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Key Points:

- Main drivers for changes in spatial heterogeneity of the Pan-Amazonian ecosystem states under climate change are decomposed
- Spatial heterogeneity of ecosystem state is suggested to increase over an extended ecosystem transition region
- Vegetation feedbacks amplify climate effects on such changes

Supporting Information:

Supporting Information may be found in the online version of this article.

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Vegetation-Climate Feedbacks Enhance Spatial Heterogeneity of Pan-Amazonian Ecosystem States Under Climate Change

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Abstract Amazonian ecosystems range from rainforest to open dryland vegetation, with a following decrease in biomass along the moisture gradient. Biomass can vary greatly at the ecological transition zone between grass dominated savannahs and the forest. It is not well understood if the transition zone could expand under climate change, and thereby reduce ecosystem stability and carbon storage in biomass. Here, we quantify such changes by using a high-resolution regional Earth system model under RCP 8.5 climate scenario. We disentangle the effects of climate, CO₂, and land use by considering vegetation-climate feedbacks. Our results suggest that future climate change combined with elevated atmospheric CO₂ concentration tends to induce a larger spatial gradient of ecosystem states, increasing the transition area by ~110% at the end of the century. Vegetation feedbacks generally amplify the climate effect by intensifying the climate-induced warming and drought, further enhancing spatial heterogeneity.

Plain Language Summary Deforestation and the changing climate are threatening the Amazonian ecosystems, making the fate of this vast biological carbon stock remain largely uncertain under future climate change. Previous studies suggest that the Amazon rainforest may lose a certain degree of capacity to recover under continuous warming and increasing drought. However, changes in rainforest could affect climate at local to regional scale, and in turn affect rainforest. Assessments of Amazonian ecosystem changes considering such vegetation feedbacks could therefore be more promising. Here, we assess the future changes in Pan-Amazonian ecosystem states by employing a fully coupled biosphere-atmosphere numerical model that can capture local and regional climate phenomena. By considering vegetation feedbacks, effects of the main drivers, including climate, elevated CO₂, and land use, can be more realistically quantified. Our results suggest that the Amazonian region will be at a higher risk of abrupt change in ecosystem composition and will have a larger area with unstable vegetation state under future climate change compared with the present-day climate. We point out that vegetation feedbacks, with a substantial contribution to the simulated changes in ecosystem transition, could be important to understand the capacity of ecosystems to recover and should gain necessary attention in regional climate change studies.

1. Introduction

The Amazonian rainforest is a complex dynamical system hosting one of the largest terrestrial carbon stocks in the Earth system (Pan et al., 2011), and has been experiencing rapid and extensive changes in the last decades (Baccini et al., 2017; Brando et al., 2014). Recent studies link these changes to changes in climate, land use, and atmospheric CO₂ concentrations (Fleischer et al., 2019; Huntingford et al., 2013; Malhi et al., 2008; Oyama & Nobre, 2003), giving essential implications to the long-term vegetation dynamics over the Amazonian regions (Ahlström et al., 2017; Betts et al., 2004; Cox et al., 2000). Emergent transition in ecosystem composition and structure usually follow a particular spatial pattern (Holling, 1973; Scheffer et al., 2009), which can serve as an early-warning indicator for ecological management (von Hardenberg et al., 2001; van Nes & Scheffer, 2005; Rietkerk et al., 2004). For the Amazonian ecosystems, the transition

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can be characterized between two distinct states: a stable high-biomass rainforest state in the wet Amazon basin and a stable low-biomass state characterized by savanna and open dryland. They are generally controlled by hydrological conditions with a transitional area in which both states can occur in proximity within a relatively sharp hydrological gradient (Ahlström et al., 2017; Hirota et al., 2011; Staver et al., 2011). The vulnerable balance between these two states in the transitional area usually self-organize through small-scale land-atmosphere interactions, and can be easily broken by local disturbances, such as fire (Brando et al., 2014; Staver et al., 2011) and land use (D’Almeida et al., 2007; Spracklen et al., 2018), which could tip ecosystems to either a high- or low-biomass state and result in a heterogeneously vegetated land surface.

