

# Analysis of critical transitions at the Global Forest

## Abstract

One of the most important changes produced in the biosphere is the replacement of forest areas with human dominated landscapes. These areas contain much less species than the natural ecosystem they replaced, and are one of the main drivers of extinctions in the anthropocene. The forest cover is also coupled to atmospheric dynamics and the balance of gases in the atmosphere. The dynamics of forest fragments or patches is central to its function as ecosystem. In different kinds of vegetation including forests the patch size distributions follow power laws or approximate power law, but all these patterns have been observed at relatively small scales. Here we studied the distribution of forest patch sizes at a global level and its changes in the last fourteen years. We hypothesize that the global forest patches should follow a power law distribution. Power laws are a signal of critical phase transitions, where the system changes suddenly of state at a critical point, in the case of forest patches this change implies an abrupt change in the connectivity that poses a risk on the functioning of forest as an habitat and as an ecosystem. Thus we used early warning indicators derived from phase transition theory to estimate the closeness of forest at the continental level to a possible critical transition. We found that all the regions of the world follow power laws in its forest patch structure, except Eurasia that fits a very similar distribution: the log-normal. The observation of power laws is a requirement to assume that a critical transition exists but other indicators are needed. We calculated early warning indices based on the temporal dynamics of the largest patch. We observed that the tropical forest of South America is approaching a critical transition in its patch structure, and the tropical forest of Africa is going through this transition. This is the first time that early warning indicators are applied to a continental scale and the signals of these transitions are detected. The forest fragments that are involved in these transitions are in the order of millions of  $\text{km}^2$ , thus there is some time until this tendency compromises its internal functioning as ecosystems. This emphasizes the urgent need of a coordinate management crossing the borders of individual countries to protect these two fundamental tropical ecosystems.

## Introduction

Forest is one of the most important ecosystems on earth providing habitat for a large proportion of species and contributing extensively to global biodiversity [1]. In the previous century human activities have reached the global scale changing influencing the bio-geochemical cycles [2]. One of the most dramatic human induced changes is the replacement of 40% of Earth's formerly biodiverse land areas with landscapes that contain

only a few species of crop plants, domestic animals and humans [3]. These changes have been happening locally but they have been accumulated over time and have reached a global scale that constitutes a global forcing [4]. That means a force that can induce changes at the level of the whole biosphere. Another global scale forcing that is tied to habitat destruction is fragmentation. Fragmentation is defined as the division of a continuous habitat into separated portions that are smaller and more isolated, this produces multiple interwoven effects: reductions of biodiversity between 13% and 75%, decreasing forest biomass and changes in nutrient cycling [5].

Complex interaction between species and feedbacks at different levels of organization [6] can produce abrupt changes called critical transitions [7]. These abrupt state shifts can not be linearly forecasted from past changes so they are difficult to predict and manage [7]. Critical transitions had been detected mostly at local scales [8,9], but the accumulation of changes in local communities that overlap geographically can propagate and cause an abrupt change of the entire system [4], this is coupled with the existence of global scale forcings implies the possibility that a critical transition occurs at a global scale [10,11].

There are two general classes of critical transitions: one where the sudden shift between states is mostly irreversible showing the presence of two stable states. These show hysteresis that is a catastrophic regime shift [12], also called first order transitions. This could be the result of a positive feedback mechanisms [13], for example the growth of forest in a site is more probable if it is surrounded by forest than if it is surrounded cultivated or degraded land [14]. This is observed in semiarid regions where the transition from a vegetated state to a desertic one occurs as a result of human pressures and climatic change [15], in biological invasions [16], and biology and social sciences in general [17].

The second are continuous critical transitions [18], or second order transitions. In this case there is a narrow region where the system changes from one domain to another, besides the change is also sudden it is continuous and theoretically reversible. These transitions are linked to spatial patterns: at the critical point we can observe scale invariant fractal structures characterized by power law patch distributions [19]. The simplest model where we can observe this kind of transitions is a random map: each site has an independent probability  $p$  of being occupied. Even in this simple setting, starting with  $p = 0$ , when  $p$  reaches a certain value the landscape changes from fragmented to a connected state. Another more relevant model is about forest fires, the key factor in this case is the existence of an ecological memory: after a fire biomass is consumed so there must be some time to build up fuel before a recurring fire [20].

The spatial phenomena studied by percolation theory is related to the concept of connection, in a very general way we can find a path between the objects that belongs to a system [17], thus connectivity is a

1 fundamental property of general systems and also, ecosystems from forests [21] to marine ecosystems [22] and  
2 the whole biosphere [23]. Percolation is characterized by two domains or phases. One dominated by short  
3 range interactions where information can not spread and another where long range interactions are possible  
4 and information can spread over the whole area. In this context information is taken in a broad sense and  
5 can represent species dispersal or movement. Thus, there is a critical point that defines a threshold boundary  
6 between the two phases and the system could be driven close or far of the critical point by an external force.  
7 Climate change and deforestation are the main forces that could be the drivers of a phase change in forests  
8 [5,24].

9 Percolation thresholds are important to understand forest growth dynamics: when the system is above the  
10 critical point is in a connected state and the dispersal of species inside the forest is enhanced. Dispersal  
11 strategies are influenced by percolation thresholds in three-dimensional forest structure [25]. Recently has  
12 been show that not only the patches but species distributions also have percolation thresholds [26]. If we  
13 push the system below the percolation threshold the system will be in an unconnected state, which could  
14 produce a biodiversity collapse [27,28]. In an opposite direction being in a connected state could produce the  
15 acceleration of an invasion of forest into a prairie [29,30].

16 One of the problems with critical transitions is that the value of the critical threshold is not known in advance,  
17 and near that point a small change can precipitate a state shift of the system, thus they are very difficult to  
18 anticipate. Several methods were developed to detect the closeness of the critical point such as a deceleration  
19 in recovery from perturbations, an increase in variance in the spatial or temporal pattern. Besides some of  
20 these methods have been experimentally tested [8,31], still there is a debate about the its reliability [32,33].

21 In most real systems where spatial dynamics is important we could observe processes like: demographic  
22 fluctuations, spatial heterogeneities and/or dispersal limitation. This processes that introduce stochasticity  
23 can convert a catastrophic transition to a second order transitions [13]. Forest is a system where these three  
24 processes are ubiquitous so continuous transitions should be more probable than catastrophic transitions,  
25 moreover some evidence of a second order critical transition related to drought and fire has been found in  
26 tropical forest [34].

27 From the point of view of percolation theory, the necessary condition we need to be near a critical transition  
28 is that the patch size distribution follows a power-law. But this is not a sufficient condition because power-law  
29 distributions are present in a wide range of conditions in vegetation of arid ecosystems [35,36] and ant colonies  
30 [37] and attached microalgae [38,39]. The origin of these power-laws is attributed to a facilitation mechanisms  
31 [40,41], that is likely to be present in forest [42].

Our objectives were to evaluate what models best describe forest patch distribution at a continental scale; examine how patch size and connectivity change between regions and across time; and look for evidence that forests are near critical fragmentation thresholds. The advantage of using data at a continental scale is that for very large systems the transitions are very sharp thus much easier to detect than at smaller scales, where noise can mask the signals of the transition.

## Methods

### Area definition

We choose mainland zones at a continental scale to analyze based in the possibility of connection, close patches of continuous forest must connect the region, big islands of more than XXXX km<sup>2</sup> like Madagascar were included as a separate regions, smaller islands where not included, we considered big islands connected to the mainland when they are at one km or less distance away. With this criteria we defined three regions in America, one corresponding to South America temperate forest (SAT), another to subtropical and tropical forest up to Mexico (SAST), and the last covering USA and Canada forest (NA). Europe and north Asia were all connected and they are included in one region (EUAS), the other regions are south Asia (SEAS), Africa (AF), and Australia and islands (OC) (Supplementary figure S1-S6). Each regions have subregions that correspond to nearby islands (Table 1).

