Growing aridity and seasonality can drive catastrophic changes in the Amazon forest

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The consolidation of a non-analogous climate shortly will likely affect the structure and functioning of Amazon, the most biodiverse terrestrial ecosystem on the planet. However, the ecological mechanisms underlying these potential events are still poorly understood. Here, we investigate the mechanism responsible for controlling the forest-savanna transition regime through an objective measure of resilience, based on the multidimensional climatic niche of ecosystems. Our results suggest that there is an alternating dominance, where forest and savanna have their respective basins of attraction. However, we note that the two stable states can coexist only in a narrow ecotonal zone of bistability. In this particular region, there is an equivalence between forest and savanna in quantitative terms and its presence indicates, in addition to a low hysteresis, a propensity for a catastrophic transition regime between forest and savanna. In this sense, we determine the critical levels of resilience that intermediate the dynamics of transition between forest and savanna through such bistable ecotonal zone. Also, we found that bistable region is strongly associated with critical climatic thresholds, mainly on the axis of the moisture availability and climatic seasonality, but with the lower effect of the average annual temperature. Thus, we can expect that if such climatic thresholds are reached, due to ongoing climate change, and forest resilience limits are exceeded; large-scale catastrophic events will suddenly be triggered. The expected effects are the erosion of Amazonian biodiversity, with the massive extinction of species, culminating in the consolidation of a stable state with simplified ecosystems, with a lower density of tree cover.

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Abstract

The consolidation of a non-analogous climate shortly will likely affect the structure and functioning of Amazon, the most biodiverse terrestrial ecosystem on the planet. However, the ecological mechanisms underlying these potential events are still poorly understood. Here, we investigate the mechanism responsible for controlling the forest-savanna transition regime through an objective measure of resilience, based on the multidimensional climatic niche of ecosystems. Our results suggest that there is an alternating dominance, where forest and savanna have their respective basins of attraction. However, we note that the two stable states can coexist only in a narrow ecotonal zone of bistability. In this particular region, there is an equivalence between forest and savanna in quantitative terms and its presence indicates, in addition to a low hysteresis, a propensity for a catastrophic transition regime between forest and savanna. In this sense, we determine the critical levels of resilience that intermediate the dynamics of transition between forest and savanna through such bistable ecotonal zone. Also, we found that bistable region is strongly associated with critical climatic thresholds, mainly on the axis of the moisture availability and climatic seasonality, but with the lower effect of the average annual temperature. Thus, we can expect that if such climatic thresholds are reached, due to ongoing climate change, and forest resilience limits are exceeded; large-scale catastrophic events will suddenly be triggered. The expected effects are the erosion of Amazonian biodiversity, with the massive extinction of species, culminating in the consolidation of a stable state with simplified ecosystems, with a lower density of tree cover.

Keywords: Tipping point, Resilience, Bistability, Forest-savanna transitions.

Introduction

Observational data indicate that the 2016 year was the warmest and driest in the Amazon basin since the beginning of observations (Jiménez-Muñoz et al., 2016). In this context, El Niño (ENSO) plays an essential role as a determining factor of extreme interannual climatic events in the Amazon. This climate pattern, with higher temperatures and longer dry season duration, seems to compose a trend for the biome, especially in its eastern to southwestern borders (Li et al., 2008b; Fu et al., 2013; Jiménez-Muñoz et al., 2013). For the foreseeable future, this scenario is expected to accentuate. Climate simulations predict that by the end of the 21st century the Amazon basin will suffer from non-analogous conditions with little overlap with the current climate (Williams et al., 2007; Malhi et al., 2009; Garcia et al., 2014).

Terrestrial ecosystems are known to depend on energy and moisture availability to maintain their structure and functioning (Murphy & Bowman, 2012; Donoghue & Edwards, 2014; Oliveras & Malhi, 2016)(Murphy & Bowman, 2012; Donoghue & Edwards, 2014; Oliveras & Malhi, 2016). However, forests are not only a passive recipient of abiotic conditions (Zemp et al., 2017)(Zemp et al., 2017). Amazon forest, with its immense biological richness (Mittermeier et al., 2003), plays a vital role in the global climate system, integrating an intricate network of material and energy feedbacks at large scales (Aragão et al., 2014; Nobre et al., 2016). Therefore, it is expected that ongoing climate change, promoted mainly by the increasing rate of greenhouse gas emissions to the atmosphere (IPCC, 2014), will affect the integrity and functioning of the Amazon forest (Davidson et al., 2012). Such climate state will entail the commitment of a vast set of goods and services provided to humans (Cardinale et al., 2012; Pecl et al., 2017).

