(Reviewer comments in italics; Responses in bold)

# Response to Anonymous Referee #1 Received and published: 11 July 2017

5 General Comments:

Reviewer summary:

The manuscript presents results from the DGVM INLAND evaluating the effect of climate variability, fire and phosphorus limitation on vegetation structure and dynamics in the transitional zone between the forested Amazon and grassland savanna of the Cerrado. Changes in net primary production, aboveground biomass, and leaf area index are assessed between simulations, and simulated aboveground biomass is compared to observations. Transects along the Amazon-Cerrado transition zone are analyzed in subsets, as well as the region as a whole. Inclusion of climate variability, fire and maps phosphorus limitation improves simulation of vegetation structure across the region and for four of five transects. The cerrado transect has the lowest correlation to observations. Fire has the strongest impact on vegetation characteristics, followed by phosphorous limitation. Overall, INLAND with these included factors appears effective at simulating vegetation across the region, but regional deficiencies show that more improvements can be made.

*Article contribution and overall impact:* 

This study highlights the need for improved simulation of vegetation in a key forest-savanna transition zone. A shift in vegetation in this region has the capacity to impact the cycling of water and nutrients as well as energy fluxes beyond the area of forest-savanna transition. Uncertainty in future climate and fire behavior as well as the feedback between these factors make the vegetation state of this region difficult to predict. The manuscript does a good job of presenting the challenges of simulating vegetation in this transitional zone where climate, nutrients and fire are essential contributors to vegetation state. The inclusion of phosphorous limitation in the simulations for the region is an important addition to the evaluation of vegetation state. The discussion would benefit from a more detailed description of the fire model and fire activity during simulation. The concluding recommendations for future work also need to be clarified. Discussion of the importance of vegetation size structure and how this is or is not represented in INLAND should also be added. A key component of the mortality of woody vegetation to fire is its size at the time of fire and the ability to accumulate size between fires. This is central to the work of many of W. Hoffman's papers in the region (Hoffman et al 2003, Hoffman et al 2009, Hoffman et al 2012). Please add discussion of size structure to the manuscript.

Response: We are grateful to the reviewers for their insightful comments and helpful suggestions. We have included a better fire model description and have described how it works throughout the discussion of its impact on the vegetation structure. We have included a more complete discussion about the influence of fire on size structure along the transition. Details about recommendations for future work were also included.

Detailed comments:

1. Page 6 line 101-107: Add the 1x1 degree grid size to this section.

Response: This information was added. See below:

"The present study focuses on the Amazon-Cerrado transition (Figure 1). We use the official delimitation of the Brazilian biomes proposed by IBGE (2004), and define five transects along the transition border with  $1^{\circ} \times 1^{\circ}$  grid size (the terms "transition", "Amazon-Cerrado transition" and "Forest-Savanna transition" are used interchangeably with the same meaning throughout this manuscript)."

2. Page 9 line 159-164: Provide more detail concerning fire model. Is the fire ignition probability the same in every pixel, or is there spatial variability? If there is spatial variability what drives this parameterization? Does flammability vary by PFT?

Response: The fire ignition probability is spatially varied in INLAND. INLAND incorporates all fire components of the CTEM (Canadian Terrestrial Ecosystem Model) model (Arora and Boer, 2005). These components simulate fire at the daily timescale (instead of the yearly timescale of earlier models) by computing the probability of fire occurrence, which is based on biomass availability, flammability and ignition source for each pixel (using observed lighting frequency). Burned area is modeled as an ellipse of dimensions determined by wind and fuel conditions. The fire model of CTEM uses an arbitrary anthropogenic fire probability which is summed to the natural ignition probability. In summary, the natural ignition probability is represented by a lightning scalar, which varies from 0 to 1 as cloud-to-ground lightning frequency varies from a specified lower value of essentially no lightning to an upper value close to the maximum observed. The probability of fire ignition due to human causes may be selected depending on location and human activity and determines the lower limit of ignition constraint. In INLAND, we use 0.50 for the probability of fire ignition due to human cause. Additionally, we suggest the reviewer to verify the arbitrary ignition scheme in Figure 3c in Arora and Boer (2005), which we do not have permission to reproduce. Moreover, in INLAND the vegetation structure is represented by two layers. The fire occurrence reduces the upper canopy decreasing the trees LAI (LAI upper), and opening the canopy. The opening canopy implicates in more luminosity penetration and consequently increase of photosynthesis rates by grasses (increasing of LAI lower) initializing a competition between PFTs for light resource. We have included these details concerning fire model in the Methods section.

 3. Page 16 line 316: define "transition" here and throughout manuscript. The reference is not always clear. Most often it appears to be Amazon-Cerrado transition or forest-savanna transition, if that is correct please add the extra detail here and throughout manuscript (Pg 20 line 403, pg 21 line 419, pg 22 line 426,428,443, pg 23 line 451)

Response: We agree with the reviewer that this term was not always clear and may generate doubts. To clarify, we included in Page 6 line 105-106 a brief reference: "The terms Amazon-

82 Cerrado transition, forest savanna transition or transition are used interchangeably with the 83 same meaning throughout this manuscript".

4. Page 17 line 323-325: Update sentence to "responsible for altering the simulated AGB to approach the observed AGB" or some variant. Current sentence structure is unclear.

87 Response: The sentence has been changed. See below:

 "In T2, T3 and T4, however, fire is responsible for altering the simulated AGB to the observed AGB in the eastern pixels of the Cerrado domain (Figure 5)".

5. Page 18 line 345-349: What observational data set is this being compared to for current vegetation state? Is this a by pixel comparison of the same grid size?

Response: We use the official delimitation of the Brazilian biomes proposed by IBGE (2004), which reconstructs in more detail the probable location of the vegetation before the anthropogenic interference. This database is a vector database and is available in http://downloads.ibge.gov.br/downloads\_geociencias.htm.

6. Page 18 line 359-364: Do the climate datasets used in simulation include reduced rainfall and ENSO effects? Explain this further.

Response: The CRU climate database, which is used in our study, included reduced rainfall and ENSO effects. The CRU gridded climate dataset is a database developed from monthly observations at meteorological stations across the world's land areas (Harris et al., 2014). These dataset includes six mostly independent climate variables (mean temperature, diurnal temperature range, precipitation, wet-day frequency, vapor pressure, and cloud cover). Maximum and minimum temperatures have been arithmetically derived from these. This gridded product will be publicly available, including the input station series (http://www.cru.uea.ac.uk/and http://badc.nerc.ac.uk/data/cru/).

7. Page 21 line 409: Update to "for the most part Dynamic Vegetation Models"

Response: That has been changed.

8. Page 22 line 435-437: Add more detail clarifying how the INLAND model differs from reality. Is it able to simulate rapid restoration following fire? If not, what would need to be added to the model's fire or vegetation characteristics?

Response: In our model, the restoration of vegetation after fire occurrence is exclusively due to the canopy opening and consequently more luminosity penetration into lower canopy. Two layers in the INLAND represent the vegetation structure. The fire occurrence reduces de upper canopy decreasing the trees LAI (LAI upper), and opening the canopy. Thus, we have more luminosity penetration and consequently increase of photosynthesis rates by grasses (increase of LAI lower)

initializing a competition for light resource. The dynamic vegetation module computes for each PFT: gross and net primary productivity, changes in biomass pools, simple mortality disturbance processes and resultant LAI, with the same manner before the fire occurrence, thus allowing vegetation type and cover to change with time. We have included more details about fire model (in section 2.2) describing the INLAND Surface Model and added more details about restoration after fire occurrence in the discussion.

9. Page 22 line 444: Update to "but the inclusion of these effects"

#### Response: That has been changed.

 10. Page 22 line 442-445: This needs more explanation. Is the vegetation simulation insufficient because of the presence of transitional and robust pixels in the certado in fig 5? Or is this because of comparisons to observed data of vegetation in the certado?

**Res** 

Response: The sentence was re-written. See below:

"From Figure 5, it is clear that CV, F and P limitation in the transition zone reduce the AGB, approaching the simulated to the observed data. However, the inclusion of these effects is still insufficient to represent the actual vegetation structure in the Amazon-Cerrado border (Figure 6L)."

11. Page 23 line 449: what is meant by residence time?

Response: Residence time is the average time a particle resides (passes) in a pool or system. In INLAND, the residence time is a parameter of the vegetation used by the PFTs to allocate carbon in the different compartments of biomass (leaves, roots and stems). The residence time of carbon in a biomass compartment is intended to represent the loss of biomass through mortality and tissue turnover.

12. Page 24 line 477-479: Explain this in more detail: "It does not dynamically change the allocation"

Response: Parameters can be fixed or dynamically allocated, which means that they can change over time. Fixed parameters for a given PFT are assumed during the carbon allocation in INLAND. For tropical evergreens trees, for example, we have 50% of carbon allocation in stems, 25% in leaves and 25% in roots. Even though there is evidence that in the Amazonia-Cerrado transition the carbon allocation rates may vary in some situations of water stress, the INLAND model do not represent this strategy.

13. Page 25 line 495-496: Reword this sentence. The meaning is not clear.

Response: We agree to the reviewer. This sentence was changed. See below:

"Obtaining ecophysiological parameters is a challenge to the scientific community once the field measurements depend on fieldwork conducted throughout all the transition area."

14. Page 26 line 522-525: Inclusion of spatially explicit parameters may or may not improve DGVM simulation. This assumes that the existing processes are accurate, and that it is merely parameters. Provide more discussion of this possibility, or re-word this section.

Response: There are evidences that the inclusion of spatially explicit parameters may improve DGVM simulation. Castanho et al. (2013) showed that the simulated aboveground biomass in Amazonia improved with spatially biophysical parameters such as woody biomass residence clearer time, maximum, carboxylation capacity ( $V_{max}$ ), and NPP allocation to wood. They found that using single values for key ecological parameters in the tropical forest biome severely limits simulation accuracy. We believe that the same limitation occurs along the transition. The use of spatial parameters allows represent the spatial heterogeneity along the Amazon-Cerrado border and may lead to simulated spatial variability of biomass. However, the lack of data observed in this region limits the representation and understanding of how biophysical parameters vary throughout the transition. Thus, it is necessary obtain physiological and structural parameters to establish numerical relationships between the environment and the vegetation dynamic models.

Page 26 line 525-527: What is meant by temporal variability? Size structure?

Response: Currently the physiological parameters of vegetation are fixed, each PFT uses a fixed carbon allocation parameter, mortality, carboxylation capacity and others from start to finish of the simulation. We suggest that these parameters should be dynamically allocated, i.e. temporal variability in physiological parameters of vegetation, as a function of other simulated variables should be included, to improve the simulation results.

- (Reviewer comments in italics; Responses in bold)
- Response to Anonymous Referee #2 Received and published: 23 July 2017 195
- This work uses the vegetation model INLAND to evaluate the individual and combined effects of the 196
- climate variability, the fire and the Phosphorus (P) limitation on the Brazilian ecosystem. The changes 197
  - on the NPP, ] and AGB were evaluated in relation to 12 climate simulations. The AGB was also
- 199 evaluated in function of observed data. In addition to climate variability, this work shows the
- 200 importance of considering the soil nutrient limitation as well as the disturbances caused by the biomass
- 201 burning in the study of vegetation dynamics. It is also presented some deficiencies of the DGVMs and
- 202 the databases used to feed the INLAND model. Understanding the mechanisms that affect the vegetation
  - and the efforts to improve numerical models in order to simulate such effects is of paramount important
- 203 204 to the scientific progress. Therefore, this study is of great relevance and, in my opinion, it is suitable for
- publication in the BG. However, I have some recommendations and doubts that I would like to see being 205
- 206 clarified before publication.
- 207 Specific comments

