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SPECIAL FEATURE

GRASS–WOODLAND TRANSITIONS

# Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas

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## Summary

**1.** Transition areas between biomes are particularly sensitive to environmental changes. Our understanding of the impacts of ongoing climate change on terrestrial ecosystems has significantly increased during the last years. However, it is largely unknown how climatic change will affect transitions among major vegetation types.

**2.** We modelled the distribution of three alternative states (forest, savanna and treeless areas) in the tropical and subtropical Americas by means of climate-niche modelling. We studied how such distribution will change by the year 2070 by using 17 downscaled and calibrated global climate models from the Coupled Model Intercomparison Project Phase 5 and the latest scenarios provided by the 5th Assessment Report of the IPCC.

**3.** Our results support the savannization of the tropical and subtropical Americas because of climate change, with an increase in savannas mainly at the expense of forests.

**4.** Our models predict an important geographical shift in the current distribution of transition areas between forest and savannas, which is much less pronounced in the case of those between savannas and treeless areas. Largest shifts, up to 600 km northward, are predicted in the forest–savanna transitions located in the eastern Amazon.

**5.** Our findings indicate that climate change will promote a shift towards more unstable states: the extent of the transition areas will notably increase, and largely stable forest areas are predicted to shrink dramatically.

**6.** *Synthesis.* Our work explores dimensions of the impact of climate change on biomes that have received little attention so far. Our results indicate that climate change will not only affect the extent of savanna, forest and treeless areas in the tropical and subtropical Americas, but also will: (i) promote a significant geographical shift and an increase of the extent of transition areas between biomes and (ii) decrease the stability of the equilibrium between forest, savanna and treeless areas, yielding a more unpredictable system.

**Key-words:** climate-change impacts, forest, plant–climate interactions, savanna, treeless vegetation, vegetation transitions

## Introduction

The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) provides unequivocal evidence of ongoing climate change, which is characterized by an increase in temperature globally and important modifications in rainfall patterns (IPCC 2013). Climate change will have major impacts on the structure and functioning of terrestrial ecosystems (Peñuelas *et al.* 2013) and is already promoting important changes in the spatial extent and distribution of vegetation types worldwide (Gang *et al.* 2013). Our understanding of the impacts of ongoing climate change on terrestrial ecosystems has significantly increased in recent years (see Paruelo *et al.* 1995; Parmesan & Yohe 2003; Parmesan 2006; Walther 2010; Peñuelas *et al.* 2013 for reviews). In tropical areas, forests might retreat yielding more open

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savanna-like systems, a pattern particularly well identified for the Amazonian region (Salazar, Nobre & Oyama 2007; Zelazowski *et al.* 2011; Franchito, Rao & Fernandez 2012).

Climate-induced changes in vegetation types will have direct effects on the provisioning of ecosystem services for humans (MEA 2003). Shifts from grasslands into woodlands results in a significant reduction in livestock production (Anadón *et al.* 2014), which can be offset by an increase in carbon sequestration (Havstad *et al.* 2007) and soil fertility (Eldridge *et al.* 2011). The shift from forest to grassland can also have impacts on ecosystem services other than the provisioning of timber or food, such as carbon sequestration, regulation of climate and provisioning of clean water (MEA 2003).

Biome transitions are areas of high socio-ecological interest for many reasons. These areas have a unique and high biological diversity at multiple levels (from genes to communities; see Kark & Van Rensburg 2006 for a review) and are areas of high conservation interest (Smith *et al.* 1997, 2001). These areas are also particularly sensitive to human activities such as grazing (Hudak 1999) and to important components of climate change such as the increase in precipitation intensity and rainfall variability predicted for many terrestrial ecosystems worldwide (Meehl, Arblaster & Tebaldi 2005; IPCC 2013). In this direction, rapid vegetation shifts in responses to recent changes in climatic conditions are already being detected in areas such as the Arctic tundra (Sturm, Racine & Tape 2001), the Alps (Gehrig-Fasel, Guisan & Zimmermann 2007) and the dry lands of the south-western U.S. (Van Auken 2009). Recent studies have highlighted how climate-change drivers, such as an intensification of the rainfall regime, may favour the recruitment and expansion of woody plants in savannah ecosystems (Holmgren *et al.* 2013; Kulmatiski & Beard 2013), a vegetation transition with major ecological effects on biodiversity, nutrient cycling and carbon sequestration in dry lands worldwide (Eldridge *et al.* 2011). As such, forecasting how vegetation in transitional areas will respond to climate change is an urgent ecological question that has been poorly studied to date.

Understanding how climatic variables such as rainfall and temperature determine woody vegetation cover in grassland–woodland transition areas has been an area of active research in the last decades (Williams *et al.* 1996; Sankaran *et al.* 2005; Hirota *et al.* 2011; Staver, Archibald & Levin 2011). Continental-scale analyses of tree cover in African savannas have found that mean annual precipitation largely limits the maximum cover of woody species and that disturbance dynamics control savanna structure below this maximum (Sankaran *et al.* 2005). More recent analyses have reported the presence of three alternative stable states (forest, savanna and treeless) in the world′s savannas (Hirota *et al.* 2011). These authors found that the tree cover values characterizing savannas (~20%) and forests (~80%) were found over multiple rainfall conditions, suggesting that woody cover is not controlled by gradual increases in precipitation and that there is a shifting probability of being in either of the three stable states identified. The reverse side of this multiple stable state equilibrium is the existence of highly unstable tree cover values (~5% and ~60%) that can be then identified as transition areas between biomes. A key property of the findings reported by Hirota *et al.* (2011) is that any given locality will have a probability of being forest, savanna and desert according to their climatic characteristics, and thus, they allow us to quantify how likely transitions between vegetation types are probably to occur. For example, in a locality with very high probability of being forest and low of being savanna or treeless, the probability of transition between vegetation states in very low. As a consequence, the uncertainty of the locality is very low as it is highly probable that it will be a forest. On the contrary, the uncertainty of a locality with similar and high probabilities of being forest and savanna (and low probability of being treeless) is very high, as it is very difficult to predict whether this locality will be a forest or a savanna. In localities of high uncertainty, small changes in tree cover due to human activities (e.g. fires, selective logging) might have a large effect on the system and promote the transition from one state to another. On the contrary, localities with low uncertainty are probably to be more resilient to human-induced changes to tree cover (Hirota *et al.* 2011).

