest plant functional types
(PFTs), each with a different bark investment strategy. We evaluated our model's predictions against observations of
savanna and forest tree growth rates, tree inventories, and total aboveground carbon (AGB) for different fire frequencies
370 using field data from savannas and forests in the Cerrado region of Brazil. We then [used the model to](#) ~~tested whether the~~
[following](#) two hypotheses ~~were consistent with model simulations~~: (1) Including bark investment as a tree fire survival
strategy decreases simulated carbon losses to increasing fire frequency, regardless of precipitation regime, due to the higher
probability of survival for thicker-barked, larger trees. (2) Including bark thickness as a fire survival strategy expands the
environmental conditions under which trees and grasses coexist by allowing for increased tree survival in frequently burned
375 savannas, [but also coming at a growth-rate cost that limits their ability to shade out grasses](#). Finally, we considered the
effects of changing fire frequency and fire survival strategy on ecosystem composition and aboveground carbon vulnerability
along a rainfall gradient in the Neotropics.

2 Materials and Methods

380 2.1 Model Description

Our model simulations were carried out in a cohort-based terrestrial biosphere model, ED2, [using parameterizations](#)
[from Xu et al. \(2016\) unless otherwise specified](#). ED2 explicitly scales up tree-level competition for light, water, and
nutrients to the ecosystem level (Medvigy et al., 2009; Medvigy and Moorcroft, 2012). The effects of water limitation on
photosynthesis have been previously identified to be important for simulating savanna-grass dynamics (Baudena et al., 2015;
385 Lasslop et al., 2016). Correspondingly, a novel aspect of the version of ED2 used in this study is the mechanistic
representation of water-limited photosynthesis, whereby leaf and stem water potential are tracked and used to solve for root
zone water uptake, transport of water vertically through the sapwood, and transpiration of water into the atmosphere.
Variability in hydraulic traits such as turgor loss point, xylem water conductivity, and marginal water use efficiency
determine PFT-specific responses to changes in leaf and stem water potential. Importantly, this mechanistic water limitation

390 scheme has been demonstrated to better resolve vegetation dynamics in water limited tropical ecosystems (Xu et al., 2016),
such as tropical savanna and forest regions.

We have incorporated in ED2 the following new processes important to ecosystem fire resistance in the Neotropics:
(1) a PFT-specific bark investment strategy in two updated tropical PFTs; (2) a carbon tradeoff between bark production and
tree height, canopy area, sapwood area, rooting depth, and leaf carbon; (3) a fire survivorship function dependent on
395 individual tree bark thickness; and (4) a dynamic feedback between tree size, survivorship probability, and grass biomass
availability. Updated model codes are included as Supplementary Materials file S1. The two new PFTs represent a generic
tropical forest tree PFT and tropical savanna tree PFT. Both are based on the tropical brevideciduous PFT from Xu et al.
(2016). Previous PFT versions do not include a bark thickness trait. The brevideciduous PFT was chosen because its
intermediate wood density and specific leaf area represent a drought survival strategy incorporating both drought avoidance
400 and resistance. This intermediate strategy is utilized by a broad array of tropical tree species (Xu et al., 2016). The savanna
and forest PFTs differ only in their bark investment strategy and the associated trade-offs. In the model, individual tree bark
thickness is calculated according to the following equation (Thonicke et al., 2010):

$$bt(PFT, dbh) = \beta(PFT) * dbh . \quad (1)$$

405

In Equation (1), bt is tree bark thickness in cm, β is the bark thickness slope coefficient (Table 1) that varies with PFT, and
 dbh is tree diameter at breast height in cm. In Neotropical savannas and forests, β ranges from ~0.068- 0.087 for trees of the
forest functional guild and from ~0.087-0.142 for trees of the savanna functional guild (Pellegrini et al., 2016a). We assigned
 $\beta = 0.077$ and $\beta = 0.110$ to our forest and savanna PFTs, respectively, based on the average of the observed ranges in bark
410 thickness.

The carbon cost of a tree investing in bark is difficult to quantify. Here, we incorporated a cost through the tree
allometric relations. Bark turnover rate in these systems is assumed to be negligible. Ordinarily in cohort- or individual-
based models, dbh is allometrically related to woody biomass, leaf biomass, crown height, crown area, rooting depth, and
sapwood area. The model also uses a standard allometric relationship between dbh and woody biomass. However, the new
415 model relates the other derived properties to dbh with bark excluded (denoted dbh'). Thus, for a given dbh , a PFT with a
large β will have a smaller dbh' , fewer leaves, a shorter height, a shallower rooting depth, a smaller crown, and a smaller
sapwood area for water transport than a PFT with a small β . A similar tradeoff has been used previously to quantify the costs
and benefits associated with growing thick bark (Lawes et al., 2013) and accounts for the observed increased bark
investment only in trees growing in fire-prone areas (Charles-Dominique et al., 2017; Pellegrini et al., 2017a). This approach
420 probably exaggerates the cost of bark because the relative cost of a tree growing outer bark for the purpose of stem insulation
may be substantially less than the cost of growing xylem. Thus we performed an additional set of simulations with no carbon
cost associated with tree bark investment to capture the end members of the spectrum of carbon tradeoff associated with bark
investment strategy.