To define patches we use the MODerate-resolution Imaging Spectroradiometer (MODIS) Vegetation Continuous Fields (VCF) Tree Cover dataset. This dataset is produced at 250-meters resolution, globally from 2000 to 2014, we used the version 051 [43]. There are several definition of forest [44], but we choose a 30% threshold to convert the percentage tree cover to a binary image of forest and non-forest pixels. This was the definition used by the United Nations' International Geosphere-Biosphere Programme [45], and studies of global fragmentation [5]. Patches of contiguous forest were determined in the binary image by grouping connected pixels using a neighborhood of 8 forest units (Moore neighborhood). To fit the patch size distributions we set a minimal patch size ( $X_{min}$ ) at nine pixels to avoid artifacts at patch edges due to discretization [46].

### Percolation theory

A more indeep introduction of percolation theory can be found elsewhere [19] and a review from an ecological point of view is available [47]. Here to explain the basic elements of percolation theory we formulate a simple model: we represent our area of interest by a square lattice and each site of the lattice can be occupied—e.g. by

forest—with a probability  $p$ . The lattice will be more occupied when  $p$  is greater, but the sites are randomly distributed. We are interested in the connection between sites so we have to establish a neighborhood, for this example we define the eight sites surrounding the focal site as neighbors. The sites that are neighbors define a patch. When there is a patch that connects the lattice from opposite sides it is said that the system percolates. The percolating patch suddenly appears at some value of  $p$  called the critical point  $p_c$ .

Thus percolation is characterized by two well defined phases: the unconnected phase (called subcritical in physics) when  $p < p_c$ , a individual of a species cannot travel far away inside the forest, the forest is fragmented, or in a general sense information cannot spread. The second is the connected phase (supercritical) when  $p > p_c$ , species can move inside a forest patch from side to side of the area, information can spread over the whole area. Near the critical point several scaling laws arise: the structure of the patch that spans the area is fractal, the size distribution of the patches is power-law, and other quantities also follow power-law scaling [19].

The value of the critical point  $p_c$  depends on the geometry of the lattice and on the definition of the neighborhood, but other power-law exponents only depend on the lattice dimension. Close to criticality is found that the distribution of patch sizes is:

$$(1) \ n_s(p_c) \propto s^{-\alpha}$$

where  $n_s(p)$  is the number of patches of size  $s$ . The exponent  $\alpha$  does not depend on the details of the model and it is called universal [19]. These scaling laws can be applied for landscape structures that are approximately random, with correlations if the forest sites are correlated over short distances [48]. This called in physics isotropic percolation universality class, and corresponds to an exponent  $\alpha = 2.05495$ , if we observe that the patch size distribution has another exponent it will not belong to this universality class and other kind of mechanisms should be invoked. Percolation thresholds can also be generated by models that have some kind of memory [49,50]: a patch that has been exploited for many years will recover different than a recently deforested forest patch. In this case the system can belongs to a different universality class or in some cases there is no universality and the value of  $\alpha$  will depend on the parameters and details of the model [51].

## Patch size distributions

We fitted the empirical distribution of forest patch areas to four distributions using maximum likelihood estimation [52,53]. The distributions were: power-law, power-law with exponential cut-off, log-normal, and exponential distributions. We assume that the patch size distribution is a continuous variable that was

1 discretized by remote sensing data acquisition procedure.

2 Besides the hard  $X_{min}$  limit we set due to discretization, the power-law distribution needs a lower bound for its  
3 scaling behaviour. This lower bound is also estimated from the data by maximizing the Kolmogorov-Smirnov  
4 (KS) statistic comparing empirical to fitted cumulative distribution function [53]. We also calculate the  
5 uncertainty of the parameters using a non-parametric bootstrap method [54].

6 The corrected Akaike Information Criteria ( $AIC_c$ ) and the Akaike weights were computed for each model  
7 [55]. Akaike weights ( $w_i$ ) are the weight of evidence in favor of model  $i$  being the actual best model for the  
8 situation at hand given that one of the  $N$  models must be the best model for that set of  $N$  models.

9 Additionally, we computed the goodness of fit of the power-law model following the bootstrap approach  
10 described by Clauset et. al [53], where simulated data sets following the fitted model are generated, and a  
11 p-value equal to the proportion of simulated data sets that has a KS statistic less extreme than empirical  
12 data. The criterion to reject the power law model was  $p \leq 0.1$  but as we have a very large n negligible small  
13 deviations could produce a rejection [56], thus we chose a  $p \leq 0.05$  to reject the power law model.

14 To test for differences between the fitted power law exponent for regions and subregions we used a weighted  
15 linear regression with a residual auto-correlation structure. For this we use a generalized least squares  
16 procedures: function gls from package nlme [57]. The weights were the bootstrapped 95% confidence intervals  
17 and we added an auto-regressive model of order 1 to the residuals to account for temporal autocorrelation.

18 Image processing were done in MATLAB (Version??). All statistical analyses were done using the GNU R  
19 version 3.3.0 [58], using code provided by Cosma R. Shalizi for power law with exponential cutoff model and  
20 the powerLaw package [59] for fitting the other distributions. The complete source code for the processing  
21 of images and analysis, the patch size data and the figures with each fit (year by region by subregion) are  
22 available at figshare <http://dx.doi.org/10.6084/m9.figshare.XXXXX>.

## 23 **Largest patch dynamics**

24 The largest patch is the one that connects the highest number of sites in the area, it has been used extensively  
25 to indicate fragmentation [21,60]. The relation of the size of the largest patch  $S_{max}$  with critical transitions  
26 has been extensively studied in relation to percolation phenomena [19], but seldom used in ecological studies  
27 (but see [48]). When we are in a connected state ( $p > p_c$ ) the landscape is almost insensitive to the loss of a  
28 small fraction of forest, but close to the critical point the same loss can have an important effects [18,47]. At  
29 this point the largest patch will have a filamentary structure, extended forest areas will be connected by thin

1 threads, thus small losses could produce big fluctuations.

2 One way to evaluate the fragmentation of the forest is to calculate the proportion of the largest patch against  
3 the total area [61], as is very difficult to evaluate the total area that the forest could potentially occupy  
4 we use the total forest area. Thus we calculate the proportion of the largest patch for each year, dividing  
5  $S_{max}$  by the total forest area of the same year:  $RS_{max} = S_{max} / \sum_i S_i$ . This has the effect of eliminate the  
6 fluctuations produced  $S_{max}$  due to environmental or climatic changes affecting all the region considered.  
7 When the proportion  $RS_{max}$  is big (more than 60%) the largest patch contains most of the forest so there  
8 are less small forest patches and the system is probably in a connected phase. When this proportion is low,  
9 20% or less there are a greater quantity of forest patches and we are probably at the fragmented phase. But  
10 it is possible that with a high  $RS_{max}$  the system is near a percolation threshold, this has to be evaluated  
11 using the temporal fluctuations.

12 We calculate the fluctuations around the mean with the absolute values  $\Delta S_{max} = S_{max}(t) - \langle S_{max} \rangle$ , and  
13 also using the proportions of  $RS_{max}$ . To characterize the fluctuations we fitted three empirical distributions:  
14 power-law, log-normal, and exponential; using the same methods described previously. We expect that large  
15 fluctuation near a critical point have heavy tails (log-normal or power-law) and that fluctuations far from  
16 a critical point have exponential tails, corresponds to Gaussian processes. As the data set spans 15 years  
17 we have do not have enough power to reliably detect which distribution is better [53]. To improve this we  
18 performed the goodness of fit test described above for all the distributions. We generated animated maps  
19 showing the fluctuations of the 2 largest patches to aid in the interpretations of the results.