The land-atmosphere interactions tend to be strong over semi-arid regions (Koster et al., 2004; Seneviratne et al., 2010) where changes in the vegetated land surface may lead to a deviated evolution of climate over time, resulting in multiple vegetation-climate equilibria (Claussen, 1998; Oyama & Nobre, 2003; Zeng & Neelin, 2000). Changes in regional climate further affect vegetation through local ecological processes, such as tree mortality induced by drought and fire (Allen et al., 2010; Brando et al., 2014) that in turn may extend the heterogeneous land surface. Nevertheless, the land-atmosphere interactions resolved by climate models are usually scale-dependent, in particular for those processes related to water exchanges (Kitoh et al., 2011; Prein et al., 2015, 2016; Wu et al., 2020). For example, on top of an expected stronger seasonality of precipitation under future climate change, the simulated future precipitation at higher horizontal resolution generally results in increase in extremes, characterized by a prolonged drought and an increase in extreme rainfall over the Amazonian heterogeneous regions, for example, the Cerrado (Kitoh et al., 2011). Hence, representation of land-atmosphere interaction without considering a proper scale in conventional Earth system models (ESMs) makes it a challenge to capture realistic ecosystem states over a vegetation-transition landscape, which, however, is critical to understand the fate of Amazonian ecosystems under future climate changes. Here, we further explore the questions: (1) will the spatial heterogeneity, which acts as one of the important characteristics of the overall Amazonian ecosystem dynamics, change under continued anthropogenic forcing? And (2) what is the role of land-atmosphere interaction in such changes when considering the drivers—climate, CO₂ concentration, and land use—that are expected to be the primary controls for future changes in Amazonian ecosystems?

2. Methods

2.1. Factorial Simulations With RCA-GUESS

To understand the underlying mechanisms for the possible future changes in spatial heterogeneity of Amazonian ecosystems, we conducted numerical simulations using a coupled vegetation-atmosphere regional Earth system model (RESM), RCA-GUESS, running at high-resolution (Smith et al., 2011). Four factorial simulations with switching on and off the drivers of interests were conducted to disentangle the potential long-term biophysical effects under future climate change. They are summarized in Table S1 with more details in Section 1 of Supporting Information (S1), and are briefly described here: (1) the *transient land use and land cover change (LULCC) simulation with vegetation feedbacks* (X_{LVC} , all effects) with transient LULCC forcing derived from the ‘harmonized’ RCP 8.5 global land-use scenario (Hurtt et al., 2011), in which vegetation feedbacks to climate were enabled. (2) The *LULCC-fixed simulation with vegetation feedbacks* (X_{0VC}), which was conducted with the same setup as the X_{LVC} simulation except that LULCC forcings were fixed to the year 2006 for the period 2006–2100. (3) The *LULCC-fixed simulation without vegetation feedbacks* (X_{00C}), which was conducted with the same setup as the X_{0VC} simulation except that vegetation feedbacks were not enabled. (4) To further isolate the atmospheric CO₂ effects on physiology, we performed the *LULCC-fixed offline simulation without elevated CO₂ forcing* (X_{000}) based on the experiment X_{00C} .

2.2. Factorial Effects

The factorial effects for future changes in the Pan-Amazonian regions are decomposed by utilizing the numerical simulations conducted in Section 2.1. The all effects including biogeophysical feedbacks are represented as the differences between the future and present-day simulated quantities in the X_{LVC} simulation, denoted as Δ_{all} (Equation 1). The disentangled climate change effect on vegetation (Δ_{CC} , Equation 2) is quantified as the differences between the future and the present-day quantities from X_{000} simulation. For