The advantage of having thicker bark is incorporated through our fire survivorship function. This function
425 prescribes that trees with thicker bark are more likely to survive a fire event than trees with thinner bark. Thus, large trees
and trees with a large β at a given height are more likely to survive than small trees and trees with a small β . Survivorship is
also dependent on the amount of grass biomass present. This grass dependence comports with observations that an
abundance of grass biomass results in higher ecosystem flammability and hotter fires that cause increased tree mortality
(Hoffmann et al., 2012b). These ideas are incorporated in the following equation based on Pellegrini et al. (2016a) derived
430 from data in Hoffmann et al. (2009):

$$survivorship = \begin{cases} \min(1, 0.618 * bt + 0.0383) & \text{for } g_b > 25 \\ \min(1, 0.602 * bt + 0.1484) & \text{for } g_b \leq 25 \end{cases} \quad (2)$$

In Equation (2), *survivorship* is the tree survivorship fraction of a given tree size class and functional guild, g_b is grass
435 biomass (in g C m⁻²), and 25 is the threshold for increased fire intensity based on grass biomass curves of savanna
flammability from Hoffmann et al. (2012b). In the model, fire intensity is based only on grass biomass present and grass
survivorship after fire is always zero. However, grass is able to reseed by continuous seed deposition from adjacent unburnt
patches. We used the updated model to assess the joint effects of precipitation, fire disturbance, and bark investment strategy
on (1) tree demography and AGB and (2) tree-grass coexistence.

440 2.2 Simulations

We conducted two classes of single-grid cell simulations. We first evaluated our model performance against
observed datasets within the Cerrado region of Brazil at different fire frequencies. We then performed model experiments to
assess the influence of bark investment strategy on vegetation carbon and tree-grass coexistence across a rainfall and fire
gradient in the Cerrado. Our model experiments included two sets of simulations. First, we ran a control simulation that
445 included C₄ grass and our updated savanna and forest PFTs, but no investment in bark or fire survival benefit ($bt=0$). Second,
we ran simulations including [the following 3 PFTs run simultaneously](#): C₄ grass ~~and~~, our updated [savanna savanna PFT](#), and
[our updated forest tree PFT](#). ~~Both savanna and forest tree PFTs included~~ [the with bark](#) a fire survival strategy and allometric
tradeoffs based on bark investment. This scenario assumes that bark and xylem have the same construction cost per unit
volume. Given that bark construction cost may be lower than xylem construction costs, we also ran simulations including C₄
450 grass and our updated savanna and forest tree PFTs with a fire survival strategy but no cost associated with bark production.
Excluding this bark-growth tradeoff did not change the overall results. We include these simulations with fire survival
strategy but no bark investment tradeoff for comparison in the Supplementary Material.

In our simulations, ecosystems were spun up from tree seedlings initialized at a density of 1.0 seedling m⁻². C₄ grass
was able to seed in at a rate of 0.001 kg C month⁻¹ m⁻². Simulations were forced with 0.5°, 3-hourly meteorology from the
455 Princeton Global Forcing dataset (Sheffield et al., 2006). To isolate the effects of precipitation and fire frequency, all

simulations were forced with a constant 370 ppm atmospheric CO₂ and meteorology looped over the same 20-year period (1980-2000). This twenty-year period is long enough to ensure a majority of the years are not anomalous, but short enough to reduce the effects of trends in climate with global change. Median fire frequency was prescribed at the beginning of a simulation and fire interval varied stochastically within ± 3 years of the user input value. Fire disturbance occurred at most
460 once per year and the fraction of the landscape that burned was kept constant at 30% during a given fire event. Thus, there were no climate feedbacks on fire, and grass biomass only affected fire intensity (i.e. tree fire survival probability), but not the frequency or burned area fraction. Windthrow disturbance affected 1% of the landscape each year, resulting in 100% mortality of trees taller than 5 m and 20% mortality of trees smaller than 5 m.

465 2.2.1 Model Evaluation

We evaluated performance of the updated model using ecosystem measurements from study sites located in IBGE and the adjacent JBB Ecological Reserves within the Cerrado region of Brazil at approximately 15.95° S and 47.85° W. In these reserves, mean annual temperature is ~ 22.5 °C and mean annual precipitation (MAP) totals ~ 1460 mm with a ~~distinct~~
dry season [during which precipitation is <50 mm/month](#) from May to September. From the 1910s until reserve formation in
470 the 1970s, the whole landscape was subject to frequent fire at ~ 2 year intervals (Pellegrini et al., 2014). Since reserve formation, the initiation of fire management strategies has provided a landscape with diverse disturbance histories: fire return interval ranges from a few years in savannas to half a century in some adjacent forest patches (Pellegrini et al., 2014).