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- 1. L55-L60: observing the Figure 6d (CV+PC), all the Amazon region became "very robust", so we can 208
- 209 assume that the simulation that considers only the climatic effect didn't indicate the "savannization of
- 210 the Amazon", in other words, the results obtained in this study don't agree with the mentioned works.
- 211 Can you comment on this?
- Response: The "savannization of the Amazon" have been appointed by studies that use future 212
- climate scenarios (Oyama and Nobre, 2003; Betts et al., 2004; Cox et al., 2000; Cox et al., 2004; 213
- Salazar et al., 2007 Pereira et al., 2012) or climate scenarios associated to changes on vegetation in 214
- 215 the deforestation case (Shukla et al., 1990; Malhi et al., 2009; Pires and Costa, 2013). Our results
  - do not indicate the "savannization of the Amazon" because they are based on past climate.
- 2. L140: "values smaller than 0.8 m<sup>2</sup>m<sup>-2</sup> characterize a grassland vegetation type" Grassland can 217
- have LAI values much higher than 0.8 m<sup>2</sup>m<sup>-2</sup>. Darvishzadeh et al., 2008 found out grassland's average 218
- values of 2.76  $\text{m}^2\text{m}^{-2}$  and maximum value of 7.34  $\text{m}^2\text{m}^{-2}$ . Please check if the INLAND really utilizes this 219
- 220 threshold of LAI to define grassland.
- Response: We agree with the reviewer, although we think the reviewer misunderstood the text. 221
- 222 The total LAI for grasslands can definitely be much higher than 0.8 m<sup>2</sup>m<sup>-2</sup>. In this sentence, we
  - refer to the LAI upper (tree LAI). That means that grassland vegetation type cannot have trees
- with LAI greater than 0.8 m<sup>2</sup>m<sup>-2</sup> while the LAI lower (grasses) is not limited. 224

- 225 3. 3. L85-L87: According to Oliveira et al. (in press), the weather also has influence in the nutrients.
- 226 Then, the climate change's effect cannot be higher due to the indirect effects in the nutrients? Can you
- 227 comment on this?
- 228 Response: Certainly, there is influence between weather and nutrients. For example, a very
- 229 intense rain can leach nutrients, such as nitrogen, as well as strong winds can carry clay particles
  - where numerous nutrients are adsorbed. However, in this work the nutritional conditions are
- prescribed and fixed. In this way, we cannot assert that the climate change's effect is higher due to
- the indirect effects in the nutrients. Oliveira et al (in press) has also been updated to Oliveira et al.
- 233 **(2017).**

- 4. L157-L158: How are the other PFTs affected by the availability of P?
- 235 Response: Tropical evergreen and deciduous trees are affected by availability of P in INLAND
- while other PFTs are unaffected. The lack of scientific reports about the influence of phosphorus
- on shrub and grass vegetation along the Amazon basin justify why only these two PFTs are
- affected. The phosphorus limitation in INLAND is based on regression equation developed by
- 239 Castanho et al. (2013), which use results of Fyllas et al. (2009) and Mercado et al. (2009). Fyllas et
  - al. (2009) show that soil fertility is one of the most important predictors for observed higher
- 241 nutrient concentration in Amazon tree leaves, while Mercado et al. (2009) report that the
- 242 correlation between observed Vmax and P concentration in Amazon tree leaves. Thus, Castanho
- et al. (2013) developed a similar regression equation to that of Mercado et al. (2009, 2011) between
- 244 Vmax and total P concentration in soil, instead of P concentration in leaves, allowing estimate
- 245 Vmax for the whole Amazon.
- 5. L262: I didn't understand where the 8.7% came from. Could you make it clearer?
- 247 Response: We calculated the average biomass values for each biome area (Amazon and Cerrado)
- 248 using the biomes delimitation from IBGE showed in Figure 1. This average biomass value was
- calculated for all simulations (Table 1), to compare the difference in the average value of each
- 250 simulation. In Cerrado, average biomass is 8.7% lower in the simulation with inter-annual
- climate variability (CV) than with average climate (CA).
- 252 6. L339-L344: It can be seen in Figure 6 large differences between CA + F (Line3) and CV + F (Line
- 253 4). However, the differences between CA (Line 1) and CA + F (Line 3) and the ones between PC
- 254 (Column 1), PR (Column 2) and PG (Column 3) are not very significant. Thus, the climatic variability
- 255 is dominant when considering the three effects. Probably, if a fifth map showing CA + PG + F
- 256 CA+PG is constructed in Figure 4, it will be quite distinct from Figure 4d. Therefore, it should be
- exposed more clearly how it came up to the conclusion described in L513-515.

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      difference between the vegetation types along the central Cerrado domain in CA (Line 1) and CA
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      + F (Line 3), the most part of these changes is very robust when fire is considered. We do not use
      the vegetation types to infer which are the main determinant drivers on the transition, we use the
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      Figure 6 only to show how these drives affect the distribution of vegetation. It is clear, however,
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      that the CV+F combinations yield the best vegetation patterns, with minor differences associated
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      with soil P.
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      The difference between CA + PG +F - CA+PG shows similar behavior that on CV simulations,
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      but we did not plot this difference because in our statistical analyses only the interannual climate
      variability showed significant influence on AGB and LAI. Finally, to write the sentence in L513-
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      515 ("fire is in the main determinant factor of the vegetation changes along the transition. The
      nutrient limitation is second in magnitude, stronger than the effect of inter-annual climate
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      variability"), we use F-statistics in Tables 3, 4 and 5, which permits infer the magnitude of fire,
      phosphorus limitation, and climate on AGB and LAI. To clarify this, we rewrote this sentence to
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      "Based on the F-statistic in Tables 3, 4 and 5, this work shows that fire is in the main determinant
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      factor of the changes in vegetation structure (LAI, AGB) changes along the transition. The
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      nutrient limitation is second in magnitude, stronger than the effect of inter-annual climate
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Response: In Figure 6, we evaluate only the robustness of the simulations. Although there is little

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- 7. L342: I think it is unlikely that an area with "deciduous forest" will turn into "evergreen forest" after being consumed by fire. Please comment if this is possible or if it is a model deficiency.
- 279 Response: In INLAND simulation, the "deciduous forest" is turning into "evergreen forest" after
- being consumed by fire happens in only 5 pixels and in average climate condition only, in a clay
- soil with large water retention capacity (Figure 6G-I) In this situation, where there is little water
- 282 stress in the CA simulation, both evergreen and drought deciduous PFTS have each one very high
- LAI, and the PFT that dominates can be defined by minor effects. Fire, although active, is
- probably too small to be relevant in a non-stressed ecosystem. However, when the interannual
- probably too small to be relevant in a non-stressed ecosystem. However, when the interaminal
- climate variability is considered, INLAND replaces the "evergreen forest" in Figures 6G-I to
- "Savanna and Grasslands" (Figure 6J-L). These results show the limitations of CA and the
- 287 importance to consider the interannual climate variability on simulations to improve the
- 288 vegetation simulated.

variability."

- 289 Technical corrections
- 290 1. L22: "1960 1990"  $\rightarrow$  "1961 1990", as described in L204.
- 291 Response: This has been changed in the revised manuscript.

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- 293 2. L23: "two regional datasets"  $\rightarrow$  "two datasets".
- 294 Response: This has been changed in the revised manuscript.
- 3. L62: "particularly the P limitation."  $\rightarrow$  "particularly the Phosphorus (P) limitation."
- 296 Response: This has been changed in the revised manuscript.
- 297 4. L72: "Phosphorus (P) is  $a" \rightarrow "P$  is a" or "Phosphorus is a".
- 298 Response: This has been changed in the revised manuscript.
- 299 5. L103: Transects 1 and 2 are more related to "Cerrado" than "Amazon", as shown in Figures 1, 2
- 300 and 5. Please rewrite this sentence.
- 301 Response: We do not agree with this technical correction. The transects were located 50% in
- 302 Amazon domain and 50% in Cerrado domain, as we described.
- 303 6. L105: "Transect 1 (T1, 43 °-49 °W; 5 °-7 °S)"  $\rightarrow$  "Transect 1 (T1, 44 °-50 °W; 5°-7 °S)".
- 304 Response: This has been changed in the revised manuscript.
- 305 7. L107: "Transect 5 (T5, 53 °-61 ° W; 13 °-15 ° S)" \rightarrow "Transect 5 (T5, 52 °-60°W;13°-15 ° S)".
- 306 Response: This has been changed in the revised manuscript.
- 307 8. L138: "annual mean LAI<sub>upper</sub> above"  $\rightarrow$  "annual mean LAI<sub>upper</sub> below".
- 308 Response: We do not agree with this technical correction. The annual average of "LAI upper" in
- 309 INLAND needs to be above 0.8 m<sup>2</sup> m<sup>-2</sup>. This value is prescribed by the model.
- 310 9. L173: "We used the P-mehlich-1"  $\rightarrow$  "We used the Pmehlich-1".
- 311 Response: This has been changed in the revised manuscript.
- 312 10. L176: "resulting in 12 additional pixels" Wouldn't it be 6?
- 313 Response: There are 12 pixels, as described in Suplementary Materials.
- 314 11. L176: "pixels with observed total P content" → "pixels without observed total P content"

- 315 Response: These additional pixels with the observed total P content are described in
- 316 Suplementary Materials.
- 317 12. L186: "Above-Ground AGB (AGB) database" → "Above-Ground Biomass (AGB database"
- 318 Response: This has been changed in the revised manuscript.
- 319 13. L194-L196: There are two pixels for each longitude in each transects. Do the Figures 3 and 5 show
- 320 the mean of the two pixels, or only the upper or the lower one?
- 321 Response: The Figures 3 and 5 show the average of two pixels. This information was added to the
- 322 caption of both figures.
- 323 14. L212: Remove the phrase: "The model simulations were run for the time period 1582-2008, a total
- 324 of 427 years." The boundary condition begins in 1948, so it can't be said that the model began in
- 325 1582. This was only an artifice used to simulate the same period for seven times.
- 326 Response: This has been changed in the revised manuscript.
- 327 15. L224: "the simulations (CV + PC) (CA + PC) = (CV CA)|PC"  $\rightarrow$  "the simulations (CV + PC)
- 328 and (CA+PC)" The notation "(CV-CA)|PC" is interesting, but it wasn't used. Then it can be
- 329 removed.
- 330 Response: This has been changed in the revised manuscript.
- 331 16. L228: "and CA+PC, so that (CA+PC+F)-(CA+PC)=F|CA,PC. Similarly,"  $\rightarrow$  "and CA+PC.
- 332 Similarly,".
- 333 Response: This has been changed in the revised manuscript.
- 334 17. L230: "between CV + PC + F and CV + PC, so that (CV + PC + F) (CV + PC) = F|CV, PC. The
- 335 different"  $\rightarrow$  "between CV +PC +F and CV +PC. The different".
- Response: This has been changed in the revised manuscript.
- 337 18. L273: "TB declined by 2% for PR", In Figure 4b it looks positive, so it would be an increase
- 338 instead of a decrease. Please check it.
- 339 Response: This 2% refers to the area average of Cerrado domain.
- 340 19. L393: "compared to CV + PC"  $\rightarrow$  "compared to CV + PC CA + PC".

- Response: In this sentence, we are comparing CV+PG CV+PC.
- 342 20. Figure 4d: "CV + PG + F CV + PC"  $\rightarrow$  "CV + PG + F CV + PG".
- 343 Response: This has been changed in the revised manuscript. Although this is not a regionally
- relevant event, we modified the text to include this discussion.
- 346 References:

- Fyllas, N. M., Pati no, S., Baker, T. R., Bielefeld Nardoto, G., Martinelli, L. A., Quesada, C. A.,
- Paiva, R., Schwarz, M., Horna, V., Mercado, L. M., Santos, A., Arroyo, L., Jimenez, E. M.,
- 349 Luizao, F. J., Neill, D. A., Silva, N., Prieto, A., Rudas, A., Silviera, M., Vieira, I. C. G., Lopez-
- 350 Gonzalez, G., Malhi, Y., Phillips, O. L., and Lloyd, J.: Basin-wide variations in foliar properties of
- 351 Amazonian forest: phylogeny, soils and climate, Biogeosciences, 6,2677-2708, doi:10.5194/bg-6-
- 352 **2677-2009, 2009.**
- 353 Mercado, L. M., Lloyd, J., Dolman, A. J., Sitch, S., and Pati<sup>\*</sup>no,S.: Modelling basin-wide
- 354 variations in Amazon forest productivity- Part 1: Model calibration, evaluation and upscaling
- functions for canopy photosynthesis, Biogeosciences, 6, 1247-1272, doi:10.5194/bg-6-1247-2009,
- 356 **2009.**

- Mercado, L. M., Patiño, S., Domingues, T. F., Fyllas, N. M., Weedon, G. P., Sitch, S., Quesada, C.
- 358 A., Phillips, O. L., Aragão, L.E. O. C., Malhi, Y., Dolman, A. J., Restrepo-Coupe, N., Saleska, S.
- 359 R., Baker, T. R., Almeida, S., Higuchi, N., and Lloyd, J.: Variations in Amazon forest productivity
- 360 correlated with foliar nutrients and modelled rates of photosynthetic carbon supply, Philos. T.
- 361 Roy. Soc. B, 366, 3316–3329, doi:10.1098/rstb.2011.0045, 2011.

