

Analysis of critical transitions at the Global Forest

Abstract

Global forests provide critical habitat for many species, ecosystem services, and are coupled to atmospheric dynamics and gases. One of the most important changes produced in the biosphere is the replacement of forest areas with human dominated landscapes. These areas contain many fewer species than the natural ecosystem they replaced, and this change is one of the main drivers of extinctions in the Anthropocene. The dynamics of forest fragments or patches are central to its function as an ecosystem. In different kinds of vegetation, including forests, the patch size distributions follow (perhaps approximate) power laws, laws that can be used as a signal of critical phase transitions, where the system state changes suddenly at a critical point; in the case of forest patches, this implies an abrupt change in connectivity that poses a risk to forest function as a habitat and ecosystem. All these patterns have been observed at relatively small scales, however. Here we studied the distribution of forest patch sizes at a global level and its changes over the last fourteen years, using the closeness of forest at the continental level as a possible early warning indicator of critical transitions, and combining five separate criteria to detect closeness to a fragmentation threshold. The conditions that indicate that a region is near a critical fragmentation threshold are: patch size distributions follow a power law; temporal fluctuations of the largest patch follow a power law; variance of largest patch fluctuations increase in time; and skewness is negative. Most regions, except the Eurasian mainland, followed a power-law distribution. We found that only the tropical forest of Africa and South America met the five criteria and thus seemed to be near a critical fragmentation threshold. This implies that the combined influence of human pressures and climate forcings might trigger undesired effects of fragmentation such as species loss and [TODO] in these regions. The simple models proposed here could be used to estimate fragmentation thresholds, and inform the management practices needed to stop this trend.

Introduction

Forests are some 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 influenced global bio-geochemical cycles [2], with one of the most dramatic changes being 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 local have accumulated over time now constitute a global forcing [4].

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]. The effects of fragmentation are not only important from an ecological point of view but also human activities and ecosystem services supply and flow are deeply influenced by the level of landscape fragmentation [6].

Complex interactions between species and feedbacks at different levels of organization [7] can produce abrupt changes called critical transitions [8]. These abrupt state shifts cannot be linearly forecasted from past changes, and are thus difficult to predict and manage [8]. Critical transitions had been detected mostly at local scales [9,10], but the accumulation of changes in local communities that overlap geographically can propagate and cause an abrupt change of the entire system at larger scales [4]. Coupled with the existence of global scale forcings, this implies the possibility that a critical transition could occur at a global scale [11,12].

There are two general classes of critical transitions. In the first, a sudden shift between states is mostly irreversible because of the presence of two stable states and no coexistence between these states is allowed. This behavior is called hysteresis and represents a catastrophic regime shift [13], also called first order transitions. This could be the result of positive feedback mechanisms [14], for example the growth of forest in a site is more probable if it is surrounded by forest than if it is surrounded by cultivated or degraded land [15]. This has been observed in semiarid regions where the transition from a vegetated to a desertic state occurs as a result of human pressures and climatic change [16], in biological invasions [17], and biology and social sciences in general [18].

The second class are continuous critical transitions [19], or second order transitions. In this case there is a narrow region where the system changes from one domain to another, pushed by external conditions. The change in this case is sudden, but continuous and theoretically reversible. This region of change can be characterized by a critical point where the change begins. At the critical point we can observe distinctive spatial patterns: scale invariant fractal structures characterized by power law patch distributions [20]. The simplest model where we can observe this kind of transition is a random map, in which 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 concerns forest fires and ecological memory: biomass is consumed in a fire, and afterwards some time must pass to build up fuel before a subsequent fire can occur [21]. [TODO which is the critical parameter here, explain]

1 The spatial phenomena observed in continuous critical transitions deal with connectivity, a fundamental
2 property of general systems and ecosystems from forests [22] to marine ecosystems [23] and the whole
3 biosphere [24]. When a system goes from a fragmented to a connected state we say that it percolates
4 [18]. Percolation implies that there is a path of connections that involves the whole system. Thus we can
5 characterize two domains or phases: one dominated by short-range interactions where information cannot
6 spread, and another in which long range interactions are possible and information can spread over the whole
7 area. (The term “information” is used in a broad sense and can represent species dispersal or movement.)