At the tree level, we compared annual diameter increments in the simulation with bark and without fire disturbance to annual diameter increments of twelve paired savanna and forest species measured over the years 2006-2007 (Rossatto et
475 al., 2009). We performed a 35-year model spin up from seedlings in accordance with the disturbance history and age structure of the site (Rossatto et al., 2009) and then examined the range of average annual diameter increments of our savanna and forest PFTs over a 20-year period to the range of observed annual diameter increments. In our simulations, the dbh size classes included in the calculation for the savanna PFT ranged from 5-9 cm with a mean of ~ 7 cm and from 6-10 cm with a mean of ~ 8 cm for the forest PFT in accordance with the Rossatto et al. (2009) observations.

480 Next, we assessed the ability of the model to predict observed tree size class distributions and measurements of AGB at sites with different fire frequencies to evaluate if the updated model with bark could more accurately capture ecosystem-level carbon dynamics and tree size abundance in response to fire compared to the control model without bark.

We compared model ~~simulations~~ [simulated tree size distributions for trees with dbh >2 cm](#) to inventories of trees with dbh > 2 cm along 200-300 m² transects made in July 2012 within the IBGE and JBB Ecological Reserves. Total AGB was
485 calculated from diameter inventories using the allometric relations from Xu et al. (2016) and accounting for bark carbon investment assuming $\beta = 0.077$. We performed a 35-year model spin up in accordance with the disturbance history of the reserves after 1970 (Pellegrini et al., 2014) and then compared the range in simulated AGB over the next 10-year period in a simulation with bark fully included and a control simulation without bark investment to observed AGB estimates and tree

size class distributions. In our simulations, our high fire frequency scenario was forced with a fire return interval that ranged from 2-8 years, our intermediate fire frequency scenario was forced with a return interval that ranged from 9-15 years, and our low fire frequency scenario was forced with a return interval that ranged from 57-63 years, in accordance with the disturbance regimes of Pellegrini et al. (2014) plots 3, 4-5, and 6, respectively. In these validations, the range in the model output represents the range in simulated AGB or tree size over the 10-year period. Variation in the observations is due to variation between plot biomass or in variation across individuals within plots sampled at a single point in time. Although the errors are not analogous, we intend to represent the range in model output resulting from growth and variable meteorological forcing over the 10-year time period following model spin-up.

2.2.2 Model Experiments

To assess the outcome of including bark investment as a fire survival strategy on carbon vulnerability and tree-grass coexistence, we conducted experiments along a-sites with a rainfall gradient within the Cerrado. We included locations with MAP within the first (MAP=820 mm), central (MAP=1150 mm), and fourth quartiles (MAP=1660 mm) of the distribution from a network of sites, one with a low MAP of ~820 mm, one with an intermediate MAP of ~1150 mm, and one with a high MAP of ~1660 mm. At each location we included simulations with bark investment and a growth tradeoff, and with no bark at four forced fire return intervals ranging from 1-6, 5-11, 9-15, and 22-28 years. Additionally, we included a simulation with no fire. For each simulation we performed a 100-year model spin up from seedlings and then analysed the subsequent 20-year average total AGB, AGB by tree size, and tree crown area fraction (Fig. 1). Tree crown area fraction ranged from zero, corresponding to open grassland, to one, corresponding to closed canopy forest and were calculated by summing the crown area of each cohort (up to a maximum crown area of one). Savanna regions were defined as regions having a crown area fraction of 0.2-0.8.

3 Results

3.1 Agreement between emergent tree growth in simulations and observations

Simulated growth rates for both the savanna and forest PFTs fell well within the observed range for Cerrado species when the allometric growth tradeoff with bark thickness was included (Fig. S1). The median growth rate for the savanna PFT was within < 0.1% different from of the observed median savanna species growth rate (Fig. S1a). Additionally, both observed and simulated savanna species had similar minimum diameter increments. However, the model did not capture the upper limit of faster growing savanna species, possibly due to additional differences in physiological traits such as allocation or the maximum rate of carboxylation. The model overestimated the median growth rate for the forest species by ~23%, but

was able to capture a wide range of the variability in growth rates seen in the observations (Fig. S1b). Further, the
520 interquartile range of observed and simulated diameter increments overlapped broadly.