Reviewer comments in italics; Responses in bold)

## Response to Anonymous Referee #3 Received and published: 25 July 2017

- General Comment: This manuscript mainly focuses on Amazon-Cerrado transitional vegetation. For this region, a mechanistic model is used to determine the effects of various processes on aboveground biomass (AGB). In particular, the effects of fire phosphorus (P) limitation, and interannual climate variability are evaluated. It is concluded that all of these effects are important, but that fire is the main driver of vegetation change along the transition. The manuscript also reports that the model simulates
- >80% of the spatial variability in AGB in the transition zone.
- Understanding the spatial distribution of tree biomass in the tropics is a very active area of research.
- 373 The questions asked by the authors, especially in regard to P limitation, are open ones and quite worthy
  - of investigation. It is very reasonable to approach questions about mechanisms, such as those asked by
  - the authors, using a mechanistic model. Nevertheless, I was unconvinced by the analysis that was
- 376 presented. I have major concerns about the implementation of P limitation and the statistical analysis.
- 377 The phenology scheme was not described in much detail, but could strongly influence the results.
  - Several claims in the discussion were weakly, if at all, supported by the results.

Specific Comments

- I do not think that the authors really implemented P-limitation in their model. As I understood the manuscript, simulated P dynamics do not affect vegetation biomass. Instead, the authors prescribe a map of Vmax based on a statistical regression between Vmax and soil P. As such, there is no mechanistic representation of P limitation in this model. Without a mechanistic link, I do not think it is correct to ascribe variation in AGB to variations in P. This manuscript can be improved by investigating the effects of different mechanistic implementations of P cycling and P limitation on the simulated vegetation.
- Response: Indeed, we did not implement a full P cycle model, but rather we parametrized what we believe is the most important relationship between soil P and photosynthesis. In this study, we only use the P-limitation through the linear relation developed by Castanho et al. (2013) to evaluate the biomass along the Amazon-Cerrado transition. The P cycle is slow, and a full representation of the soil P may be advantageous only over a time scale of several decades to centuries. In the shorter term (a few decades), starting from a known point in soil fertility as we did, seems to be a more appropriate approach. The values of P in the map influence Vmax, which

- 395 mechanistically influences NPP and biomass. This has been demonstrated before by Castanho et
- 396 al. (2013).
- 397 The implementation of a full P cycling and is out of the scope of this manuscript. The main
- 398 objective of this manuscript is investigate the influence of P-limitation, climate and fire
- 399 occurrence on AGB, and not implement P cycling.
- 400 1. Ptotal may indeed have some positive relation with Vmax, but Equation (1) still seems problematic to
- 401 me. What happens when Ptotal is very large, and vegetation is presumably no longer limited by P? This
- 402 equation would say that Vmax would still increase, but surely there must be some maximum value when
- 403 other factors become limiting.
- 404 Response: Equation (1), being an empirical equation, represents the relationship between P and
- 405 Vcmax in the range where there are observed values. In the hypothetical case of a very high
- 406 Ptotal, and a consequent very high Vmax, other bottlenecks in the model code (limitation by light
  - or by water or by temperature) would limit gross photosynthesis. However, this is unlikely, given
- 408 that the Amazon and Amazon-Cerrado transition soils are known for being nutrient poor.
- 409 More generally, I was not convinced that the most important way P affects plants is through Vmax. For
- 410 example, what about maintenance of some approximate C:N:P stoichiometry, carbon costs of P
- 411 acquisition, etc.?

- 412 Response: Castanho et al. (2013) provided empirical evidence that Vmax is influenced by P-total.
- 413 The other processes described by the reviewer, along with other process not described, may also
- be important, but they have yet to be implemented and tested. Our study, however, falls in line
- 415 with the common use of parameterizations in the modeling literature, to quickly test some effects
- 416 before a full and more complex model is implemented.
- 417 2. The statistical analyses are inappropriate and do not support the conclusions. The statistical tests
- 418 used by the authors are only appropriate when there is some random variable. I did not identify
- 419 anything in the simulation design that could lead to a random effect (for example, some stochastic
- 420 process). I recommend cutting the whole statistical analysis.
- 421 Response: With all due respect to the reviewer, we believe that this point is not correct. There are
- 422 several sources of random variability in the data, such as (from lower to higher): spatial
- 423 variability in the soils texture (in both CA and CV simulations), spatial variability in soil fertility
  - (in PR and PG simulations), the interannual climate variability (in the CV case), and the random
- 425 ignition in the fire module.

- 426 3. The model description incomplete. Is the source code available somewhere? Exactly how does this
- 427 version of the model differ from previous versions? Any new equations or new parameter values need to
- 428 be documented here.

- 429 Response: The source code can be downloaded from http://biosfera.dea.ufv.br/en-US, clicking on
- 430 models and, then, on INLAND. The INLAND project was mainly a revision of the IBIS code,
  - through assembly and standardization of different IBIS versions, and improvements in software
- 432 engineering. We used the version described by Senna et al. (2009) as starting point for INLAND.
- 433 No changes in tuning were done since that paper, except the addition of the P parameterization,
  - which was described in detail. Some of the key equations and parameterizations, however, were
- described by Foley et al. (1996) and Kucharik et al. (2000).
- 436 4. The manuscript indicates (lines 120-121) that a temperature-based phenology scheme was used. But
- 437 a drought phenology scheme is more appropriate for the tropics. I can imagine that the results would
- 438 change dramatically if a drought phenology scheme were used. The original IBIS model had a drought
- 439 phenology scheme, right? I guess that was not implemented here?
- 440 Response: We agree and thanks the reviewer for this commentary. That was our mistake. This
- 441 sentence has been modified. The INLAND, such as IBIS, has phenology scheme based on winter-
- 442 deciduous and drought-deciduous behavior of particular PFTs. For winter-deciduous plants
- 443 (outside the area of study), the temperature based is used, while for tropical drought-deciduous
- plants, the PFTs drop their leaves during the least productive months of the year, defined in
- 445 terms of the previous year's carbon balance. This phenology scheme is extensively described in
- 446 Foley et al. (1996) and Kucharik et al. (2000). Lines 120-121 were changed to "The vegetation
- 447 phenology module simulates the processes such as budding and senescence based on drought
- 448 phenology scheme for tropical deciduous trees."
- 449 5. I was surprised that the manuscript did not discuss alternative stable states in terms of either the
- 450 AGB database or the simulations. How was the AGB database constructed, given that there may be
- 451 alternative stable states? I found it remarkable that the model was able to capture 80% of the
- 452 variability. Would this result indicate that the idea of alternative stable states is not really appropriate
- 453 in the Amazon-Cerrado transition?
- 454 Response: We are not sure we understand this comment. Alternatives states in this region would
- 455 arise as a consequence of climate change and antropogenic disturbance. This is clearly outside the
- 456 scope of this study, which aims at representing the actual non-disturbed status of the vegetation,
- and attribute the processes responsible for its present status, in terms of climate variability, fire
- 458 and P limitation.

- 459 Additional comments
- 460 Lines 88-89: This is too vague. A discussion of the failures would be welcome.
- 461 Response: In accordance with the referees's wishes, we included references and have now
- 462 changed this paragraph to "Currently, no model has demonstrated to be able to accurately
- 463 simulate the vegetation transition between Amazon and Cerrado. In general the DGVMs simulate
- 464 evergreen forest along the Amazon-Cerrado border neglect savanna occurrence (Botta and Foley,
- 465 2002; Bond et al., 2005; Salazar et al., 2007; Smith et al., 2014). This difficulty may be due to
- 466 absence or not well represented disturbances such as fire, nutritional limitation or soil proprieties.
- 467 Thus, we need a better understanding of the drivers on transitional vegetation to determine the
- 468 parameters and establish relations between the environmental and transitional vegetation
- 469 physiognomies."
- 470 Line 155: This equation needs more description. Is the same Vmax assigned to all PFTs? Is it meters
- 471 square of leaf area or meters squared of ground?
- 472 Response: There is reference to equation and specified the PFTs limited by phosphorus on the
- 473 manuscript. Please check Line 157: "This equation has been developed by Castanho et al. (2013)
- 474 based on data for tropical evergreen and deciduous trees, and is applied only to these two PFTs in
- 475 the model."
- 476 Lines 269-276: It is arbitrary as to whether there are increases or decreases. Whether there is an
- 477 increase or a decrease depends on the chosen baseline. Also on this paragraph, I am wondering
- 478 *whether tree biomass simply follows soil P?*
- 479 Response: The increase or decrease biomass in PG and PR was evaluated from PC using the
- 480 subtraction between the simulations: (CV+PR)-(CV+PC) and (CV+PG)-(CV+PC). These
- 481 differences represents the isolated effect of P limitations on tree biomass along the simulated area.
- 482 Line 280: Note that the word "inflammable" actually means easily ignited.
- 483 Response: We agree with the reviewer. This sentence was changed to "The small or null fire effect
- in the Central Amazon rainforest is related the greater water availability on the Amazonia, which
- 485 makes the forest naturally not flammable as well as a gradient towards seasonally dryer climate
- 486 increases the intensity and magnitude of fire effects towards the Cerrado (Figure 4d)."
- 487 Lines 278-281: Not justified. Where is water availability shown, and how is it defined?

- 488 Response: We agree with the reviewer. This sentence was changed to "The small or null fire effect
- 489 in the Central Amazon rainforest is related the greater water availability on the Amazonia, which
- 490 makes the forest naturally not flammable as well as a gradient towards seasonally dryer climate
- 491 increases the intensity and magnitude of fire effects towards the Cerrado (Figure 4d)."
- 492 Lines 300-302: Why does fire cause LAI to increase?
- 493 Response: In INLAND the vegetation structure is represented by two layers: upper and lower
- 494 canopy. The fire occurrence reduces the upper canopy decreasing the trees LAI (LAI upper),
- 495 opening the canopy, and leading to more luminosity available to the lower layer, and consequently
- 496 increasing the photosynthesis rates by grasses (increase of LAI lower). In general, the LAI lower
  - increases quickly after the fire occurrence contributing with the increases of the LAI total that
- 498 represents the sum of the two layers.

- 499 *Line 409-411: There are exceptions (Goll et al, Yang et al).*
- 500 Response: We agree to the reviewer. This sentence was changed.
- 501 Lines 416-424: This paragraph seems too speculative given the model results.
- 502 Response: We excluded this paragraph.
- 503 Lines 425-428: This is also not strongly supported.
- Response: This is supported by Tables 3, 4 and 5.
- 505 Lines 460-462: But does it help explain the spatial variability?
- 506 Response: Yes. Patterns along the eastern part of the transects are determined by fire, which is
- 507 less important in the western part of the transects.
- 508 Line 502: Showing the climate data would make this point more convincing.
- 509 Response: This is well known in the literature, but anyway. We provide three figures in this
- response to clarify this point to the reviewer. The seasonality of precipitation for Amazon and
- Cerrado biomes used in this study is shown in Figure R1. The dry season duration is larger in the
- 512 Cerrado domain (Figure R1a) than in the Amazonia domain (Figure R1b). In the Cerrado, dry
- season comprise a period of about 6 months with little or no rain.
- 514 Spatial variability of precipitation and temperature are shown in Figures R2 and R3, respectively.
- 515 These figures plot the difference between the average of 1999-2008 (a subset of CV) and CA
- (average of 1961-1990) highlighting the spatial variability of these climate variable throughout the

study area. Comparing the interannual climate variability with the average climate, precipitation decreases (Figure R2) and temperature increases up 1.5°C (Figure R3) in central Cerrado in October, November, December and January. The lower precipitation associated with higher temperatures in central Cerrado can explain a low biomass, low LAI vegetation and savanna existence without fire disturbance. Note that this is a 10-year subset of the CV database. The actual year-to-year variations present much more intense amplitudes.

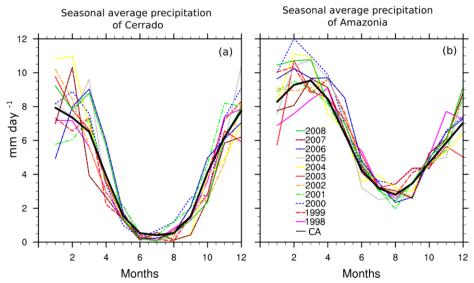


Figure R1. Seasonal of precipitation for Amazon and Cerrado domains for average climate (CA) -black line - and the last ten years of interannual- climate variability (CV) - color lines.

Figure R2. Spatial variability of precipitation for study area considering the average of the last 10 years of CV (1999-2008) and average climate CA (1961-1990).

