

(Reviewer comments in *italics*; Responses in **bold**)

**Response to Associate Editor Received: 20 Dec 2017**

We appreciate the suggestions. The manuscript has been completely revised by a professional editor to provide better wording for unclear sentences and bring the manuscript more in line with the style conventions in *Biogeosciences*. This includes a minor change in the title of the manuscript. Also, we reviewed the discussion and removed some non-essential points. However, most of the discussion that was explicitly requested by previous reviewers was retained. In addition, all referee's suggestions have been included and are detailed below.

With these modifications, we hope you find that the manuscript is now acceptable for publication.

*Line 22: Update to: "to an observed AGB map."*

**Response: This has been changed in the revised manuscript. Please check line 31 in marked-up manuscript version.**

*Lines 71-73: Revise "unlike the temperate forests" and "adsorvided"*

**Response: This has been changed in the revised manuscript. Please check lines 155-156 in marked-up manuscript version.**

*Lines 80-81: Revise: "However, N is not a limiting nutrient for trees in the tropics (Davidson et al. 2004), while P availability affects the trees dynamics."*

**Response: This has been changed in the revised manuscript. Please check line 163-165 in marked-up manuscript version.**

*How much does this AGB map differ from other AGB maps (e.g. from Mitchard et al., Saatchi et al.) and why did you choose to use this one? It might be helpful to add 1-2 sentences in the discussion about the uncertainties in the "observational" maps when comparing them to model results.*

**Response: Although Saatchi et al., (2009), Baccini et al., (2012) and Mitchard et al., (2014) are maps of pantropical biomass, they were for present day biomass, including deforested pixels. Deforestation is widespread in the region, compromising the comparison with our results, since the goal of this study is to understand the drivers of natural vegetation structure and dynamics in the transition zone. The same justification is valid for the Avitabil data, since this map represents the data combination of Saatchi and Baccini. Thus, we prefer to use the biomass database of Nogueira et al. (2015) that includes aboveground measures in the original vegetation (before extensive clearing), and uses 74 different classes of vegetation and better representing the many physiognomies in the region. The areas that are currently degraded were identified, and biomass was assigned according to information about the original vegetation.**

**Response to Report#1** Received: 20 Dec 2017

*General Comments:*

*Revision: The revision comments here are mainly associated with language and wording.*

*Detailed comments:*

*Abstract: line 25-26: Update phrase “gradually improve simulated vegetation types” What is meant by “improve” vegetation?*

**Response: This has been changed in the revised manuscript. Please check line 35 in marked-up manuscript version.**

*Page 3 line 40-42: Update “physiognomies” and “woodland formations” to something more clearly descriptive of vegetation.*

**Response: This has been changed in the revised manuscript. Please check lines 86-87 in marked-up manuscript version.**

*Page 3 line 42-44: Update to “ecotonal vegetation around this transition includes a mix of tropical forest and savanna species.”*

**Response: This has been changed in the revised manuscript. Please check lines 88-89 in marked-up manuscript version.**

*Page 6 line 115: Update to “INLAND is a revision of the IBIS model”*

**Response: This has been changed in the revised manuscript. Please check line 268 in marked-up manuscript version.**

*Page 7 line 117-119: Update to “We used the version described by Senna et al. (2009) as the starting point for INLAND without changes in tuning, aside from the addition of P parameterization, described below.”*

**Response: This has been changed in the revised manuscript. Please check lines 271-272 in marked-up manuscript version.**

*Page 7 line 131: Update to “based on a drought phenology scheme”*

**Response: This has been changed in the revised manuscript. Please check line 284 in marked-up manuscript version.**

*Page 8 line 152-153: Include a basic description of Cerrado and Camp sujo. Some papers describe cerrado as “savanna woodland with 10-60% tree cover”.*

**Response: We used the Ribeiro and Walter, 2008 definition for both physiognomies. The reference to the definition was explicitly included in Line 374 of the marked-up manuscript version.**

*Page 15 line 293: Update to “is much higher in magnitude than due to P”*

**Response: This has been changed in the revised manuscript. Please check line 735 in marked-up manuscript version.**

*Page 15 line 294-297: Split this into two sentences.*

**Response: This has been changed in the revised manuscript. Please check lines 736-739 in marked-up manuscript version.**

*Page 18 line 344: Update to “cover in the last 10 years of simulation”*

**Response: This has been changed in the revised manuscript. Please check line 881 in marked-up manuscript version.**

*Page 18 line 350: Update to “deciduous forest with evergreen forest”*

**Response: This has been changed in the revised manuscript. Please check line 888 in marked-up manuscript version.**

*Page 18 line 360: Update to “PFTs each have a very high LAI”*

**Response: This has been changed in the revised manuscript. Please check line 898 in marked-up manuscript version.**

*Page 18 line 361: Explain what is meant by “minor effects” determining dominance, or delete this phrase.*

**Response: This has been removed in the revised manuscript.**

*Page 18 line 362: Update to “fire results in the replacement”*

**Response: This has been changed in the revised manuscript. Please check line 899 in marked-up manuscript version.**

*Page 18 line 363: Update to “grasses in the entire central Cerrado region”*

**Response: This has been changed in the revised manuscript. Please check line 900 in marked-up manuscript version.**

*Page 19 line 364: Update to: “the importance of considering the interannual climate”*

**Response: This has been changed in the revised manuscript. Please check line 901 in marked-up manuscript version.**

*Page 19 line 369-370: Update to “indicating difficulty in simulating transitional vegetation in these regions”*

**Response: This has been changed in the revised manuscript. Please check lines 969-970 in marked-up manuscript version.**

*Page 22 line 449: Should “according to fire probability” be updated to fire occurrence or size? How does the fraction of reduction relate to fire? Is there a fuels component?*

**Response: This has been changed in the revised manuscript. Please check lines 410-432 and 1153-1157 in marked-up manuscript version.**

*Page 23 line 447-453: Suggest moving this section (Sentence beginning “In INLAND, fire...”) to Section 2.2, and include one sentence to remind reader of these details. (As stated in section 2.2, fire acts on upper and lower LAI according to fire intensity, triggering competition.)*

**Response: This has been changed in the revised manuscript. Please check lines 1153-1157 in marked-up manuscript version.**

*Page 23 line 458-462: In 458 you state that “the model does not include ...fire intensity...” but then state that trees and grasses “are equally exposed to the same fire intensity” Update this so that these statements are consistent. Update line 462 to state what aspect of fire is modifying PFTs.*

**Response: This has been changed in the revised manuscript. Please check line 1154 in marked-up manuscript version.**

*Page 24 line 475-480: “...other important factors are still needed...” improved representation of fire and vegetation fire resistance would also improve these results.*

**Response: This has been changed in the revised manuscript. Please check lines 1272-1278 in marked-up manuscript version.**

*Page 24 line 482: Update “for modeling are peculiar” to “for modeling the transition area are unique.”*

**Response: This has been removed in revised manuscript version.**

*Page 25 line 492: Update to “and P have a smaller influence”*

**Response: This has been changed in the revised manuscript. Please check lines 1283-1284 in marked-up manuscript version.**

*Page 25 line 496: Replace “phytophysionomies distribution” to “vegetation structure and distribution”*

**Response: This has been changed in the revised manuscript. Please check line 1288 in marked-up manuscript version.**

*Page 26 line 514: Update to “indicating that INLAND has difficulty representing the ABG...”*

**Response: This has been changed in the revised manuscript. Please check line 1401 in marked-up manuscript version.**

*Page 26 line 516: Suggest updating “physiognomies” to “vegetation characteristics” or “vegetation types”*

**Response: This has been changed in the revised manuscript. Please check line 1403 in marked-up manuscript version.**

*Page 26 line 522: Update to “Amazon-Cerrado border are influenced not only”*

**Response: This has been changed in the revised manuscript. Please check line 1437 in marked-up manuscript version.**

*Page 28 line 553: Update to “lack of measured field parameters”*

**Response: This has been changed in the revised manuscript. Please check line 1525 in marked-up manuscript version.**

1 **Influence of climate variability, fire and phosphorus limitation on**  
2 **vegetation structure and dynamics of the Amazon-Cerrado border**

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4 Emily Ane Dionizio da Silva<sup>1</sup>, Marcos Heil Costa<sup>1</sup>, Andrea Almeida Castanho<sup>2</sup>, Gabrielle Ferreira  
5 Pires<sup>1</sup>, Beatriz Schwantes Marimon<sup>3</sup>, Ben Hur Marimon-Junior<sup>3</sup>, Eddie Lenza<sup>3</sup>, Fernando Martins  
6 Pimenta<sup>1</sup>, Xiaojuan Yang<sup>4</sup>, Atul K. Jain<sup>5</sup>

8 <sup>1</sup> Department of Agricultural Engineering, Federal University of Viçosa (UFV), Viçosa, MG [36570-](#)  
9 [000](#), Brazil.