However, there are still many uncertainties about how the forest will respond if there is a consolidation of such changes in the climate. In this regard, in large part, is due to the non-inclusion

of biological mechanisms in the construction of predictive models (Urban et al., 2016). According to the ecological stability theory (Scheffer et al., 2001), along with an environmental gradient, a catastrophic transition regime can be triggered suddenly between stable states if a given resilience threshold is reached. In this way, it is possible to identify the effects of bistability (Hirota et al., 2011; Staver, Archibald & Levin, 2011). A central concept in ecological stability theory is that of resilience. Resilience, in the context of complex ecological systems, can be interpreted as the ability of an ecosystem to recover after suffering a disturbance (Holling, 1973; Pimm, 1984; Scheffer et al., 2001; Folke et al., 2004).

In this study, to understand the potential responses of the Amazon forest to changes in climate, we propose to investigate the ecological mechanism that controls forest-savanna transition regimes and the implications for the forest ecosystem. To achieve this goal, we measured and mapped the resilience of forest and savanna by modeling the multidimensional climatic niche of ecosystems using high spatial resolution remote sensing data. This new approach, which integrates different theoretical and methodological bodies, represents a significant advance for the conservation of Amazonian biodiversity in order to will improve our predictive capacity in anticipating catastrophic transitional events.

Material & Methods

Modeling the multidimensional climate niche of forest and savanna

The presence-absence data of the stable ecosystem states, used as input in ecological niche modeling, were defined from a trimodal frequency histogram of the tree cover variable (0-100%) from the MODIS (Moderate Resolution Imaging Spectroradiometer Satellite) (Townshend et al., 2011). The spatial resolution of the raster is 6 km inside and covers all of South America. The

stable savanna state presents tree cover values between 5 and 60%, while forest presents values over 60% (Hirota et al., 2011). Within this range, the steady state in question assumes the presence value (1), and out is considered as absent (0). After correction of classification inaccuracies due to the historical land use bias, based on a consensual basis of high-resolution vegetation classes (Tuanmu & Jetz, 2014), the raster was converted to the point vector format, where each observation received its geographical coordinate of longitude and latitude.

As bioclimatic predictors for ecological niche modeling, we used the climatic dataset CHPclim (v.1.0) produced by the Climate Hazards Group's Precipitation Climatology with a spatial resolution of 0.05 ° (~6 km) to describe the precipitation patterns of South America (Funk et al., 2015). The temperature patterns along the continent were represented with the WorldClim database (Hijmans et al., 2005) with a spatial resolution of 0.041° (~ 5 km). We have selected four bioclimatic predictors related to energy availability (temperature) and humidity (precipitation), which are recognized as essential factors from the ecophysiological point of view of ecosystems (Lehmann et al., 2014; Oliveras & Malhi, 2016): annual cumulative precipitation (ACP); (2) precipitation seasonality coefficient (PSC); (3) annual average of temperature (AAT) and (4) annual range of temperature (ART).

To model the ecological niche of ecosystems as stable states, we used the biomod2 package implemented in the R software (Thuiller et al., 2009). Niche models were calibrated using presence-absence data from each ecosystem combined with the four bioclimatic predictors described above. We have adopted the ensemble strategy, which emphasizes the most consensual predictions among different modeling methods (Araújo & New, 2007; Franklin, 2010), thus minimizing the effect of uncertainties on model prediction (Diniz-Filho et al., 2009)(Diniz-Filho et al., 2009). We utilized ten different methods for build the models: Bioclim (SRE), Classification

Tree Analysis (CTA) (Scull, Franklin & Chadwick, 2005); Maxent (Phillips et al., 2006, 2016); Random Forest (RF) (Breiman, 2001); Generalized Linear Models (GLM) (Guisan, Edwards & Hastie, 2002); Generalized Aditive Models (GAM) (Hastie & Tibshirani, 1986); Function Discriminant Analysis (FDA) (Manel, Dias & Ormerod, 1999); Artificial Neural Networks (ANN) (Manel, Dias & Ormerod, 1999); Multiple Aditive Regression Splines (MARS) (Friedman, 1991). For each method, we ran ten replicates with 75, and 25% partition for training and test, respectively. We evaluated the quality of the models produced by the different methods with the True Skill Statistics (TSS) and Receiver Operating Characteristic (ROC) metrics. The best models to compose the ensemble were selected using the TSS metric that measures quality combining sensitivity and specificity (Allouche, Tsoar & Kadmon, 2006). For threshold effect, only the models with TSS>=0.6 were considered to compose the ensemble. The model of consensual distribution was then obtained through the arithmetic mean among the best models of the different methods (Diniz-Filho et al., 2010).