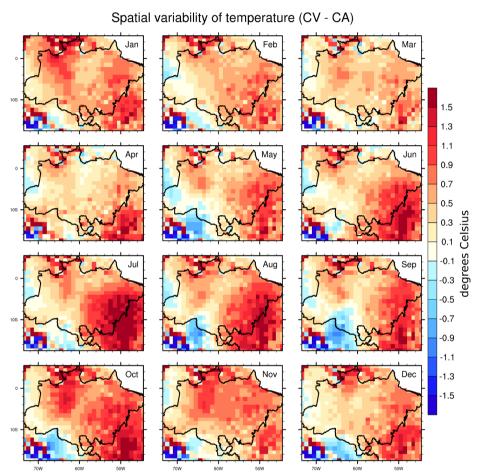


Figure R3. Spatial variability of temperatures for the study area considering the average of the last 10 years of CV (1999-2008) and average climate CA (1961-1990).

## **References:**

Bond, W. J., Woodward, F. I. and Midgley, G. F.: The global distribution of ecosystems in a world without fire, New Phytol., 165(2), 525–538, doi:10.1111/j.1469-8137.2004.01252.x, 2005

539 Smith, B., Waarlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J. and Zaehle, S.: 540 Implications of incorporating N cycling and N limitations on primary production in an individual-541 based dynamic vegetation model, Biogeosciences, 11(7), 2027–2054, doi:10.5194/bg-11-2027-2014, 542 2014

border 546 547 Emily Ane Dionizio da Silva<sup>1</sup>, Marcos Heil Costa<sup>1</sup>, Andrea Almeida Castanho<sup>2</sup>, Gabrielle Ferreira 548 Pires<sup>1</sup>, Beatriz Schwantes Marimon<sup>3</sup>, Ben Hur Marimon-Junior<sup>3</sup>, Eddie Lenza<sup>3</sup>, Fernando Martins 549 Pimenta<sup>1</sup>, Xiaojuan Yang<sup>4</sup>, Atul K. Jain<sup>5</sup> 550 551 <sup>1</sup> Department of Agricultural Engineering, Federal University of Viçosa (UFV), Viçosa, MG, Brazil 552 <sup>2</sup> The Woods Hole Research Center, 149 Woods Hole Rd., Falmouth, MA USA 553 <sup>3</sup> Federal University of Mato Grosso, Nova Xavantina Campus, Nova Xavantina, MT, Brazil 554 <sup>4</sup> Oak Ridge National Laboratory, Oak Ridge, TN, USA Excluído: t 555 Excluído: ot <sup>5</sup> Department of Atmospheric Sciences, University of Illinois at Urbana-Champaign 556 557

Influence of climate variability, fire and phosphorus limitation on

the vegetation structure and dynamics in the Amazon-Cerrado

Correspondence to: Emily Ane D. da Silva (emilyy.ane@gmail.com)

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#### Abstract

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Climate, fire and soil nutritional limitation are important elements that affect the vegetation dynamics in areas of forest-savanna transition. In this paper, we use the dynamic vegetation model INLAND to evaluate the influence of inter-annual climate variability, fire and phosphorus (P) limitation on the Amazon-Cerrado transitional vegetation structure and dynamics. We assess how each environmental factor affects the net primary production, leaf area index and aboveground biomass (AGB), and compare the AGB simulations to observed AGB map. We used two regional datasets – the 1961-1990 average seasonal climate and the 1948 to 2008 inter-annual climate variability, two datasets of total soil P content in soil, based on regional (field measurements) and global data and the INLAND fire module. Our results show that inter-annual climate variability, P limitation and fire occurrence gradually improve simulated vegetation types and these effects are not homogeneous along the latitudinal/longitudinal gradient, showing a synergistic effect among them. In terms of magnitude, the effect of fire is stronger, and is the main driver of vegetation changes along the transition. The nutritional limitation, in turn, is stronger than the effect of inter-annual climate variability acting on the transitional ecosystems dynamics. Overall, INLAND typically simulates more than 80% of the AGB variability in the transition zone. However, the AGB in many places is clearly not well simulated, indicating that important soil and physiological factors in the Amazon-Cerrado border, such as lithology and water table depth, carbon allocation strategies and mortality rates, still need to be included in the model.

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#### 1 Introduction

The Amazon and Cerrado are the two largest and most important phytogeographical domains in South America. The Amazon forest has been globally recognized and distinguished not only for its exuberance in diversity and species richness, but also for playing an important role in the global climate by regulating water (Bonan, 2008; Pires and Costa, 2013) and heat fluxes (Shukla et al., 1990; Rocha et al., 2004; Roy et al., 2002). The Cerrado is recognized worldwide for being the richest savanna in the world (Myers et al., 2000; Klink and Machado, 2005). It is characterized by different physiognomies, ranging from sparse physiognomies to dense woodland formations, and the latter are commonly mixed with Amazon rainforest forming transitional areas. The Amazon-Cerrado transition extends for 6270 km from northeast to southwest in Brazil, and the ecotonal vegetation around this transition is a mix of the characteristics of the tropical forest and the savanna (Torello-Raventos et al., 2013).

Gradients of seasonal rainfall and water deficit, fire occurrence, herbivory and low fertility of the soil have been reported as the main factors that characterize the transition between forest and savanna globally (Lehmann et al., 2011; Hoffman et al., 2012; Murphy and Bowman, 2012). However, few studies have evaluated the individual and combined effects of these factors on Brazilian ecosystems ecotones (Marimon-Junior and Haridasan, 2005; Elias et al., 2013; Vourtilis et al., 2013).

It is challenging to assess the degree of interaction among these various environmental factors in the transitional region and to infer how each one influences the distribution of the regional vegetation. In this case, Dynamic Global Vegetation Models (DGVMs) can be powerful tools to isolate the influences of climate, fire and nutrients, therefore helping to understand their large-scale effects on vegetation (House et al., 2003; Favier et al., 2004; Hirota et al., 2010; Hoffman et al., 2012).

Previous modelling studies using DGVMs that investigate climate effects in the Amazon indicate that the rainforest could experience changes in rainfall patterns which would either transform the forest into an ecosystem with more sparse vegetation – similar to a savanna, what has been called as the "savannization of the Amazon" (Shukla et al., 1990; Cox et al., 2000; Oyama and Nobre, 2003; Betts et al., 2004; Cox et al., 2004; Salazar et al., 2007) - or to a seasonal forest (Malhi et al., 2009; Pereira et al., 2012; Pires and Costa, 2013). These studies had great importance to the improvement of terrestrial biosphere modeling, but they neglect two important processes in tropical ecosystem dynamics: fire occurrence and nutrient limitation, particularly the Phosphorus (P) limitation.

In tropical ecosystems, fire plays an important ecological role and influences the productivity, the biogeochemical cycles and the dynamics in the transitional biomes, not only by changing the phenology and physiology of plants, but also by modifying the competition among trees and lower canopy plants such as grasses, shrubs and lianas. Fire occurrence, depending on its frequency and intensity, may increase the mortality of trees and transform an undisturbed forest into a disturbed and flammable one (House et al., 2003; Hirota et al., 2010; Hoffmann et al., 2012). Fires also affect the dynamics of nutrients in the savanna ecosystem, changing mainly the N:P relationship and P availability in the soil (Nardoto et al. 2006).

Studies suggest that P is the main limiting nutrient within tropical forests (Malhi et al., 2009; Mercado et al., 2011; Quesada et al., 2012) unlike the temperate forests. Phosphorus is a nutrient that is easily adsorvided by soil minerals due to the large amount of iron and aluminum oxides in the Amazon and Cerrado acidic and strongly weathered soils (Dajoz, 2005; Goedert, 1986). In the tropics, the warm and wet climate favors the high biological activity in the soil and the litter decomposition, not limiting

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the nitrogen for plant fixation. In Cerrado, higher soil fertility is related to regions with greater woody plants abundance and less grass cover, similarly to the features found in the Amazon rainforest (Moreno et al., 2008; Vourtilis et al., 2013; Veenendaal et al., 2015). However, the phosphorus limitation is often neglected by DGVMs. which usually assume unlimited P availability and consider nitrogen as the main limiting nutrient. However, N is not a limiting nutrient for trees in the tropics (Davidson et al. 2004), while P availability affects the trees dynamics.

In principle, in transitional forests, where the climate is intermediate between wet and seasonally dry, the heterogeneous structure and phenology make it difficult to represent these forests in models. The Amazon-Cerrado border is the result of the expansion and contraction of the Cerrado into the forest (see Marimon et al., 2006; Morandi et al., 2016), especially in the Mato Grosso state, where extreme events, such as intense droughts, influence the vegetation dynamics (Marimon et al., 2014) and the nutrient (Oliveira et al., 2017) and carbon cycling (Valadão et al., 2016).

Currently, no model has demonstrated to be able to accurately simulate the vegetation transition between Amazonia and Cerrado. In general the DGVMs simulate evergreen forest along the Amazon-Cerrado border and neglect savanna occurrence (Botta and Foley, 2002; Bond et al., 2005; Salazar et al., 2007; Smith et al., 2014). This difficulty may be due to absence or not well represented disturbances such as fire, nutritional limitation or soil proprieties. Thus, we need a better understanding of the drivers on transitional vegetation to determine the parameters and establish relations between the environmental and transitional vegetation physiognomies.

In this paper we use the dynamic vegetation model INLAND (Integrated Model of Land Surface Processes) to evaluate the influence of inter-annual climate variability, fire occurrence and P limitation Excluído: in press

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Excluído: Currently, no model has demonstrated to be able to accurately simulate the vegetation transition between Amazon and Cerrado. A better understanding of the main drivers that determine the distribution of different vegetation physiognomies in the region is crucial for more reliable simulations of the transitional tropical ecosystems in future climate scenarios.

in the Amazon-Cerrado transitional vegetation dynamics and structure. We assess how each element affects the net primary production (NPP), leaf area index (LAI) and aboveground biomass (AGB) and compare the model simulated AGB to observed AGB data. The results presented here are important to build models that accurately represent the transition vegetation, and show the need to include the spatial variability of eco-physiological parameters in these areas.

#### 2 Materials and methods

# 2.1 Study Area

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The present study focuses on the Amazon-Cerrado transition (Figure 1). We use the official delimitation of the Brazilian biomes proposed by IBGE (2004), and define five transects along the transition border with 1° × 1° grid size (the terms "transition", "Amazon-Cerrado transition" and "Forest-Savanna transition" are used interchangeably with the same meaning throughout this manuscript). Transects 1 to 4 are established considering approximately 330 km into the Amazon and 330 km into the Cerrado domain, while Transect 5 is 880 km long on the southern Amazon-Cerrado border. The transects are located as follows: Transect 1 (T1, 44°-50°W; 5°-7°S), Transect 2 (T2, 46°-51° W; 7°-9S), Transect 3 (T3, 48°-54° W; 9°-11° S), Transect 4 (T4, 49°-55° W; 11°-13° S), and Transect 5 (T5, 52°-60° W; 13°-15° S) (Figure 1).

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## 2.2 Description of the INLAND Surface Model

The Integrated Model of Land Surface Processes (INLAND) is the land-surface component of the Brazilian Earth System Model (BESM). INLAND is <u>basically a revision of the IBIS model</u> (Integrated Biosphere Simulator, <u>described</u> by Foley et al., 1996; Kucharik et al., 2000), through

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assembly and standardization of different IBIS versions, and improvements in software engineering. We used the version described by Senna et al. (2009) as starting point for INLAND. No changes in tuning were done since that paper, except the addition of the P parameterization, described below.

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The model considers changes in the composition and structure of vegetation in response to the environment and incorporates important aspects of biosphere-atmosphere interactions. The model simulates the exchanges of energy, water, carbon and momentum between soil-vegetation-atmosphere. These processes are organized in a hierarchical framework and operate at different time steps, ranging from 60 minutes to 1 year, coupling ecological, biophysical and physiological processes. The vegetation structure is represented by two layers: upper (arboreal PFTs) and lower (no arboreal PFTs, shrubs and grasses) canopies, and the composition is represented by 12 plant functional types (PFTs) (e.g., tropical broadleaf evergreen trees or C4 grasses, among several others). The photosynthesis and respiration processes are simulated in a mechanistic manner using the Ball-Berry-Farquhar model (details in Foley et al., 1996). The vegetation phenology module simulates the processes such as budding and senescence based on drought phenology scheme for tropical deciduous trees. The dynamic vegetation module computes the following variables yearly for each PFT: gross and net primary productivity (GPP and NPP), changes in AGB pools, simple mortality disturbance processes and resultant LAI, thus allowing vegetation type and cover to change with time. The partitioning of the NPP for each PFT resolves carbon in three AGB pools: leaves, stems and fine roots. The LAI of each PFT is obtained by simply dividing leaf carbon by specific leaf area, which in INLAND is considered fixed (one value) for each PFT.