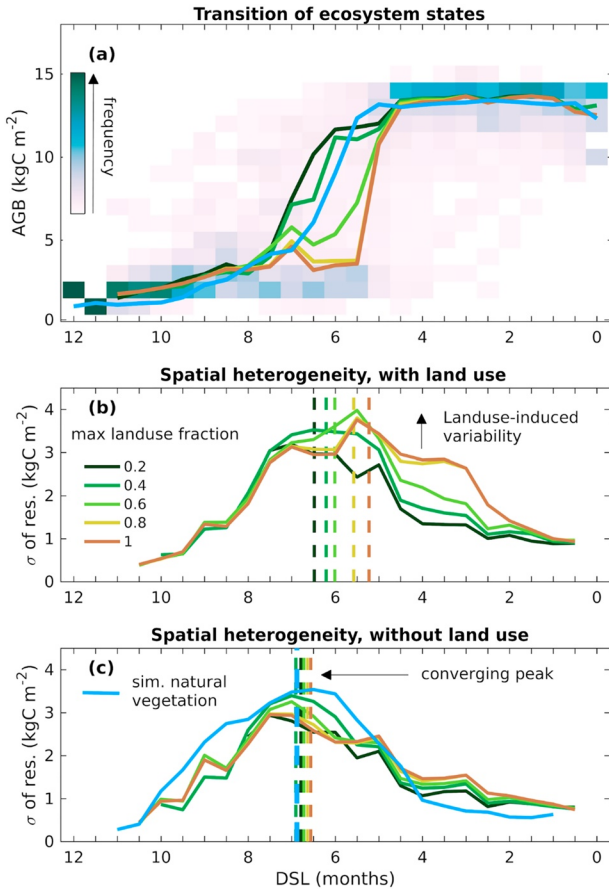


Figure 1. Observed and model-estimated transition between low and high above-ground biomass (AGB) states for the Pan-Amazonian ecosystem as a function of dry season length (DSL) during 1993–2012. (a) $AGB \sim f(DSL)$ functional relation, calculated from the mean of AGB over DSL bin for different levels of maximum land-use area (green to brown lines). Colored frequency fields describe the standardized frequency of grid points of each AGB and DSL bin to the total number of grid points within the corresponding DSL bin for all land classes. (b) Spatial heterogeneity along the DSL gradient, shown as the standard deviation (σ) of the AGB residuals (computed as the spatial variation of the mean values for 1993–2012) from the $AGB \sim f(DSL)$ relation. Residuals are derived from linear regression of AGB against DSL for each 0.5 months DSL bin. Vertical dashed lines represent DSL with the largest σ , indicating the maximum spatial heterogeneity (MSH). (c) Similar to (b), but residuals are derived from multilinear regression against DSL and land-use fraction. Lines and shading in (a)–(c) are calculated based on the global estimates of AGB (Liu et al., 2015), and the gauge-based precipitation dataset CRU TS3.21 (Harris et al., 2014), except that blue lines in (a) and (c) are derived from the simulated natural vegetation by RCA-GUESS.

assessing the impacts of vegetation dynamics, we separate the impact of atmospheric CO_2 on vegetation (Δ_C , Equation 3) and the feedbacks that originate from physiological changes (Δ_V , Equation 4). A similar analysis is applied to quantifying future land-use effects (Δ_L , Equation 4). Numerical expressions are as follows:

$$\Delta_{all} = X_{LVC}(t_f) - X_{LVC}(t_p), \quad (1)$$

$$\Delta_{CC} = X_{000}(t_f) - X_{LVC}(t_p), \quad (2)$$

$$\Delta_C = X_{00C}(t_f) - X_{000}(t_f), \quad (3)$$

$$\Delta_V = X_{0VC}(t_f) - X_{00C}(t_f), \quad (4)$$

$$\Delta_L = X_{LVC}(t_f) - X_{0VC}(t_f), \quad (5)$$

where the subscript ‘ p ’ and ‘ f ’ for the time period t represent the present-day (1993–2012) and future (2080–2099), respectively. The decomposed effects are calculated based on the temporal mean of simulated quantities in the analysis period. Based on this approach, all the decomposed effects are numerically closed, i.e., $\Delta_{all} = \Delta_{CC} + \Delta_C + \Delta_V + \Delta_L$.

3. Results

We define the spatial heterogeneity of ecosystem states (σ) as the standard deviation of the above-ground biomass (AGB) residuals within a specific range of dry season length (DSL) from the $AGB \sim f(DSL)$ relation (see Analysis approaches in supporting information S1). After assessing RCA-GUESS’s performance in simulating DSL, productivity, evapotranspiration, temporal variability of AGB, and recovery rate from disturbances (Figures S1 and S2; see Model evaluation in supporting information S1), $AGB \sim f(DSL)$ relation and its corresponding spatial heterogeneity are further examined.

3.1. Estimating the Spatial Heterogeneity of the Pan-Amazonian Ecosystem States

We first examine the dependence of the AGB on DSL over the Pan-Amazonian domain (Figure 1). Figure 1a presents $AGB \sim f(DSL)$ functional relation with a sharp transition between a high ($>10 \text{ kgC m}^{-2}$) and a low ($<5 \text{ kgC m}^{-2}$) AGB states in areas with short and long DSL, respectively. The transitional semi-arid regions with a range of DSL between 4 and 8 months are characterized by a steep increase in mean AGB along a relatively narrow DSL gradient and by a large σ (Figure 1b), signifying a mosaic of high- and low-biomass vegetation patches with high-spatial

heterogeneity of ecosystem states. The transition curves, moreover, are substantially influenced by land use, presenting a shift in the shape of the transition curve when grid cells above a certain threshold of land-use fraction (i.e., land-use maxima) are excluded (Ahlström et al., 2017). The maximum spatial heterogeneity (MSH) generally coincides with the occurrences of the steep sections of the individual transition curves, presenting different corresponding DSLs of MSH when land-use maxima decrease. It is reasonable to expect that the transition curve and MSH for natural ecosystems without anthropogenic interferences, as an ecological response to climate, can be derived in theory when the land-use impacts are fully excluded.