10 <sup>2</sup> The Woods Hole Research Center, 149 Woods Hole Rd., Falmouth, MA, [02540](#), USA.

- Excluído: .

11 <sup>3</sup> [Plant Ecology Laboratory](#), [State](#) University of Mato Grosso, Nova Xavantina Campus, Nova  
12 Xavantina, MT [78690-000](#), Brazil.

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13 <sup>4</sup> Oak Ridge National Laboratory, Oak Ridge, TN, [37831](#), USA.

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14 <sup>5</sup> Department of Atmospheric Sciences, University of Illinois at Urbana-Champaign, [Urbana](#), [IL 61801](#),  
15 [USA](#).

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

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25 **Abstract**

26 Climate, fire and soil **nutrient** limitation are important elements that affect vegetation dynamics  
27 in areas of forest-savanna transition. In this paper, we use the dynamic vegetation model INLAND to  
28 evaluate the influence of interannual climate variability, fire and phosphorus (P) limitation on Amazon-  
29 Cerrado transitional vegetation structure and dynamics. We assess how each environmental factor  
30 affects net primary production, leaf area index and aboveground biomass (AGB), and compare the AGB  
31 simulations to an observed AGB map. We used two climate data sets, (monthly average climate for  
32 1961-1990 and interannual climate variability for 1948-2008), two data sets of total soil P content (one  
33 based on regional field measurements and one based on global data), and the INLAND fire module. Our  
34 results show that the inclusion of interannual climate variability, P limitation and fire occurrence, each  
35 contribute to simulating vegetation types that more closely match observations. These effects are  
36 spatially heterogeneous and synergistic. In terms of magnitude, the effect of fire is strongest and is the  
37 main driver of vegetation changes along the transition. Phosphorus limitation, in turn, has a stronger  
38 effect on transitional ecosystem dynamics than interannual climate variability does. Overall, INLAND  
39 typically simulates more than 80% of the AGB variability in the transition zone. However, the AGB in  
40 many places is clearly not well simulated, indicating that important soil and physiological factors in the  
41 Amazon-Cerrado border region, such as lithology, water table depth, carbon allocation strategies and  
42 mortality rates, still need to be included in the model.

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## 80 1 Introduction

81 The Amazon and the Cerrado are the two largest and most important phytogeographical domains  
82 in South America. The Amazon forest has been globally recognized not only for its species diversity  
83 and richness, but also because it plays important roles in the global climate by regulating water (Bonan,  
84 2008; Pires and Costa, 2013) and heat fluxes (Shukla et al., 1990; Rocha et al., 2004; Roy et al., 2002).

85 The Cerrado is recognized as the most species-rich savanna in the world (Myers et al., 2000; Klink and  
86 Machado, 2005). It is characterized by landscapes ranging from sparse fields to dense woodlands, which  
87 may mix with Amazon rainforest vegetation in transitional areas. The Amazon-Cerrado transition  
88 extends 6270 km from northeast to southwest in Brazil, and ecotonal vegetation around this transition  
89 includes a mix of tropical forest and savanna species (Torello-Raventos et al., 2013).

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

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

100 Previous modeling studies using DGVMs that investigated climate effects in the Amazon  
101 indicate that the rainforest could experience changes in rainfall patterns that would transform the forest  
102 into either an ecosystem with sparse vegetation, similar to a savanna - what has been called the  
103 "savannization of the Amazon" (Shukla et al., 1990; Cox et al., 2000; Oyama and Nobre, 2003; Betts et  
104 al., 2004; Cox et al., 2004; Salazar et al., 2007) - or into a seasonal forest (Malhi et al., 2009; Pereira et

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143 | al., 2012; Pires and Costa, 2013). These studies have had great importance for the improvement of  
144 | terrestrial biosphere modeling, but they neglect two important processes in tropical ecosystem  
145 | dynamics: fire occurrence and nutrient limitation, particularly phosphorus (P) limitation.

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

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154 | Studies suggest that P is the main limiting nutrient within tropical forests (Malhi et al., 2009;  
155 | Mercado et al., 2011; Quesada et al., 2012), unlike in temperate forests, where nitrogen is the main  
156 | nutrient that limits productivity. Phosphorus is easily bound by soil minerals due to the large amount of  
157 | iron and aluminum oxides in the acidic and strongly weathered soils of the Amazon and the Cerrado  
158 | (Dajoz, 2005; Goedert, 1986). In the tropics, the warm and wet climate favors high biological activity in  
159 | the soil and rapid litter decomposition, therefore nitrogen is not generally limiting for plant fixation. In  
160 | the Cerrado, higher soil fertility is related to regions with greater woody plant abundance and less grass  
161 | cover, similar to conditions found in the Amazon rainforest (Moreno et al., 2008; Vourtilis et al., 2013;  
162 | Veenendaal et al., 2015). However, phosphorus limitation is often neglected by DGVMs, which usually  
163 | assume unlimited P availability and consider N to be the main limiting nutrient. Although N does affect  
164 | tree growth (Davidson et al. 2004), it is not a limiting tropical soil nutrient when compared to total P  
165 | availability, which affects competition between trees,

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166 | In principle, in transitional forests, where the climate is intermediate between wet and seasonally  
167 | dry, the heterogeneous structure and phenology make it difficult to represent these forests in models.

203 The Amazon-Cerrado border is the result of the expansion and contraction of the Cerrado into the forest  
204 (see Marimon et al., 2006; Morandi et al., 2016), especially in Mato Grosso state, where extreme events,  
205 such as intense droughts, influence the vegetation dynamics (Marimon et al., 2014) and the nutrient  
206 (Oliveira et al., 2017) and carbon cycling (Valadão et al., 2016).

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207 Currently, no model has been able to accurately simulate the vegetation transition between the  
208 Amazon and the Cerrado. In general DGVMs simulate evergreen forest along the Amazon-Cerrado  
209 border and miss savanna occurrence (Botta and Foley, 2002; Bond et al., 2005; Salazar et al., 2007;  
210 Smith et al., 2014). This difficulty may be because these models neglect or poorly represent nutrient  
211 limitation, soil properties or disturbances such as fire. Thus, we need a better understanding of the  
212 controls on transitional vegetation in order to determine the appropriate model parameters and simulate  
213 relations between environmental factors and transitional vegetation physiognomies.

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214 In this paper we use the dynamic vegetation model INLAND (Integrated Model of Land Surface  
215 Processes) to evaluate the influence of interannual climate variability, fire occurrence and P limitation  
216 on Amazon-Cerrado transitional vegetation dynamics and structure. We assess how each element  
217 affects net primary production (NPP), leaf area index (LAI) and aboveground biomass (AGB) and  
218 compare the simulated AGB to observed AGB data. The results presented here are important for  
219 building models that accurately represent transitional vegetation, and show the need for including the  
220 spatial variability of ecophysiological parameters for these areas.

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## 211 2 Materials and methods

### 222 2.1 Study area

223 The present study focuses on the Amazon-Cerrado transition region (Fig. 1). We use the official  
224 delimitation of the Brazilian biomes proposed by IBGE (2004), and define five transects along the  
225 transition border with a 1° × 1° grid size (the terms “transition”, “Amazon-Cerrado transition” and  
226 “Forest-Savanna transition” are used interchangeably throughout this manuscript). Transects 1 to 4 all

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261 span the Amazon-Cerrado border, extending approximately 330 km into each biome, while Transect 5  
262 is 880 km long and runs along the southern Amazon-Cerrado border. The transects are located as  
263 follows: Transect 1 (T1: 44°-50° W, 5°-7° S), Transect 2 (T2: 46°-51° W, 7°-9° S), Transect 3 (T3:  
264 48°-54° W, 9°-11° S), Transect 4 (T4: 49°-55° W, 11°-13° S), and Transect 5 (T5: 52°-60° W, 13°-  
265 15° S) (Fig. 1).

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## 266 2.2 Description of the INLAND surface model

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267 The Integrated Model of Land Surface Processes (INLAND) is the land-surface component of  
268 the Brazilian Earth System Model (BESM). INLAND, a revision of the IBIS model (Integrated  
269 Biosphere Simulator, described by Foley et al., 1996; Kucharik et al., 2000), has been developed by  
270 assembling and standardizing different IBIS versions, and adding improvements in software  
271 engineering. We used the version described by Senna et al. (2009) as the starting point for INLAND  
272 without changes in tuning, aside from the addition of the P parameterization, described below. Code is  
273 available from <http://www.biosfera.dea.ufv.br/en-US/download-inland>.