20 A robust way to detect if the system is near a critical transition is to analyze the increase of variance of the  
21 forest's density [62], the problem is that the variance increase appears when we are very close to the transition  
22 [51]. An alternative is to analyze the variance of the fluctuations of the largest patch  $\Delta S_{max}$ , a maximum  
23 is attained at the critical point but a significant increase occurs well before the system reach the threshold  
24 [51]. Also before the critical fragmentation the skewness of the distribution of  $\Delta S_{max}$  should be negative,  
25 this implies that the fluctuations below the average are more frequent. We characterized the increase in the  
26 variance using quantile regression: if variance is increasing the slopes of upper or/and lower quartiles should  
27 be positive or negative.

## 28 Results

29 The power law distribution was selected as the best model in most of the cases (Supplementary Figure S7).  
30 In a small number of cases (4 of 300) the power law with exponential cutoff was selected but the value of the

parameter  $\alpha$  was similar by  $\pm 0.02$  to the pure power law. Moreover the patch size where the exponential tail begins is very large (determined by the inverse of the exponential decay parameter), thus we use the power law parameters (See Supplementary data, region EUAS3). In finite-size systems the favored model should be the power law with exponential cutoff, because the power-law tails are truncated to the size of the system [19]. Here the regions are so large that the cutoff is practically not observed.

There is only one region that does not follow a power law: Eurasia mainland, and it follows a log-normal distribution. The log-normal and power law are both heavy tailed distributions and they are difficult to distinguish. In our case Akaike weights have very high values for log-normal (near 1), meaning that this is the only possible model. Additionally the goodness of fit tests clearly rejected the power law model in all cases for this region (Supplementary table S1, region EUAS1). In general the goodness of fit test rejects the power law model in less than 10% of cases. In large forest areas like Africa mainland (AF1) or South America tropical-subtropical (SAST1), larger deviations are expected and the rejections rates are higher so the proportion is 30% or less (Supplementary Table S1).

Taking into account the bootstrapped confidence intervals of each power law exponent ( $\alpha$ ) and the temporal autocorrelation, there is no significant differences between  $\alpha$  for the regions with biggest forest areas—greater than  $10^7$  km<sup>2</sup> (Figure 1 and Supplementary figure S8). And also there is no differences between these regions and the ones with forest areas smaller than  $10^7$  km<sup>2</sup> (Supplementary Table S2 & S3), and all the slopes of  $\alpha$  are not different from 0. Thus we can talk about global average  $\alpha = 1.908$  with a bootstrapped 95% confidence interval between 1.898 and 1.920.

The proportion of the largest patch relative to total forest area  $RS_{max}$  for regions with more than  $10^7$  km<sup>2</sup> of forest is showed in figure 2. South America tropical and subtropical (SAST1) and North America (NA1) have a higher  $RS_{max}$  of more than 60%, the other big regions have 40% or less. For regions with less total forest area (Supplementary figure S9 & Table 1), United Kingdom (EUAS3) has a very low proportion near 1%, and other regions have a very high proportion like New Guinea (OC2) and Malaysia/Kalimantan (OC3). The case of SEAS2 (Philippines) is very interesting because it seems to be under 30% until the year 2005, then fluctuates in the range 30-60% then keeps over 60% (supplementary figure S9). Thus this seems to be an example of a transition from a unconnected state to a connected state, that deserves an in-depth further study.

We analyzed the distributions of relative fluctuations of the largest  $\Delta RS_{max}$  and absolute fluctuations  $\Delta S_{max}$ . The model selection for  $\Delta S_{max}$  results in power laws distributions for all regions (Supplementary table S6). The goodness of fit test (GOF) did not reject power laws in any case, but either can not reject the other models except in few cases, this is due to the small number of observation we have for this analysis. When



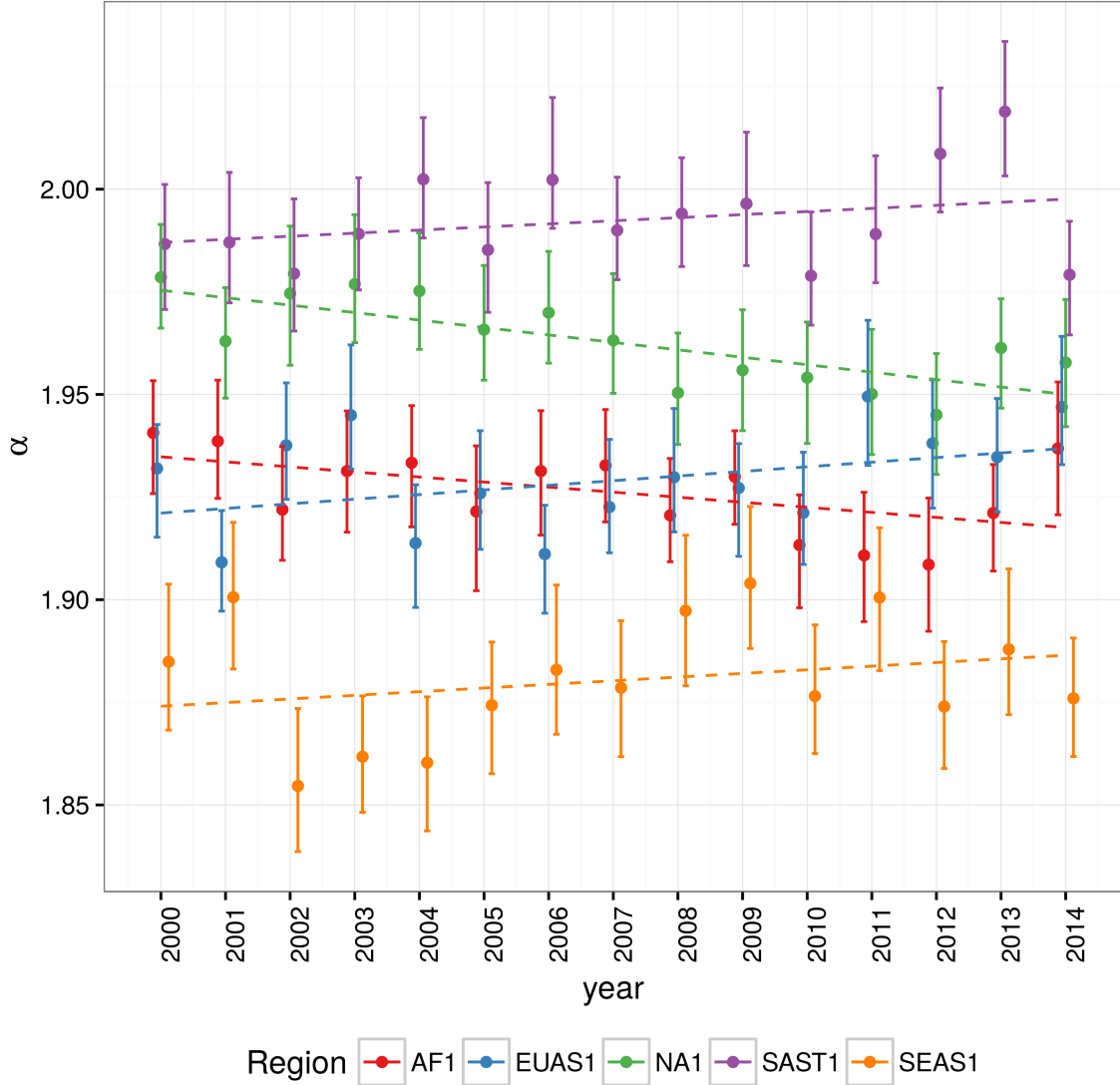


Figure 1: Power law exponents ( $\alpha$ ) of forest patch distributions for regions with total forest area  $> 10^7$  km<sup>2</sup>. Dashed horizontal lines are the fitted generalized least squares linear model, error bars are 95% confidence intervals estimated by bootstrap resampling. The regions are AF1: Africa mainland, EUAS1: Eurasia mainland, NA1: North America mainland, SAST1: South America subtropical and tropical, SEAS1: Southeast Asia mainland. For EUAS1 the best model is log-normal but the exponents are included here for comparison.