To minimize the land-use effect for a natural vegetation response to climate, we include land-use fraction as an additional predictor to derive σ using multilinear regression for each DSL bin, avoiding abiotic spatial variances induced by land use that biases the estimated MSH. We find that land-use-corrected σ decreases substantially on the low-DSL (wet) shoulder but declines more gradually over the high-DSL shoulder (Figure 1c). This likely reflects a larger influence of land use on vegetation fragmentation occurring over the fringe of the Amazon rainforest, while a mosaic of vegetation patches over savanna and grassland landscapes is maintained by frequent disturbances, such as wildfires (Figure S3), that occur at different states of regrowth following past disturbances. The locations of MSH converge at around seven-month DSL regardless of the thresholds of land-use maxima used (Figure 1c). Results from the simulated natural vegetation by RCA-GUESS are in close proximity to the observational estimates (Figures 1a and 1c). Together with the reasonable responses of gross primary productivity (GPP) and evapotranspiration (ET) to DSL (Figures S2a–S2f), it confirms that the model adequately represents the spatial heterogeneity of ecosystem states under a reasonable land-atmosphere interaction over the study region.

3.2. Assessing Changes in Spatial Heterogeneity in Future Climate Scenario

To assess the possible future changes in spatial heterogeneity of Amazonian ecosystems, we run RCA-GUESS with boundary conditions from a simulation with HadGEM2-ES for the high-emission scenario RCP 8.5. RCA-GUESS projects significant changes in DSL over Amazonia, in a magnitude comparable to the ensemble mean of changes realized by other ESMs (Figures S1f and S1g). Employing a high-emission scenario allows to probe ecological resilience (Folke et al., 2004; Holling, 1973) by imposing a large perturbation of climate to the simulated ecosystem dynamics and assesses if ecosystems in different parts of the domain can absorb perturbation and persist. Under the simulated future climate, the results of RCA-GUESS point to a weakening of the present-day steep DSL gradient from the wet Amazonian forest to the Cerrado savanna area and its adjacent semi-arid regions (Figures S1a, S1d, and S1f). It exhibits an extension of the area with increased DSL over parts of the eastern Amazon basin, resulting in a significant increase in corresponding DSL location of MSH (Figure S6).

Change in the corresponding DSL of MSH simulated by RCA-GUESS is in general agreement with the overall changes projected by CMIP5 ESMs, in which five out of seven ESM simulations showing a significant shift of DSL ($p_{\text{DSL-ESM}} < 0.05$) (Figure S6). Changes in the magnitude of MSH are nevertheless not consistent among CMIP5 ESMs. Compared to HadGEM2-ES, RCA-GUESS shows a similar shift toward high DSL but with higher σ (+33%). This is expected due to the explicit representation of demographic processes of mortality and disturbance in RCA-GUESS that could induce larger spatial stochastic variation in vegetation age and successional stage compared to the area-based vegetation representation in HadGEM2-ES. Also, RCA-GUESS simulations at higher horizontal resolution (0.44×0.44 deg. vs. 1.25×1.88 deg. in HadGEM2-ES) could better capture landscape details (e.g., topography) and local climate phenomena, which are crucial to represent the spatial heterogeneity of ecosystem states. An additional test using the post-processed re-gridded RCA-GUESS results presents merely marginal differences of the computed σ of MSH (Figure S4), indicating that the simulated large σ in RCA-GUESS is mainly induced by model formulation instead of data resolution.

Future changes in σ are also reflected by its changes in spatial pattern across the Amazonian region (Figure 2). For the present day, areas with low σ are concentrated over the western high-biomass rainforest (dominated by tropical evergreen trees, Figure S5) and the severe low-biomass drought regions (dominated by herbaceous species, e.g., the eastern part of the continent). The region intermediate between the low and high DSL is an extensive zone of transitional areas co-occurring low- and high-biomass vegetation. The present-day pattern simulated in our study (Figure 2a) is coherent with previous resilience maps proposed for the Amazon based on the relation of tree cover to climate (Hirota et al., 2011; Staver et al., 2011). Under future climate change, the present-day pattern is altered by an expansion of the semi-arid area into the presently high-biomass region, with an increase in σ and increased dominance of short-lifespan species (e.g., tropical shade-intolerant broadleaved evergreen tree, Figure S5) occurring over an extended transition area of the central Amazon (+110%) and Cerrado savanna region, in which the original ecosystem states tend to be stable and deterministic under prevailing hydrological conditions (Figures 2b and 2c). The increase in σ is attributed to the combined or single effect of changes in AGB and DSL (Figure S1; Boisier et al. 2015). For