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274 The model considers changes in the composition and structure of vegetation in response to the  
275 environment and incorporates important aspects of biosphere-atmosphere interactions. The model  
276 simulates the exchanges of energy, water, carbon and momentum between soil, vegetation, and  
277 atmosphere. These processes are organized in a hierarchical framework and operate at different time  
278 steps, ranging from 60 minutes to 1 year, coupling ecological, biophysical and physiological processes.  
279 The vegetation composition is represented by 12 plant functional types (PFTs) (e.g., tropical broadleaf  
280 evergreen trees or C4 grasses), and the vegetation structure is represented by two canopy layers: upper  
281 (arboreal PFTs) and lower (shrubs and grasses, but no arboreal PFTs). The photosynthesis and  
282 respiration processes are simulated in a mechanistic manner using the Ball-Berry-Farquhar model  
283 (details in Foley et al., 1996). The vegetation phenology module simulates processes such as budding  
284 and senescence based on a drought phenology scheme for tropical deciduous trees. The dynamic

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350 vegetation module computes the following variables yearly for each PFT: gross and net primary  
351 productivity (GPP and NPP), changes in AGB pools, simple mortality disturbance processes and  
352 resultant LAI; this allows vegetation type and cover to change with time. The partitioning of the NPP  
353 for each PFT resolves carbon into three AGB pools: leaves, stems and fine roots. The LAI of each PFT  
354 is obtained simply by dividing leaf carbon by specific leaf area, which in INLAND is considered fixed  
355 (one value) for each PFT.

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

360 Using these aspects of vegetation dynamics and soil physical properties, the model can simulate  
361 plant competition for light and water between trees, shrubs and grasses through shading and differences  
362 in water uptake (Foley et al., 1996). These PFTs can coexist within a grid cell, and their annual LAI  
363 values indicate the dominant vegetation type within a grid cell. For example, the dominant vegetation  
364 type is Tropical Evergreen Forest if the tropical broadleaf evergreen tree PFT has an annual mean upper  
365 canopy LAI ( $LAI_{upper}$ ) above  $2.5 \text{ m}^2 \text{ m}^{-2}$ . On the other hand, the dominant vegetation type is Tropical  
366 Deciduous Forest if the tropical broadleaf drought-deciduous tree PFT has an annual mean  $LAI_{upper}$   
367 above  $2.5 \text{ m}^2 \text{ m}^{-2}$ . Where total tree LAI ( $LAI_{upper}$ ) is between  $0.8$  and  $2.5 \text{ m}^2 \text{ m}^{-2}$ , the dominant  
368 vegetation type is Savanna, and  $LAI_{upper}$  values smaller than  $0.8 \text{ m}^2 \text{ m}^{-2}$  represent a Grassland vegetation  
369 type.

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370 We assume that the vegetation types Tropical Evergreen Forest and Tropical Deciduous Forest  
371 in INLAND represent the Amazon rainforest, while Savanna and Grassland represent the Cerrado.  
372 INLAND's Savannas would be equivalent to the Cerrado physiognomies *Cerradão* and *Cerrado sensu*  
373 *strictu*, while INLAND's Grasslands would be equivalent to the physiognomies *Campo sujo* and *Campo*  
374 *Limpo* (*sensu* Ribeiro and Walter, 2008).

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389 Soil chemical properties are represented by carbon (C), nitrogen (N) and phosphorus. The  
 390 carbon cycle is simulated through vegetation, litter and soil organic matter, where the biogeochemical  
 391 module is similar to the CENTURY model (Parton et al., 1993; Verberne et al., 1990). The amount of C  
 392 existing in the first meter of soil is divided into different compartments characterized by their residence  
 393 time, which can vary from just hours for microbial AGB and organic matter to several years for lignin.  
 394 The model considers only soil N transformations and C decomposition, but the N cycle is not fully  
 395 simulated, and N does not influence the vegetation productivity; i.e., there is a fixed C:N ratio. The P  
 396 cycle also is not fully implemented; instead, P limitation is spatially parameterized through the linear  
 397 relationship developed by Castanho et al. (2013) to limit the gross primary productivity. A map of total  
 398 P available in the soil ( $P_{total}$ ) is used by the model to estimate the maximum capacity of carboxylation by  
 399 the Rubisco enzyme ( $V_{max}$ ) for each grid cell using Eq. (1):

$$V_{max} = 0.1013P_{total} + 30.037 \quad (1)$$

400 where  $V_{max}$  and  $P_{total}$  are given in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and  $\text{mg P kg}^{-1} \text{ soil}$ , respectively. This equation has  
 401 been based on data for tropical evergreen and deciduous trees, and is applied only to these two PFTs; the  
 402 other PFTs are unaffected.

404 INLAND also contains a spatial fire module, based on the Canadian Terrestrial Ecosystem  
 405 Model CTEM (Arora and Boer, 2005). In this module, three aspects of the fire triangle are considered:  
 406 the availability of fuel to burn, the flammability of vegetation, and the presence of an ignition source.  
 407 Each is represented daily by an independently calculated probability, and the product of the three is the  
 408 probability of fire occurrence, calculated daily. Availability of fuel to burn depends on biomass,  
 409 flammability depends on soil moisture, and ignition depends on a random lightning occurrence and a  
 410 constant anthropogenic ignition probability. The daily fire occurrence probability is equal to the daily  
 411 AGB burned fraction. The AGB burned fraction is accumulated throughout the year, and its ratio is  
 412 applied at the end of each year to the grid cell area, reducing the leaf, wood and root biomass pools.  
 413 After fire occurrence, the carbon allocation and mortality rates are not modified, and the recovery of

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431 [vegetation dynamics from a fire follows the model standard procedure, where](#) upper and lower LAI are  
432 decreased, [triggering competition between both canopies for light](#),

**Excluído:** In INLAND, the fire disturbance reduces the biomass of all pools and PFT's by the same fraction inside each pixel at the end of every year. Thus,

## 433 [2.3.Observed data](#)

### 434 **2.3.1 Phosphorus databases**

435 We used two P databases to estimate  $V_{max}$  ([Eq. \(1\)](#)): one regional (referred to as PR) and one  
436 global (referred to as PG). In addition, a control P map (PC) represents the unlimited nutrient  
437 availability case, equivalent to a  $V_{max}$  of  $65 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , or  $350 \text{ mg P kg}^{-1}$  soil, according to [Eq.](#)  
438 [\(1\)](#).

**Excluído:** , according to the fire probability,

**Excluído:** , and increasing the photosynthesis rates and stocks of carbon in leaves, stems and roots pools in the lower canopy. The carbon allocation and mortality rates in INLAND are fixed parameters for each PFT and are not modified after fire occurrence. Thus, during recovery from a fire, the vegetation dynamics follows the model standard procedure

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439 The PR database was developed [using data on](#) total P in the soil for the Amazon basin published  
440 by Quesada et al. (2011), plus 54 additional [samples measuring](#) available  $P_v$  (P extracted via Mehlich-1  
441 [extraction,  \$P\_{Mehlich-1}\$](#) ) ([Fig. 2a](#)). We used the [P<sub>Mehlich-1</sub> values](#) and clay contents measured in a forest-  
442 [savanna transition region in Brazil \(Mato Grosso state\)](#) to estimate  $P_{total}$  and expand the coverage area of  
443 the P data (Section S1). These 54 samples were gridded to a  $1^\circ \times 1^\circ$  grid to be compatible with the  
444 spatial resolution used by INLAND, resulting in 12 additional pixels with observed total P content ([Fig.](#)  
445 [2a](#)). For pixels without observed  $P_{total}$ , the  $P_{total}$  was assumed to be  $350 \text{ mg P kg}^{-1}$  soil, similar [to the PC](#)  
446 [conditions](#).

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447 A global data\_set of  $P_{total}$  ([PG; Fig. 2b](#)) was also used to estimate  $V_{max}$ . This global data set is  
448 part of a database containing six global maps of the different forms of P in the soil (Yang et al., 2013).  
449 [The uncertainties and limitations associated with this database are restricted to the Hedley fractionation](#)  
450 [data used, which are 17% for slightly weathered soils, 65% for soils at an intermediate stage of](#)  
451 [weathering and 68% for highly weathered soils \(Yang et al., 2013\)](#),

**Excluído:** The  $P_{total}$  was estimated from lithologic maps, distribution of soil development stages, fraction of the 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 (Ya[...]

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### 452 **2.3.2 Aboveground biomass (AGB) database**

453 The AGB database used was created by Nogueira et al. (2015) and considered undisturbed (pre-  
454 deforestation) vegetation existing in the Brazilian Amazon. This database was compiled from a

507 vegetation map at a scale of 1:250000 (IBGE, 1992) and AGB averages from 41 published studies that  
508 conducted direct sampling in either forest (2317 plots) or non-forest or contact zones (1830 plots). We  
509 bilinearly interpolated the AGB (dry weight) for each transect to a resolution of  $1^\circ \times 1^\circ$  to ensure  
510 compatibility of the observed and simulated data.