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**Excluído:** The vegetation phenology module simulates the processes such as budding and senescence based on empirically-based temperature thresholds for each PFT

INLAND has eight soil layers to simulate the diurnal and seasonal variations of heat and moisture. Each layer is described in terms of soil temperature, volumetric water content and ice content (Foley et al., 1996; Thompson and Pollard, 1995). Furthermore, all of these processes are influenced by soil texture and amount of organic matter within the soil profile.

Considering these aspects of vegetation dynamics and soil physical properties the model can simulate plant competition for light and water between trees, shrubs and grasses through shading and differences in water uptake (Foley et al., 1996). These PFTs can coexist within a grid cell and their annual LAI values indicate the dominant vegetation type within a grid cell. For example, the dominant vegetation type is a Tropical Evergreen Forest if the PFT tropical broadleaf evergreen tree has an annual mean upper canopy LAI (LAI<sub>upper</sub>) above 2.5 m<sup>2</sup> m<sup>-2</sup>. On the other hand, the dominant vegetation type is a Tropical Deciduous Forest if the tropical broadleaf drought-deciduous tree has an annual mean LAI<sub>upper</sub> above 2.5 m<sup>2</sup> m<sup>-2</sup>. Where total tree LAI (LAI<sub>upper</sub>) is between 0.8 and 2.5 m<sup>2</sup> m<sup>-2</sup>, dominant vegetation type is savanna, and LAI<sub>upper</sub> values smaller than 0.8 m<sup>2</sup> m<sup>-2</sup> characterize a grassland vegetation type.

We assume that the vegetation types Tropical Evergreen Forest and the Tropical Deciduous Forest in INLAND <u>represents</u> the Amazon rainforest, while Savanna and Grasslands represent the Cerrado. Savanna would be equivalent to the Cerrado physiognomies *Cerradão* and *Cerrado sensu strictu*, while Grasslands would be equivalent to the physiognomies *Campo sujo* and *Campo Limpo* (sensu Ribeiro and Walter, 2008).

The soil chemical properties are represented by the carbon, nitrogen and phosphorus. The carbon cycle is simulated through vegetation, litter and soil organic matter, where the biogeochemical module

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is similar to the CENTURY model (Parton et al., 1993; Verberne et al., 1990). The amount of C existing in the first meter of soil is divided into different compartments characterized by their residence time, which can vary in an interval of hours for microbial AGB and organic matter to several years for lignin. The model considers only the soil N transformations and carbon decomposition, but the N cycle is not fully simulated and N does not influence the vegetation productivity, i.e., there is a fixed C:N ratio. The P cycle also is not fully implemented, instead the P-limitation is spatially parameterized through the linear relation developed by Castanho et al. (2013) to limit the gross primary productivity. A map of total P available in the soil (Ptotal) is used by the model to estimate the maximum capacity of carboxylation by the Rubisco enzyme (Vmax) for each grid using Equation (1):

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$$V_{max} = 0.1013 P_{total} + 30.037 \tag{1}$$

where  $V_{max}$  and  $P_{total}$  are given in  $\mu molCO_2$  m<sup>-2</sup> s<sup>-1</sup> and mg kg<sup>-1</sup>, respectively. This equation has been based on data for tropical evergreen and deciduous trees, and is applied only to these two PFTs, while the other PFTs are unaffected.

INLAND also contains a spatial fire module, from the Canadian Terrestrial Ecosystem Model CTEM (Arora and Boer, 2005). In this module, three aspects of the fire triangle are considered – the availability of fuel to burn, the flammability of vegetation, and the presence of an ignition source. Each is represented daily by an independently calculated probability, and the product of the three is the probability of fire occurrence. Availability of fuel to burn depends on biomass, flammability depends on soil moisture and ignition depends on a random lightning occurrence and a constant anthropogenic ignition probability (in these runs prescribed to 0.50). The burned area fraction is calculated daily and depends on the probability of ignition, spread rate (as function of wind speed, soil moisture), simulated

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**Excluído:** The individual probabilities are calculated at the daily timescale based on soil, climate and vegetation conditions to generate a daily burned gridcell area fraction for each PFT. Following Arora and Boer (2005), a

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length to breadth ratio of fire, and extinguishing rate. The daily area burned is accumulated through the year and its ratio to the grid cell area is applied at the end of each year as a "penalization fraction" to leaf, wood and root biomass pools. For more details, see Arora and Boer (2005).

## 2.3 Observed data

# 2.3.1 Phosphorus databases

We used two P databases to estimate  $V_{max}$  (Equation 1): one regional (referred to as PR) and one global database (referred to as PG). In addition, a control P map (PC) represents the unlimited nutrient availability case, equivalent to a  $V_{max}$  of 65  $\mu$ molCO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>, or 350 mg P kg<sup>-1</sup> soil, according to Equation 1.

The PR database was developed from total P in the soil for the Amazon basin published by Quesada et al. (2011) plus 54 additional available P samples (P extracted via Mehlich-1 extractor,  $P_{mehlich-1}$ ) (Figure 2a). We used the  $P_{mehlich-1}$  and clay contents measured in a forest-savanna transition region in Brazil (Mato Grosso state) to estimate  $P_{total}$  and expand the coverage area of the P data (Section S1). These 54 samples were gridded to a  $1^{\circ} \times 1^{\circ}$  grid to be compatible with the spatial resolution used by INLAND, resulting in 12 additional pixels with observed total P content (Figure 2a). For pixels without observed  $P_{total}$ , the  $P_{total}$  was assumed to be 350 mg P kg<sup>-1</sup> soil, similarly to the PC conditions.

A global dataset of  $P_{total}$  (Figure 2b) was also used to estimate  $V_{max}$ . This global data set is part of a database containing six global maps of the different forms of P in the soil (Yang et al., 2013). The  $P_{total}$  was estimated from lithologic maps, distribution of soil development stages, fraction of the

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**Excluído:** Therefore, at the end of each year both upper and lower LAI are decreased, according to the amount burned, triggering competition.

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remaining source material for different stages of weathering using chronosequence studies (29 studies), and P distribution in different forms for each soil type based on the analysis of Hedley fractionation (Yang and Post, 2011), which are part of a worldwide collection of soil profile data. The uncertainties and limitations associated with this database are restricted to the Hedley fractionation data used, which are 17% for low weathered soils, 65% for intermediate soils and 68% for highly weathered soils (Yang et al., 2013).

# 2.3.2 Above-Ground Biomass (AGB) database

The AGB database used was created by Nogueira et al. (2015) and considered undisturbed (predeforestation) vegetation existing in the Brazilian Amazonia. This database was compiled from a vegetation map at a scale of 1:250000 (IBGE, 1992) and AGB averages from 41 published studies that had conducted direct sampling in either forest (2317 plots) or non-forest or contact zones (1830 plots). We bi-linearly interpolated the AGB (dry weight) for each transect considering  $1^{\circ} \times 1^{\circ}$  to ensure compatibility of the observed and simulated data.

Five longitudinal transects (Figure 1) were used separately to characterize AGB in the Amazon-Cerrado border (Figures 3a and 3b). In T1, T2, T3 and T4, the higher AGB values in the west and lower values in the east are consistent with the transition from a dense and woody vegetation (the Amazon forest) towards a sparse vegetation with lower AGB (the Cerrado). However, T1 shows a more gradual reduction of AGB along the west to east gradient, while in T2, T3 and T4 the transition is more abrupt. In T5 no west-east gradient is present with high AGB heterogeneity and predominant low AGB across

the transect (Figure 3b).

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#### 2.4 Simulations

The model was forced with the prescribed climate data based on the Climate Research Unit (CRU) database (Harris et al., 2014). Two climate boundary conditions were used: the first is referred to as the monthly climatological average (CA) that represents the average climate for the period 1961-1990. The second climate boundary condition is the historical dataset, for the continuous period between 1948 and 2008 (CV). For both boundary conditions, the variables used are rainfall, solar radiation, wind velocity and maximum and minimum temperatures. The CRU database has been widely used by the scientific community in case studies, because these data preserve the spatial mean of the rainfall data, although, they do not provide adequate representation of their variance precipitation (Beguería et al., 2016). The dataset has a 1-degree spatial resolution and a monthly time resolution.

Soil texture data is based on the IGBP-DIS global soil (Global Soil Data Task 2000) (Hansen and Reed, 2000). In the CV group of runs, the model was spin-up by cycling the 1948-2008 climate data (61-year) seven times, totaling 427 years. In the CA group of runs, the annual mean climate data was cycled 427 times. In both cases, CO<sub>2</sub> varied from 278 to 380 ppmv, according to observations in the period, updated annually. In both cases, only the model results of the last 10 years were used to analyze the results.

The experiment design is a factorial combination of the climate scenarios (CA, monthly climatological average, 1961-1990; CV, monthly climate time series, 1948-2008), the nutrient limitation on  $V_{max}$  (PC, no P limitation ( $V_{max} = 65 \mu molCO_2 m^{-2} s^{-1}$ ); PR, regional P limitation; PG, global P limitation) and the occurrence of fire (F) or not (Table 1). The 12 combinations in Table 1 allow the evaluation of individual and combined effects of climate, soil chemistry, and the incidence of fire on the

**Excluído:** The model simulations were run for the time period 1582-2008, a total of 427 years

variables: Net Primary Production (NPP), tree AGB, and LAI of the upper and lower canopies (LAI<sub>upper</sub>, LAI<sub>lower</sub>).

We consider that the subtraction between the simulations (CV+PC) and (CA+PC) represents the isolated effect of inter-annual climate variability without P limitations. The same logic is applied to isolate other factors such as fire and P in different climate scenarios. For example, the fire effect under average climate without P limitation case is calculated by the difference between CA+PC+F and CA+PC, Similarly, the isolated effect of fire under a climate with inter-annual variability scenario without influence of P limitation is calculated by the difference between CV+PC+F and CV+PC, The different combinations of climate scenarios with and without fire effects and with and without P limitations are described in Table 2.

#### Statistical analysis and determination of the best model configuration

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The statistical analysis is divided in four parts. First, we present maps of the isolated effects for all simulated area calculated as the average of the last ten years of simulated spatial patterns. The statistical significance of the isolated effects on NPP, LAI and AGB are determined using the t-test with p < 0.05. The results are tested in each pixel, for all the simulated domain (n = 10).

Second, we present an analysis of variance using the one-way ANOVA and the Tukey-Kramer test in the transition zone. We consider all 31 pixels which fall in transects T1 to T5 (npixels). The results presented are based on the set of last 10 years of simulation (1999-2008, n<sub>years</sub>) for the 12 combinations (n<sub>simulation</sub>) in Table 1. Moreover, we grouped treatments according to climate regardless of P limitation, presence or absence of fire, where all sets with CV vs CA are tested (Group 1, n=1860,  $(n_{pixel} \ x \ n_{year} \ x)$ (n<sub>simulation</sub>/2)). Similarly, in Group 2 we tested if PC, PR or PG were significantly different from each

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other regardless the F or climate used (Group 2, n=1240,  $(n_{pixel} \ x \ n_{year} \ x \ (n_{simulation}/3))$ . In Group 3 we tested if fire introduced a significant effect regardless of climate and P limitation (Group 3, n=1860,  $(n_{pixel} \ x \ n_{year} \ x \ (n_{simulation}/2))$ . Finally, all treatments were tested to each simulation assessing their individual effects on NPP, LAI and AGB  $(n_{pixel} \ x \ n_{year} = 310)$ .

Third, a correlation coefficient between the simulated and observed values for AGB was calculated for each transect. The simulated variables are averaged for the last 10 years of simulations (1999 - 2008) and compared to AGB from Nogueira et al. (2015) within a grid cell.

Finally, we evaluate INLAND's ability to assign the dominant vegetation type by analyzing 10 years of probability of occurrence. If the dominant vegetation type (evergreen tropical forest, or deciduous forest for the Amazon rainforest, and savanna or grasslands for Cerrado) in a pixel is the same in more than 90% of the simulated years (9 out of 10), then the simulated vegetation type is defined as "very robust" for that pixel; if it occurs in 70 - 90% of the simulated years, the simulated result is considered to be "robust". If the dominant vegetation occurred in less than 70% of simulated years, the pixel is considered "transitional" vegetation.