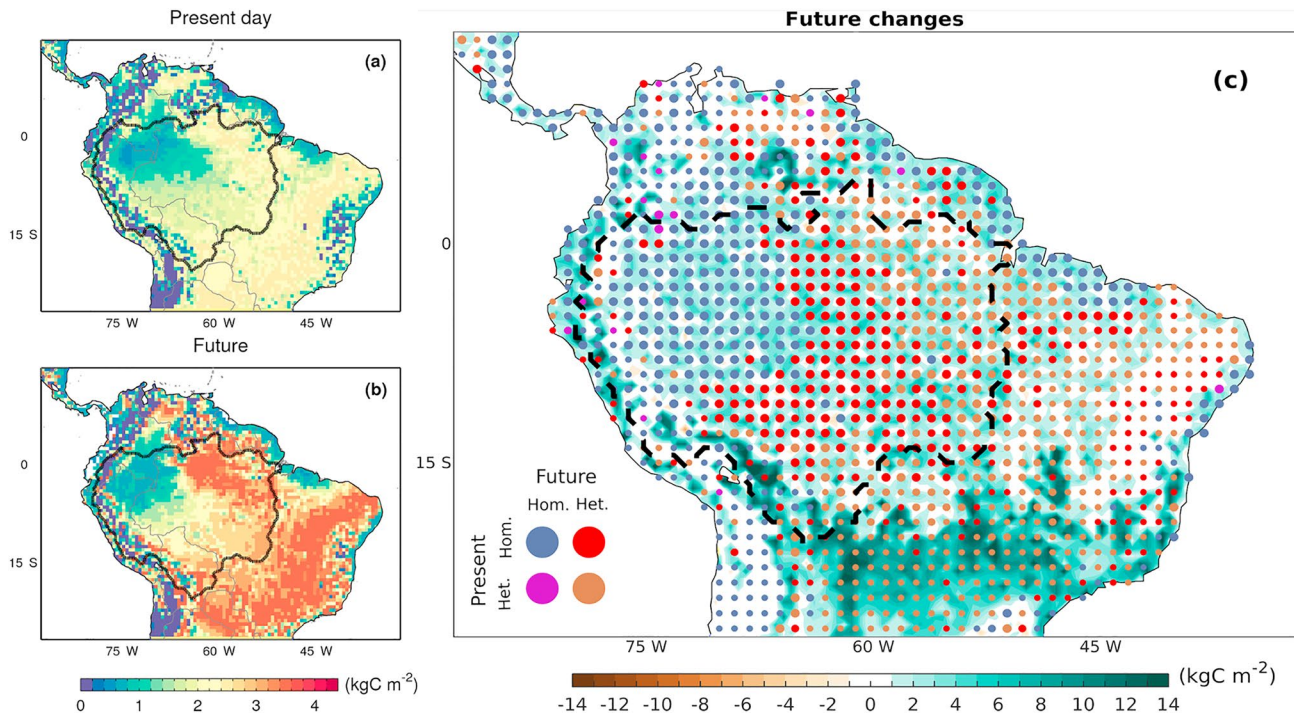


Figure 2. Future changes in spatial heterogeneity of ecosystem states for the Amazon basin and its adjacent areas. (a–b) Present-day (1993–2012) and future (2080–2099) spatial heterogeneity (σ) in terms of the standard deviation of AGB residuals derived from the polynomial $\sigma \sim f(\text{DSL})$ functional relation (its uncertainty and goodness of fit can be found in Figure S8). (c) Changes from present day to future, blue stippling indicates the area with small spatial heterogeneity ($\sigma < 2 \text{ kgC m}^{-2}$) both in present day and future, representing the unchanged homogenous state. Orange stippling indicates large spatial heterogeneity ($\sigma \geq 2 \text{ kgC m}^{-2}$) common for both present day and future. Red and purple stipplings represent new heterogeneous and new homogenous states in the future, respectively. Dot sizes reflect present-day AGB (large, $\text{AGB} > 10 \text{ kgC m}^{-2}$, median, $5 \leq \text{AGB} \leq 10 \text{ kgC m}^{-2}$, small, $< 5 \text{ kgC m}^{-2}$), color shading shows projected changes in AGB. Results are from natural vegetation simulation by RCA-GUESS with boundary conditions from the RCP 8.5 simulation of HadGEM2-ES ESM.

example, the increased σ in the central Amazon is mainly related to an increase in DSL given the limited changes in AGB. The expansions of the high σ area are also found in four ESMs (Figures S9c–S9e and S9g), with a shift in MSH to dryland similar to the dynamics presented by RCA-GUESS (Figure S8).