511 Five longitudinal transects (Fig. 1) were individually used to characterize AGB at the Amazon-  
512 Cerrado border (Figs. 3a, 3b). For T1, T2, T3 and T4, the higher AGB values in the west and lower  
513 values in the east are consistent with the transition from a dense and woody vegetation (the Amazon  
514 forest) towards a sparse vegetation with lower AGB (the Cerrado). However, T1 shows a more gradual  
515 reduction of AGB along the west to east gradient, while for T2, T3 and T4 the transition is more abrupt.  
516 For T5 there is no west-east gradient; AGB heterogeneity is high and low AGB predominates across the  
517 transect (Fig. 3b).

## 519 2.4 Simulations

520 The model was forced with prescribed climate data based on the Climate Research Unit (CRU)  
521 database (Harris et al., 2014). Two climate boundary conditions were used: the first is referred to as the  
522 monthly climatological average (CA) that represents the average climate for the period 1961-1990. The  
523 second climate boundary condition is the historical data set for the continuous period between 1948 and  
524 2008, which provides information on interannual climate variability (CV). For both boundary  
525 conditions, the variables used are rainfall, solar radiation, wind velocity and maximum and minimum  
526 temperatures. The CRU database is developed from observations at meteorological stations across the  
527 world's land areas; it has been widely used by the scientific community in case studies to evaluate El  
528 Niño-Southern Oscillation (ENSO) effects and other modes of interannual climate variability (Foley et  
529 al., 2002; Marengo, 2004; Wang et al., 2014), because these data preserve the spatial mean of rainfall

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555 data, although they do not provide adequate representation of precipitation variance (Beguiría et al.,  
556 2016). The data\_set has a 1-degree spatial resolution and a monthly time resolution.

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557 Soil texture data is based on the [International Geosphere-Biosphere Programme – Data and](#)  
558 [Information System](#) global [IGBP-DIS](#) (Hansen and Reed, 2000). In the CV group of runs, the model  
559 was spun-up by cycling the 1948–2008 climate data (a 61-year data set) seven times, totaling 427 years.

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560 In the CA group of runs, the annual mean climate data was cycled 427 times. In both cases, CO<sub>2</sub> varied  
561 from 278 to 380 ppmv, according to observations in the period, updated annually. In both cases, only  
562 the model results of the last 10 years were used to analyze the results.

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563 The experimental design is a factorial combination of (1) the two climate scenarios (CA,  
564 monthly climatological average, 1961–1990; CV, monthly climate time series, 1948–2008), (2) the  
565 three scenarios for P limitation on V<sub>max</sub> (PC, no P limitation (V<sub>max</sub> = 65 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>); PR, regional  
566 P limitation; PG, global P limitation), and (3) the scenarios including (F) or excluding fire (Table 1).

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567 The 12 combinations in Table 1 allow the evaluation of individual and combined effects of climate, soil  
568 chemistry, and fire incidence on the variables Net Primary Production (NPP), tree AGB, and LAI of the  
569 upper and lower canopies (LAI<sub>upper</sub>, LAI<sub>lower</sub>).

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570 We consider that the difference between the simulations (CV+PC) and (CA+PC) represents the  
571 isolated effect of interannual climate variability without P limitation. The same logic is applied to  
572 isolate other factors, fire and P limitation, in different climate scenarios. For example, the fire effect  
573 under average climate without P limitation case is calculated by the difference between CA+PC+F and  
574 CA+PC. Similarly, the isolated effect of fire under a climate scenario with interannual variability  
575 without influence of P limitation is calculated by the difference between CV+PC+F and CV+PC. The  
576 different combinations of climate scenarios with and without fire effects and with and without P  
577 limitations are described in Table 2.

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605 **2.5 Statistical analysis and determination of the best model configuration**

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

610 Second, we present an analysis of variance using one-way ANOVA and the Tukey-Kramer test  
611 in the transition zone. We consider all 31 pixels that fall in transects T1 to T5 ( $n_{\text{pixels}}$ ). The results  
612 presented are based on the last 10 years of simulation (1999-2008,  $n_{\text{years}}$ ) for the 12 combinations  
613 ( $n_{\text{simulation}}$ ) in Table 1. We group the 12 treatments in three different ways in order to assess separately  
614 the effects of climate, P limitation, and fire. In Group 1 we group treatments according to climate  
615 treatment and compare results for all simulations that used CV versus those that used CA, regardless of  
616 P limitation or inclusion of fire (Group 1,  $n = 1860$ , ( $n_{\text{pixel}} \times n_{\text{year}} \times (n_{\text{simulation}}/2)$ ). Similarly, in Group 2  
617 to look at P limitation, we test if the PC, PR and PG scenarios differed significantly regardless of the  
618 fire or climate scenario used (Group 2,  $n = 1240$ , ( $n_{\text{pixel}} \times n_{\text{year}} \times (n_{\text{simulation}}/3)$ ). In Group 3 we test if fire  
619 introduced a significant effect regardless of climate and P limitation scenario (Group 3,  $n = 1860$ , ( $n_{\text{pixel}}$   
620  $\times n_{\text{year}} \times (n_{\text{simulation}}/2)$ ). Finally, all treatments are tested for each simulation in order to assess the  
621 individual and combined effects of climate, P limitation, and fire on NPP, LAI and AGB ( $n_{\text{pixel}} \times n_{\text{year}} =$   
622 310).

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

626 Finally, we evaluate INLAND's ability to assign the dominant vegetation type by analyzing 10  
627 years of probability of occurrence. If the dominant vegetation type (evergreen tropical forest or  
628 deciduous forest for the Amazon rainforest, and savanna or grasslands for Cerrado) in a pixel is the  
629 same in more than 90% of the simulated years (9 out of 10), then the simulated vegetation type is

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682 defined as “very robust” for that pixel; if it occurs in 70 - 90% of the simulated years, the simulated  
683 result is considered to be “robust”. If the dominant vegetation occurred in less than 70% of simulated  
684 years, the pixel is considered “transitional” vegetation.

### 685 3 Results

#### 686 3.1 Influence of climate, fire and phosphorus on the Amazon-Cerrado transition region

##### 687 3.1.1 Spatial patterns

688 Overall, the inclusion of interannual climate variability (CV) decreased the simulated average  
689 tree biomass (TB) by 3.8% for the entire Brazilian Amazon, and by 8.7% for the entire Cerrado in  
690 comparison to results obtained using average climate (CA), calculated as  $(CV+PC) - (CA+PC)$  (Fig.  
691 4a). The spatial differences between CV and CA for TB simulations are statistically significant and  
692 range from  $-3 \text{ kg C m}^{-2}$  to  $+2 \text{ kg C m}^{-2}$ . The state of Pará, with higher influence of the El Niño  
693 phenomenon, experienced the largest decrease in TB in the CV simulation. In the state of Roraima, on  
694 the other hand, there was an increase of about  $2 \text{ kg C m}^{-2}$  in TB when CV was considered. Bolivia and  
695 southwestern Mato Grosso state also presented, in some grid points, a significant increase in TB,  
696 exceeding  $2 \text{ kg C m}^{-2}$ .

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

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735 The tree biomass reduction due to fire events is much higher in magnitude than the effect of P  
 736 limitation or interannual climate variability (Fig. 4d). The small or null fire effect in the central Amazon  
 737 rainforest is mainly related to that region's greater water availability, which makes the forest naturally  
 738 fire resistant. Moving into the Cerrado region, on the other hand, a gradient towards seasonally dryer  
 739 climate increases the intensity and magnitude of fire effects (Fig. 4d). The fire effect on TB over the  
 740 Amazon domain was 21% to 24% of the P limitation effect (range for PR and PG cases), while the fire  
 741 effect on TB over the Cerrado was more than 250% of the P limitation effects in CV simulations, due to  
 742 quick growth of grasses after fire occurrence in the latter.

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743 **3.1.2 Influence of climate, fire and phosphorus in the transects**

744 Results of the ANOVA and Tukey-Kramer tests indicate that the inclusion of CV, P limitation  
 745 (PR and PG) and fire in INLAND led to significantly different results for average NPP, LAI and AGB  
 746 in the transition zones. The influences of climate, P and fire are shown separately in Tables 3 to Table 5  
 747 and combined in Table 6.

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748 The inclusion of 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  
 749 the P-limitation effect reduces NPP 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> (for both PR and PG)  
 750 (Table 4). The fire effect, on the other hand, has a positive effect on NPP, increasing it from  
 751 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  
 752 statistically significant (Table 5).

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753 In addition, both CV and P limitation reduce the LAI<sub>total</sub> in the canopy (Table 3 and Table 4),  
 754 while the inclusion of fire increases LAI<sub>lower</sub> more than threefold and decreases LAI<sub>upper</sub> (Table 5). The  
 755 effect of including fire on AGB (a 46.7% decrease, Table 5) is greater in magnitude than the effect of  
 756 including CV (a 5% decrease, Table 3) or P limitation (a 14% decrease, Table 4).