While research conducted over the last decades has provided key insights into advance our understanding of the mechanisms driving grass/woody vegetation coexistence in savanna systems and has improve our ability to predict their responses to climate change, no previous studies so far have explicitly evaluated how forest–savanna–treeless transitions will change under future climatic conditions at regional to continental scales (but see Hutyra *et al.* 2005; Salazar, Nobre & Oyama 2007; Salazar & Nobre 2010 for forest–savanna transitions). We aimed to assess forest–savanna–treeless transitions under climate change for the tropical and subtropical Americas; a region that is crucial for preserving global biodiversity (Myers *et al.* 2000), regulating the Earth′s climate (Gedney & Valdes 2000) and that directly supports the livelihood of more than 700 million people. Our objectives were to: (i) assess the climatic determinants of the occurrence of treeless vegetation, savannas and forest in the tropical and subtropical Americas, (ii) predict the future extent and distribution under climate-change scenarios of treeless vegetation, savannas and forest in that region, (iii) evaluate how climate change will affect the distribution of the transition areas among them and (iv) assess how climate change will affect the uncertainty of the occurrence of different vegetation types. To achieve these objectives, we modelled the spatial distribution of grasslands and woodlands and their transition areas in the studied region using the alternative stable state framework provided by Hirota *et al.* (2011) and large-scale remote sensing and climate data and employed the latest climate-change scenarios provided by the 5th Assessment Report of the IPCC (Taylor, Stouffer & Meehl 2012) to forecast how such distribution will change by the year 2070.

## Materials and methods

### MODELLING THE DISTRIBUTION OF FOREST, SAVANNA AND TREELESS AREAS

Our study area comprises the tropical and subtropical Americas, here, defined as those areas between latitude 35°N and 35°S. Hirota *et al.*

(2011) suggested that the different vegetation types in tropical areas, as described by tree cover, are actually alternative states, exhibiting sharp transitions between them at so-called tipping points. These authors identified three alternative states in the tropical areas of the Americas (forest, savanna and treeless areas) that were defined by the cutting levels of 5% and 60% of tree cover (i.e. treeles = 0–5%, savanna = 5–60%, forest = 60–100%).

We modelled the distribution of the three states (forest, savanna or treeless) according to climatic variables by means of generalized linear models with a binomial distribution of errors, with the presence/absence of the state as independent variables, and with climatic descriptors (Mean annual temperature [T], Mean annual precipitation [P], T + P, P/T ratio and Aridity Index [P/Potential evapotranspiration]) as independent variables. Our models rely on the understanding that climate governs the broadest outlines of distributions of species and biomes. This statement is well supported by current knowledge (see Araújo & Peterson 2012 for a review). In this sense, our models capture the main controls of biome distribution at a continental scale (i.e. climate), as shown by the high values of explained deviance obtained (see Results section). Models were fitted to a random sample of 3000 2.5′ × 2.5′ (~4.5 × 4.5 km) cells from the study area in natural areas. Tree cover percentage was assessed from the MOD44B Collection 3 product from MODIS (Hansen *et al.* 2003) originally at a 500 m resolution. 2.5 arc-minute resolution values were obtained by averaging the 500 m side cells within each 2.5 arc-minute side cell. Average tree cover values were then transformed to a categorical map describing the three alternative states in the present time, using the 5% and 60% cutting levels described previously. Mean annual precipitation, temperature and evapotranspiration were also assessed for each 2.5 arc-minute side cell. Precipitation and temperature were obtained from Worldclim data base (www.worldclim.org; Hijmans *et al.* 2005). Evapotranspiration was obtained from the Global Potential Evapo-Transpiration (Global-PET) data set (http://www.cgiar-csi.org/). Both data bases describe climatic average values of the period 1950–2000 and are available at a 2.5 arc-minute resolution.

Eleven candidate models were fitted to the MOD44B data, including linear and quadratic responses to the different climatic descriptors (Table 1). Models for each state were ranked according to the Akaike Information criterion (Burnham & Anderson 2002). In accordance with previous works showing that tree cover and climate relationships at the continental scale are insensitive to the spatial resolution (Staver, Archibald & Levin 2011), our results at 2.5 arc-minutes resolution were very similar to those obtained using a 30 second (~1 km) resolution (data not shown). We used the Global Land Cover 2000 (GLC2000) map to filter out areas undergoing human activities (categories 16–18 and 22; (Bartholome & Belward 2005) from our analyses. These areas cover 5.1 × $10^6$ km$^2$, comprising 23% of our study area (Fig. S1 in Supporting information). By only using natural areas, we maximize the decoupling of climate and land-use controls on the dynamics of biomes and their transitions areas. As such, our predictions are based solely on climatic controls and are largely independent of land-use change.

As it will be detailed in the Results section, a global model (i.e. including all the study area) for forest and treeless states presented high explanatory power ($D^2$ > 40%; Table 1). For the savanna state, however, the best global model according to the Akaike Information criterion performed poorly ($D^2$ = 12%; Table 1), suggesting spatial non-stationarity (i.e. the response of the savanna state to climatic condition changes within our study area). To obtain a more robust model, and starting from the best global model ($P^2$+$T^2$; Table 1), we developed models with a spatial factor describing different subareas within our study area. This factor was included as an interaction term in the models. Because of the latitudinal organization of macroclimatic control and major biomes on the Earth (Bailey & Ropes 1998), this factor divided our study area latitudinally in two or three areas. As we did not know which areas were *a priori* responsible for the presence of non-stationarity in our data, we fitted models with different spatial factors describing all possible two and three latitudinal subareas within our study area. To make the number of latitudinal subareas tractable, the minimum latitudinal width of the subareas were 5° (e.g. from 15°N to 20°N, see Table S1 in Supporting Information for examples of factors including different latitudinal subareas). In total, we fitted 91 models, each one including the best global model and a spatial factor. As detailed in the Results section below, a large number of models had a very similar explanatory power (Table S1 in Supporting information). Hence, the model for the savanna state was built using a weighted average consensus approach (Marmion *et al.* 2009). For doing so, we first selected a subset of models with the