8 Thus, there is a critical “percolation threshold” between the two phases, and the system could be driven
9 close to or beyond this point by an external force; climate change and deforestation are the main forces that
10 could be the drivers of such a phase change in contemporary forests [5,25]. Species’ dispersal strategies are
11 influenced by percolation thresholds in three-dimensional forest structure [26], and it has been shown that
12 species distributions also have percolation thresholds [27]. This implies that pushing the system below the
13 percolation threshold could produce a biodiversity collapse [28,29]; conversely, being in a connected state
14 (above the threshold) could accelerate the invasion of forest into prairie [30,31].

15 One of the problems with critical transitions is that the value of the critical threshold is not known in
16 advance; in addition, because near that point a small change can precipitate a state shift of the system,
17 they are difficult to predict. Several methods have been developed to detect the closeness of the critical
18 point, e.g. a deceleration in recovery from perturbations, or an increase in variance in the spatial or temporal
19 pattern [9,32–34].

20 In forests, we can observe processes such as demographic fluctuations, spatial heterogeneities, and/or disper-
21 sal limitation, all processes that introduce stochasticity that can convert a catastrophic transition to a second
22 order transitions [14]. Thus a continuous transitions should be more probable than catastrophic transitions,
23 and some evidence of a continuous critical transition related to drought and fire has been found in tropical
24 forest [35], and grasslands [36,37].

25 The necessary condition we need to be near a continuous critical threshold is that the patch size distribution
26 follows a power-law. This distributions are present in a wide range of conditions, for example in arid
27 ecosystem vegetation [38,39], ant colonies [40], and attached microalgae [41,42]. The presence of power-laws
28 is not a sufficient condition because they can be produced by different mechanisms. One hypothesis is that
29 these power-laws were produced by facilitation mechanisms [43,44], that are likely to be present in forest
30 [45].

31 In this study, 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 [18] and thus much easier to detect than at smaller scales, where noise can mask the signals of the transition.

Methods

Area definition

We analyzed mainland zones at a continental scale, specifying that close patches of continuous forest must connect the region [TODO: what does this mean?], big islands of more than XXXX km²—like Madagascar—were treated as separate areas, unless they were < 1 km from the mainland, while smaller islands were excluded. With these criteria we defined three regions in America: South America temperate forest (SAT), subtropical and tropical forest up to Mexico (SAST), and USA and Canada forest (NA). Europe and north Asia were all connected and treated as one region (EUAS). Other regions were south Asia (SEAS), Africa (AF), and Australia and islands (OC) (Supplementary figure S1-S6). Each region have subregions that correspond to separate areas inside a continent or 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-m resolution, globally from 2000 to 2014. We used version 051 [46]. There are several definition of forest [47], 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 [48], 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 [49].

Percolation theory

A more in-depth introduction to percolation theory can be found elsewhere [20] and a review from an ecological point of view is available [50]. 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 define a neighborhood, the eight adjacent sites surrounding any particular site. 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 $p < p_c$, in which species cannot travel far inside the forest, as it is fragmented; 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 (lattice), i.e. 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 [20].

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 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 α does not depend on the details of the model and it is called universal [20]. These scaling laws can be applied for landscape structures that are approximately random, with correlations if the forest sites are correlated over short distances [51]. In physics this is called “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 some other mechanism should be invoked to explain it. Percolation thresholds can also be generated by models that have some kind of memory [52,53]: for example, a patch that has been exploited for many years will recover different than a recently deforested forest patch. In this case the system can belong to a different universality class, or in some cases there is no universality, in which case the value of α will depend on the parameters and details of the model [54].