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757 Although CV effects on NPP and AGB for each simulation are not statistically significant, the  
 758 effects of fire and P limitation (regardless of phosphorus map) are. Fire effects are significant only for  
 759 structural variables: AGB, LAI<sub>total</sub>, LAI<sub>upper</sub> and LAI<sub>lower</sub>. Simulations showed that LAI<sub>total</sub> was

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826 1.52 m<sup>2</sup> m<sup>-2</sup> greater for CV+PG+F as compared to CV+PG, and 1.32 m<sup>2</sup> m<sup>-2</sup> greater for CV+PR+F as  
827 compared to CV+PR (Table 6).

### 828 3.1.3 West-East patterns of AGB in the Amazon-Cerrado transition

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

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

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

848 In T2, T3 and T4, however, fire changes the simulated AGB, making it closer to the observed  
849 AGB in the eastern pixels of the Cerrado domain (Fig. 5). In T5 these relationships are similar, with  
850 climate having a smaller influence than P on AGB; fire appears mainly to reduce AGB.

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879 **3.2 Simulated vegetation composition,**

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

885 The vegetation composition in all P-limitation scenarios for CA simulations resulted in robust  
886 simulations for nearly all pixels, except for the northern Cerrado domain (Figs. 6a, 6b, 6c). The CA+PC  
887 and CA+PR simulations had the same vegetation composition, while CA+PG replaced the deciduous  
888 forest with evergreen forest in the central Cerrado region, around 8° S, 46° W (Figs. 6A, 6B, 6C). This  
889 behavior might be related to the higher  $P_{total}$  values in PG than PR and PC for the Cerrado region (Fig.  
890 S1). Cerrado was better represented in CV+PC, CV+PR and CV+PG than in the same CA combinations  
891 (Fig. 6). The occurrence of forested areas in the central Cerrado decreased in CV treatments, where it  
892 was replaced by the savanna or grassland vegetation class.

893 When the effect of fire was added to CA simulations, the model simulated an increase in the  
894 uncertainty of the vegetation cover classification in the Cerrado region. Fire in the CA+PC+F  
895 simulation reduced the deciduous forest in the central Cerrado biome, and the vegetation was replaced  
896 by evergreen forest in about five pixels that have clay soils with large water retention capacity (Figs.  
897 6G, 6H, 6I). In this situation, where there is little water stress, both evergreen and drought-deciduous  
898 PFTs have a very high LAI. Fire, although active, is probably too small to be relevant in a non-stressed  
899 ecosystem. In CV simulations, however, fire results in the replacement of the deciduous and perennial  
900 forest by savanna and grasses in the entire central Cerrado region (Figs. 6J, 6K, 6L). These results show  
901 the limitations of CA and the importance of considering interannual climate variability in simulations to  
902 improve the accuracy of simulated vegetation as compared to observed.

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966 For all treatments, transitional forest areas in the northern and southwestern Cerrado biome are  
967 not adequately represented. With >90% of concordance, INLAND assigns tropical evergreen forest  
968 rather than deciduous forest in some pixels in the north of the transition area, and tropical evergreen  
969 forest rather than savanna in the southwest, indicating difficulty in simulating transitional vegetation in  
970 these regions.

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#### 971 4 Discussion

972 The inclusion of CV, PR and PG and fire in INLAND revealed significant influences on the  
973 simulated vegetation structure and dynamics of the Amazon-Cerrado border (Fig. 4 and Table 6),  
974 suggesting that these factors play a key role in determining vegetation structure of the forest-savanna  
975 border and can improve the simulated representation of the current contact zone between these biomes.  
976 This is broadly consistent with the literature that investigated causes of savanna existence in the real  
977 world (Hoffmann et al., 2012; Dantas et al., 2013; Lehmann et al., 2014). In this study, the spatial  
978 analysis and the Tukey-Kramer test (TK) show a difference in magnitude among these factors in  
979 vegetation, with fire occurrence and P limitation being stronger than interannual climate variability  
980 along the transects (Fig. 4).

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981 The spatial analysis showed that CV reduces AGB especially in eastern Amazonia (Fig. 4a).  
982 Climate of this region is intensely affected by ENSO, which can reduce precipitation by 50%, placing  
983 the vegetation under intense water stress (Botta and Foley, 2002; Foley et al. 2002; Marengo et al.,  
984 2004; Andreoli et al., 2012; Hilker et al., 2014). This reduction in rainfall in dry years induces direct  
985 changes in carbon flux (NPP) and stocks in leaves and wood, leading to changes in vegetation structure.

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986 In addition to interannual changes in rainfall, interannual variability in other climate variables in CV  
987 also affects AGB (namely, average, maximum and minimum temperatures, wind speed, and specific  
988 humidity), and influences photosynthesis in the model, both directly (through Collatz and Farquhar  
989 equations) and indirectly (e.g. through evapotranspiration). Our results showed significant differences  
990 for most parts of the biomes, except central Amazonia (Fig. 4a), where CV and precipitation seasonality

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1018 have been noted as secondary effects on vegetation (Restrepo-Coupe et al., 2013), since there is no  
 1019 shortage of water available during the dry season.  
 1020 Across the Cerrado, lower water availability in some years in CV affects tree biomass, despite  
 1021 the fact the vegetation is predominantly grassy herbaceous. The AGB decline is significant for most of  
 1022 the simulated Cerrado domain (Fig. 4a), and average values could represent half the amount of typical  
 1023 tree biomass in this biome, reflecting INLAND's ability to simulate similar Cerrado conditions and  
 1024 expose the few trees to high water stress.  
 1025 However, no significant difference in average AGB was found throughout the transects between  
 1026 CV+PC and CA+PC (TK,  $p < 0.05$ ) (Table 6). On the other hand, when we analyzed the influence of  
 1027 CV for the same pixels across all simulations (Table 3), the results showed that the decrease in AGB by  
 1028  $0.38 \text{ kg C m}^{-2}$  (5.7%) is statistically significant along the transition, regardless of P limitation and fire  
 1029 occurrence.  
 1030 The P limitation effect was statistically significant for PR and PG throughout the Amazon  
 1031 domain, and the main differences between these simulations were the spatial patterns of reduced tree  
 1032 AGB, (Figs. 4b and 4c). We cannot affirm which of these databases is better, since they were derived  
 1033 using different methodologies and observations (Quesada et al., 2009; Yang et al., 2014). However, PG  
 1034 showed a higher AGB decrease in central Amazonia, northeastern Pará and northeastern Mato Grosso  
 1035 state, indicating that in these areas the P limitation is higher. This result does not corroborate the  
 1036 northwest southeast AGB gradient found in the Amazon basin, where studies have shown, higher  
 1037 productivity in the west, where soils are more fertile than those found in the southeast (Aragão et al.,  
 1038 2009; Saatchi et al., 2007; Nunes et al., 2012; Lee et al., 2013). On the other hand, PR AGB agrees with  
 1039 the northwest southeast gradient, suggesting less P limitation in the soils of central Amazonia, with  
 1040 declines in AGB mainly in the southeastern part of the rainforest (between Pará and northeastern Mato  
 1041 Grosso states) (Fig. 4b).

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1081 In the Cerrado, P limitation also influenced vegetation (Fig. 4c) and presented statistically  
1082 significant differences when we compared CV+PG  $\rightarrow$  CV+PC. In this biome, as well as in the Amazon,  
1083 tree abundance, richness and diversity have been generally associated with higher soil fertility (Long et  
1084 al., 2012; Vourtilis et al., 2013), highlighting the importance of P in the composition and maintenance  
1085 of vegetation, especially in transition areas.

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1086 Compared to the Amazon domain, the effects of P limitation are smaller in the Cerrado.  
1087 However, few pixels in PR that have P limitation showed a significant decrease in arboreal AGB (Fig.  
1088 4b). In PG, we found reduction of AGB for most of the Cerrado domain, except for the southern part of  
1089 Tocantins state (Fig. 4c). Despite the differences in spatial patterns, there were no statistically  
1090 significant differences between PR and PG within the transects (Table 4 and Table 6).

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1091 The spatial differences between PG and PR revealed that PG is lower than PR in western  
1092 Amazonia and higher in northern Amazonia. Moreover, PG has lower P values in the southern part of  
1093 the transition compared to PR, while in the Cerrado domain P values ranged from 120 to 200 mg kg<sup>-1</sup>  
1094 (Fig. S1). Although the PR data set includes all known P data collected in the region, these differences  
1095 reinforce the need to improve the data on P<sub>total</sub> for the soils of the Amazon and the Amazon-Cerrado  
1096 transition domains. Currently, P<sub>total</sub> data for the Cerrado is scarce, making it unfeasible to establish a  
1097 proxy similar to Castanho et al. (2013), which was specific for the Amazon.