Spatial resilience boundary for forest and savanna

This study emphasizes the natural transition mechanisms between the Amazonian forest and adjacent savanna ecosystems (e.g., cerrado) from a resilience gradient based on the multidimensional climatic niche of steady states. Therefore, the study area comprises the entire Amazon basin and the adjacent regions bordering the biome, located between latitudes 10 °N and 20 °S and longitudes 40 ° W and 80 °W. The spatial resolution of the raster is 0.05 ° (~ 6 km) containing 432,042 pixels.

Here, climate suitability models derived from ecological niche modeling are used alternatively as a direct and objective measure of ecosystem resilience. To identify the geographical limits of

resilience between the Amazon forest and adjacent savannas, we calculated the amplitude between the resilience gradients of the two stable states over all the pixels in the study area to identify the dominance zones and those where there is bistability in spatially explicit ways. Regions with high amplitude values indicate that forest or savanna, depending on the area, dominate regarding resilience, while low amplitude values (close to zero) suggest that there is a counterbalance of the resilience between the two ecosystems, ecosystems would be equivalent to having bistability.

Predicting resilience thresholds in transition regimes

To identify critical resilience thresholds before forest-savanna transition regimes, we calculated the observed proportion of each stable state (forest or savanna) along each measured unit of forest resilience to the study area. We counted a total of 446 independent and non-autocorrelated samples, where the forest and savanna ratio were calculated, ranging from 0 (zero) to 1 (one) along the resilience gradient. The observed proportions, such as response variable, were then plotted as a function of the forest resilience gradient. Then, we fitted a non-linear local regression statistical model (LOESS) to the observed data to estimate the critical cut points under the resilience gradient at the moment the curves assumed independent behavior and diverged each other.

Calculating the trend towards a transition regime and its associated climatic thresholds

We measured the propensity for transitions regimes from the spatial anomaly of resilience calculation between the rasters of the two stable states. The values of the output of the operation vary between [+1000] (positive), which are related to the increase of the forest resilience, and [-1000] (negative) indicating an increase of the resilience of savanna. Using this gradient, we counted the number of forest and savanna observations under each unit of the measured anomaly

to calculate the observed proportion of forest and savanna along the gradient of the anomaly. After this procedure, which generated a set of 1,805 observations with statistical independence and without spatial autocorrelation, we plot the observations under a two-dimensional scatterplot, where the respective bioclimatic predictors are the axes.

We separate the factors under the two-dimensional climate space in (a) energy availability and humidity and (b) climatic seasonality. After this, we then fit a linear model, which the orientation of the line will indicate the type of statistical relationship between the predictors and the tendency to transformations between the ecosystems. By assigning a color gradient, related to the trend variable to a transition regime, it was also possible to identify the climatic thresholds critical to the transition between stable states from abrupt color changes.

Results

We map the distribution of ecosystem resilience of stable forest and savanna states based on the occupation of their respective multidimensional climatic niches (Figure 1A and B). The models presented high sensitivity in predicting the alternating dominance of stable states over space with synchronized geographic substitution between ecosystems. Such pattern of alternating dominance between the two stable states is further evident in Figure 1C, where high resilience amplitude values dominate almost the entire study area. However, we have detected only a narrow boundary of bistability between the two ecosystems, where low values of resilience amplitude (close to zero) prevail, highlighted by the black rectangles in Figure 1C. Such a bistable ecotonal zone should be responsible for the mediation of transition events between the two stable states, being described in the theoretical field as Maxwell's point. Its presence indicates, in addition to bistability among the ecosystems, a low hysteresis, in case the return to the original stable state occurs.