#### 3 Results

## 3.1 Influence of climate, fire and phosphorus in the Amazon-Cerrado transition region

# 3.1.1 Spatial patterns

Overall, the inclusion of inter-annual climate variability (CV) resulted in a decrease in the simulated average tree biomass (TB) by 3.8% in the entire Brazilian Amazonia, and by 8.7% in the entire Cerrado in comparison to average climate (CA), with values obtained by the difference CV+PC —

<u>CA+PC</u> (Figure 4a). The spatial differences between CV and CA for TB simulations are statistically significant and range from 3 kg-C m<sup>-2</sup> to +2 kg-C m<sup>-2</sup>. The state of Pará, with higher influence of the El Niño phenomenon, experienced the highest decrease in TB in the CV simulation. In the state of Roraima, on the other hand, there was an increase of about 2 kg-C m<sup>-2</sup> in TB when CV was considered. Bolivia and southwest of Mato Grosso state also presented, in some grids points, a significant increase in AGB higher than 2 kg-C m<sup>-2</sup>.

On average, P acts as a limiting factor in the simulated TB, decreasing by 13% in regional P (PR) simulation and 15% in global P (PG) simulation. In PR, TB decreased mainly in the southeastern Amazonia (between Pará and northeastern Mato Grosso states) and northwestern Amazonas state (Figure 4b). In PG, the largest TB decline occurred in central Amazonia, northeastern Pará and northeastern Mato Grosso (Figure 4c). In Cerrado, on the other hand, TB declined by 2% for PR and 9% for PG with respect to the control simulation. In PR, the few pixels in the Cerrado that have P limitation showed a significant decrease in TB (Figure 4b), while in PG the TB reduction was statistically significant for most of the Cerrado domain, except in southern Tocantins state (Figure 4c).

The tree biomass reduction due to fire events is much higher in magnitude than due to P limitation or inter-annual climate variability (Figure 4d). The small or null fire effect in the Central Amazon rainforest is related to the greater water availability in Amazonia, which makes the forest naturally not flammable as well as a gradient towards seasonally dryer climate increases the intensity and magnitude of fire effects towards the Cerrado (Figure 4d). The fire effect on TB over the Amazon domain was 21-24% of the P limitation effect (range for PR and PG cases), while the fire effect on TB

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over the Cerrado was more than 250% of the P limitation effects in CV simulations, which is due to quick growth of grasses after fire occurrence in the latter.

# 3.1.2 Influence of climate, fire and phosphorus in the transects

Results of the ANOVAs and Tukey-Kramer test indicate that the inclusion of CV, limitation by P (PR and PG) and fire in INLAND led to significantly different averages of NPP, LAI and AGB in the transition zones. This influences of climate, P and fire are shown separately in Tables 3 to Table 5 and combined in Table 6.

The effects of climate and P on productivity show that CV reduces the NPP from 0.68 kg-C m<sup>-2</sup> yr<sup>-1</sup> to 0.64 kg-C m<sup>-2</sup> yr<sup>-1</sup> (Table 3) and the P effect results in NPP decline from 0.71 kg-C m<sup>-2</sup> yr<sup>-1</sup> to 0.64 kg-C m<sup>-2</sup> yr<sup>-1</sup> (both PR and PG) (Table 4). The fire effect, moreover, has a positive effect on NPP from 0.66 kg-C m<sup>-2</sup> yr<sup>-1</sup> when fire is off to 0.67 kg-C m<sup>-2</sup> yr<sup>-1</sup> when fire is on. This difference, albeit low, is statistically significant (Table 5).

In addition CV and P limitation reduce the  $LAI_{total}$  in the canopy (Table 3 and Table 4),

increasing three times  $LAI_{lower}$  and decreasing  $LAI_{upper}$  (Table 5). The magnitude of fire effect on AGB

 $(46.7\%, Table\ 5)\ is\ greater\ in\ relation\ to\ the\ CV\ (5\%, Table\ 3)\ and\ P\ (14\%, Table\ 4)\ limitation\ effects.$ 

Even though CV effects on NPP and AGB for each simulation is not statistically significant, the effects of fire and P limitation (regardless of phosphorus map) are. Fire effects are significant only for structural variables as AGB, LAI<sub>total</sub>, LAI<sub>upper</sub> and LAI<sub>lower</sub>. It presents an increase of LAI total of 1.52 m<sup>2</sup> m<sup>-2</sup> in CV+PG+F in relation to CV+PG, and of 1.32 m<sup>2</sup> m<sup>-2</sup> in CV+PR+F in relation to CV+PR (Table 6).

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## 3.1.3 West-East patterns of AGB in the Amazon-Cerrado transition

The model used in this study simulates > 80% of the observed AGB variability in all treatments along the transition area except in T5 (Table 7). It shows that the model is able to capture AGB variability along the transition area, which is relevant when compared to studies that simulate 50% of the observed AGB variability (Senna et al., 2009; Castanho et al., 2013).

It is not possible to identify a treatment that best represents AGB in all transects (Table 7). A combined analysis of Table 7 and Figure 5 indicates a general agreement that observed AGB decreases from W to E in T1 to T4, and this is well captured by several configurations of the model, with specific differences among them. Overall, CA and PC configurations, being the least disturbed treatments, yield higher AGB, while the introduction of CV, PG and F reduce the AGB. However, the simulated results may be above or below the observed ones, which suggests that additional local factors are not included in the model.

The curves of AGB (Figure 5) show the impact of CV, PG and F along the W-E transition. PG has a high influence on the transition, decreasing the ABG especially in the western part of the transects, where the Amazon vegetation is predominant. This feature is particularly simulated in T3 and T4, where PG decrease the AGB by 2 kg-C m<sup>-2</sup> in the west pixels of these transects (Figure 5). In T1, T2 and T5, AGB decline is also higher with P limitation when compared to the curves limited only by CV. However, in T1 model simulations tend to underestimate the highest and the lowest AGB extremes, and the absolute values were always underestimated, despite the improvement in correlation with the inclusion of the fire component (Table 7).

In T2, T3 and T4, however, fire is responsible for altering the simulated AGB to the observed AGB in the eastern pixels of the Cerrado domain (Figure 5). In T5 these relations are similar, with climate presenting less influence on AGB decrease than P, and fire appears mainly as an AGB reduction factor.

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## 3.2 Simulated composition of vegetation

Most of the pixels in CA show very robust simulations, with more than 90% of the same vegetation cover in the simulated last 10 years (Figure 6a-c and 6g-i). A larger number of pixels with transitional vegetation were simulated in CV (Figure 6d-f and and 6j-l). An even higher variability in CV compared to CA simulations was observed when we added the effects of P limitation and fire (Figure 6a and 6j-l).

The vegetation composition in all P limitation scenarios for CA simulations resulted in robust simulations for nearly all pixels, except for the north of Cerrado domain (Figures 6a, 6b and 6c). The CA+PC and CA+PR simulations had the same vegetation composition, while CA+PG replaced the deciduous forest by evergreen forest in the central Cerrado region, around 8°S 46°W (Figures 6A, 6B and 6C). This behavior might be related to the higher P<sub>total</sub> values in PG than PR and PC for the Cerrado region (Figure S1). Cerrado was better represented in CV+PC, CV+PR and CV+PG than in the same CA combinations (Figure 6). The occurrence of forested areas in central Cerrado decreased in CV combinations, these being replaced by the savanna or grassland vegetation class.

When the effect of fire was added to CA simulations, the model simulated an increase in the uncertainty on the vegetation cover classification in the Cerrado region. The effect of fire reduced the presence of deciduous forest in central Cerrado biome as well as in CA+PC, and the vegetation was

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replaced by evergreen forest in about 5 pixels with clay soils with large water retention capacity in CA+PC+F (Figures 6G, 6H, 6I). In this situation, where there is little water stress in the CA simulation, both evergreen and drought deciduous PFTs have each one very high LAI, and the PFT that dominates can be defined by minor effects. Fire, although active, is probably too small to be relevant in a non-stressed ecosystem. In CV simulations, however, fire effect results in the replacement of the deciduous and perennial forest by savanna and grasses in all central Cerrado region (Figures 6J, 6K and 6L). These results show the limitations of CA and the importance to consider the interannual climate variability on simulations to improve the vegetation simulated.

For all combinations used, transitional forest areas in the northern and southwestern Cerrado biome are not adequately represented. With >90% of concordance, INLAND assigns the existence of tropical evergreen forest rather than deciduous forest in some pixels in the north of the transition, and the existence of tropical evergreen forest rather than savanna in the southwest, indicating difficulty to simulate transitional vegetation in these regions.

## 4 Discussion

The inclusion of CV, PR and PG and fire in INLAND showed significant influences on the simulated vegetation structure and dynamics in the Amazon-Cerrado border (Figure 4 and Table 6), suggesting that these factors play key role on vegetation structure in the forest-savanna border and can improve the simulated representation of the current contact zone between these biomes. This is broadly consistent with the literature that investigated causes of savanna existence in the real world (Hoffmann et al., 2012; Dantas et al., 2013; Lehmann et al., 2014). In this study, the spatial analysis and the Tukey-Kramer test (TK) show a difference in magnitude among these factors in vegetation, with fire

occurrence and P limitation being stronger than inter-annual climate variability along the transects (Figure 4).

The spatial analysis showed that CV declines AGB predominantly in eastern Amazonia (Figure 4a). Climate of this region is intensely affected by El Niño–Southern Oscillation (ENSO), which could reduce precipitation by 50%, placing the vegetation under intense water stress (Botta and Foley, 2002; Foley et al. 2002; Marengo et al., 2004; Andreoli et al., 2012; Hilker et al., 2014). This reduction in rainfall in dry years brings in direct changes in carbon flux (NPP) and stocks in leaves and wood, leading to changes in vegetation structure. In addition to inter-annual changes in the rainfall, interannual variability in other climate variables in CV also affect AGB, as average, maximum and minimum temperature, as well as wind speed and specific humidity, and influence photosynthesis on the model both directly (through Collatz and Farquhar equations) and indirectly (e.g. through evapotranspiration). Our results showed significant differences for most part of the biomes, except central Amazonia (Figure 4a), where CV and precipitation seasonality have been pointed as secondary effects on vegetation (Restrepo-Coupe et al., 2013), since there is no shortage of water availability during the dry season.

Along the Cerrado, lower water availability in some years in CV affects tree biomass, although that vegetation is predominantly grassy-herbaceous. The AGB decline is significant for most part of the simulated Cerrado domain (Figure 4a) and average values could represent half the amount of typical tree biomass in this biome. This reduction in AGB reflects INLAND's ability to simulate similar Cerrado conditions and expose the few trees to high water stress.

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Throughout the transects, however, no significant difference was found for average AGB between CV+PC and CA+PC by TK at p<0.05 (Table 6). On the other hand, when we analyzed the influence of CV for the same pixels, but using all simulations (Table 3), regardless of P limitation and fire occurrences, the results showed that the decrease in AGB by 0.38 kg-C m<sup>-2</sup> (5.7%) is statistically significant along the transition.

P limitation effect was statistically significant for PR and PG along all the Amazon domain and the main differences between these simulations were the spatial patterns of tree AGB decrease (Figure 4b and Figure 4c). We cannot affirm which of these databases is better because they are the results of different methodologies and observations (Quesada et al., 2009; Yang et al., 2014). However, PG showed a higher AGB decrease in central Amazonia, northeastern Pará and northeastern Mato Grosso state, indicating that in these areas the P limitation is higher. This result does not corroborate the northwest-southeast AGB gradient found in the Amazon basin, which showed a higher productivity in the west where soils are more fertile than those found in the southeast (Aragão et al., 2009; Saatchi et al., 2007; Nunes et al., 2012; Lee et al., 2013). On the other hand, PR AGB agrees with the northwest-southeast gradient, presenting less limitation in the soils of central Amazonia with declines in AGB mainly in the southeastern part of the rainforest (between Pará and northeastern Mato Grosso states) (Figure 4b).

In Cerrado, P limitation also influenced vegetation (Figure 4c) and presented statistically significant differences when compared <u>CV+PG - CV+PC</u>. In this biome, as well as in the Amazon, tree

abundance richness and diversity have been generally associated with increases of soil fertility (Long et

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al., 2012; Vourtilis et al., 2013), highlighting the importance of P in the composition and maintenance of vegetation, especially in transition areas.