**Table 1.** Candidate climatic models fitted to the distribution of forest, savanna and treeless areas in the tropical and subtropical Americas. For each model, the explained deviance ($D^2$) and Akaike Information Criterion (AIC) value are shown. For each state, the selected model is in bold. For the Savanna, the best global model (i.e., that with $D^2$ = 12.29%) was not used and the value in brackets represents the explained deviance of the model finally employed. In this case, the $D^2$ value represents weighted mean of the $D^2$ values of the 20% best multizone models (see Materials and methods and Table S1 in Supporting Information)

| | Forest | | Savanna | | Treeless | |
|---|---|---|---|---|---|---|
| Model | $D^2$ | AIC | $D^2$ | AIC | $D^2$ | AIC |
| P | 39.30 | 2230.60 | 1.69 | 4029.92 | 65.02 | 946.43 |
| $P^2$ | 44.52 | 2041.20 | 10.35 | 3677.38 | 56.97 | 1165.07 |
| T | 24.79 | 2762.85 | 0.01 | 4098.74 | 28.05 | 1942.20 |
| $T^2$ | 24.81 | 2764.23 | 4.29 | 3925.37 | 29.37 | 1908.62 |
| $P^2$+T | 45.64 | 2002.16 | 10.35 | 3679.19 | 56.79 | 1172.06 |
| $T^2$+P | 41.76 | 2144.44 | 5.35 | 3884.16 | **66.84** | **901.23** |
| $P^2$+$T^2$ | **45.88** | **1995.36** | **12.29 (30.34)** | **3601.67** | 56.97 | 1169.33 |
| ARIDITY | 32.38 | 2484.60 | 0.99 | 4058.49 | 58.97 | 1109.37 |
| ARIDITY$^2$ | 38.65 | 2256.38 | 4.02 | 3936.52 | 59.50 | 1096.95 |
| P/T | 15.30 | 3111.09 | 0.32 | 4086.00 | 27.80 | 1948.89 |
| $(P/T)^2$ | 33.02 | 2462.86 | 0.43 | 4083.42 | – | – |

P = Mean annual precipitation; T = Mean annual temperature, ARIDITY = Aridity Index (P/Potential evapotranspiration).

highest accuracy and then calculated a weighted average according to a model performance metric (Hartley, Harris & Lester 2006; Marmion *et al.* 2009). In our case, and given the differences in the explanatory power of the models, we selected the 20% best models according to their explained variance ($n = 18$ models, range of explained variance of these models = 27.6–33.6%). Models were weighted according also to their explained deviance (Araújo & New 2007). We did not use the Akaike weights (Burnham & Anderson 2002) for model averaging because this approach led us to the selection of only one best model (i.e. weight of the first ranked model = 0.996).

Our distribution models for forest, savanna and treeless areas were projected to the study area using present conditions (1950–2000) and climate-change scenarios. For the scenarios, we used 17 downscaled and calibrated global climate models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Taylor, Stouffer & Meehl 2012) (See Table S2). We selected for our projections the Representative Concentration Pathway 8.5 (RCP8.5) for the year 2070. Within the Fifth IPCC Assessment Report, RCP8.5 represents the scenario with the highest concentration of greenhouse gases and with a predictive radiative forcing of + 8.5 W m$^{-2}$ (IPCC 2013). Our rationale behind the selection of the worst (but possible) scenario is that we are more interested in capturing the overall directions of the changes than in quantifying exactly the extent of the changes. To describe the extent of forest, savanna and treeless areas in the present time and for the year 2070, each cell was assigned to the state with largest probability of occurrence.

### MODELLING TRANSITIONS

Our study system is comprised by three states (forest, savanna and treeless areas) and two possible transitions (forest–savanna and savanna–treeless). To model these two transitions, we first divided our study area in the forest–savanna and savanna–treeless systems. These two subareas are mutually exclusive. The forest–savanna system is defined as those areas where the probability in the present time of being savanna or forest is larger than the probability of being treeless. Conversely, the savanna–treeless system is defined as those areas where the probability of being savanna or treeless in the present time is larger than the probability of being forest (Figs 2 and 3). Starting from the distribution maps of the three alternative states for the present time and the climate-change scenario of the 17 CMIP5 global climate models, we calculated transition maps between forest and savanna, and between savanna and treeless areas for these two periods. In the transition maps, we calculated for each cell a transition index ($Trans_{AB}$) calculated as $Trans_{AB} = p(A) - P(B)$, Where *P(A)* and *P(B)* are the probability of being in state A and B, as described by the distribution maps. The transition index ranges between 1 and -1, with 1 being those cells with the largest probability of being in state A and least probability of being in state B, and −1 the other way around (maximum probability of being in state B and least of being in state A). Values close to 0 indicate high uncertainty, being difficult to predict whether the cell will be in state A or B, and cells with $Trans_{AB} = 0$ are those that have exactly the same probability of being in state A or B, according to their climatic conditions. From the transition maps, we identified transition areas, that is, areas with the highest uncertainty, which were defined as those with $Trans_{AB}$ absolute values below 0.2. In the same vein, we defined the core areas of the biomes, that is, areas with the lowest uncertainity, as those with $Trans_{AB}$ absolute values above 0.5. The modelling approach described previously was performed for each one of the 17 CMIP5 global climate models. Final projection maps for biome distribution, transition areas and their changes were built from the ensemble mean of the projections provided by the 17 models (Araújo & New 2007).