Figure 1. Ecosystem resilience gradient and Maxwell point detection. Estimated climate resilience for the forest (A) and savanna (B). In (C), the amplitude of resilience between forest and savanna gradients. The rectangles in (C) under the lowest values indicate the boundary between the two ecosystems, where a bistability pattern and low hysteresis prevail.

In Figure 2, we observed empirically, under the forest resilience gradient, that, from a given boundary, towards the highest values, there is a predominance of the stable state of forest (green balls), reflected in the highest proportion of observations when compared to savannas (purple balls). Below an absolute limit of resilience, toward the lower values, the pattern reverses, since there is proportionately more savanna than forest. However, between the two extremes of the gradient, we identified an ecotonal resilience zone (green-moss rectangle), where the observed values between forest and savanna are proportionally similar (~ 0.5). Such pattern indicates the presence of mosaics of habitats in the landscape, where there is a dominance of either of the two stable states (Figure 2). With the aid of a non-linear local regression model fitted to the data, we observed that critical resilience values before catastrophic transition events between forest and savanna are between 704 to 448 under the forest resilience gradient.

Figure 2. Critical resilience thresholds and the bistable ecotonal zone. Under high resilience values (>= 704) dominance of forests (green balls), while in low values (<= 448) savannas stand out (purple balls). Under an intermediate zone of the resilience gradient (green-moss polygon), there is a balance of the observed proportions of forest and savanna, indicating an area of bistability. This transition zone should play a vital role in the mediation of stable state change events between forest and savanna.

In Figure 3, we present a trend metric for catastrophic transition regimes under the two-dimensional climate space of the study area. In the graph of energy availability and humidity for ecosystems (Figure 3A), we observed that there is a strong tendency towards catastrophic transformations between forest and savanna associated with a critical threshold of moisture availability. At precipitation levels below the threshold of 1500 mm/year (ACP), there is a sudden change with an evident increase in the chance to savanna, independent of the observed mean annual temperature (AAT) values. On the other hand, in the climatic seasonality graph (Figure 3B), the results indicate that the increase in climatic seasonality, both regarding temperature (ART) and precipitation (PSC), are positively correlated with the tendency to more open environments in the area of study. Such pattern may lead to events of sudden transitions from forest to savanna.

Figure 3. The propensity for catastrophic transition regimes under bidimensional climate space. In (A) on the X-axis is the average annual temperature gradient (AAT) and on the Y-axis the annual cumulative precipitation (ACP). In (B) on the X-axis is the annual range of temperature (ART) and on the Y-axis is the seasonal precipitation coefficient (PSC). In all, we used n=1805 observations.

Discussion

The evidence presented here, such as Maxwell's point detection in a spatially explicit way, reinforces that a possible transition regime between forest and savanna would occur suddenly and in catastrophic proportions, if the critical resilience threshold is reached (Staal et al., 2016). The erosion of biodiversity, with the massive extinction of forest species through a phenomenon described as die-back forest (Cox et al., 2004), would result in the systematic loss of resilience

induced by anthropogenic environmental changes. This process of degradation, in theory, would culminate in the consolidation of another level of ecological stability on the Amazon basin, with a lower density of tree cover (e.g., savannas) (Zemp et al., 2017). This result is possible because forests are more vulnerable to climate change shortly than other terrestrial ecosystems (Perez, Stroud & Feeley, 2016).

It appears that the transition process over the Amazon basin has already begun (Malhi et al., 2008; Davidson et al., 2012). Observed empirical evidence, with data from different sources, has shown that the forest is losing its natural self-regeneration capacity. In general, slower recovery of these ecosystems has been observed in structural and functional terms after disturbances, mainly under the southeastern and eastern edges of the biome, near the ecotonal zone with the cerrado. For example, the ability of forests to retain carbon in biomass in this region has been compromised as a function of the observed moisture deficit (Phillips et al., 2009; Brienen et al., 2015; Feldpausch et al., 2016; Baccini et al., 2017). Amazonian floodplain forests have also shown a slower recovery rate after fire events and prolonged dry periods (Flores et al., 2017). In the same sense, severe drought events are also associated with high tree mortality rates (Allen et al., 2010; Greenwood et al., 2017), with effects aggravated by forest fires (Barlow & Peres, 2008; Brando et al., 2014).