Including a bark investment strategy in the model resulted in trees becoming more fire resistant with increasing
size. ~~As a result, which reproduced the observed size class distribution in the data.~~ For higher fire frequencies, simulations
where bark was ~~used to determine fire-driven mortality and growth tradeoffs~~ ~~represented included?~~ ~~as a fire survival strategy~~
~~better reproduced~~ ~~predict a larger the observed~~ maximum tree size, ~~which more closely reflects observed size class~~
525 ~~distribution~~ compared to the model without bark (Fig. S2). Further, at high fire frequencies, simulations with bark had the
smallest percent difference in predictions of the median size class (23.0% compared to 25.9% for the simulation without
bark) (Fig. S2a). At intermediate fire frequencies, simulations with bark also had ~~the smallest~~ ~~a smaller~~ percent difference in
predictions of the median size class (27.0% compared to 51.7% for the simulation without bark) ~~and better predict the skew~~
~~in number count towards larger tree size classes~~ (Fig. S2b). For low fire frequencies, including a bark investment strategy did
530 not improve predictions of maximum tree size, however a better prediction for median tree size ~~and skew towards larger~~
~~trees~~ was achieved (38.6% compared to 44.1% for the simulation without bark) (Fig. S2c). ~~Consequently, and as expected,~~
~~the importance of bark investment for capturing ecological dynamics was greatest in frequently burning environments.~~

Size-specific survivorship affected predictions of ecosystem AGB under different fire frequencies. At high fire
frequencies, simulations with a bark investment strategy captured the observed AGB within its predicted range and had the
535 lower percent error between simulated and observed mean AGBs (an overestimation by 36.2% compared to an
underestimation by 38.8% for the simulation without bark) (Fig. 3a2a). Under intermediate fire frequencies, simulations with
a bark investment strategy overestimated mean AGB by 0.8%, and the observed AGB was fully within the simulated
interquartile range, whereas the simulation without bark underestimated mean AGB by 20.2% and did not capture the
observed AGB within the range of predicted values (Fig. 3b2b). At low frequency fire, the simulation without bark
540 ~~predicted~~ ~~predicts~~ the observed AGB marginally more accurately than the model with a bark investment strategy (percent
errors of +4% and -6.7%, respectively) (Fig. 3e2c).

3.2 Bark investment decreases carbon losses at high fire frequencies

We found substantial differences in the fraction of AGB present in different tree size classes between the original
545 model without bark and the updated model with a bark investment strategy, but these differences depended on fire frequency
and precipitation. The impact of including bark thickness increased with MAP and fire frequency, ~~likely~~ because the higher
~~potential~~ growth rates allowed for trees to grow larger faster but the increased fire frequency restricted the growth of species
that did not invest in thick bark (Figs. 34, S2S3). When fire was frequent, the model without the bark investment strategy
~~predicted~~ ~~predicts~~ a ~~smaller absolute AGB and a~~ large contribution of small and intermediate-sized trees to ~~total~~
550 ~~AGB biomass~~ -whereas the model version with bark investment strategy ~~predicted~~ ~~predicts~~ a ~~much higher absolute AGB with~~
~~that~~ virtually all biomass ~~was allocated~~ in the larger tree size classes (Figs. 43-4). These results were robust regardless of the

cost of bark investment to tree growth (see Section 2.1) (Fig. S3S4). The greater proportion of biomass in large trees was due to the low probability of mortality during a fire because of the insulating capacity of bark and the relationship between tree size and bark thickness (eq.1). However, it should be noted that the biomass fraction of small trees is not illustrative of the frequency (i.e., abundance) frequency of small trees, as small tree biomass comprises a very small fraction of AGB when large trees are present. Thus, small trees grow between fires even in the simulations with a bark investment strategy, though they comprise very little of the absolute biomass. -Indeed, the model with bark investment strategy predicts cumulative AGB mortality (resulting from fire, windthrow disturbance, age related mortality, and carbon starvation) to occur almost exclusively in the small and large tree size classes, excluding midsized trees (Fig. S5). This absence of midsized trees mortality is reflective of indicative of an absence of midsized trees high-due to the high fire-driven mortality rate of small, low biomass trees. AGB mortality in large trees results from a low but persistent age related mortality and windthrow disturbance. In contrast, trees of all size classes are present in the no bark simulation, and correspondingly the model predicts AGB mortality across all size classes, consistent with a large number of smaller trees, fewer intermediate and large sized trees, and an overall lower total AGB (Fig. 4,S5). Trends in AGB growth reflect almost identical biomass patterns. As would be expected, the difference in tree size distributions between the model without bark and the model with a bark investment strategy decreased substantially when fires were eliminated (Fig. 4b3b,d,f,S5 b,d,f).

We also found that tree size distributions were largely unaffected by MAP in the presence of frequent fire in both simulations with a bark investment strategy (Figs. 34a,c,e,S43); only minor impacts were found at intermediate fire frequency and high MAP (Fig. S2eS3c). In contrast, the model without a bark investment strategy predicts that small size classes comprised a substantial fraction of AGB ~~were prevalent~~ for high fire frequency simulations-using the original model without a bark investment strategy, particularly at low MAP (Fig. 4a3a,c,e).