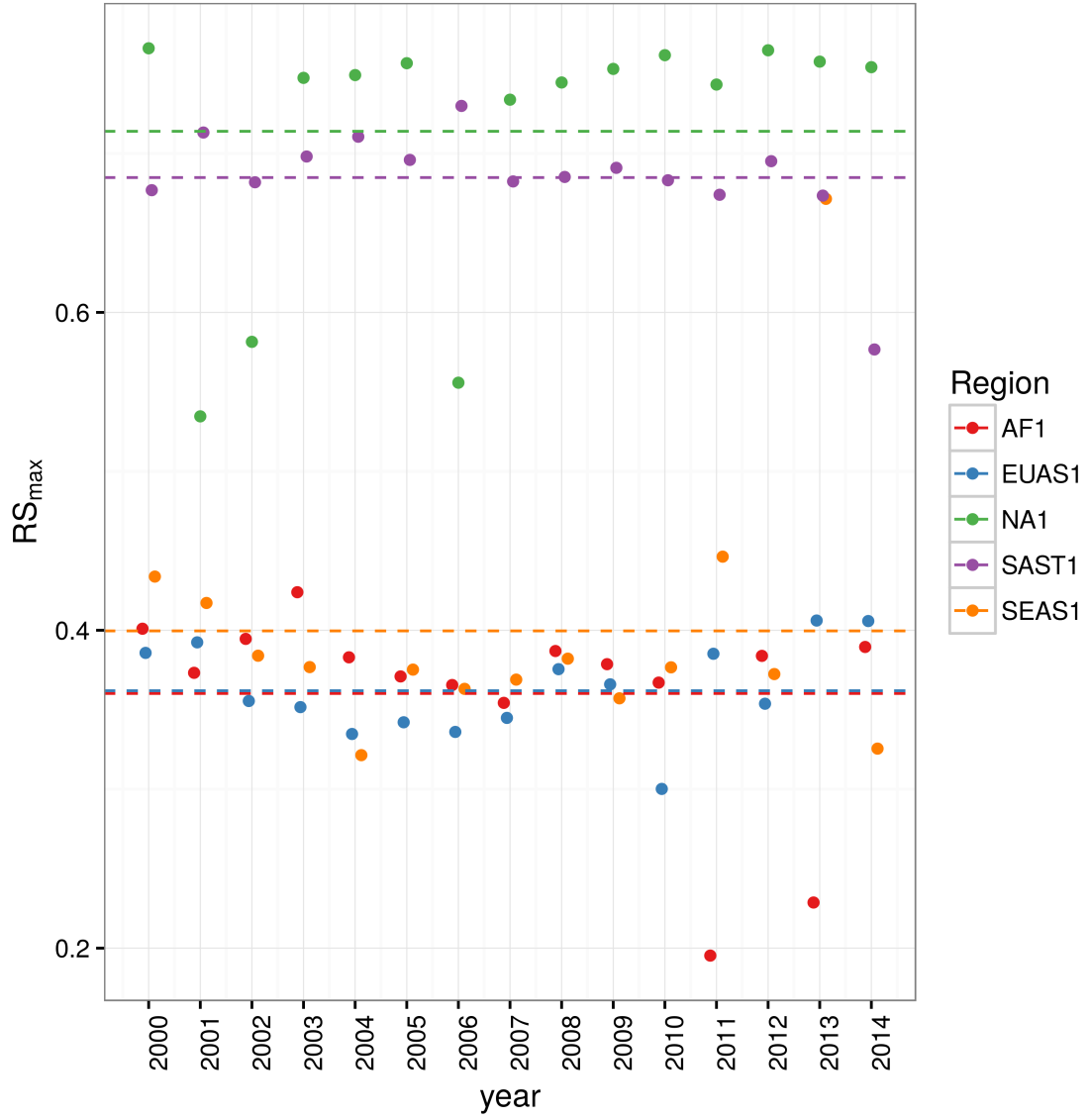


Figure 2: Largest patch proportion relative to total forest area  $RS_{max}$ , for regions with total forest area  $> 10^7$  km<sup>2</sup>. Dashed lines are averages across time. The regions are AF1: Africa mainland, EUAS1: Eurasia mainland, NA1: North America mainland, SAST1: South America tropical and subtropical, SEAS1: Southeast Asia mainland.

we analyzed  $\Delta RS_{max}$  we found some differences: Eurasia mainland (EUAS1), New Guinea (OC2), Malaysia (OC3), New Zealand (OC6, OC8) and Java (OC7) all follow an exponential distribution (Supplementary Table S7). We only considered that fluctuations follow a power law when this distribution is selected for both absolute and relative fluctuations.

The animations of the two largest patches (Supplementary data) qualitatively shows the nature of fluctuations and if the state of the forest is connected or not. If the largest patch is always the same patch is most probably that the forest is not fragmented and this happens for regions with a  $RS_{max}$  of more than 40%, like AF2 (Madagascar), NA1 (North America), OC3 (Malaysia), etc. Moreover these regions maintain always the same largest patch, which could represent a core area for conservation. In the regions with  $RS_{max}$  between 40% and 30% the identity of the largest patch changes could change or stay the same in time. For OC7 (Java) the largest patch changes and for AF1 (Africa mainland) it stays the same, this reflects the fact that this is the zone where the critical transition occurs. Only for EUAS1 (Eurasia mainland) we observed that the two patches largest patches are always the same, this means that this region is probably composed of two independent domains and should be divided in further studies. For regions with less than the 30% the identity always change like in SAST2 (Cuba) and EUAS3 (United Kingdom), reflecting that they are in a fragmented state. The case of SEAS2 (Philippines) a transition is observed, in the first period the identity of the largest patch changes and then after 2010 it becomes constant.

The results of quantile regressions are identical for  $\Delta RS_{max}$  and  $\Delta S_{max}$  (supplementary table S4). In the biggest regions, Africa (AF1) have the upper and lower quantiles significant with negative slopes, but the lower quantile slope is lower so we conclude that negative fluctuations and variance are increasing (Figure 3). Eurasia mainland (EUAS1) have only the upper quantile significant with a positive slope so it presents an increase of the variance. North America mainland (NA1) have only the lower quantile is significant with positive slope thus variance is decreasing. For Australia mainland all quantiles are significant, the slope of the lower quantiles is greater than the upper ones thus variances is decreasing (Supplementary figure S10). A summary of the results about variances and all the other indicators is shown in table 1.

Thus the conditions that indicate that a region is near a critical fragmentation threshold are that patch size distributions follows a power law, temporal  $\Delta RS_{max}$  fluctuations also follow a power law, variance of  $\Delta RS_{max}$  is increasing in time and skewness is negative, all these conditions are given only for: Africa mainland (AF1) and South America tropical & subtropical (SAST1).