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1098 In INLAND, the inclusion of P limitation, parameterized simply through the linear relationship  
1099 between V<sub>max</sub> and P<sub>total</sub>, showed significant spatial differences in simulated AGB and an improvement in  
1100 simulation accuracy, highlighting the importance of P limitation in modeling studies. For the most part,  
1101 Dynamic Global Vegetation Models (DGVMs) do not consider the complete phosphorus cycle (see  
1102 exceptions in Goll et al., 2012 and Yang et al., 2014), despite the importance of nutrient cycling for  
1103 AGB maintenance and tropical vegetation dynamics in dystrophic soils. For example, nutrient cycling  
1104 in the Amazon-Cerrado transition region is closely related to the hyper-dynamic turnover of AGB  
1105 (Valadão et al. 2016). Vegetation sustains the constant input of nutrients, including large annual

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1143 amounts of available P, and in fact some key species might be crucial to the hyper-cycling of nutrients  
1144 (Oliveira et al. 2017). In addition, weather can affect nutrient fluxes; intense rain can leach nutrients,  
1145 such as nitrogen, and strong winds can transport clay particles on which nutrients are adsorbed.  
1146 However, in this work nutrient conditions are prescribed and fixed.

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1147 Fire occurrence is another important factor that controls s AGB dynamics in the Cerrado and in  
1148 transitional vegetation (Hoffman et al., 2003; Hoffman et al., 2012; Silvério et al., 2013; Couto-Santos  
1149 et al., 2014; Balch et al., 2015). This study clearly corroborates these findings, showing statistically  
1150 significant influences of fire when compared to control simulations (Fig. 4d and Table 5). In the  
1151 transition region, the fire effect may reduce average AGB by 50% (Table 5), which under climate  
1152 change or deforestation conditions may lead to an even stronger change in the vegetation structure and

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1153 dynamics. As stated in section 2.2, fire in INLAND acts on upper- and lower-canopy LAI according to  
1154 fire occurrence, triggering competition. The changes in canopy structure after fire occurrence are  
1155 exclusively due to the canopy opening and consequently allowing more penetration of photosynthetic  
1156 radiation into the lower canopy. This competition induces a significant increase of the lower canopy,  
1157 resulting in increased LAI<sub>lower</sub> (Table 5).

**Excluído:** In INLAND, the fire disturbance reduces the biomass of all pools and PFT's by the same fraction inside each pixel at the end of every year. Thus, upper and lower LAI are decreased, according to the fire probability, 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 and mortality rates in INLAND are fixed parameters for each PFT and are not modified after fire occurrence. Thus, during recovery from a fire, the vegetation dynamics follows the model standard procedure. ¶

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1158 The model does not include fire characteristics such as velocity, intensity and duration of  
1159 burning (Hoffman et al., 2003; Rezende et al., 2005; Elias et al., 2013; Reis et al., 2015) or the  
1160 representation of some tree morphological adaptations, such as bark thickness, that confer fire resilience,  
1161 to Cerrado species. Thus, trees and grasses throughout the Amazon-Cerrado border area are equally  
1162 affected by occurrence of fire within a grid cell. However, despite these limitations in the representation  
1163 of fire characteristics and morphological attributes of fire resistance, our results show that simulated  
1164 biomass is closer to observed biomass in Cerrado areas when the fire module is activated (Fig. 5). An  
1165 improvement in distribution of biomes along the simulated transition area is also observed (Fig. 6g-i),  
1166 highlighting fire as an essential factor in representing the Amazon-Cerrado border.

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1264 This study shows better correlation between simulated and observed AGB when compared to  
 1265 previous modeling studies, regardless of treatment. The correlation coefficients are generally above 0.80  
 1266 for the transects, except for T5, for which the correlation coefficient is generally below 0.5 (Table 7).  
 1267 Senna et al. (2009) found a maximum correlation coefficient between simulated and observed ABG of  
 1268 0.20, while Castanho et al. (2013) showed a correlation coefficient of 0.80 for the Amazon domain.  
 1269 From Fig. 5, it is clear that CV, F and P limitation in the transition zone reduce AGB, causing the  
 1270 simulated data to approach the observed data. However, the inclusion of these effects is still insufficient  
 1271 to represent the correct distribution of vegetation types throughout the Amazon-Cerrado border region  
 1272 (Fig. 6L). In our interpretation, this means that other important factors still need to be represented,  
 1273 especially in T5, where soils are rocky and shallow. Better spatial representation of soil physical  
 1274 properties (including shallow, rocky soils), as well as spatially varying physiological parameterizations  
 1275 of the vegetation (such as carbon allocation, deciduousness of vegetation and residence time), and  
 1276 improved representation of fire and vegetation fire resistance are probably needed to improve the  
 1277 accuracy of simulations, in particular in the northern and southern extremes of the border region (T1  
 1278 and T5).

1279 For all transects, the AGB curves have similar patterns (Fig. 5); smaller differences are observed  
 1280 between the CA+PC and CV+PG curves, while larger differences are observed when fire is present. The  
 1281 effect of P limitation is intermediate in magnitude, but it reduces AGB more than including interannual  
 1282 climate variability does. In the east, it is observed that there is little or no difference among AGB  
 1283 simulated with CA+PC, CV+PC and CV+PG, revealing that interannual climate variability and P have a  
 1284 smaller influence on the AGB there. In the east of T2, T3 and T4, fire is the factor that brings the  
 1285 simulated results closest to the observed data (Fig. 5); this differs from the results for the western grid  
 1286 points, where CV+PG appears to be a better proxy for observed data.

1287 These results are interesting because they reflect the different mechanisms that regulate the  
 1288 structure of these ecosystems and probably the vegetation structure and distribution in different

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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  $K_s = 1.5 \cdot 10^{-4} \text{ m} \cdot \text{s}^{-1}$  ( $540 \text{ mm} \cdot \text{h}^{-1}$ ) in reality into an impervious brick with  $K_s = 3.3 \cdot 10^{-7} \text{ m} \cdot \text{s}^{-1}$  ( $1.2 \text{ mm} \cdot \text{h}^{-1}$ ) in the model.
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1384 locations. For example, P limitation seems to be the factor that improves simulated AGB in regions  
1385 where the predominant vegetation type is tropical rainforest. Fire, on the other hand, improves the  
1386 representation of AGB in grid points where Cerrado vegetation occurs. Moreover, important factors  
1387 such as partitioning productivity into leaves, roots and wood carbon pools are assumed to be fixed in  
1388 space and time within a given PFT, neglecting the natural capacity of transitional forests to adapt and to  
1389 adjust their metabolisms to local environmental conditions (Senna et al., 2009). In years of severe  
1390 drought, or under frequent fire occurrence, transitional forests can prioritize the stock of carbon in fine  
1391 roots instead of the basal or leaf increment in order to maximize access to water, undergo hydraulic  
1392 redistribution of soil moisture to maintain greenness and photosynthesis rates, or increase the capacity  
1393 to resprout after fire occurrence (Hoffman et al., 2003; Brando et al., 2008). Brando et al. (2008) found  
1394 changes in carbon allocation after an artificial drought in eastern Amazonia, with wood production  
1395 reduced 13%–60%, and an associated increase in root production. Although in INLAND low soil  
1396 moisture can reduce photosynthetic rates, carbon allocation rates are fixed (Fig. 5a),  
1397 T2, T3 and T4, located in the central part of the Amazon–Cerrado transition, showed the highest  
1398 average correlations between observed and simulated data (Table 7). For these transects, INLAND  
1399 seems to be able to capture the high variability of the AGB gradient.  
1400 At T5, located at the south of the transition area, average correlations were low for all  
1401 treatments, indicating that INLAND has difficulty representing the AGB gradient in that region (Table  
1402 7). However, it captures the lower AGB as compared to the northern areas. In this region, the vegetation  
1403 is characterized by a wide diversity of characteristics, which vary along with other important factors,  
1404 such as lithology, soil depth, topography and soil fertility. The observed data also showed high AGB  
1405 variability, indicating that there are changes in the vegetation structure for this area, featuring medium-  
1406 sized and small vegetation types on different soil types. In INLAND, however, features such as  
1407 lithology and water-table depth are not considered due to the complexity of representing them on a large

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1435 scale: this limits the model's ability to represent heterogeneous environments throughout the transitional  
1436 region.

1437 Patterns of vegetation distribution along the Amazon-Cerrado border are influenced not only by  
1438 interannual climate variability, P limitation, and fire, but also by ecophysiological parameters.  
1439 Additional field experiments are needed to understand relationships among currently fixed parameters  
1440 (such as carbon allocation, residence time, and deciduousness), environmental conditions and soil  
1441 properties.