Incorporating bark thickness decreased predicted carbon losses with increasing fire frequency (Fig. 54) because larger, thick-barked trees made up the majority of AGB (Fig. 43) and had a very low probability of mortality during a fire. When a bark investment strategy was included, fire caused almost no reduction in biomass at the wettest site (1660 mm yr⁻¹ MAP), (Figs. 5a4a,S4aS6a). In simulations with no bark investment strategy, trees were highly vulnerable to fire, so burning at ~3-year intervals resulted in a 73% reduction in biomass relative to when fire was excluded (Fig. 5b4b). However, the effect of including a bark investment strategy on reducing carbon losses decreased as MAP decreased (i.e., the difference in simulated carbon loss between scenarios without and with bark investment strategy was lowest in the driest site). For example, at an intermediate MAP (1150 mm yr⁻¹), a 3-year fire return interval caused a 36% reduction in AGB in the model with a bark investment strategy and an 81% reduction in AGB using the control model without bark investment, relative to ecosystems without fire. At the driest site, a 3-year fire return interval caused a 70% reduction in AGB in simulations with a bark investment strategy and a 76% reduction in AGB for the simulations without bark, relative to ecosystems without fire.

There was a strong interaction between precipitation, fire, and bark investment strategy. When no bark investment strategy was included, both fire frequency and precipitation exerted an equivalently strong control on total AGB, and the range in AGB after 100 years of growth increased substantially with increasing precipitation, but strongly depended on fire

frequency (Fig. 5b4b). However, when bark investment was included as a fire survival strategy, MAP exerted a much stronger control than fire on the total AGB (Figs. 5a4a, S4a, S6a), indicating the important role of water availability regulating growth when species become fire resistant.

590 3.3 Environment and biological traits jointly affect simulated tree-grass coexistence

Both fire frequency and precipitation were important in maintaining tree-grass coexistence and thus in controlling the distribution of grasslands, savannas, and tropical forests (Fig. 65). At high fire frequencies and low precipitation, we simulated grasslands with minimal tree cover regardless of the model scheme (Figs. 6a5a,c, S5a, S7a,c). However, simulations with bark investment as a fire survival strategy expanded conditions under which there was 20-80% tree-grass coexistence. At fire return intervals of 1-6 years and intermediate MAP (1150 mm yr⁻¹) and at less frequent fire return intervals (9-15 years) and intermediate MAP (1150 mm yr⁻¹), bark investment mitigated either complete tree loss or complete grass loss (Figs. 65, S5S7). Thus, including bark investment as a fire survival strategy moderated the transition between grassland and forest at intermediate MAP under varying fire frequencies.

600 4 Discussion

We documented that tree bark investment strategy interacts with precipitation and fire frequency to determine both (i) the stability of ecosystem carbon to fire and (ii) the coexistence of grasses and trees, illustrating that species traits, in addition to climate and fire, are critical for the stability of savanna and forest biomes. Bark investment strategy increased the stability of the carbon stock in large trees, which decreased ecosystem carbon losses with increased fire frequency under a range of precipitation conditions. Investment in bark was especially important in wetter savannas and forests, illustrating that the distribution of functional traits is fundamental to the resilience of wet forests to increased fire and changing rainfall regimes.

610 4.1 Implications for carbon ~~resistance~~ losses

Our simulations illustrate that tree bark thickness as a fire survival ~~mechanism~~ trait substantially decreases fire-driven carbon losses, but the magnitude of the effect depends on precipitation regime (Fig. 5a4a-b). We found that bark investment was particularly important at reducing carbon losses at higher fire frequencies in locations with a high MAP (1660 mm). This is because trees had ample water availability, enabling ~~smaller trees~~ them to grow rapidly and quickly become fire resistant, ~~and decreasing the probability of fire mortality to near zero~~. In contrast, the effect of bark investment ~~on~~ offered little to no benefit in reducing carbon losses ~~diminished~~ at the lowest MAP and highest fire frequency because small trees were not able to grow rapidly and accumulate thick enough bark to escape fire mortality. The decreasing utility of bark investment as a survival strategy at the lowest MAP and highest fire frequency likely occurred because bark investment

[slowed growth and prolonged the period during which trees were more susceptible to fire-driven mortality](#). Taken together, these results suggest that current models that do not account for bark investment strategies may underpredict Neotropical carbon resistance to fire in both savannas and forests. Such models would over-predict mortality of large thick-barked trees that make up a majority amount of aboveground woody biomass (Slik et al., 2013; Hanan et al., 2008). However, further work understanding the spatial distribution of tree species and their corresponding bark investment strategies is also critical (Pellegrini et al., 2017a; Rosell, 2016; Pausas, 2015; Dantas et al., 2013) because observations show that even large trees in rainforests have thin enough bark that they suffer substantial fire mortality (Uhl and Kauffman, 1990), although the forests with high mortality have precipitation values much higher than the maximum we consider (1660 mm).