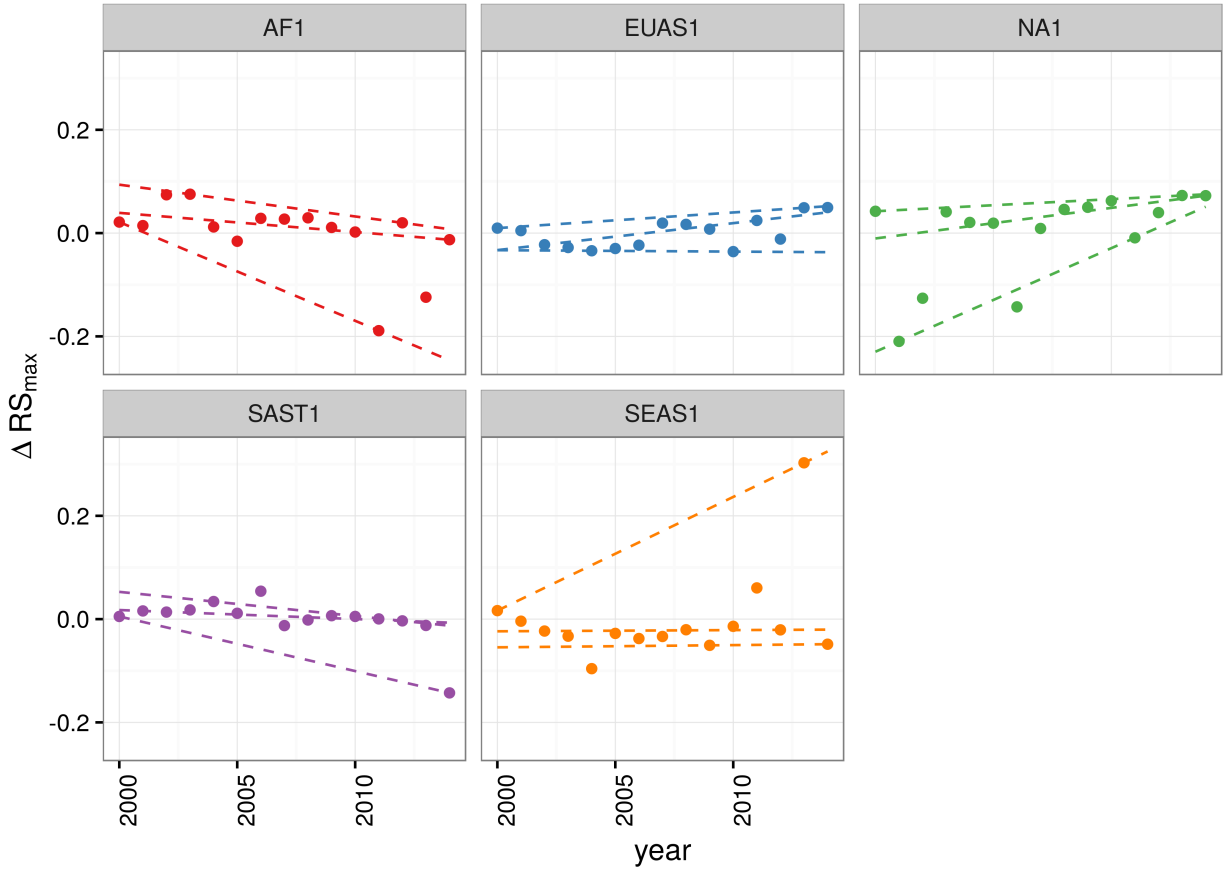


Figure 3: Largest patch fluctuations for regions with total forest area  $> 10^7 \text{km}^2$ . The patch sizes are relative to the total forest area of the same year. Dashed lines are 90%, 50% and 10% quantile regressions, to show if fluctuations were increasing. The regions are AF1: Africa mainland, EUAS1: Eurasia mainland, NA1: North America mainland, SAST1: South America tropical and subtropical, SEAS1: Southeast Asia mainland.

Table 1: Regions, subregions and indicators of closeness to a critical fragmentation threshold. Where,  $RS_{max}$  is the largest patch divided by the total forest area,  $\Delta RS_{max}$  are the fluctuations of  $RS_{max}$  around the mean, skewness was calculated for  $RS_{max}$  and the increase or decrease in the variance was estimated using quantile regressions, NS means the results were non-significant.

Region			Average	Patch Size	$\Delta RS_{max}$	Skewness	Variance
Description			$RS_{max}$	Distrib	Distrib.		
AF	1	Africa mainland	0.36	Power	Power	-1.8630	Increase
	2	Madagascar	0.65	Power	Power	-0.2478	NS
EUAS	1	Eurasia, Mainland	0.36	LogNormal	Exp	0.4016	Increase
	2	Japan	0.94	Power	Power	0.0255	NS
	3	United Kingdom	0.07	Power	Power	2.1330	NS
NA	1	North America	0.71	Power	Power	-1.5690	Decrease
	5	Newfoundland	0.87	Power	Power	-0.7411	NS
OC	1	Australia, Mainland	0.28	Power	Power	0.0685	Decrease
	2	New Guinea	0.97	Power	Exp	0.1321	Decrease
	3	Malaysia/Kalimantan	0.97	Power	Exp	-0.9633	NS
	4	Sumatra	0.92	Power	Power	1.3150	Increase
	5	Sulawesi	0.87	Power	Power	-0.3863	NS
	6	New Zealand south island	0.76	Power	Exp	-0.6683	NS
	7	Java	0.38	Power	Exp	-0.1948	NS

Region			Average	Patch Size	$\Delta RS_{max}$	Skewness	Variance
		Description	$RS_{max}$	Distrib	Distrib.		
	8	New Zealand north island	0.75	Power	Exp	0.2940	NS
SAST	1	South America, Tropical and subtropical forest up to Mexico	0.68	Power	Power	-2.7760	Increase
	2	Cuba	0.21	Power	Power	0.2751	NS
SAT	1	South America, Temperate forest	0.60	Power	Power	-1.5070	Decrease
SEAS	1	Southeast Asia, Mainland	0.40	Power	Power	3.0030	NS
	2	Philippines	0.54	Power	Power	0.3113	Increase

## 1 Discussion

2 We found that the forest patch distribution of most regions of the world followed power laws spanning seven  
3 orders of magnitude. These include tropical rainforest, boreal and temperate forest. Power laws have been  
4 found for several kinds vegetation, but never at global scales as we found in this study. Eurasia does not  
5 follow a power law, but it is a geographically extended region, that probably consist of different domains as  
6 we observed in the patch dynamics animations. The union of two independent power law distribution gives  
7 a lognormal [63], thus in further studies we should split this region in two and test if the distributions are  
8 power laws.

9 Several mechanisms have been proposed for power laws: the first was related self organized criticality (SOC),  
10 in this case the system is driven by its internal dynamics to the critical state, this was suggested mainly for  
11 fire-driven forests [20,64]. Real ecosystems do not seem to meet the requirements of SOC dynamics: their  
12 dynamics is influenced by external forces, interactions are non-homogeneous—they might vary from place to  
13 place [65]. Moreover, SOC for forest-fire dynamics requires the memory effect: fire scars in a site should  
14 accumulate and interfere with the propagation of a new fire. Pueyo et al. [34] do not found that effect so  
15 they suggested that other mechanisms produce the power laws patterns.

The mechanism suggested by Pueyo et al. [34] was isotropic percolation, when a system is near the critical point power law structures arise. This is equivalent to the random forest model that we explained previously, and requires the tuning of an external environmental condition to carry the system to this point. We did not expect that forest growth is a random process at local scales but it could be that combinations of factors cancel out and at large scales the forest dynamics would seem random. If this is the case the power law exponent should be near  $\alpha = 2.05495$ , that is the theoretically predicted, but this value is outside the confidence interval we found for  $\alpha$  (1.898–1.920), thus other explanations are needed.

The mechanism of facilitation has been suggested as an explanation of pervasive power laws in patch size distribution [40], thus we hypothesize that models that include this process should explain this patterns. Scanlon et al. [36] represent the dynamics of savanna trees using a model including a global constraint (mean rainfall), a local facilitation mechanism and two states: tree/non-tree. This model produced power laws across a rainfall gradient without the need of tuning an external parameter. The results for this model showed an  $\alpha = 1.34$  which is also different than our results. Another model but with three states (tree/non-tree/degraded) including local facilitation and grazing was also used to obtain power laws patch distributions without external tuning. This model also captures the deviations of power laws at high grazing pressures [35]. At the scales of this study grazing does not seem to be important as we did not observe exponential cut-offs, but the combination of three states, local facilitation, and global constraints seems to be the most general way of modeling forest at global scales. In this case the power law structures are present in all the range external conditions and two critical transitions are present, assuming that the original state is with trees covering most of the area, the first was the fragmentation transition where the trees passed from a connected to a disconnected state. The second is the extinction transition: the non-tree and degraded sites go from an unconnected to a connected state.