Compared to the Amazon domain, the magnitude of effects of P limitation is lower in the Cerrado. However, few pixels in PR that have P limitation showed a significant decrease in arboreal AGB (Figure 4b), while in PG, we found reduction of AGB for most of the Cerrado domain, except only for the southern Tocantins state (Figure 4c). Despite the differences in spatial patterns, there was no statistically significant differences between PR and PG within the transects (Table 4 and Table 6).

The spatial difference between PG and PR showed that PG is lower than PR in the western Amazonia, and higher in northern Amazonia. Moreover, PG have low P values in south of the transition compared to PR, while in Cerrado domain P values ranged between 120 to 200 mg kg<sup>-1</sup> (Figure S1). Although the PR dataset includes every known P data collected in the region, these differences reinforce the need to improve the data of P<sub>total</sub> in the soils of the Amazon and Cerrado/Amazon transition domains. Currently, P<sub>total</sub> data in Cerrado is scarce, and make unfeasible to establish a proxy similar to Castanho et al. (2013), which was specific for the Amazon.

In INLAND, the simple P-limitation parameterized through the linear relation Vmax and P<sub>total</sub>, showed significant spatially differences in AGB simulated and an improvement in simulations, highlighting the importance of P-limitation in modeling studies. For the most part, Dynamic Global Vegetation Models (DGVMs) do not consider the complete phosphorus cycle (see exceptions in Goll et al., 2012 and Yang et al., 2014), despite the importance of nutrient cycling for AGB maintenance and tropical vegetation dynamics in dystrophic soils. For example, nutrient cycling in the Amazon/Cerrado transition is closely related to the hyper-dynamic turnover of the AGB (Valadão et al. 2016), in which

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some key species might also be crucial to the hyper-cycling of nutrients through which vegetation sustain the constant input of nutrients, including large annual amounts of available P (Oliveira et al. 2017).

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The fire occurrence is an important factor controlling the AGB dynamics in the Cerrado or in the transition vegetation (Hoffman et al., 2003; Hoffman et al., 2012; Silvério et al., 2013; Couto-Santos et al., 2014; Balch et al., 2015), which this study clearly replicates, showing statistically significant influences when compared to control simulations (Figure 4d and Table 5). In the transition, the fire effect may reduce average AGB by 50% (Table 5), which under climate change or deforestation conditions may lead to an even stronger change in the vegetation structure and dynamic. According to Hoffmann et al. (2009) the undisturbed forests in the Amazon-Cerrado border appear to be more resilient to fire in relation to the other tropical forests and the vegetation-fire dynamics is mainly controlled by tree "topkill" (defined by the authors as complete death of the aerial biomass). In INLAND, the effect of fire on AGB is similar to the "topkill" presented by Hoffmann et al. (2009), being represented by the penalization fraction described earlier, and applied annually to the leaf, wood and root biomass pools of the pixel. Therefore, at the end of every year both upper and lower LAI are decreased, according to the amount burned, triggering competition between both canopies for light, and increasing the photosynthesis rates and stocks of carbon in leaves, stems and roots pools in the lower canopy. The carbon allocation in INLAND is fixed and is not modified after fire occurrence, as observed in some species of the savanna-forest transition (Hoffman et al., 2009; 2012). Thus, during recovery from a fire, the vegetation dynamics follows the model standard procedure.

Excluído: The decrease in tree AGB occasioned by P limitation can contribute to a decrease in litter production and consequently could affect nutrient cycling in tropical ecosystems. According to Oliveira et al. (2017), the litter produced by vegetation corresponds to the main return route to the available fraction of P for plants, especially in the transition areas where Pavailable in the soil is very low. In our model, however, P acts directly in the photosynthesis limitation through V<sub>max</sub> and cannot be reabsorbed by the roots. Thus, the litter produced in vegetation contribute only to dry matter and fire occurrence increase In nature, the litter affected by fire occurrence volatilizes the small amount of P available to plants, increasing the nutrient losses of the ecosystem. Despite this simplified representation in INLAND, it can represent the P influence on woody AGB in the Amazon and Cerrado ¶

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In the Cerrado domain, the simulated fire effect implies in significant increases <u>in</u> shrubs and herbaceous vegetation and decreases <u>in</u> the arboreal component, resulting in increment of LAI<sub>lower</sub> and decrease of LAI<sub>upper</sub> (Table 5). These changes in canopy structure after fire occurrence are exclusively due to the canopy opening and consequently more penetration of photosynthetic radiation into the lower canopy.

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The model does not include neither characteristics related to resilience such as velocity, intensity and duration of the burning (Hoffman et al., 2003; Rezende et al., 2005; Elias et al., 2013; Reis et al., 2015) nor the representation of some tree morphological adaptation that confers to Cerrado species resilience to fire occurrence, such as bark thickness. Thus, trees and grasses throughout the Amazon-Cerrado border are equally exposed to the same fire intensity inside the grid cell, without fire resistance differences. However, despite the limitations in the representation of resilience characteristics and morphological attributes of fire resistance, our results show that simulated biomass is more close to observed biomass in Cerrado areas when the fire module is activated (Figure 5). An improvement in distribution of biomes along the simulated transition area is also observed (Figure 6g-i), highlighting fire as an essential factor to represent the Amazonia-Cerrado border.

This study shows an improvement in the correlations between simulated and observed AGB when compared to previous modeling studies, regardless of treatment, with correlation coefficients usually above 0.80 for the transects, except for T5, for which the correlation coefficient value is usually below 0.5 (Table 7). Senna et al. (2009) found 0.20 as maximum correlation coefficient between simulated and observed ABG while Castanho et al. (2013) showed 0.80 for Amazonia domain. From Figure 5, it is clear that CV, F and P limitation in the transition zone reduce the AGB, causing the

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simulated data to approach the observed data. However, the inclusion of these effects is still insufficient to represent the correct distribution of the vegetation types throughout the Amazon-Cerrado border (Figure 6L). In our interpretation, this means that other important factors are still missing from the simulation, especially in T5, where soils are rocky and shallow. A better spatial representation of soil physical properties, including shallow rocky soils, as well as spatially varying physiological parameterizations of the vegetation such as carbon allocation, deciduousness of vegetation, residence time and tree structure that may discern thick from thin trees, are probably needed to improve the simulations, in particular in the northern and southern extremes of the border (T1 and T5).

In addition, literature shows that in the transition area, soils are very different than Amazon soils, and that essential proprieties for modeling are peculiar (Silva et al., 2006; Vourlitis et al., 2013; Dias et al. 2015). For example, Dias et al. (2015) recently showed that the pedological functions normally used by DGVMs may underestimate the saturated hydraulic conductivity ( $K_s$ ) by >99%, transforming a well-drained soil with  $K_s = 1.5.10^{-4} \text{ m.s}^{-1}$  (540 mm.h<sup>-1</sup>) in reality into an impervious brick with  $K_s = 3.3.10^{-7} \text{ m.s}^{-1}$  (1.2 mm.h<sup>-1</sup>) in the model.

For all transects, the AGB curves have similar patterns (Figure 5); the smaller difference is observed between CA+PC and CV+PG curves, while the larger difference is when fire is present. The effect of P limitation appears as an effect of intermediate magnitude, reducing the AGB by more than the effect of inter-annual climate variability. In the east, it is observed that there is little or no difference among AGB simulated by CA+PC, CV+PC and CV+PG, revealing that inter-annual climate variability and P have smaller influence in the AGB. However, in the east of T2, T3 and T4, fire is the factor that

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adjusts the simulated to the observed data (Figure 5), differently than the grid points in the West, where CV+PG is a better proxy between observed and simulated data.

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Such conditions are interesting because they reflect the different mechanisms that regulate the structure of these ecosystems and probably the phytophysiognomies distribution. For example, P limitation seems to be the factor that improves simulated AGB in regions where the predominant vegetation type is the tropical rainforest. Fire, on the other hand, improves the AGB in grid points where the Cerrado occurs. Moreover, important factors such as productivity partitioning into leaves, roots and wood carbon pools are assumed to be fixed in space and time within a given PFT, neglecting the natural capacity of transitional forests to adapt itself and to adjust their metabolism to local environmental conditions (Senna et al., 2009). In years of severe drought, or under frequent fire occurrence, transitional forests could prioritize the stock of carbon in fine roots instead of the basal or leaf increment to maximize access to available water, make hydraulic redistribution of soil moisture to maintain the greenness and photosynthesis rates, or increase the capacity to resprout after fire occurrence (Hoffman et al., 2003; Brando et al., 2008). Brando et al. (2008) found high sensitivity in carbon allocation for eastern Amazon basin trees, which reduced wood production by 13-60% in response to an artificial drought. Although in INLAND soil moisture can reduce the photosynthetic rates during the months of lower rainfall, it does not dynamically change the allocation rates, exposing the PFTs in these areas to severe water stress and underestimating the AGB, such as in the west of T1 (Figure 5a).

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T2, T3 and T4, located in the central part of the Amazon-Cerrado transition, showed the highest average correlations between observed and simulated data (Table 7). For these transects, INLAND seems to be able to capture the high variability of AGB gradient.

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At T5, located at the south of the transition, the average correlations were low for all treatments, indicating that INLAND has difficulty to represent the AGB gradient there (Table 7). However, it captures the lower AGB as compared to the northern ones. In this region, the vegetation is characterized by a wide diversity of physiognomies, which varies with other preponderant factors, such as lithology, soil depth, topography and fertility. The observed data also showed high AGB variability, indicating that there are changes in the vegetation structure, featuring medium-sized and small vegetation types on different soil types. In INLAND, however, features such as lithology and water-table depth are not considered due to the complexity of its representation on the large scale, limiting the representation of a heterogeneous environment throughout the transition.

Patterns of vegetation distribution along the Amazon-Cerrado border exist are influenced not only by inter-annual climate variability, P limitation, and fire, but also by the ecophysiological parameters, Additional field experiments are needed to understand the relationship between currently fixed parameters (such as carbon allocation, residence time, and deciduousness, among others) to the environmental conditions and soil proprieties.

Another point to discuss is that the model simulates, in a few pixels in southeastern Cerrado, very robust simulations of the presence of savanna and grassland even in the absence of fire (Figure 6A-F and 6a-f). This is, in our view, a result of the intense water and heat stress in this region. In the Brazilian Cerrado, the high temperatures (> 35 °C) combined to the dry season duration (as long as 6

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**Excluído:** Obtaining these parameters is a challenge to the scientific community once the field measurements are difficult due to the extension of the transition area

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months with little or no rain) exposes the vegetation to a severely stressed situation, so that a low biomass, low LAI vegetation may exist without the need of a frequent disturbance.

**Conclusions** 

This is the first study that uses modeling to assess the influence of inter-annual climate variability, fire occurrence and phosphorus limitation to represent the Amazon-Cerrado border. This study shows that, although the model forced by a climatological database is able to simulate basic characteristics of the Amazon-Cerrado transition, the addition of factors such as inter-annual climate variability, phosphorus limitation and fire gradually improves simulated vegetation types. These effects are not homogeneous along the latitudinal/longitudinal gradient, which makes the adequate simulation of biomass challenging in some places along the transition. Based on the F-statistic in Tables 3, 4 and 5, this, work shows that fire is in the main determinant factor of the changes in vegetation structure (LAL AGB) along the transition. The nutrient limitation is second in magnitude, stronger than the effect of inter-annual climate variability.

Overall, although INLAND typically simulates more than 80% of the variability of biomass in the transition zone, in many places the biomass is clearly not well simulated. Situations for clearly wet or markedly dry climate conditions were well simulated, but the simulations are generally poor for transitional areas where the environment selected physiognomies that have an intermediate behavior, as is the case of the transitional forests in northern Tocantins and Mato Grosso.

There are evidences that the inclusion of spatially explicit parameters such as woody biomass residence time, maximum carboxylation capacity (V<sub>max</sub>), and NPP allocation to wood may improve

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Amazon rainforest AGB simulation by DGVMs (Castanho et al., 2013). However, in the transition, the lack of field parameters measured limits the inclusion of the variability of these biophysical parameters in DGVMs. Additional field work and compilation of existing ones, are necessary to obtain physiological and structural parameters through the Amazon-Cerrado border to establish numerical relationships between soil, climate and vegetation. With the help of these data, the vegetation dynamic models will be able to correctly simulate current patterns and future changes in vegetation considering climate change scenarios. In addition, it is also needed to include not only the spatial variability, but also temporal variability in physiological parameters of vegetation, allowing a more realistic simulation of the soil-climate-vegetation relationship. Finally, our results reinforce the importance and need of the DGVMs to incorporate the nutrient limitation and fire occurrence to simulate the Amazon-Cerrado border position.