3.3. The Role of Vegetation Feedbacks in the Future Changes of Spatial Heterogeneity

To unfold the underlying mechanism behind the simulated shifts, we isolated the drivers and feedbacks—i.e., climate, CO₂ concentration, land use, and vegetation feedbacks related to the modified land surface—by performing a set of factorial simulations (Table S1), which provide a useful basis for quantifying the factorial effects.

Figure 3 presents an affected $\text{AGB} \sim f(\text{DSL})$ relation associated with individual drivers. Specifically, climate change alone overall decreases σ and reduces the average of biomass density over the Amazon basin (Figures 3b, 3f, and S11) by increased DSL, increased temperature, and reduced precipitation–evaporation balance that governs soil water availability (Figures S1 and S13 and Malhi et al., 2008). The monsoon-controlled savanna region experiences an increase in precipitation with a relatively small change in seasonality, which reduces water stress and enhances vegetation growth for savanna species (Figures S13f and S14d). Overall, the $\text{AGB} \sim f(\text{DSL})$ relation of the entire region shifts significantly toward the drier end with a decrease in σ (see arrows for the tendency of convergence in Figures 3b and S11b), presenting a shallower biomass gradient between moist forest and savanna. In isolation, CO₂ fertilization, without vegetation feedback, does not influence DSL. But an increase in vegetation growth due to an enhancement of photosynthesis and water use efficiency (Huntingford et al., 2013; Long, 1991) introduces overall higher levels of AGB for the high biomass state and larger σ over the rainforest than the savanna, resulting in a small shift of the MSH toward the rainforest region (Figures 3c and 3f).