## 1443 5 Conclusions

1444 This is the first study that uses modeling to assess the influence of interannual climate  
1445 variability, fire occurrence and phosphorus limitation to represent the Amazon-Cerrado border. This  
1446 study shows that, although the model forced by a climatological database is able to simulate basic  
1447 characteristics of the Amazon-Cerrado transition, the addition of factors such as interannual climate  
1448 variability, phosphorus limitation and fire improves simulation of vegetation types. These effects are not  
1449 homogeneous throughout the region, which makes the adequate simulation of biomass challenging in  
1450 some places. Based on the F-statistic reported in Tables 3, 4 and 5, fire is the main factor determining  
1451 changes in vegetation structure (LAI, AGB) along the transition. Phosphorus limitation is second in  
1452 magnitude, stronger than the effect of interannual climate variability.

1453 Overall, although INLAND typically simulates more than 80% of the variability of biomass in  
1454 the transition zone, in many places the biomass is clearly not well simulated. Situations for markedly  
1455 wet or dry climate conditions were well simulated, but the simulations are generally poor for  
1456 transitional areas where the environment selected physiognomies that have an intermediate behavior, as  
1457 is the case for transitional forests in northern Tocantins and Mato Grosso.

1458 There is evidence that the inclusion of spatially explicit parameters such as woody biomass  
1459 residence time, maximum carboxylation capacity ( $V_{max}$ ), and NPP allocation to wood may improve

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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 months with little or no rain) exposes the vegetation to a severely ...
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1524 Amazon rainforest AGB simulation by DGVMs (Castanho et al., 2013). However, in the transition~~al~~  
1525 ~~area~~, the lack of ~~measured field parameters~~ limits ~~inclusion~~ of the variability of these biophysical  
1526 parameters in DGVMs. Additional field work and compilation of existing ~~data~~ are necessary to obtain  
1527 physiological and structural parameters throughout the ~~Amazon-Cerrado~~ border ~~area~~ to establish  
1528 numerical relationships between soil, climate and vegetation. With the help of these data, dynamic  
1529 vegetation models will be able to improve simulation of current patterns and future changes in  
1530 vegetation considering climate change scenarios. In addition, it is ~~necessary~~ to include not only ~~spatial~~  
1531 variability, but also temporal variability in physiological parameters of vegetation, allowing ~~more~~  
1532 realistic simulation of ~~soil-climate-vegetation relationships~~. Finally, our results reinforce the ~~need for~~  
1533 DGVMs to incorporate ~~nutrient limitation and fire occurrence~~ ~~for simulating~~ the ~~Amazon-Cerrado~~  
1534 border position.

## 1536 6 Acknowledgements

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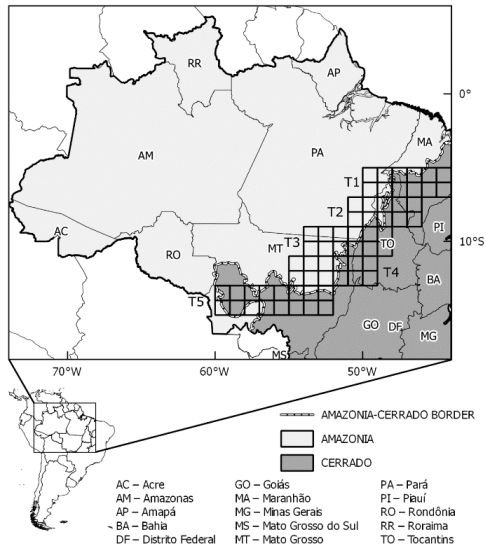
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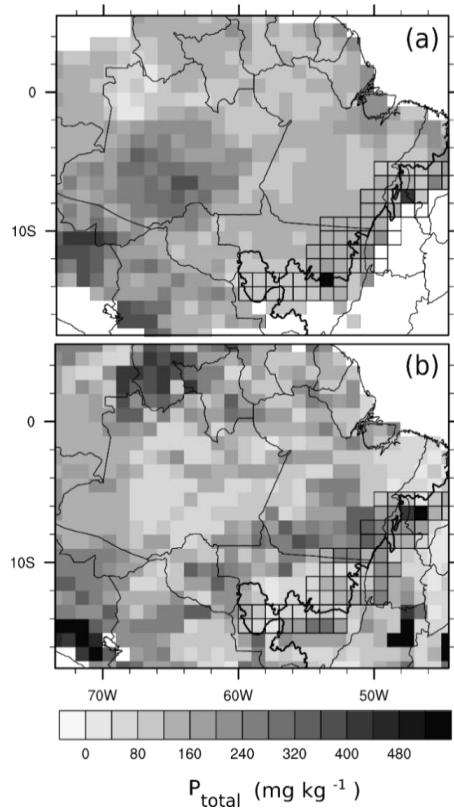
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1837 **Figure 1.** Delimitation of the study area, showing Amazonia (in light gray) and the Cerrado (in dark  
 1838 gray) (IBGE, 2004), and the location of five west-east transects used in this work (from T1 to T5). The  
 1839 dashed line represents the border between biomes.

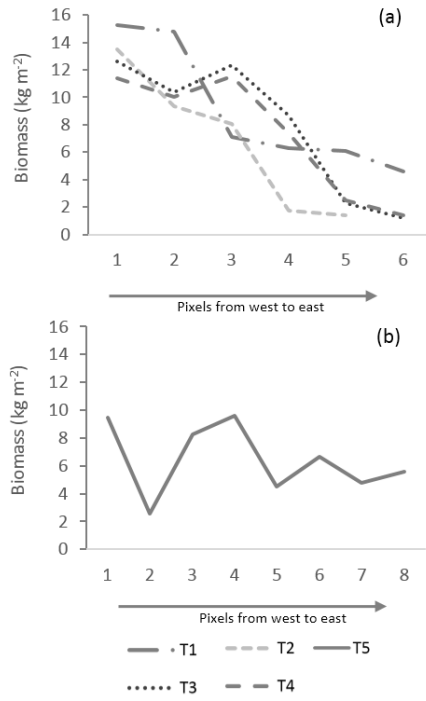


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1841 **Figure 2.** (a) Regional map of total P in the soil (PR), (b) Global map of total P in the soil (Yang et al.,  
 1842 2013) (PG).

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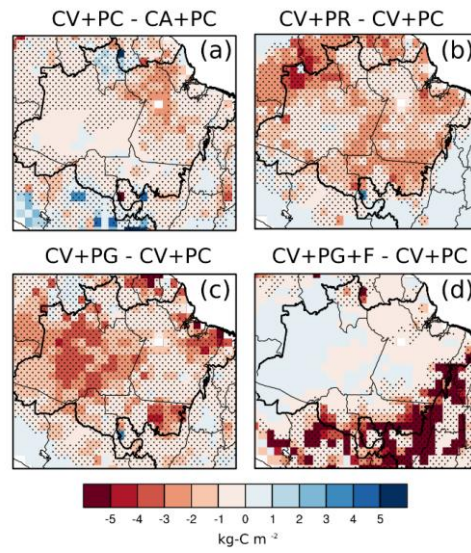
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**Figure 3.** Average variations of aboveground biomass (AGB) in pixels from west to east in the Amazon-Cerrado transition for transects (a) T1, T2, T3 and T4, and (b) T5.

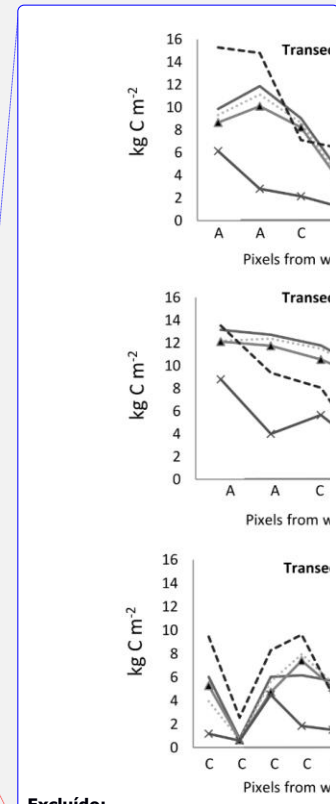
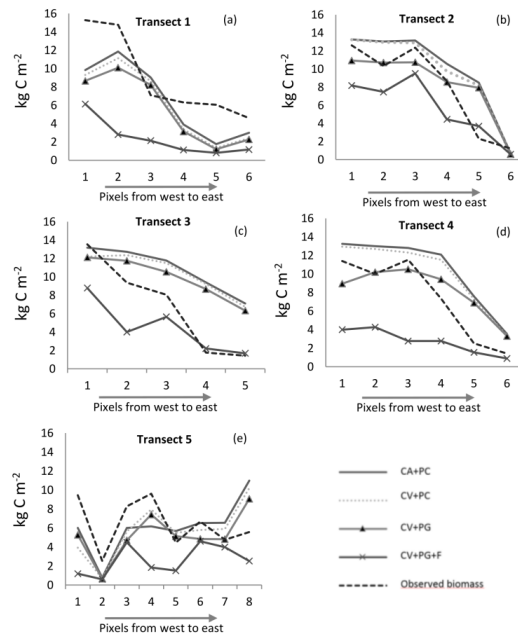
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1858 **Figure 4.** Effects of interannual climate variability (a), regional P limitation (b), global P limitation (c),  
 1859 and fire (d) on AGB. The hatched areas indicate that the variables are significantly different compared  
 1860 to the control simulation at the level of 95% according to the *t*-test. The thick black line indicates the  
 1861 geographical limits of the biomes.