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# 6 Acknowledgements

We gratefully thank the Brazilian agencies FAPEMIG and CAPES for their financial support.

Atul K Jain is funded by the U.S. National Science Foundation (NSF-AGS- 12-43071).

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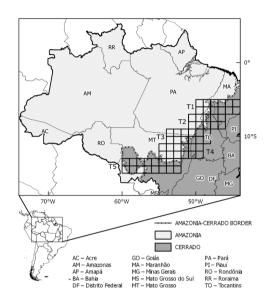
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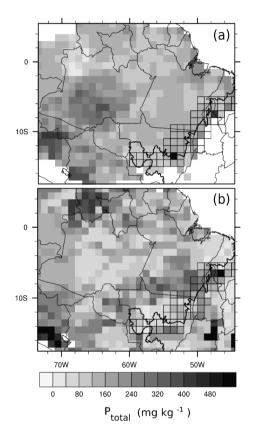
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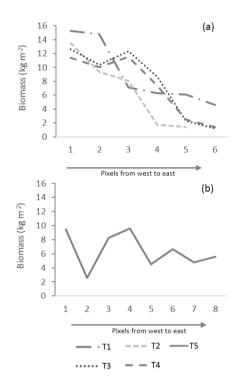
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**Figure 1.** Delimitation of the study area Amazonia (in light gray) and Cerrado (in dark gray) (IBGE, 2004), and the location of five transects used in this work (from T1 to T5). The dashed line represents the border between biomes.



**Figure 2.** (a) Map of regional total P in the soil (PR), (b) Map of global total P in the soil (Yang et al., 2013) (PG).



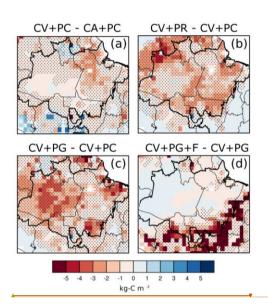
1723 | Figure 3. Average variations of AGB in pixels from West to East in the Amazonia-Cerrado transition

for transects T1, T2, T3 and T4 (a), and T5 (b).

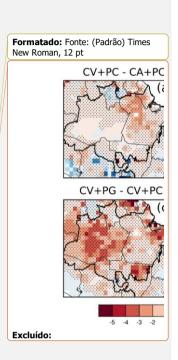
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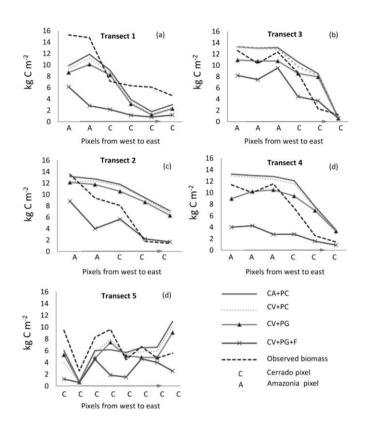
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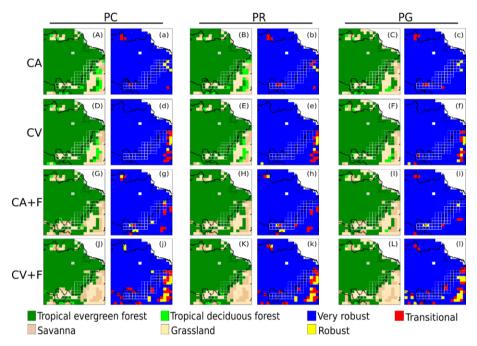
**Figure 4.** Effects of inter-annual climate variability (a), Regional P limitation (b), Global P limitation (c), and fire (d) on AGB. The hatched areas indicate that the variables are significantly different compared to the control simulation at the level of 95% according to the t-test. The thick black line is the geographical limits of the biomes.





**Figure 5.** Average longitudinal AGB gradient in Amazonia-Cerrado transition simulated for T1 to T5 considering different combinations: observed data; seasonal climate control simulation (CA+PC); interannual climate variability (CV+PC); inter-annual climate variability + global P limitation (CV+PG); and inter-annual climate variability + P + fire occurrence (CV+PG+F).

Excluído: Longitudinal



**Figure 6.** Results for the dominant vegetation cover simulated by INLAND for the different treatments (A-L) and a metric of variability of results (a-l). Simulations are considered very robust if the dominant vegetation agrees on 9-10 of the last 10 years of simulation, robust if it agrees on 7-8 years, and transitional if on 6 or fewer years.

**Table 1.** Simulations with different scenarios evaluated by INLAND model in Amazonia-Cerrado transition. CA, climatological average, 1961-1990; CV, monthly climate data, 1948-2008; the nutrient limitation on  $V_{max}$  - PC, no P limitation ( $V_{max}$  = 65 µmol-CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>); PR, regional P limitation; PG, global P limitation).

	-	•		$\mathbf{V}_{ ext{max}}$	
Climate	$CO_2$	Fire (F)	PC	PR	PG
CA	Variable	Off	CA+PC	CA+PR	CA+PG
CA	Variable	On	CA+PC+F	CA+PR+F	CA+PG+F
CV	Variable	Off	CV+PC	CV+PR	CV+PG
CV	Variable	On	CV+PC+F	CV+PR+F	CV+PG+F

**Table 2.** Individual and combined effects for each simulation in Amazonia-Cerrado transition. CA, climatological seasonal average, 1961-1990; CV, monthly climate data, 1948-2008; the nutrient limitation on  $V_{max}$  - PC, no P limitation ( $V_{max}$  = 65  $\mu$ molCO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>); PR, regional P limitation; PG, global P limitation)

Phosphorus (P)	Fire (F)
CA+PR)-(CA+PC)	(CA+PC+F)-(CA+PC)
CV+PR)-(CV+PC)	(CV+PC+F)-(CV+PC)
CA+PG)-(CA+PC)	(CA+PR+F)-(CA+PR)
CV+PG)-(CV+PC)	(CV+PR+F)-(CV+PR)
	(CA+PG+F)-(CA+PG)
	(CV+PG+F)-(CV+PG)
	CA+PR)-(CA+PC) CV+PR)-(CV+PC) CA+PG)-(CA+PC)

**Table 3.** Summary of average NPP, LAI and AGB for the Amazonia-Cerrado transition at the transects domains, considering all simulations with CA and CV regardless of fire presence or P limitation. The results of a one-way ANOVA are also shown, including the F statistic, and p value. Values within each column followed by a different letter are significantly different (p < 0.05) according to the Tukey–Kramer test (n=1860: 31 pixels x 10 years x  $n_{simulation/2}$ ).

Group 1	NPP		LAI <sub>total</sub>		LAI <sub>lowe</sub>	r	LAI <sub>upper</sub>		AGB	
	kg-C m <sup>-2</sup> yr	-1	$m^2 m^{-2}$		$m^2 m^{-2}$		$m^2 m^{-2}$		kg-C m <sup>-2</sup>	!
CA	0.68	a	7.47	a	1.98	a	5.49	a	6.68	a
CV	0.64	b	7.15	b	2.11	a	5.04	b	6.30	b
F	40.2		57.2		2.96		36.0		11.3	
p	< 0.001		< 0.001		ns		< 0.01		<0.001	

**Table 4.** Summary of average NPP, LAI and AGB for the transition at the transects domains, considering different P limitation, regardless of climate and fire presence. The results of a one-way ANOVA are also shown, including the F statistic, and p value. Values within each column followed by a different letter are significantly different (p < 0.05) according to the Tukey–Kramer test (n=1240: 31 pixels x 10 years x  $n_{simulation/3}$ ).

Group 2	NPP		LAItotal		LAI <sub>lower</sub>	•	LAI <sub>upper</sub>		AGB	•
	kg-C m <sup>-2</sup> yr <sup>-1</sup>		$m^2 m^{-2}$		$m^2 m^{-2}$		$m^2 m^{-2}$		kg-C m <sup>-2</sup>	2
PC	0.71	a	7.64	a	1.84	b	5.80	a	7.15	a
PR	0.64	b	7.15	b	2.19	a	4.95	b	6.20	b
PG	0.64	b	7.14	b	2.10	a	5.04	b	6.12	b
$F_{2.99}$	62.8		61.0		8.75		53.5		33.6	
p	< 0.001		< 0.001		< 0.01		< 0.01		< 0.001	

**Table 5.** Summary of average NPP, LAI and AGB for the transition at the transects domains, considering presence or absence of fire. The results of a one-way ANOVA are also shown, including the F statistic, and p value. Values within each column followed by a different letter are significantly different (p < 0.05) according to the Tukey–Kramer test (n=1860: 31 pixels x 10 years x  $n_{\text{simulation/2}}$ ).

Group 3	Group 3 NPP		LAI <sub>total</sub> LAI <sub>lower</sub>		LAI <sub>upper</sub>	AGB	
kg-C m <sup>-2</sup> yr <sup>-1</sup>		$m^2 m^{-2}$	$m^2 m^{-2}$	$m^2 m^{-2}$	kg-C m <sup>-2</sup>		
Fire OFF	0.66	a	6.72 b	0.88 b	5.84 a	8.47 b	
Fire ON	0.67	b	7.90 a	3.21 a	4.69 b	4.51 a	
$F_{3.84}$	8.28		937	1459	249	1719	
<i>p</i>	< 0.005		< 0.001	< 0.01	< 0.01	< 0.001	

**Table 6.** Summary of average NPP, LAI and AGB for the transition at the transects domains, considering all factor combinations. The results of a one-way ANOVA are also shown, including the F statistic, and p value. Values within each column followed by a different letter are significantly different (p < 0.05) according to the Tukey–Kramer test (n=310: 31 pixels x 10 years).

	NPP		LAI <sub>total</sub>		LAI <sub>lower</sub>		LAI <sub>upper</sub>	-	AGB	
	kg-C m <sup>-2</sup> yr <sup>-1</sup>		$m^2 m^{-2}$		$m^2 m^{-2}$		$m^2 m^{-2}$		kg-C m <sup>-2</sup>	
CV+PC	0.69	bcd	6.96	d	0.84	e	6.48	a	9.01	ab
CV+PG	0.61	f	6.24	f	0.85	e	5.60	bc	7.91	c
CV+PR	0.62	f	6.33	f	0.85	e	5.74	bc	8.04	c
CV+PC+F	0.69	abc	7.92	b	2.91	cd	4.61	ef	4.89	de
CV+PG+F	0.63	ef	7.76	b	3.73	a	5.81	bc	3.91	f
CV+PR+F	0.63	ef	7.65	bc	3.47	ab	4.69	ef	4.02	f
CA+PC	0.72	ab	7.39	c	0.91	e	6.12	ab	9.31	a
CA+PG	0.64	def	6.64	e	0.91	e	5.40	cd	8.22	c
CA+PR	0.65	cdef	6.72	de	0.91	e	5.49	cd	8.31	bc
CA+PC+F	0.74	a	8.29	a	2.69	d	5.02	de	5.40	d
CA+PG+F	0.67	cde	7.90	b	3.29	abc	4.04	g	4.45	ef
CA+PR+F	0.67	cde	7.88	b	3.19	bc	4.18	fg	4.42	ef
F	16.2		115		140		38.1		172	
p	< 0.001		< 0.001		< 0.01		< 0.01		< 0.001	

**Table 7**. Correlation coefficients of AGB simulated by INLAND and field estimates (n= 310: 31 pixels x 10 years).

	T1	T2	Т3	<b>T4</b>	T5	All transects
CA+PC	0.843	0.928	0.886	0.937	0.337	0.786
CV+PC	0.838	0.884	0.890	0.939	0.355	0.781
CA+PR	0.793	0.848	0.830	0.911	0.399	0.756
CV+PR	0.795	0.793	0.832	0.907	0.527	0.771
CA+PG	0.814	0.951	0.838	0.889	0.388	0.776
CV+PG	0.825	0.922	0.840	0.879	0.496	0.792
CA+PC+F	0.988	0.987	0.977	0.892	0.133	0.795
CV+PC+F	0.976	0.947	0.933	0.908	0.187	0.790
CA+PR+F	0.842	0.805	0.981	0.808	0.561	0.799
CV+PR+F	0.925	0.804	0.927	0.808	0.319	0.757
CA+PG+F	0.844	0.961	0.980	0.830	0.430	0.809
CV+PG+F	0.845	0.932	0.931	0.881	0.177	0.753
CA avg	0.854	0.913	0.915	0.878	0.375	0.787
CV avg	0.867	0.880	0.892	0.887	0.344	0.774