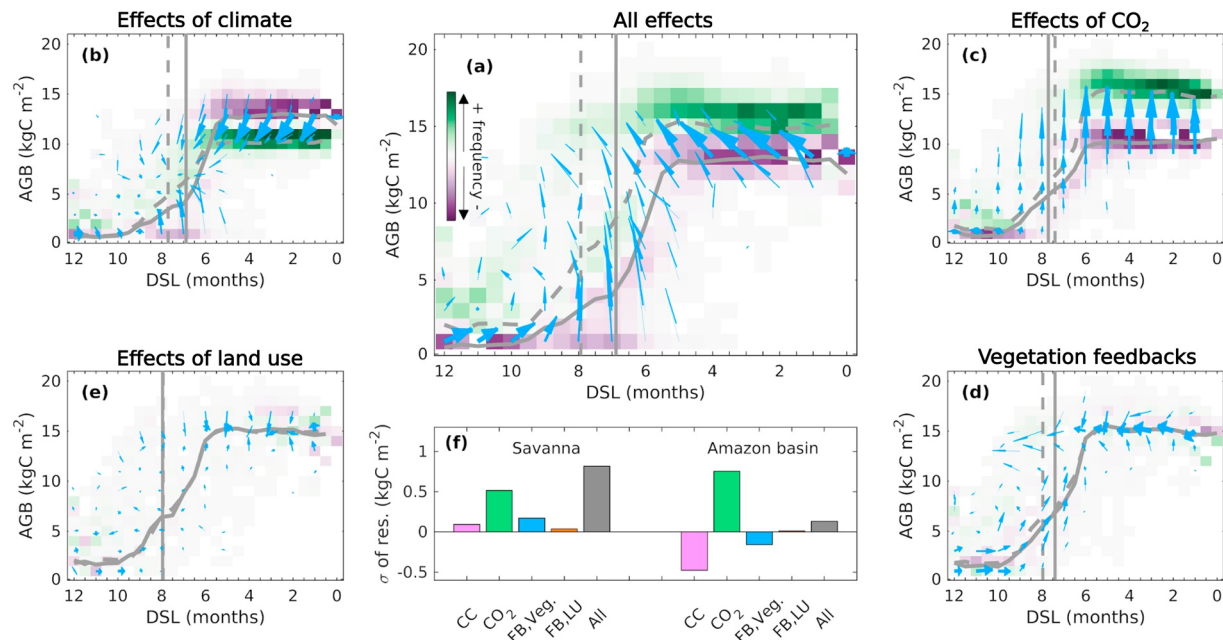


Figure 3. Potential drivers for future changes in $AGB \sim f(DSL)$ functional relation and their influences on maximum spatial heterogeneity (MSH). (a) Changes in the $AGB \sim f(DSL)$ functional relation between the simulated present-day (curve in full line) and the future (curve in dashed line). Colored contours indicate areas in the DSL-AGB space with decreasing (purple) and increasing (green) likelihood of occurrence. Arrows indicate the changing tendency of DSL-AGB space with strength (arrow length) and the number of grid points (arrow width). Vertical line indicates the estimated corresponding DSL of MSH for present day (full line) and the future (dashed line). The simulated change is decomposed into individual effects with the assistance of factorial simulations, i.e., effects of (b) climate change, (c) elevated CO₂ concentration, (d) vegetation dynamics, and (e) land use change. (f) Factorial contributions to changes in spatial heterogeneity (σ) for the wet Amazon basin and its adjacent semi-arid regions. The $AGB \sim f(DSL)$ relations (curves in full lines and dashed lines in a–e) are composed of the mean AGB of each DSL bin. Results are from natural vegetation simulation by RCA-GUESS driven by the boundary conditions from the RCP 8.5 simulation of HadGEM2-ES ESM.

When vegetation feedbacks are enabled, partial stomatal closure in response to elevated atmospheric CO₂ constrains evapotranspiration (Figure S13k), with feedbacks to the atmosphere leading to enhanced climate change-induced warming (+1 °C of the annual mean surface temperature) and decreased precipitation (–5 to –15 mm/month, Figures S13c and S13g). Vegetation feedbacks thus intensify the warming-induced reduction in σ and increase DSL over the Amazon basin (Figure 3f), imposing influences on Amazonian vegetation similar to the effect of climate change alone. For the semi-arid regions, vegetation feedbacks enhance the spread in the AGB response to DSL, which is related to two mechanisms. On the one hand, increased tolerance of a longer DSL due to elevated CO₂ causes rainforest to expand and savanna to contract (right-to-left arrows for the high-AGB section, Figure 3d), shifting the high AGB zone toward the original semi-arid climate envelope. On the other hand, shrub encroachment and woody thickening over savanna increase σ (Figure S5d). Also, increased vegetation growth with a larger leaf surface area enhances transpiration, increases precipitation, and reduces DSL through vegetation feedbacks (left-to-right arrows for the low-AGB section, Figure 3d), further sustaining the original savanna. As a result, vegetation feedbacks shift MSH significantly toward the dryland by approx. 0.5 DSL (Figures 3d and S11d). It acts as a synergy of both hydrological and physiological effects, although the hydrological effect represented as the vegetation-induced changes in DSL tends to be small (Figure S12d). Feedbacks from land-use change assumed under the RCP 8.5 harmonized scenario have a much milder impact on σ compared to the effects mentioned above (Figure 3e). Because future land-use-induced changes in land surface (Figure S15) lead only to minor changes in climate over parts of the savanna, the impact on the adjacent natural vegetation through land-atmosphere interaction is limited (Figure S14f).

4. Discussion and Conclusion

The fate of the Amazonian ecosystem is important not only due to the massive part tropical rainforests play within the global carbon cycle but also warrants attention for the ecological management of the Amazon (Scheffer et al., 2001). Numerous studies have explored the critical influence of the hydroclimate regime on the transition of ecosystem states between moist forest, dry savanna, and shrubland across the Amazon Basin, suggesting the importance of local feedback processes in sustaining Amazonian ecosystem resilience (Ciemer et al., 2019; Hirota et al., 2011; Holmgren et al., 2013; Spracklen et al., 2012; Staal et al., 2018, 2020; Staver et al., 2011; Zemp et al., 2017), such as the effects of cascading feedback process in air passage on redistributing hydroclimate conditions over rainforest (Spracklen et al., 2012; Staal et al., 2018; Zemp et al., 2017), the effects of long-term rainfall variability (Ciemer et al., 2019; Holmgren et al., 2013), and the effects of timing and amplitude of seasonal hydrological conditions as well as their interactions with other climatic drivers (Restrepo-Coupe et al., 2017) on shaping the resilience of tropical forest and savannah. However, the strong reciprocal vegetation-climate couplings in the nexus of multiple drivers usually induce nonlinear impacts on vegetation states, which challenge the assessment of the vulnerability of Amazonian ecosystems to future climate change. Our study complements recent studies that highlight significant potential effects of forest-rainfall interactions on forest degradation in the Amazon (Staal et al., 2018; Zemp et al., 2017), and quantifies the effects of interactions induced by the precursory changes of main drivers under climate change using a complementary Earth system modeling approach. In one of the first applications of a coupled biosphere-atmosphere RESM at high resolution over the Amazon, our model reproduces the observed transition of ecosystem states between rainforest and dryland vegetation along a gradient of DSL, and reveals how this relation may shift in the future, a question subject to change in the key drivers, individually and in combination. It depicts a sharper transition with an increase in spatial heterogeneity of ecosystem states along an increased gradient of AGB but against a smaller gradient of DSL from rainforest to dryland due to CO₂ effect and vegetation feedbacks (Figures 3c and 3d).