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**Figure 5.** Average longitudinal AGB gradient in the Amazon-Cerrado transition simulated for T1 to T5 (a-e) considering different combinations of factors represented in the simulations: seasonal climate simulation (control) (CA+PC); interannual climate variability simulation (CV+PC); interannual climate variability + global P limitation simulation (CV+PG); and interannual climate variability + P limitation + fire occurrence simulation (CV+PG+F). Observed AGB is also shown for comparison with simulation results.

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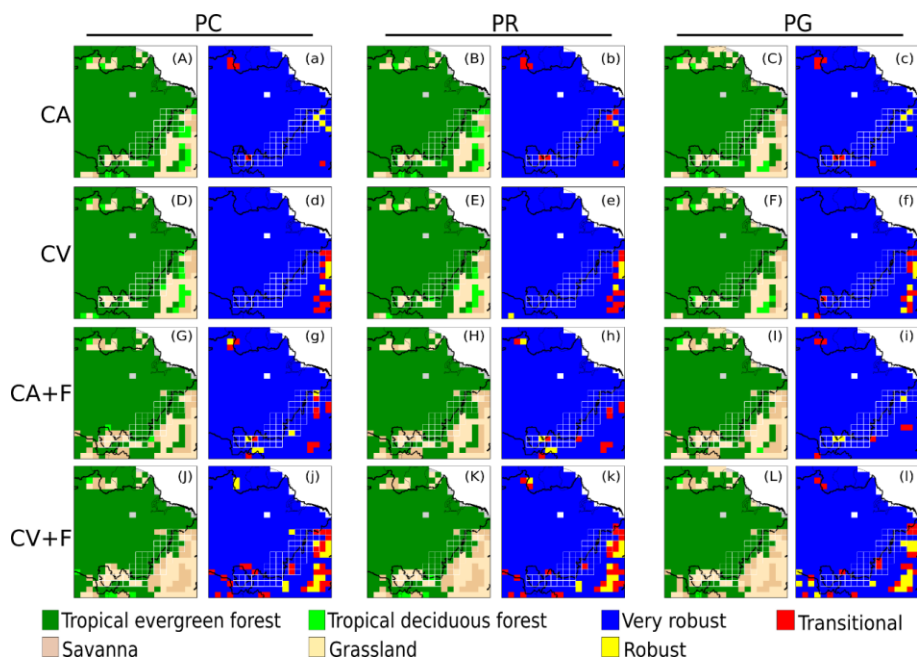
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**Figure 6.** Results for the dominant vegetation cover simulated by INLAND for the different treatments

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(A–L) and a metric of variability of results (a–l). Simulations are considered very robust if the dominant

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vegetation agrees in 9–10 of the last 10 years of simulation, robust if it agrees in 7–8 years, and

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transitional if it agrees in 6 or fewer years.

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**Table 1.** Twelve simulation treatments evaluated by the INLAND model for the Amazon-Cerrado transition zone. CA, monthly climatological average, 1961-1990; CV, monthly climate data, 1948-2008; Nutrient limitation on  $V_{max}$ ; PC, no P limitation ( $V_{max} = 65 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ); PR, regional P limitation; PG, global P limitation.

Climate	CO <sub>2</sub>	Fire (F)	V <sub>max</sub>		
			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

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**Table 2.** Individual and combined effects for each simulation treatment for the Amazon-Cerrado transition zone. CA, monthly climatological average, 1961-1990. CV, monthly climate data, 1948-2008. Nutrient limitation on V<sub>max</sub>; PC, no P limitation (V<sub>max</sub> = 65 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>); PR, regional P limitation; PG, global P limitation.

<b>Climate (C)</b>	<b>Phosphorus (P)</b>	<b>Fire (F)</b>
(CV+PC) <u>-</u> <u>-</u> (CA+PC)	(CA+PR) <u>-</u> <u>-</u> (CA+PC)	(CA+PC+F) <u>-</u> <u>-</u> (CA+PC)
(CV+PR) <u>-</u> <u>-</u> (CA+PR)	(CV+PR) <u>-</u> <u>-</u> (CV+PC)	(CV+PC+F) <u>-</u> <u>-</u> (CV+PC)
(CV+PG) <u>-</u> <u>-</u> (CA+PG)	(CA+PG) <u>-</u> <u>-</u> (CA+PC)	(CA+PR+F) <u>-</u> <u>-</u> (CA+PR)
	(CV+PG) <u>-</u> <u>-</u> (CV+PC)	(CV+PR+F) <u>-</u> <u>-</u> (CV+PR)
		(CA+PG+F) <u>-</u> <u>-</u> (CA+PG)
		(CV+PG+F) <u>-</u> <u>-</u> (CV+PG)

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1931 **Table 3.** Summary of average NPP, LAI and AGB for the Amazon-Cerrado transition zone over the  
 1932 transect domains, considering all simulations with CA and CV, regardless of fire presence or P  
 1933 limitation. One-way ANOVA results are also shown, including *F* statistics, and *p* values. Values within  
 1934 each column followed by a different letter differ significantly ( $p < 0.05$ ) according to the Tukey-  
 1935 Kramer test ( $n = 1860$ : 31 pixels  $\times$  10 years  $\times$   $n_{\text{simulation}}/2$ ).

Group	NPP	LAI <sub>total</sub>		LAI <sub>lower</sub>		LAI <sub>upper</sub>		AGB		
1	$\frac{\text{kg}}{\text{C m}^2 \cdot \text{y}}$	$\text{m}^2 \text{ m}^{-2}$		$\text{m}^2 \text{ m}^{-2}$		$\text{m}^2 \text{ m}^{-2}$		$\frac{\text{kg}}{\text{C m}^2}$		
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
<i>F</i> <sub>3,84</sub>	40.2		57.2		2.96		36.0		11.3	
<i>p</i>	<0.001		<0.001		ns		<0.01		<0.001	

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**Table 4.** Summary of average NPP, LAI and AGB for the Amazon-Cerrado transition zone over the transect domains, considering all P limitation treatments, regardless of climate and fire presence. One-way ANOVA results are also shown, including F statistics, and p values. Values within each column followed by a different letter differ significantly ( $p < 0.05$ ) according to the Tukey-Kramer test ( $n = 1240$ : 31 pixels  $\times$  10 years  $\times$   $n_{\text{simulation}}/3$ ).

Group	NPP	LAI <sub>total</sub>		LAI <sub>low</sub>		LAI <sub>upper</sub>		AGB		
	$\frac{\text{kg}}{\text{C m}^2 \text{ y r}^{-1}}$	$\text{m}^2 \text{ m}^{-2}$		$\text{m}^2 \text{ m}^{-2}$		$\text{m}^2 \text{ m}^{-2}$		$\frac{\text{kg}}{\text{C m}^2}$		
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
$F_{2,9}$	62.8		61.0		8.75		53.5		33.6	
$p$	<0.001		<0.001		<0.01		<0.01		<0.001	

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**Table 5.** Summary of average NPP, LAI and AGB for the Amazon-Cerrado transition zone over the transect domains, considering presence or absence of fire. One-way ANOVA results are also shown, including F statistics, and p values. Values within each column followed by a different letter differ significantly ( $p < 0.05$ ) according to the Tukey-Kramer test ( $n = 1860$ : 31 pixels  $\times$  10 years  $\times$   $n_{\text{simulation}}/2$ ).

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 <sup>2</sup> m <sup>-2</sup>		m <sup>2</sup> m <sup>-2</sup>		m <sup>2</sup> m <sup>-2</sup>		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
<i>F<sub>3,84</sub></i>	8.28		937		1459		249		1719	
<i>p</i>	<0.005		<0.001		<0.01		<0.01		<0.001	

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**Table 7.** Correlation coefficients between AGB simulated by INLAND and field estimates ( $n = 310$ : 31 pixels  $\times$  10 years).

	T1	T2	T3	T4	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

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**Formatado:** Nenhum, Espaço Antes: 0 pt, Espaçamento entre linhas: simples, Não manter com o próximo, Não manter linhas juntas

**Formatado:** Espaçamento entre linhas: simples

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