It was suggested that a combination of spatial and temporal indicators could be more reliable to detect critical transitions [66]. We combined five criteria to detect the closeness to a fragmentation threshold two of them were spatial: the forest patch size distribution, and the proportion of the largest patch relative to total forest area ( $RS_{max}$ ). The other three were: the distribution of temporal fluctuations in the largest patch size, the trend in the variance and skewness of the fluctuations. Each one of these in individually are not a strong indicators, but the combination of all indicators gives us an increased degree of confidence about the closeness of a critical transition.

We found that only the tropical forest of Africa and South America meet the five criteria and thus seems to be near a critical fragmentation threshold. This means that the combined influence of human pressures and climate forcings can trigger all the undesired effects of fragmentation in these extended areas. A small but

continuous increase in forest loss could produce a biodiversity collapse [28], this threshold effect has been observed in different kind of models, experimental microcosms [67], field studies [68,69] and food webs [70]. From these two areas Africa is more affected because the proportion of the largest patch relative to total forest area ( $RS_{max}$ ) is near 30%, this could indicate that the transition is already started. Moreover this region was estimated to be potentially bistable, with the possibility to completely transform into a savanna [71]. The region of South America tropical forest has a  $RS_{max}$  of more than 60% indicating that the process of the fragmentation transition is approaching but not yet started.

The  $RS_{max}$  criteria is an alternative to estimate the effects of fragmentation that can be more easily estimated than the proportion of habitat relative to total area. The total area that a particular habitat can occupy is sometimes difficult to estimate but the total area of the habitat is easily identifiable, thus  $RS_{max}$  could be estimated more precisely.

When habitat is reduced species population will decline proportionally, this happens while the habitat fragments retain connectivity but as habitat reduction continues, the critical threshold is approached and connectivity will have large fluctuations [72]. This could trigger several effects that act synergically: will enhance populations fluctuations and the possibility of extinctions will raise, this in turn will increase patch isolation that decrease connectivity [72]. This positive feedback mechanism will be enhanced when the fragmentation threshold is reached with the result of the loss of most habitat specialist species at a landscape scale [68]. Some authors argue that as species have heterogeneous responses to habitat loss and fragmentation, and that as biotic dispersal is limited, the importance of thresholds is restricted to local scales or even its existence is defied [72]. Fragmentation is by definition a local process that at some point produces an emergent phenomena that spreads over the entire landscape and this could happen even if the area considered is infinite [73]. Besides, after the fragmentation threshold connectivity over all the region decreases, there is still a large and internally well connected patch that can maintain sensitive species [69]. Which is the time needed for these large patches to become fragmented, and pose in real danger of extinction a myriad of sensitive species? Following the actual trends of habitat loss and taking into account the dynamics of forest patches, the simple models proposed here could be used to estimate this second threshold and the management practices needed to stop this trend.

The effectiveness of landscape management is related to the degree of fragmentation, and the criteria to direct the efforts could be focusing on the regions that are near a transition [47]. Regions that are in an unconnected state require big efforts to recover a connected state, but regions that are near a transition could be easily pushed to a connected state, and feedback due to facilitation mechanisms helps to maintain this state.



To know if these thresholds will sum up and produce a cascading effect to reach a planetary tipping point [4], we should extend the effects of these changes to know how it will feedback on global land-atmosphere processes that affect climate change.

## References

1. Crowther TW, Glick HB, Covey KR, Bettigole C, Maynard DS, et al. (2015) Mapping tree density at a global scale. *Nature* 525: 201–205. Available: <http://www.nature.com/nature/journal/v525/n7568/full/nature14967.html>.
2. Canfield DE, Glazer AN, Falkowski PG (2010) The Evolution and Future of Earth’s Nitrogen Cycle. *Science* 330: 192–196. Available: <http://www.sciencemag.org/cgi/doi/10.1126/science.1186120>.
3. Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, et al. (2011) Solutions for a cultivated planet. *Nature* 478: 337–342. Available: <http://www.nature.com/doifinder/10.1038/nature10452>.
4. Barnosky AD, Hadly EA, Bascompte J, Berlow EL, Brown JH, et al. (2012) Approaching a state shift in Earth’s biosphere. *Nature* 486: 52–58. Available: <http://www.nature.com/nature/journal/v486/n7401/full/nature11018.html> <http://dx.doi.org/10.1038/nature11018>.
5. Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, et al. (2015) Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* 1: e1500052. Available: <http://advances.sciencemag.org/cgi/doi/10.1126/sciadv.1500052>.
6. Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution* 25: 325–331. Available: <http://www.sciencedirect.com/science/article/pii/S0169534710000613>.
7. Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, et al. (2009) Early-warning signals for critical transitions. *Nature* 461: 53–59. Available: <http://dx.doi.org/10.1038/nature08227>.
8. Carpenter SR, Cole JJ, Pace ML, Batt R, Brock WA, et al. (2011) Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment. *Science* 332: 1079–1082. Available: <http://www.sciencemag.org/content/332/6033/1079.abstract>.
9. Drake JM, Griffen BD (2010) Early warning signals of extinction in deteriorating environments. *Nature* 467: 456–459. Available: <http://dx.doi.org/10.1038/nature09389> <http://www.nature.com/nature/journal/v467/n7314/abs/nature09389>.

information.

10. Rockstrom J, Steffen W, Noone K, Persson A, Chapin FS, et al. (2009) A safe operating space for humanity. *Nature* 461: 472–475. Available: <http://dx.doi.org/10.1038/461472a>.

11. Folke C, Jansson Å, Rockström J, Olsson P, Carpenter SR, et al. (2011) Reconnecting to the Biosphere. *AMBIO* 40: 719–738. Available: <http://link.springer.com/article/10.1007/s13280-011-0184-y>.

12. Scheffer M, Walker B, Carpenter S, Foley J a, Folke C, et al. (2001) Catastrophic shifts in ecosystems. *Nature* 413: 591–596. doi:10.1038/35098000.

13. Martín PV, Bonachela JA, Levin SA, Muñoz MA (2015) Eluding catastrophic shifts. *Proceedings of the National Academy of Sciences* 112: E1828–E1836. Available: <http://www.pnas.org/content/early/2015/03/27/1414708112>.

14. Xu C, Van Nes EH, Holmgren M, Kéfi S, Scheffer M (2015) Local Facilitation May Cause Tipping Points on a Landscape Level Preceded by Early-Warning Indicators. *The American Naturalist* 186: E000–E000. Available: <http://www.jstor.org/stable/info/10.1086/682674>.

15. Kéfi S, Rietkerk M, Baalen M van, Loreau M (2007) Local facilitation, bistability and transitions in arid ecosystems. *Theoretical Population Biology* 71: 367–379. Available: <http://www.sciencedirect.com/science/article/pii/S0040580906001250>.

16. Taylor CM, Hastings A (2005) Allee effects in biological invasions. *Ecology Letters* 8: 895–908. Available: <http://dx.doi.org/10.1111/j.1461-0248.2005.00787.x>.

17. Solé RV (2011) *Phase Transitions*. Princeton University Press. Available: <https://books.google.com.ar/books?id=8RcLuv-Ll2kC>.

18. Solé RV, Bascompte J (2006) *Self-organization in complex ecosystems*. New Jersey, USA.: Princeton University Press. Available: <http://books.google.com.ar/books?id=v4gpGH6Gv68C>.

19. Stauffer D, Aharony A (1994) *Introduction To Percolation Theory*. London: Taylor & Francis.

20. Zinck RD, Grimm V (2009) Unifying wildfire models from ecology and statistical physics. *The American naturalist* 174: E170–85. Available: <http://www.ncbi.nlm.nih.gov/pubmed/19799499>.