## Results

For the three states considered, the models with the largest values of explained deviance were those including temperature and precipitation (Table 1). The best models for forests and savannas included both variables with their quadratic terms, whereas for treeless areas the best model included the linear term of precipitation and the quadratic term of temperature. For forest and treeless states, a global model (i.e. including all the study area) presented high explanatory power ($D^2$ = 45% and 60% for forest and treeless areas, respectively). As noted in the Materials and methods, the global model performed poorly for savanna ($D^2$ = 12%). Models considering a spatial factor with multiple subareas had larger explanatory power for this area ($D^2$ values ranging from 15.4% to 33.7%; Table S1). The consensus model for this state resulting from the ensemble modelling presented an averaged explained deviance of 30.3% (Table 1).

Our results indicate that forests will decrease in area in favour of savannas by the year 2070 under the RCP8.5 climate-change scenario (Table 2 and Fig. 1). Forest areas are predicted to lose $1.5 \pm 0.9 \times 10^6$ km$^2$. This biome is expected to cover 22 ± 4% of our study area in year 2070, which means a 24% (range 9–39%) reduction in comparison with its current distribution. Results from the 16 of 17 CMIP5 global climate models indicated a reduction in forest area (Table S3). The general agreement shown by the projections of each one of the 17 CMIP5 global climate models in relation to changes in forest area indicates that our predictions

**Table 2.** Projected representation of forest, savanna and treeless areas in our study area for the present time (1950–2000) and for 2070 under the RCP8.5 scenario. For the 1950–2000 period, real values (i.e. observed from the data, not modelled) are shown in brackets

| | 1950–2000 | | 2070 RCP8.5 | | Change | |
|---|---|---|---|---|---|---|
| | Area ($\times 10^3$ km$^2$) | % | Area ($\times 10^3$ km$^2$) | % | Area ($\times 10^3$ km$^2$) | Change (%) |
| Forest | 6235 | 29 (31) | 4760 ± 896 | 22 ± 4 | −1474 ± 896 | −24 (−38 to −9) |
| Savanna | 12765 | 58 (52) | 14263 ± 921 | 65 ± 4 | 1498 ± 921 | 12 (5 to 19) |
| Treeless | 2847 | 13 (17) | 2823 ± 178 | 13 ± 1 | −24 ± 178 | −1 (−7 to 5) |

Mean values and standard deviation from the 17 downscaled and calibrated CMIP5 global climate models are indicated. Results for each CMIP5 global climate model are shown in Fig. S3.

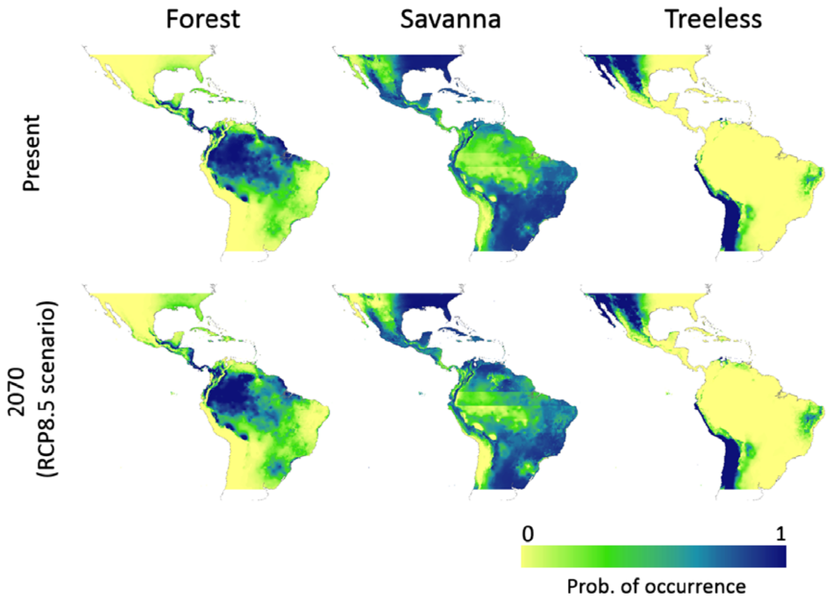

**Fig. 1.** Spatial projection of the three alternative states (forest, savanna and treeless areas) for the present time (1950–2000) and for the year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas.

are robust regarding uncertainties of the global climate models (Table 2). Changes in the extent of treeless areas are predicted to be of small extent ($-24 \pm 178 \times 10^3$ km$^2$). Results from 8 CMIP5 climate models predicted a reduction, whereas 9 models show an increase in treeless areas. This limited change actually means that the percentage of the tropical and subtropical Americas covered by treeless areas might not vary significantly due to climate change. As it will be discussed below, this result does not mean that treeless areas might remain stable but that the extension of some treeless areas might be compensated by the contraction of others.

For the forest–savanna system, the largest transition area is located in the southern portion of the Amazonian rain forest (Fig. 2). Comparatively, minor transition areas are located north of the Amazonian forest and along Central America. Within the savanna–treeless system, main transition areas are located in the southern border of the North American deserts and along Pacific coast in South America (Fig. 3). Our predictions indicate that, within the forest–savanna system, changes in the multistate equilibrium toward savanna occur mainly in the East Amazonia and North Matto Grosso regions (Fig. 4). Within the savanna–treeless transition realm, changes towards savanna occur in the Peruvian and Bolivian slopes of the Andes facing west, north of the Atacama Desert. Despite the overall reduction in the total forest area, our models predict an increase in the probability of forest in the southern Atlantic Forest region. Shifts towards treeless areas are of much lesser extent and intensity (i.e. amount of change in the transition index) than those towards forest or savanna. Main areas where our models predict a shift towards treeless areas are north-eastern Brazil and part of the Chaco, between Paraguay and Bolivia.