In this sense, the explicit determination of critical thresholds of resilience at large scales means a particularly significant advance for Amazonian conservation, since we would have a better predictive capacity to anticipate the effects of climate changes on the forest. Such information will guarantee a more precise action towards ecosystem conservation plans (Scheffer et al., 2015). Some authors have already explored this hypothesis previously based on coupled models of climate and vegetation dynamics (Oyama & Nobre, 2003; Nobre & Borma, 2009; Salazar &

256 Nobre, 2010), but without explicitly exploring the ecological mechanism underlying transition
257 regimes.

258 The bistable ecotonal zone (Maxwell point) is associated with catastrophic transition regimes and
259 also indicates the presence of an environmentally well-defined threshold (Wuyts, Champneys &
260 House, 2017). In this sense, the correlation of the observed trends to a transition regime under the
261 two-dimensional climate space allowed the design of a useful climatic metric, which indicates the
262 thresholds for the monitoring of catastrophic events. Also, with such a procedure it was possible
263 to measure the importance of bioclimatic predictors in determining potential devastating transition
264 regimes.

265 Our findings indicate that changes in mean temperature would have little influence on the
266 transition regime between forest and savanna. In other words, with a higher concentration of
267 greenhouse and increasing global temperatures, will not be the primary factor that will determine
268 catastrophic transition events between forest and savanna. Although the relevance of the effect of
269 CO2 fertilization on forest productivity is recognized (Lloyd & Farquhar, 2008; Cox et al., 2013;
270 Huntingford et al., 2013).

271 Our results indicate that the most important factor when analyzing the energy and humidity
272 availability axis is the annual cumulative volume of precipitation. According to our findings, in
273 order not to trigger catastrophic transition events between forest and savanna, it would have to rain
274 at least 1500 mm/year in a particular region. Some authors corroborate this critical climatic
275 threshold with other methodological approaches (Malhi et al., 2009; Wuyts, Champneys & House,
276 2017). In a recent study, the author indicates a breakpoint of approximately 2000 mm/year
277 (Ahlström et al., 2017) as a critical value for the maintenance of high values of gross primary
278 productivity. Although, the conclusion was not based on an objective measure of ecosystem

resilience. However, all the data observed and simulated indicate a tendency to increase aridity over the Amazon basin (Li et al., 2008a; Malhi et al., 2009; Fu et al., 2013; Boisier et al., 2015; Erfanian, Wang & Fomenko, 2017), specially on the southwest and east edges of the biome.

Under the climatic seasonality, our results indicate that the increase in seasonality of precipitation and temperature has a direct association with a higher propensity for catastrophic transition regimes between forest and savanna. These data suggest that rainfall is more frequent in the Amazon basin due to the prolongation of the dry season, mainly on the eastern edges of the southwest (Li et al., 2008a; Fu et al., 2013; Boisier et al., 2015). Another negative factor, which has further accentuated the increasing seasonality of precipitation, is the increase in the frequency of extreme drought events, mainly caused by more severe El-Niño (Jiménez-Muñoz et al., 2016).

Our results indicate that, as a function of the alternating dominance pattern through the resilience gradient, the Amazonian forest and adjacent savanna ecosystems represent two independent stable states, where each one has its basin of attraction, previous corroborating studies (Hirota et al., 2011; Staver, Archibald & Levin, 2011). However, our findings suggest that coexistence between savanna and forest is restricted to a narrow ecotonal zone of best ability, known as Maxwell's point, contrary to the hypothesis that forests and savannas have extensive areas of bimodality (Staver, Archibald & Levin, 2011). Such pattern can be explained by the fact that our models were based on the multidimensional climatic niche of stable states, which means a higher sensitivity due to better ecological resolution when compared to previous, generally two-dimensional, studies. Wuyts et al. (2017) found a similar result to this study, also indicating that human activities, such as changes in soil use, have promoted the increase of bistability in the tropical region of South America.

Conclusions

The loss of resilience due to climate change can lead to sudden catastrophic transition events between forest and savanna in the tropical region. Reducing the availability of moisture and increasing climatic seasonality appear as the main risk factors. If such critical climatic thresholds are reached, there will probably be the massive extinction of biodiversity in the Amazon rainforest.

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Figure 1

Ecosystem resilience gradient and Maxwell point detection.

Estimated climate resilience for the forest (A) and savanna (B). In (C), the amplitude of resilience between forest and savanna gradients. The rectangles in (C) under the lowest values indicate the boundary between the two ecosystems, where a bistability pattern and low hysteresis prevail.