Vegetation feedbacks modulated by vegetation physiological response to elevated atmospheric CO₂ concentrations emerge as important controls that amplify the effects of climate change on the transition (Figure 3d). The model displays medium-strength sensitivity to CO₂ compared with other physiology-based models (Walker et al., 2015) which incorporate processes of CO₂ fertilization, the strength and persistence of which remain a debated topic for estimating future changes in forest productivity in the tropics (Schimel et al., 2015). Our results point to an emergent change in ecosystem composition, with increased dominance of shade-intolerant species replacing long lifespan rainforest and short lifespan grassland for the Amazon basin and the adjacent semi-arid area, respectively (Figure S5). Such changes are identified by changes in spatial heterogeneity of AGB with a strong contribution from vegetation feedbacks (Figures 3d and S11d). The degree of feedbacks may depend on the magnitude of perturbation. One could expect a milder vegetation-feedback effect when a more moderate future climate scenario is used with a smaller increase in atmospheric CO₂ concentration. A similar inference can be applied to the land-use feedbacks when different assumptions for land-use changes are employed. The overall uncertainty may also relate to the different formulations of ESMs. For example, CESM1-BGC and MIROC-ESM-CHEM have been reported to have strong land carbon-climate feedbacks with different assumptions of nutrient limitation on vegetation growth (Arora et al., 2013), which may likely explain their distinct behavior in simulating spatial transition changes compared to other ESMs (Figure S2).

The increasing likelihood of ecosystem transition revealed by an increase in spatial heterogeneity of ecosystem states at the fringe of the Amazon basin (Figure 2) poses a risk of abrupt ecosystem change, which could be initiated by changes in hydrological conditions, interacting with additional stressors in the feedback chain such as fire (Figure S3; Brando et al., 2014; Staver et al., 2011), heatwave (Allen et al., 2015) and pest outbreaks (van Lierop et al., 2015) that affect plant mortality. Given the conspicuous effect of vegetation feedbacks on the spatial heterogeneity of ecosystem states, it also implies that the ecosystem in some regions may be more vulnerable to land surface disturbances that may tip the ecosystem into alternative states. Drastic changes in vegetation states could have similar effects of deforestation, which could result in enhanced extremes (Bagley et al., 2014; Cox et al., 2000; Zemp et al., 2017) and reduced productivity (Wu et al., 2017), and modulated basin-wise hydrological cycles (Bagley et al., 2014; Cox et al., 2000; Zemp et al., 2017) through a strengthening of positive feedback at regional scale. The propagation of these

regional-scale effects may result in self-propagating dieback of the Amazonian rainforest under the combined effects of positive biogeochemical and biogeophysical feedbacks at the global scale (Betts et al., 2004). Finally, this study highlights the potential advantage of using coupled biosphere-atmosphere ESMs to assess regional ecosystem resilience at high resolution for the studies of climate and ecosystem services in the future high-CO₂ world.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The global above-ground biomass carbon dataset (v1.0) is available from Liu et al., 2015 (<https://doi.org/10.1038/NCLIMATE2581>, https://wald.anu.edu.au/data_services/data/global-above-ground-biomass-carbon-v1-0/). CRU TS3.21 is available from Harris et al., 2014 (<https://doi.org/10.1002/joc.3711>, <https://crudata.uea.ac.uk/cru/data/hrg/#current>). The Land-Use Harmonization dataset (LUH) is available from Hurtt et al., 2011 (<https://doi.org/10.3334/ORNDAAC/1248>, http://luh.umd.edu/data.shtml#LUH1_Data). The global elevation dataset of TerrainBase is available from Row et al., 1995 (<https://doi.org/10.5065/E08M-4482>, <https://rda.ucar.edu/datasets/ds759.2/>). Data outputs of CMIP5 ESMs are available from <https://esgf-node.llnl.gov/projects/esgf-llnl/>. The numerical simulations of RCA-GUESS were performed at the National Supercomputer Center (NSC) in Linköping, Sweden. Modeling results of RCA-GUESS for analysis is available in Zenodo (<https://doi.org/10.5281/zenodo.4556094>, <https://zenodo.org/record/4556094#.YDQnIVNKixt>).

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