4.2 Implications for tree-grass coexistence

Capturing savanna distributions globally has long been difficult for vegetation models, which over-predicted the extent of either tropical forests or grasslands (Hickler et al., 2006; Cramer et al., 2001; Bonan et al., 2003; Hely et al., 2006; Schaphoff et al., 2006; Sato et al., 2007). A number of recent studies have focused on this issue: the adaptive dynamic global vegetation model (aDGVM) was able to capture savanna extent in Africa by including (i) trees with a higher fire mortality rate in small tree size classes, (ii) regenerative tree resprouting after fire events, and (iii) grass as super individuals (Scheiter and Higgins, 2009). The individual-based Populations-Order-Physiology model also included size-dependent tree mortality and was able to reproduce key vegetation structure and function along a rainfall and fire gradient in Australia (Haverd et al., 2013). Studies by Baudena et al. (2015) and Lasslop et al. (2016) have proposed several key mechanisms for capturing savannas in models: (1) water limitation on tree growth, (2) competition for water between grasses and trees, and (3) a grass-fire feedback.

The results from this study show a strong dependence of tree growth on precipitation and fire frequency, supporting observations (Pellegrini et al., 2017b; Higgins et al., 2007) and other modeling studies (Baudena et al., 2015). However, we found that including bark investment as a fire survival mechanism broadened the range of climate and fire conditions under which savannas occur by reducing the range of conditions leading to either complete tree loss or complete grass loss. This is due to the shift towards fewer, larger trees that store relatively more AGB per unit crown area than smaller trees, but are also resilient to frequent fire, resulting in ecosystems with intermediate crown cover in a wider range of precipitation and fire regimes. Thus, fire and precipitation as well as species-specific bark thickness traits have the potential to affect tree-grass coexistence, suggesting that inclusion of bark investment in models [at broader spatial scales](#) has the potential to substantially enhance our ability to accurately project changes in the tropical carbon sink with changes in fire and rainfall over the upcoming century.

4.3 Limitations and future work

650 Several avenues exist for future model improvement. Tree re-sprouting after fire has been shown to be essential in predicting the range of conditions for which tree-grass coexistence is possible (Higgins et al., 2000). Currently in our model, trees reproduce only through seedling recruitment. This has the potential to affect [model benchmarking and simulation predictions simulation outcomes](#) because initial aboveground growth rates of re-sprouts are substantially higher compared to seedlings due to (a) access to belowground carbohydrate stores and (b) elimination of the need to allocate carbon for roots. 655 Thus, re-sprouting may allow for better agreement between model predictions at higher growth rates and fire frequencies (Figs. 2,3,S1-2). Enabling tree re-sprouting may also stabilize savannas under frequent fire and low precipitation where all model versions currently simulate grassland (Fig. 65).

Additionally, the current fire model does not interact dynamically with climate or the nitrogen cycle. ED2 is capable of resolving nitrogen dynamics (Trugman et al., 2016) and we anticipate that coupling nitrogen and climate feedbacks to fire 660 will be an important step in accurately modelling the carbon cycle. Despite these current limitations, the updated model accurately predicts growth, demographics, and AGB. We believe that these results can provide important insight into tree-grass coexistence and carbon resistance with changing fire frequency in the Neotropics with global change.

5 Conclusions

665 In conclusion, our results highlight that carbon storage in tropical savannas and forests depends not only on changing environmental drivers, but also on tree fire survival strategy. Thus, we can improve projections of the tropical carbon sink with global climate change by increasing our understanding of the distribution of bark investment and incorporating this knowledge of bark investment into future vegetation models. Further, an increased understanding of the interaction between bark investment strategy and environmental drivers promises to increase our ability to project the 670 distribution of savanna in regions previously simulated as grasslands or forests by reducing the range of conditions leading to either complete tree loss or complete grass loss.

Code availability: Model codes are included as an online supplement

675 **Competing interests:** The authors declare that they have no conflict of interest

Author contributions

A.T.T., A.F.A.P., D.M., W.A.H. designed the research. A.T.T performed numerical experiments. A.T.T. and A.F.A.P. analysed the data. A.F.A.P. and W.A.H. contributed field data. A.T.T drafted the paper and all authors contributed to writing 680 of the manuscript.