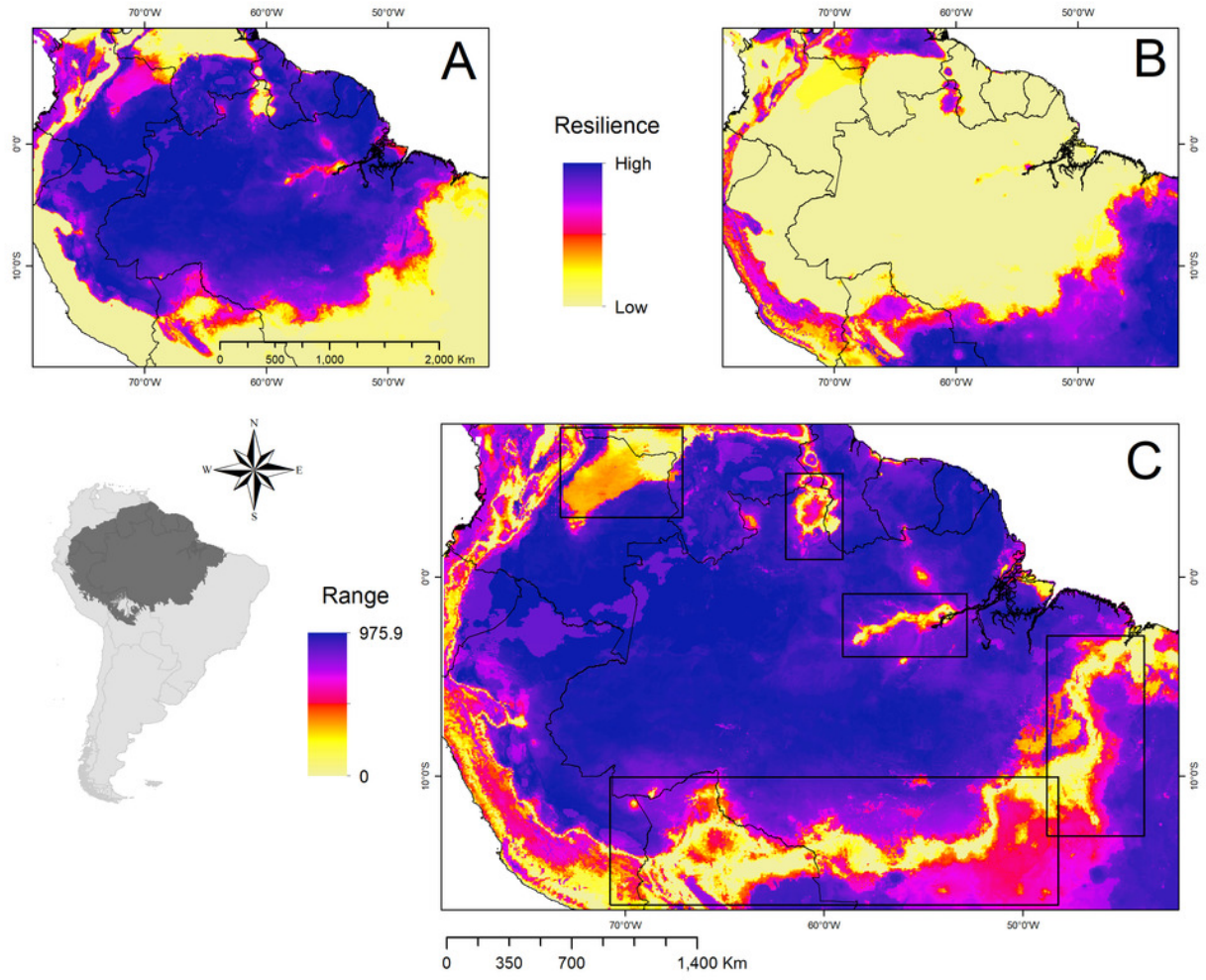

Figure 2

Critical resilience thresholds and the bistable ecotonal zone.

Under high resilience values (>= 704) dominance of forests (green balls), while in low values (<= 448) savannas stand out (purple balls). Under an intermediate zone of the resilience gradient (green-moss polygon), there is a balance of the observed proportions of forest and savanna, indicating an area of bistability. This transition zone should play a vital role in the mediation of stable state change events between forest and savanna.