Our models predict an important geographical shift in the current distribution of the forest–savanna transition, which is

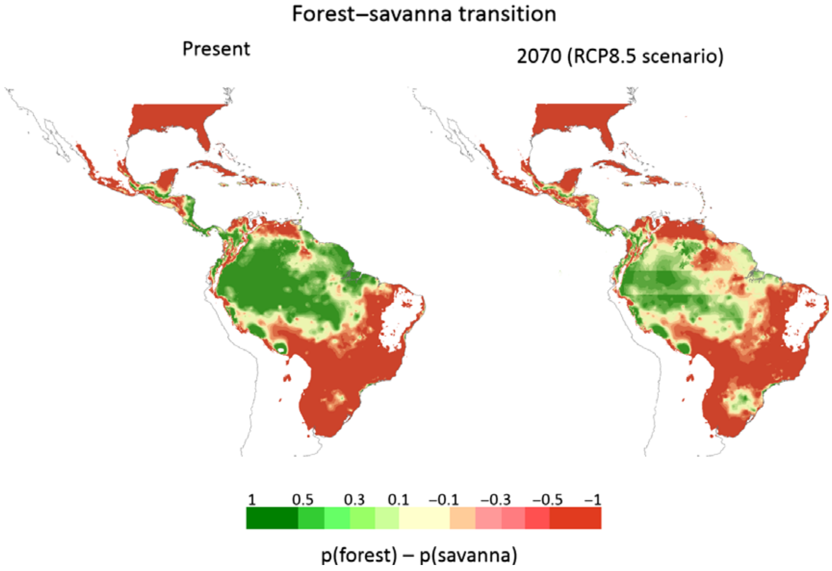

**Fig. 2.** Transition map for the forest–savanna system for the present time (1950–2000) and for the year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas. For the year 2070, the mean value of the 17 transition maps resulting from the 17 CMIP5 global climate models is shown. A histogram with the total amount of area of each class can be found in Fig. 6 (Top). The total area of each class for each one of the 17 transition maps resulting from the 17 CMIP5 global climate models can be found in Table S4.

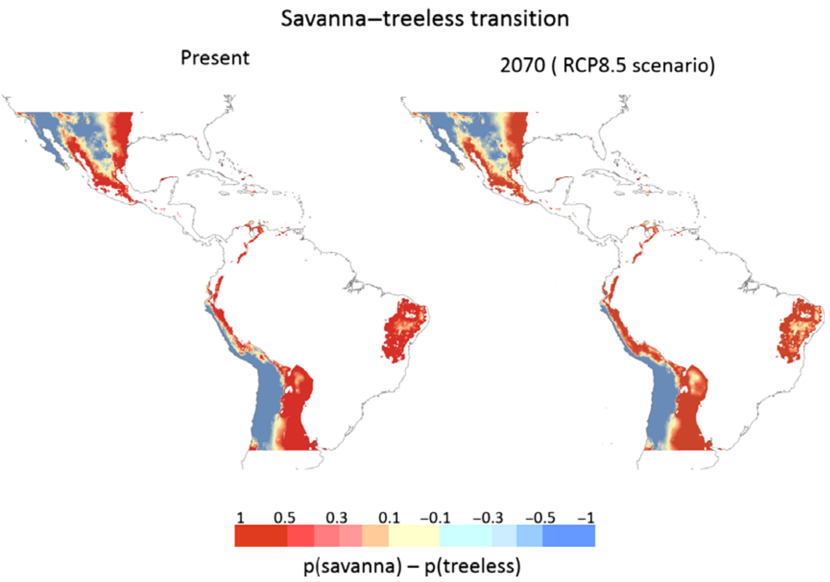

**Fig. 3.** Transition map for savanna–treeless system for the present time (1950–2000) and for the year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas. For the year 2070, the mean value of the 17 transition maps resulting from the 17 CMIP5 global climate models is shown. A histogram with the total amount of area of each class can be found in Fig. 6 (Bottom). Rest of legend as in Fig. 2.

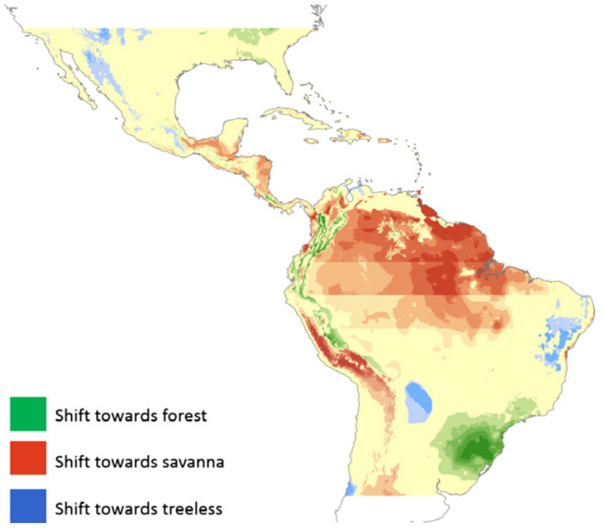

**Fig. 4.** Projected shift towards forest, savanna or treeless states for the year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas. Shifts are estimated as the difference between the transition index in the present time and the year 2070 for the forest–savanna and the savanna–treeless systems. The mean value of the projected shifts for the 17 transition maps resulting from the 17 CMIP5 global climate models is shown. Beige area indicates those cells where the change in the probability transition is below 0.1. Darker tones of green, red and blue indicate stronger shifts towards forest, savanna and treeless areas respectively.

less pronounced in the case of the savanna–treeless transition (Fig. 5). The largest move in forest–savanna transitions (up to 600 km westward) occurs in the eastern part of the Amazon, affecting the contact areas of the Amazon with three different savanna systems present in the region (Llanos, Roraima and Cerrado). Lesser shifts (up to 100 km northward) occur in the southern limit of the Amazonia. Regarding the savanna–treeless transition line, our models predict minor shifts (up to 50 km westward) in the arid and semi-arid areas of West South America (i.e. Atacama, Chaco, Monte Desert). Our models suggest that the shift in the transition line in this area increases towards the South, being maximal in the Argentinean Monte Desert. Transition areas located in the North American deserts (i.e. Mojave, Sonoran, Chihuahuan) are not expected to shift (Fig. 5).