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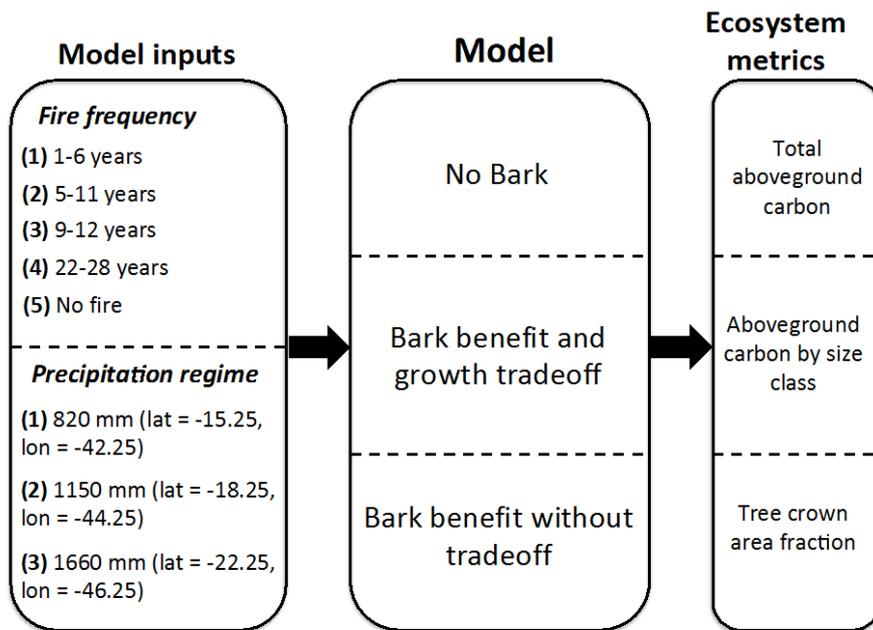
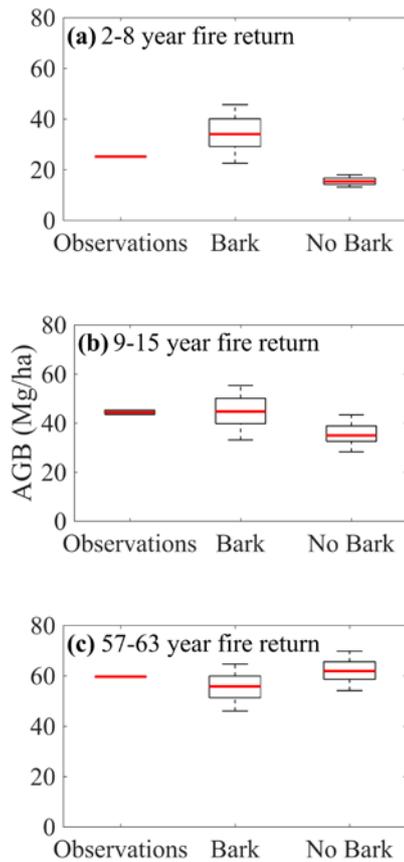
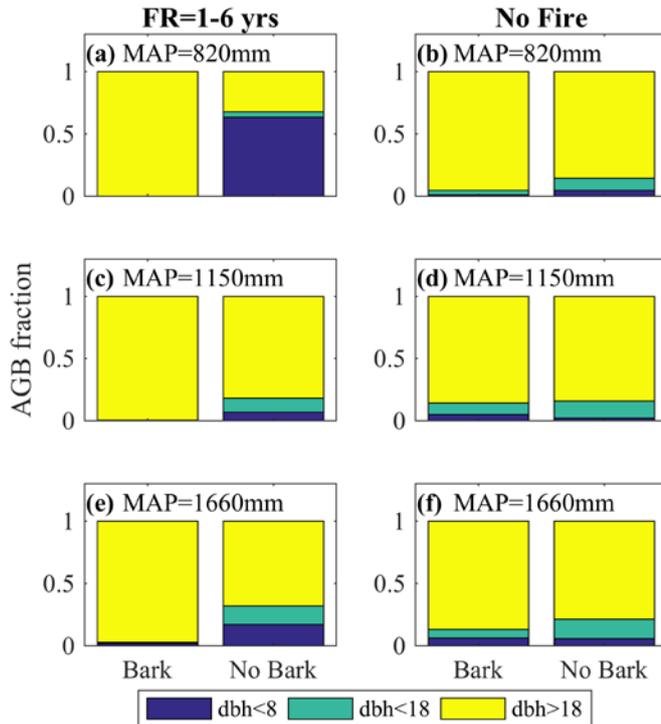


Figure 1. Schematic of model experiments along a rainfall gradient. Varied model inputs include fire frequency and precipitation regime (associated with a particular [study site locations location](#) in the Cerrado region of South America). Different model versions were used to understand the effect of including bark as a fire survival strategy on model outputs of various ecosystem metrics including aboveground woody carbon, tree size class distribution, and tree crown area fraction.

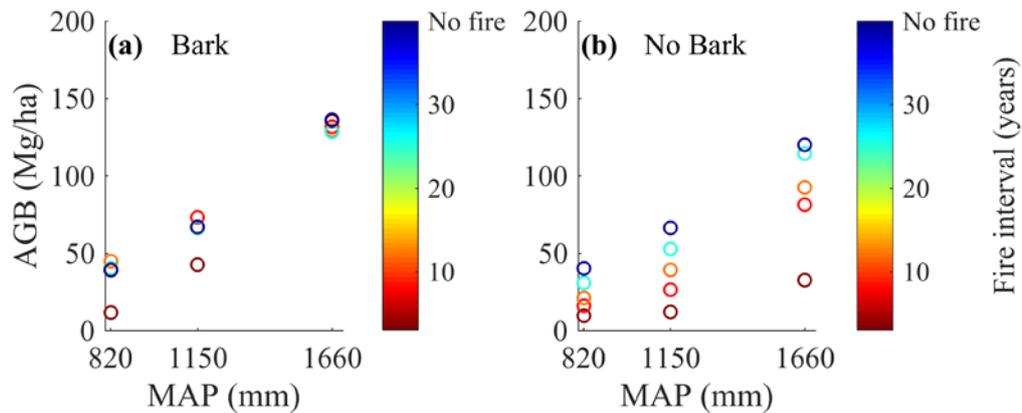
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835 **Figure 32.** Tree fire survival strategy impacts aboveground [woody carbon tree biomass](#) with fire disturbance. Observed and model-
simulated aboveground woody biomass (AGB) under **(a)** high, **(b)** intermediate, and **(c)** low frequency fire regimes. Model simulations
included a 35-year model spin up in accordance with the disturbance history of the observations (Pellegrini et al., 2014). Simulated AGB
was compared over the subsequent 10-year period for the model with bark and the model without bark. [For model output, \(T](#)
840 [he red line denotes the predicted median AGB, the black box denotes the interquartile range, and the dotted error bars denote \$\pm 2.7\$ standard deviations over the subsequent 10 year period following the 35 year spin up. For the observations, variation in AGB is due to variation in biomass across plots at the time of sampling. See Methods for additional details.](#)