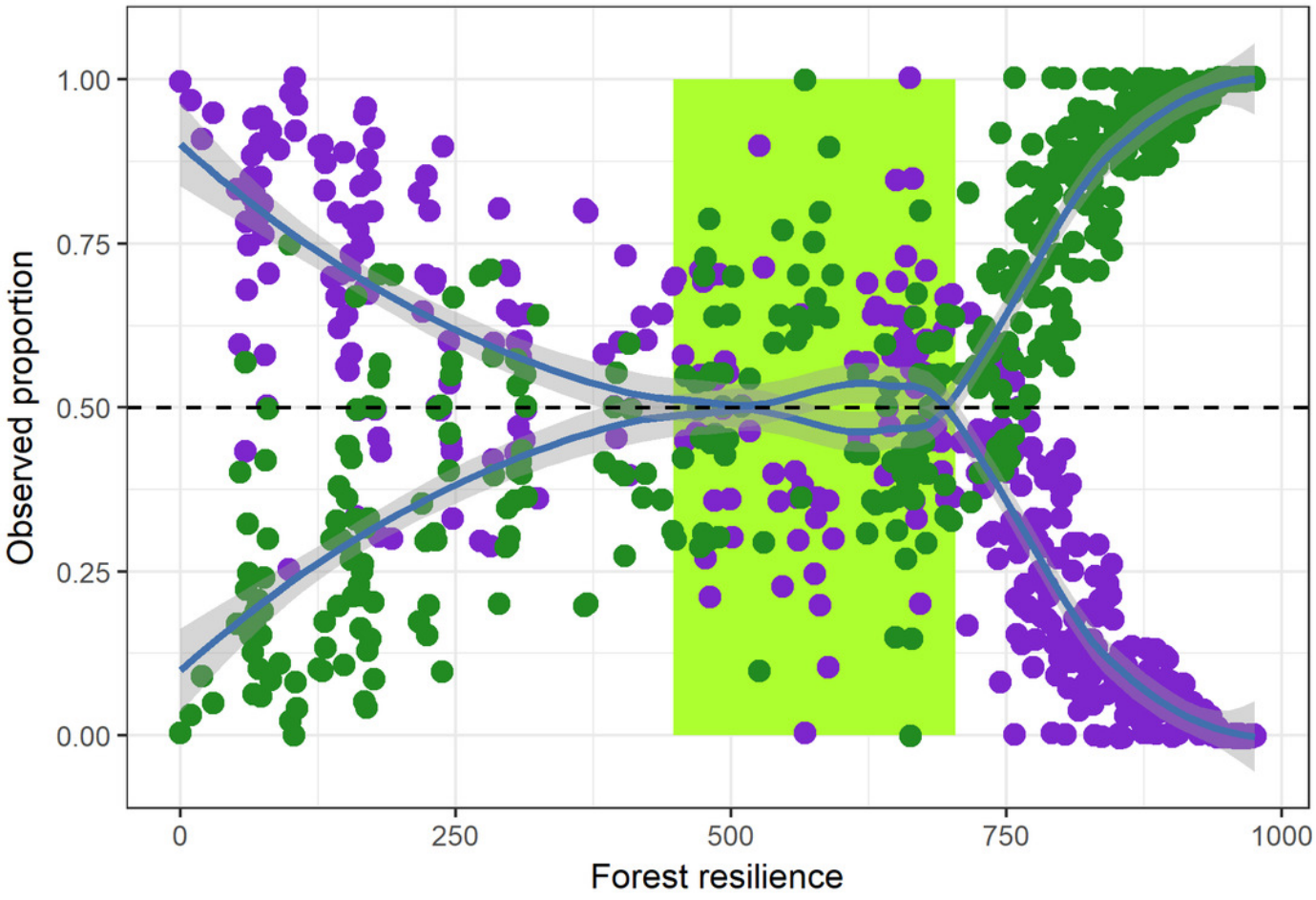

Figure 3

The propensity for catastrophic transition regimes under bidimensional climate space.

In (A) on the X-axis is the average annual temperature gradient (AAT) and on the Y-axis the annual cumulative precipitation (ACP). In (B) on the X-axis is the annual range of temperature (ART) and on the Y-axis is the seasonal precipitation coefficient (PSC). In all, we used *n*=1805 observations.