Changes in the extent and geographical location of the transition areas occur simultaneously with an increase in the uncertainty of the system state (Fig. 6). In the forest–savanna system, the reduction in forest areas is at the expense of those areas with current lowest uncertainty of being forest. A large fraction (58%) of these areas, which can be considered the core of the forest biome, shift towards areas with higher uncertainty levels (Fig. 6). As a result, core forest areas, which nowadays occupy 3.1 × $10^6$ km$^2$, are projected to cover 1.3 × $10^6$ km$^2$ (range: 0.3–2.4 × $10^6$ km$^2$, Table S4). The different projections resulting from the 17 CMIP global climate models show consistent patterns in the changes in uncertainty of the forest–savanna system, as shown by the reduced standard deviation of the predictions (Fig. 6). All 17 CIMP5 climate models predict a reduction in the areas of low uncertainty of being forest (Table S4). Forest–savanna transition areas (i.e. those where the difference in the probability of being forest and savanna is $<0.2$) increased on average by 32%, from 2 × $10^6$ km$^2$ to 2.7 × $10^6$ km$^2$ (range = 2.2–3.6 × $10^6$ km$^2$, Table S4). A similar pattern, but much less pronounced, occurs in the savanna–treeless system, with a decrease in areas with high certainty of being treeless that shift towards areas of higher uncertainty (Fig. 6 and Table S5). The largest increases in uncertainty of the system state, projected to occur on the forest–savanna system, are located around two areas: the Amazon forest, particularly in the west, and the southern portion of the Atlantic Forest, because of their shifts towards savanna and forest, respectively (Fig. 7). The largest decreases in uncertainty are located in those savanna areas on the West of South America (Llanos, Roraima, Northern Cerrado), which are clearly expected to shift towards savanna.

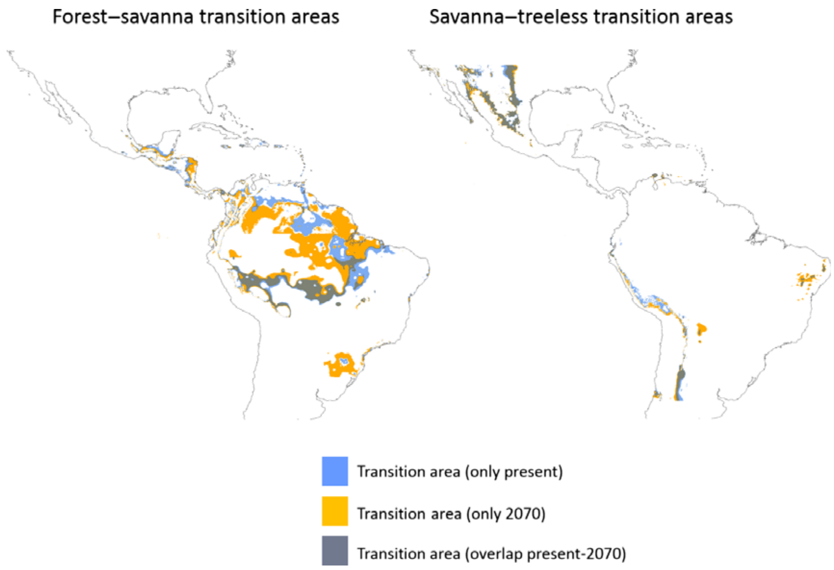

**Fig. 5.** Transition areas for the forest–savanna (left) and the savanna–treeless systems (right) in the present time and the year 2070 under the RCP8.5 scenario. For a given transition (i.e. forest–savanna), transition areas are defined as those cells in which the difference between the two alternative systems is <0.2. The mean value of the 17 transition maps for the year 2070 resulting from the 17 CMIP5 global climate models was used as base transition map.

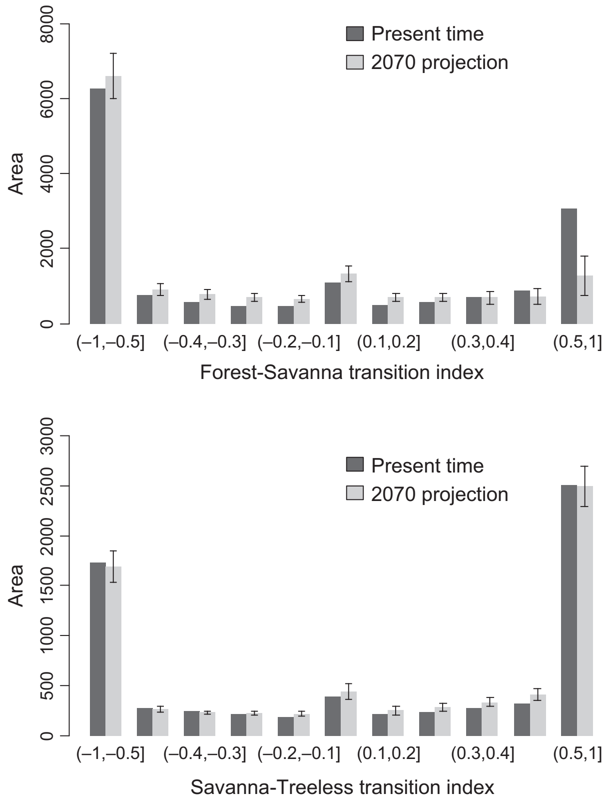

**Fig. 6.** Projected area under different classes of the transition index for the present (1950–2000) and under the RCP8.5 scenario for the year 2070 for the forest–savanna (Top) and the savanna–treeless transitions (Bottom). Forest–savanna transition index is calculated as p (forest) – p(savanna). Savanna transition index is calculated as p (savanna) – p(treeless). Values closer to 1 and -1 indicates lower uncertainty, whereas values closer to 0 indicate higher uncertainty. Mean values and standard deviation of the 17 CMIP5 global climate models are shown. Results for each CMIP5 global climate model are shown in Figs S4 and S5. Area in $10^3$ km$^2$. Note that the total area of savanna is the sum of the savanna areas in both transition systems. The spatial representation of this histogram can be found in Figs 2 and 3.