21. Ochoa-Quintero JM, Gardner TA, Rosa I, de Barros Ferraz SF, Sutherland WJ (2015) Thresholds of species loss in Amazonian deforestation frontier landscapes. *Conservation Biology* 29: 440–451. Available: <http://onlinelibrary.wiley.com/doi/10.1111/cobi.12446/abstract>.

22. Leibold MA, Norberg J (2004) Biodiversity in metacommunities: Plankton as complex adaptive systems?

- 1 Limnology and Oceanography 49: 1278–1289. Available: [http://www.aslo.org/lo/pdf/vol{\\\\_}49/issue{\\\\_}4{\\\\_}part{\\\\_}2/12](http://www.aslo.org/lo/pdf/vol{\\_}49/issue{\\_}4{\\_}part{\\_}2/12)
- 2 23. Lenton TM, Williams HTP (2013) On the origin of planetary-scale tipping points. Trends in Ecology &  
3 Evolution 28: 380–382. Available: <http://www.sciencedirect.com/science/article/pii/S0169534713001456>.
- 4 24. Bonan GB (2008) Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests.  
5 Science 320: 1444–1449. Available: <http://www.sciencemag.org/content/320/5882/1444.abstract>.
- 6 25. Solé RV, Bartumeus F, Gamarra JGP (2005) Gap percolation in rainforests. Oikos 110: 177–185.  
7 Available: <http://onlinelibrary.wiley.com/doi/10.1111/j.0030-1299.2005.13843.x/abstract>.
- 8 26. He F, Hubbell S (2003) Percolation Theory for the Distribution and Abundance of Species. Physical  
9 Review Letters 91: 198103. Available: <http://link.aps.org/doi/10.1103/PhysRevLett.91.198103>.
- 10 27. Bascompte J, Solé RV, Sole RV (1996) Habitat fragmentation and extinction thresholds in spatially explicit  
11 models. Journal of Animal Ecology 65: 465–473. Available: <http://www.jstor.org/discover/10.2307/5781?uid=3737512{\\&}uid->
- 12 28. Solé RV, Alonso D, Saldaña J (2004) Habitat fragmentation and biodiversity collapse in neutral  
13 communities. Ecological Complexity 1: 65–75. Available: [http://www.sciencedirect.com/science/article/pii/](http://www.sciencedirect.com/science/article/pii/S1476945X03000084)  
14 S1476945X03000084.
- 15 29. Loehle C, Li B-L, Sundell RC (1996) Forest spread and phase transitions at forest-prairie ecotones in  
16 Kansas, U.S.A. Landscape Ecology 11: 225–235.
- 17 30. Naito AT, Cairns DM (2015) Patterns of shrub expansion in Alaskan arctic river corridors suggest phase  
18 transition. Ecology and Evolution 5: 87–101. Available: <http://dx.doi.org/10.1002/ece3.1341>.
- 19 31. Dai L, Vorselen D, Korolev KS, Gore J (2012) Generic Indicators for Loss of Resilience Before a Tipping  
20 Point Leading to Population Collapse. Science 336: 1175–1177. Available: [http://www.sciencemag.org/](http://www.sciencemag.org/content/336/6085/1175.abstract)  
21 content/336/6085/1175.abstract.
- 22 32. Hastings A, Wysham DB (2010) Regime shifts in ecological systems can occur with no warning.  
23 Ecology Letters 13: 464–472. Available: [http://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2010.01439.](http://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2010.01439.x/abstract)  
24 x/abstract.
- 25 33. Boettiger C, Hastings A (2012) Quantifying limits to detection of early warning for critical transitions.  
26 Journal of The Royal Society Interface 9: 2527–2539. doi:10.1098/rsif.2012.0125.
- 27 34. Pueyo S, de Alencastro Graça PML, Barbosa RI, Cots R, Cardona E, et al. (2010) Testing for criticality  
28 in ecosystem dynamics: the case of Amazonian rainforest and savanna fire. Ecology Letters 13: 793–802.

- 1 Available: <http://dx.doi.org/10.1111/j.1461-0248.2010.01497.x>.
- 2 35. Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, et al. (2007) Spatial vegetation  
3 patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449: 213–217. Available:  
4 <http://dx.doi.org/10.1038/nature06111> <http://www.nature.com/nature/journal/v449/n7159/abs/nature06111.html>.
- 5 36. Scanlon TM, Caylor KK, Levin SA, Rodriguez-iturbe I (2007) Positive feedbacks promote power-law  
6 clustering of Kalahari vegetation. *Nature* 449: 209–212. doi:10.1038/nature06060.
- 7 37. Vandermeer J, Perfecto I, Philpott SM (2008) Clusters of ant colonies and robust criticality in a tropical  
8 agroecosystem. *Nature* 451: 457–460. doi:10.1038/nature06477.
- 9 38. Saravia LA, Giorgi A, Momo F (2012) Multifractal growth in periphyton communities. *Oikos* 121:  
10 1810–1820. Available: <http://doi.wiley.com/10.1111/j.1600-0706.2011.20423.x>.
- 11 39. Dal Bello M, Maggi E, Rindi L, Capocchi A, Fontanini D, et al. (2014) Multifractal spatial distribution  
12 of epilithic microphytobenthos on a Mediterranean rocky shore. *Oikos* 124: 477–485. Available: <http://onlinelibrary.wiley.com/doi/10.1111/oik.01503/abstract>.
- 13 40. Manor A, Shnerb NM (2008) Origin of pareto-like spatial distributions in ecosystems. *Physical Review*  
14 *Letters* 101: 268104. Available: <http://link.aps.org/doi/10.1103/PhysRevLett.101.268104>.
- 15 41. Irvine MA, Bull JC, Keeling MJ (2016) Aggregation dynamics explain vegetation patch-size distributions.  
16 *Theoretical Population Biology* 108: 70–74. Available: [http://www.sciencedirect.com/science/article/pii/](http://www.sciencedirect.com/science/article/pii/S0040580915001239)  
17 [S0040580915001239](http://www.sciencedirect.com/science/article/pii/S0040580915001239).
- 18 42. Bulleri F, Bruno JF, Benedetti-ecchi L (2008) Beyond Competition: Incorporating Posi-  
19 tive Interactions between Species to Predict Ecosystem Invasibility. *PLoS Biology* 6: 1136–1140.  
20 doi:10.1371/journal.pbio.0060162.
- 21 43. DiMiceli C, Carroll M, Sohlberg R, Huang C, Hansen M, et al. (2015) Annual Global Automated MODIS  
22 Vegetation Continuous Fields (MOD44B) at 250 m Spatial Resolution for Data Years Beginning Day 65,  
23 2000 - 2014, Collection 051 Percent Tree Cover, University of Maryland, College Park, MD, USA. Available:  
24 [https://lpdaac.usgs.gov/dataset{\\\_}discovery/modis/modis{\\\_}products{\\\_}table/mod44b](https://lpdaac.usgs.gov/dataset{\_}discovery/modis/modis{\_}products{\_}table/mod44b).
- 25 44. Sexton JO, Noojipady P, Song X-P, Feng M, Song D-X, et al. (2015) Conservation pol-  
26 icy and the measurement of forests. *Nature Climate Change* advance on: 192–196. Available:  
27 <http://www.nature.com/nclimate/journal/vaop/ncurrent/full/nclimate2816.html> <http://dx.doi.org/10.1038/nclimate2816>  
28 <http://10.1038/nclimate2816> [http://www.nature.com/nclimate/journal/v6/n2/abs/nclimate2816.html{\\\_}supplementary-](http://www.nature.com/nclimate/journal/v6/n2/abs/nclimate2816.html{\_}supplementary-)  
29

information.

45. Belward AS (1996) The IGBP-DIS Global 1 Km Land Cover Data Set “DISCover”: Proposal and Implementation Plans : Report of the Land Recover Working Group of IGBP-DIS. IGBP-DIS Office. Available: <https://books.google.com.ar/books?id=qixsNAAACAAJ>.