845 | **Figure 43.** Bark fire survival strategy increases the fraction of aboveground woody biomass in large trees, particularly with frequent fire. Model-simulated fraction of aboveground woody biomass (AGB) present in different tree diameter at breast height (dbh in cm) size classes for $2 < \text{dbh} < 8$ (blue), $8 < \text{dbh} < 18$ (cyan), and $18 < \text{dbh}$ (yellow) at low (a-b), intermediate (c-d), and high (e-f) MAP for a high frequency (FR) fire regime (a,c,e), and a no fire disturbance simulation (b,d,f). Simulations were initialized with tropical tree and C₄ grass plant functional types and included a 100-year model spin up from seedlings. The subsequent 20-year average AGB fraction by tree size class is shown for 850 the model with bark and the model without bark. See Fig. S2 for size class distributions associated with intermediate fire frequency.



855 | **Figure 54.** Bark fire survival strategy buffers aboveground woody biomass loss with frequent fire, particularly at high MAP. Model-simulated total aboveground woody carbon (AGB) at different MAP and forced fire regimes for the model with bark (a) and the model with no bark (b). Simulations were initialized with tropical tree and C₄ grass plant functional types and included a 100-year model spin up from seedlings. The subsequent 20-year average AGB for each disturbance and precipitation regime is shown.

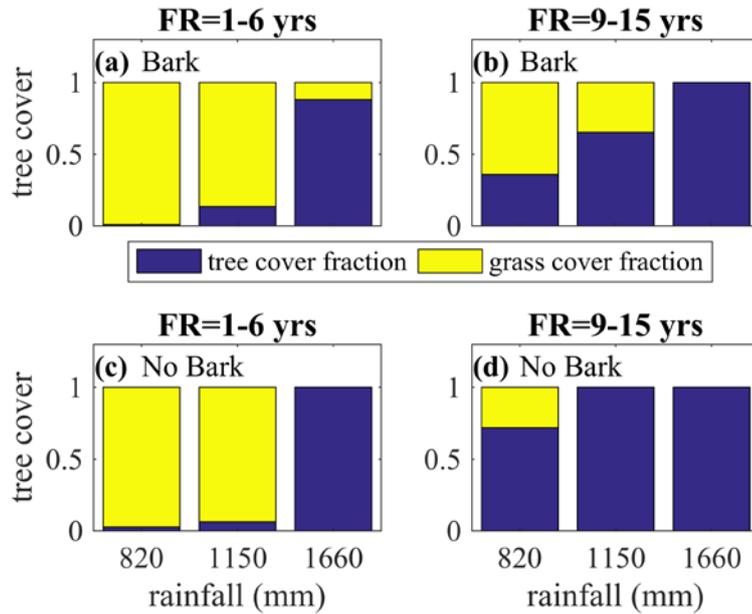


Figure 65. Bark investment can broaden the range of climate and fire conditions under which savannas occur by reducing the range of conditions leading to either complete tree loss or complete grass loss. Model-simulated tree cover fraction present at different levels of mean annual precipitation (in mm) for the model with bark (**a-b**) and the model without bark (**c-d**) for fire frequencies (FR) of 1-6 years (**a,c**) and 9-15 years (**b,d**). Simulations were initialized with tropical tree and C₄ grass plant functional types and included a 100-year model spin up from seedlings. The subsequent 20-year average tree cover fraction is shown.

Tables

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Table 1 | Model evaluations at IBGE Ecological Reserve

Metric	Fire frequency	Data source
(1) Annual diameter increments of twelve paired savanna and forest species	(1) No fire	Rossatto et al. (2009)
(2) Inventory tree size class	(1) 2-8, (2) 9-15, and (3) 57-63 years	Pellegrini et al. (2014) plots 3, 4-5, and 6
(3) Inventory aboveground biomass	(1) 2-8, (2) 9-15, and (3) 57-63 years	Pellegrini et al. (2014) plots 3, 4-5, and 6