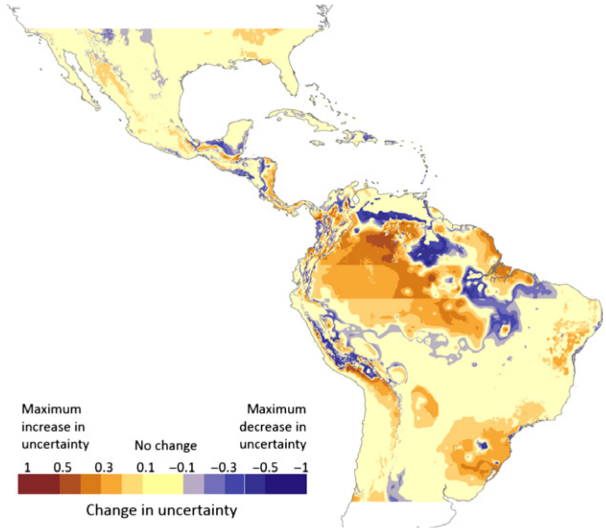

**Fig. 7.** Changes in the uncertainty of the forest–savanna transition between the present (1950–2000) and the RCP8.5 scenario (2070) in the tropical and subtropical Americas. The change in uncertainty is calculated as the change in the transition index between the two projections (i.e. 1950–2000 and 2070). The mean value resulting from analysis of the 17 CMIP5 global climate models is shown. Positive values of uncertainty indicate areas where the probability of tipping between forest and savanna will increase due to climate change.

## Discussion

Our results indicate that climate change according to the RCP8.5 scenario of the IPCC will promote the savannization of the tropical and subtropical Americas, with an increase of savannas mostly at the expense of forests. Such change will also increase the extent of transition areas between savannas and forests and will promote a dramatic reduction in stable forest areas. According to current knowledge, the shifts predicted in the distribution and stability of transitions areas are expected to bring important changes to the biota and the provision of ecosystem services such as C sequestration, climate regulation and food production in one of the most important regions worldwide for biodiversity and human well-being (MEA 2005).

Our modelling approach, which relies on niche modelling theory and focuses exclusively on the climatic controls of transitions, does not take into account other factors that have been identified as interacting with climate drivers, such as feedbacks between tree cover and climate, particularly in the rain forest (Malhi *et al.* 2008; Coe *et al.* 2013), sea surface temperature (Pereira, Costa & Malhado 2013), $CO_2$ fertilization (Lapola, Oyama & Nobre 2009) and land uses (Nepstad *et al.* 2008). In the same vein, our models use average annual values and do not consider intra- and interannual variability in rainfall and temperature, which have been described to have significant effects in driving tree cover (Malhi *et al.* 2008; Holmgren *et al.* 2013). Notwithstanding, the overall agreement between our projections and those obtained by previous studies using more complex models regarding the direction, spatial location and order of magnitude of the vegetation changes observed at a regional scale makes us confident on the results reported here.

### CLIMATE-CHANGE IMPACTS ON THE EXTENT OF SAVANNA, FOREST AND TREELESS AREAS

Our models predict that climate change will increase the extent of savannas in the Americas by 12% (range = 5–19%, average increase = $1.5 \times 10^6$ km$^2$) at the expense mostly of forests, which will decrease by 24% (range = 9–38%, average decrease = $1.5 \times 10^6$ km$^2$) and in much less extent of treeless areas. Overall this result matches the process of savannization predicted for the area for the 21st century because of climate change (Hutyra *et al.* 2005; Cook & Vizy 2008; Salazar & Nobre 2010; Franchito, Rao & Fernandez 2012). In agreement with previous results (Hutyra *et al.* 2005; Salazar & Nobre 2010; Cook, Zeng & Yoon 2012; Franchito, Rao & Fernandez 2012), our projections indicate that major increases of savanna will occur at the expense of the Amazon rain forest, particularly at its south and south-eastern portions. The amount of predicted reduction in forest, ranging from 9% to 38%, falls within the range predicted by other authors for South America (Hutyra *et al.* 2005; Salazar, Nobre & Oyama 2007; Cook & Vizy 2008; Zelazowski *et al.* 2011). Previous studies have indicated that a larger stability of the forest in the Mata Atlantica in comparison with the Amazon under a climate-change scenario (Cook, Zeng & Yoon 2012). Our results go one step further and predict a strong increase of the probability of being forest in this area. The forest of the Mata Atlantica is strongly fragmented, and only around 10% of its original area actually remains (Saatchi *et al.* 2001). Our findings indicate that in this region management actions designed to increase tree cover could take advantage of this positive inertia towards the forest.

In comparison with the transitions between forest and savanna, our prediction of transitions between savanna and treeless areas are overall small in extent, with a decrease in <1% of the treeless areas ($2.4 \times 10^4$ km$^2$). The impacts of climate change on the extent of dry lands have been much less explored than those on forests, particularly in the Amazon region. Existing work indicates an overall increase in aridity and the extent of dry lands in most the arid areas of tropical and subtropical Americas (Seager *et al.* 2007; Feng & Fu 2013). Our results partially match these patterns, because they predict a general increase in the extent of the Caatinga (NE Brazil) and Chaco Seco (Argentina and Paraguay), and a patchy increase in the extent in North American deserts. However, against current knowledge (Feng & Fu 2013), our models predict a savannization of the Atacama Desert and particularly, of the Sechura Desert, along the Peruvian Pacific coast.

Changes in vegetation type from forest into savanna and treeless groups are expected to have major effects on climate (Shukla, Nobre & Sellers 1990; Oyama & Nobre 2003). Vegetation changes affect climate directly via changes in albedo and transpiration, the later mediated through changes in rooting depth. Vegetation changes also affect climate indirectly through changes in carbon cycling. Albedo increases along the gradient from forest, savanna to treeless vegetation therefore increasing the amount of radiation reflected back to the atmosphere and reducing surface temperature (Balling 1988). Rooting depth decreases from forest to treeless vegetation, reducing the depth of the soil explored by roots and functionally reducing the soil water-holding capacity (Jackson *et al.* 1996). A reduced soil water capacity may decrease the latent heat therefore reducing the cooling capacity of the ecosystem. Finally, carbon storage is much larger in forest than in savannas and treeless vegetation in tropical areas (Saatchi *et al.* 2011), so the transition from forest into savanna may results in a net carbon emission into the atmosphere that will enhance climate warming.