46. Weerman EJ, Van Belzen J, Rietkerk M, Temmerman S, Kéfi S, et al. (2012) Changes in diatom patch-size distribution and degradation in a spatially self-organized intertidal mudflat ecosystem. *Ecology* 93: 608–618. Available: <http://www.esajournals.org/doi/abs/10.1890/11-0625.1>.

47. Oborny B, Szabó G, Meszéna G (2007) Survival of species in patchy landscapes: percolation in space and time. In: *Scaling biodiversity*. Cambridge University Press. pp. 409–440. Available: <http://dx.doi.org/10.1017/CBO9780511814938.022>.

48. Gastner MT, Oborny B, Zimmermann DK, Pruessner G (2009) Transition from Connected to Fragmented Vegetation across an Environmental Gradient: Scaling Laws in Ecotone Geometry. *The American Naturalist* 174: E23–E39. Available: <http://www.jstor.org/stable/10.1086/599292>.

49. Ódor G (2004) Universality classes in nonequilibrium lattice systems. *Reviews of Modern Physics* 76: 663–724. Available: <http://link.aps.org/doi/10.1103/RevModPhys.76.663>.

50. Hinrichsen H (2000) Non-equilibrium critical phenomena and phase transitions into absorbing states. *Advances in Physics* 49: 815–958. Available: <http://dx.doi.org/10.1080/00018730050198152>.

51. Corrado R, Cherubini AM, Pennetta C (2014) Early warning signals of desertification transitions in semiarid ecosystems. *Physical Review E* 90: 62705. Available: <http://link.aps.org/doi/10.1103/PhysRevE.90.062705>.

52. Goldstein ML, Morris SA, Yen GG (2004) Problems with fitting to the power-law distribution. *The European Physical Journal B - Condensed Matter and Complex Systems* 41: 255–258. Available: <http://link.springer.com/article/10.1140/epjb/e2004-00316-5>.

53. Clauset A, Shalizi C, Newman M (2009) Power-Law Distributions in Empirical Data. *SIAM Review* 51: 661–703. Available: <http://epubs.siam.org/doi/abs/10.1137/070710111>.

54. Efron B, Tibshirani RJ (1994) *An Introduction to the Bootstrap*. New York: Taylor & Francis. Available: <https://books.google.es/books?id=gLlpIUxRntoC>.

55. Burnham K, Anderson DR (2002) *Model selection and multi-model inference: A practical information-*

- 1 theoretic approach. 2nd. New York: Springer-Verlag.
- 2 56. Klaus A, Yu S, Plenz D (2011) Statistical analyses support power law distributions found in neuronal  
3 avalanches. *PloS one* 6: e19779. Available: <http://dx.plos.org/10.1371/journal.pone.0019779>.
- 4 57. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: Linear and Nonlinear Mixed Effects  
5 Models. Available: <http://cran.r-project.org/package=nlme>.
- 6 58. R Core Team (2015) R: A Language and Environment for Statistical Computing. Available: <http://www.r-project.org/>.
- 7  
8 59. Gillespie CS (2015) Fitting Heavy Tailed Distributions: The powerLaw Package. *Journal of Statistical*  
9 *Software* 64: 1–16. Available: <http://www.jstatsoft.org/v64/i02/>.
- 10 60. Gardner RH, Urban DL (2007) Neutral models for testing landscape hypotheses. *Landscape Ecology* 22: 15–  
11 29. Available: <http://dx.doi.org/10.1007/s10980-006-9011-4> <http://www.springerlink.com/content/2vq21v4v78461506/>.
- 12 61. Keitt TH, Urban DL, Milne BT (1997) Detecting critical scales in fragmented landscapes. *Conservation*  
13 *Ecology* 1: 4. Available: <http://www.ecologyandsociety.org/vol1/iss1/art4/>.
- 14 62. Benedetti-Cecchi L, Tamburello L, Maggi E, Bulleri F (2015) Experimental Perturbations Mod-  
15 ify the Performance of Early Warning Indicators of Regime Shift. *Current biology* 25: 1867–1872.  
16 doi:10.1016/j.cub.2015.05.035.
- 17 63. Rooij MMJW van, Nash B, Rajaraman S, Holden JG (2013) A Fractal Approach to Dynamic Inference and  
18 Distribution Analysis. *Frontiers in Physiology* 4. Available: [http://www.frontiersin.org/fractal/{\\\_}physiology/10.3389/fphys.20](http://www.frontiersin.org/fractal/{\_}physiology/10.3389/fphys.2013.00101)
- 19 64. Hantson S, Pueyo S, Chuvieco E (2015) Global fire size distribution is driven by human impact and  
20 climate. *Global Ecology and Biogeography* 24: 77–86. Available: <http://dx.doi.org/10.1111/geb.12246>.
- 21 65. Solé RV, Alonso D, McKane A (2002) Self-organized instability in complex ecosystems. *Philosophical trans-*  
22 *actions of the Royal Society of London Series B* 357: 667–681. Available: [http://rstb.royalsocietypublishing.](http://rstb.royalsocietypublishing.org/content/357/1421/667)  
23 [org/content/357/1421/667](http://rstb.royalsocietypublishing.org/content/357/1421/667).
- 24 66. Kéfi S, Guttal V, Brock WA, Carpenter SR, Ellison AM, et al. (2014) Early Warning Signals of Ecological  
25 Transitions: Methods for Spatial Patterns. *PLoS ONE* 9: e92097. Available: [http://dx.doi.org/10.1371/](http://dx.doi.org/10.1371/journal.pone.0092097)  
26 [journal.pone.0092097](http://dx.doi.org/10.1371/journal.pone.0092097).
- 27 67. Starzomski BM, Srivastava DS (2007) Landscape geometry determines community response to disturbance.  
28 *Oikos* 116: 690–699. doi:10.1111/j.2006.0030-1299.15547.x.
- 29 68. Pardini R, Bueno A de A, Gardner TA, Prado PI, Metzger JP (2010) Beyond the Fragmentation Threshold

- 1 Hypothesis: Regime Shifts in Biodiversity Across Fragmented Landscapes. PLoS ONE 5: e13666. Available:  
2 <http://dx.doi.org/10.1371/journal.pone.0013666>.
- 3 69. Martensen AC, Ribeiro MC, Banks-Leite C, Prado PI, Metzger JP (2012) Associations of Forest Cover,  
4 Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance.  
5 Conservation Biology 26: 1100–1111. Available: [http://onlinelibrary.wiley.com/doi/10.1111/j.1523-1739.2012.](http://onlinelibrary.wiley.com/doi/10.1111/j.1523-1739.2012.01940.x/abstract)  
6 01940.x/abstract.
- 7 70. Martinson HM, Fagan WF, Denno RF (2012) Critical patch sizes for food-web modules. Ecology 93:  
8 1779–1786. Available: <http://dx.doi.org/10.1890/11-1497.1>.
- 9 71. Staver AC, Archibald S, Levin SA (2011) The Global Extent and Determinants of Savanna and Forest as  
10 Alternative Biome States. Science 334: 230–232. Available: [http://www.sciencemag.org/content/334/6053/](http://www.sciencemag.org/content/334/6053/230)  
11 230.
- 12 72. Brook BW, Ellis EC, Perring MP, Mackay AW, Blomqvist L (2013) Does the terrestrial biosphere have  
13 planetary tipping points? Trends in Ecology & Evolution. Available: [http://www.sciencedirect.com/science/](http://www.sciencedirect.com/science/article/pii/S0169534713000335)  
14 article/pii/S0169534713000335.
- 15 73. Oborny B, Meszéna G, Szabó G (2005) Dynamics of Populations on the Verge of Extinction. Oikos 109:  
16 291–296. Available: <http://www.jstor.org/stable/3548746>.