### CLIMATE-CHANGE EFFECTS ON TRANSITION AREAS AND THE STABILITY OF THE SYSTEM

Using the framework of alternative stable states provided by Hirota *et al.* (2011), we were able to project how the transition areas between biomes and the stability of the system are expected to change under climate change. These two related aspects have been much less explored than the changes in the extent of the biomes themselves. As with the projected changes in the extent of biomes, shifts in the transitions between forests and savannas were much more pronounced than those between savannas and treeless areas.

Our models predict that climate change will promote a shift towards more unstable states, yielding more uncertainty in system state. Two aspects of this result deserve particular attention. On the one hand, the extent of the transition areas will increase by 32% on average (range = 10–80%), and forest–savanna transition areas, now restricted to a thin belt between both biomes might become the dominant biome in large areas, particularly in the South and Eastern part of Brazil. On the contrary, large stable forest areas are predicted to decrease by 58% on average (range = 23–90%). The climate control of vegetation types is strongest in the core (i.e. ecological optimum) of their distribution and weakens towards the edges (Sala, Lauenroth & Golluscio 1997). It is in the edges of the distribution of vegetation types where other factors such as grazing intensity, fire and logging become more important. The increase in uncertainty of large areas of the Amazon rain forest means that these areas will probably be less resilient to perturbations and thus that they might be more sensitive to human management (Hirota *et al.* 2011). In these areas of high uncertainty, positive feedbacks might make that small changes in tree cover might induce a self-propagating shift to the alternative state (i.e. from forest to savanna or from savanna to forest). In this way, fragmented landscapes with a patchy distribution of forest and savanna might be more likely to turn into solely savanna landscapes, due to, for example, an increase in fire frequency and extent (Malhi *et al.* 2008). Interestingly, and as pointed out for the Mata Atlantica above, these feedbacks can also work in the opposite direction and, in areas of high uncertainty, tree cover increases due to habitat management are more likely to trigger the conversion of savanna to forest. Land-use changes are at present the main driver of the transition between states in the study area, particularly the conversion of forest to savanna and treeless areas due to deforestation (Malhi *et al.* 2008). Overall, our results indicate that climate change will increase the importance of land use in shaping the extent of biomes during the next century.

### PREDICTED IMPACTS OF CLIMATE CHANGE ON BIODIVERSITY AND ECOSYSTEM SERVICES

The Amazon rain forest is a major component of the Earth's system, regulating Earth's climate (Malhi *et al.* 2008), and hosts up to a quarter of the world's terrestrial species (Barthlott & Winiger 1998). Rapid transition from one vegetation type to another will certainly result in major biodiversity losses (Sala *et al.* 2005). Our models predict a shift of the forest–savanna transition area of up to 600 km in the eastern Amazon for year 2070. Given the magnitude and speed of this change, a pertinent question here is to what extent species will be able to keep pace with climatic changes to reach the equilibrium (Loarie *et al.* 2009). Although our understanding of colonization processes under climate change is still limited, current models indicate that species will lag behind projected climate shifts (Nathan *et al.* 2011; Prasad *et al.* 2013). The mismatch between climatic change velocity and colonization rates is expected to be exacerbated in flat reliefs (Loarie *et al.* 2009), which are dominant in the Amazonian Basin. In this area, our models predict the largest shifts from forest to savanna suggesting a high risk of species extinctions. However, as it has been described for tree species colonization after the ice caps retreated during the Holocene, isolated habitat patches outside the core distribution range of the biome could play key role in tracking climate change (McLachlan, Clark & Manos 2005; Anderson *et al.* 2006; Parducci *et al.* 2012). In our case, for example, small savanna patches currently embedded in a forest matrix, could serve as colonizing source for the surrounding landscape when climate potentially in the area change from forest to savanna.

The portfolio of ecosystem services provided by forest, savannas and treeless vegetation types are drastically different. For example, savanna and grasslands in tropical and subtropical America constitute one of the main providers of food, particularly protein, of the world (FAO, 2007). As the reverse side of the ecosystem services linked to rain forest, predicted changes might have a positive impact on the provisioning of food (MEA 2005). We predicted an increase in the extent of transition areas and in the uncertainty of the system. This means that alternative states (i.e. forest, savanna, treeless) are probably to be more evenly distributed at a small scale (i.e. a finer grain distribution) and that localities are expected to tip from one state to another more easily. As a result, ecosystem services provided at a local scale are probably to be more diversified but also more unpredictable, because larger portions of our study area might contain a combination of different biomes that will change more frequently. Food, timber, climate amelioration, clean water, recreation and conservation are ecosystem services that will affected by vegetation transitions. These changes in the portfolio of ecosystem services resulting from vegetation transitions will affect different groups of stakeholders because they value ecosystem services differently.

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## Data accessibility

Data available from the Dryad Digital Repository (Anadón, Sala & Maestre 2014).

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## Supporting Information

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

**Figure S1.** Distribution of areas undergoing human activities (categories 16–18 and 22 in the Global Land Cover 2000 (GLC2000; Bartholome & Belward 2005) in the Tropical and Subtropical Americas (dark grey).

**Table S1.** 20% best models fitted to the distribution of savanna.

**Table S2.** List of the 17 Coupled Model Intercomparison Project Phase 5 (CMIP5) general circulation models used in this study.

**Table S3.** Predicted extent of forest, savanna and treeless areas in the tropical and subtropical Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and calibrated CMIP5 global climate models (GCM).

**Table S4.** Predicted extent of the classes of the Forest-savanna transition index in the tropical and subtropical Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and calibrated CMIP5 global climate models (GCM).

**Table S5.** Predicted extent of the classes of the Savanna-Treeless transition index in the tropical and subtropical Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and calibrated CMIP5 global climate models (GCM).