Patch size distributions

We fitted the empirical distribution of forest patch areas, based on the MODIS-derived data described above, to four distributions using maximum likelihood estimation [55,56]. The distributions were: power-law, power-law with exponential cut-off, log-normal, and exponential. We assumed that the patch size distribution is a continuous variable that was discretized by remote sensing data acquisition procedure.

Besides the hard X_{min} limit we set due to discretization, the power-law distribution needs a lower bound for its scaling behaviour. This lower bound is also estimated from the data by maximizing the Kolmogorov-

Smirnov (KS) statistic comparing the empirical to fitted cumulative distribution functions [56]. We also calculated the uncertainty of the parameters using a non-parametric bootstrap method [57], and computed corrected Akaike Information Criteria (AIC_c) and Akaike weights for each model [58]. Akaike weights (w_i) are the weight of evidence in favor of model i being the actual best model] given that one of the N models must be the best model for that set of N models.

Additionally, we computed the goodness of fit of the power-law model following the bootstrap approach described by Clauset et. al [56], where simulated data sets following the fitted model are generated, and a p-value calculated as the proportion of simulated data sets that has a KS statistic less extreme than empirical data. The criterion to reject the power law model was $p \leq 0.1$ but as we have a very large n , meaning that negligible small deviations could produce a rejection [59], we chose a $p \leq 0.05$ to reject the power law model.

To test for differences between the fitted power law exponent for regions and subregions we used a weighted linear regression with a residual auto-correlation structure. For this we use a generalized least squares procedures: function `gls` from package `nlme` [60]. The weights were the bootstrapped 95% confidence intervals and we added an auto-regressive model of order 1 to the residuals to account for temporal autocorrelation.

Largest patch dynamics

The largest patch is the one that connects the highest number of sites in the area. This has been used extensively to indicate fragmentation [22,61]. The relation of the size of the largest patch S_{max} to critical transitions has been extensively studied in relation to percolation phenomena [20], but seldom used in ecological studies (but see [51]). When in a connected state ($p > p_c$) the landscape is almost insensitive to the loss of a small fraction of forest, but close to the critical point the same loss can have important effects [19,50], because at this point the largest patch will have a filamentary structure, i.e. extended forest areas will be connected by thin threads. Small losses can thus produce large fluctuations.

One way to evaluate the fragmentation of the forest is to calculate the proportion of the largest patch against the total area [62]. The total area of the regions we are considering (Supplementary figure S1-S6) may not be the same than the total area that the forest could potentially occupy, thus a more accurate way to evaluate the weight of S_{max} is to we use the total forest area. We calculate the proportion of the largest patch for each year, dividing S_{max} by the total forest area of the same year: $RS_{max} = S_{max} / \sum_i S_i$. This has the effect of reducing the S_{max} fluctuations produced due to environmental or climatic changes influences in total forest area. When the proportion RS_{max} is large (more than 60%) the largest patch contains most of the forest so there are fewer small forest patches and the system is probably in a connected phase. Conversely, when it is

low (less than 20%), the system is probably in a fragmented phase.

It is also possible that a system with high RS_{max} is near a percolation threshold, and this has to be evaluated using the temporal fluctuations. We calculate the fluctuations around the mean with the absolute values $\Delta S_{max} = S_{max}(t) - \langle S_{max} \rangle$, using the proportions of RS_{max} . To characterize the fluctuations we fitted three empirical distributions: power-law, log-normal, and exponential, using the same methods described previously. We expect that large fluctuation near a critical point have heavy tails (log-normal or power-law) and that fluctuations far from a critical point have exponential tails, corresponding to Gaussian processes. As the data set spans 15 years we have do not have enough power to reliably detect which distribution is better [56]. To improve this we performed the goodness of fit test described above for all the distributions. We generated animated maps showing the fluctuations of the 2 largest patches to aid in the interpretations of the results.

A robust way to detect if the system is near a critical transition is to analyze the increase in variance of the density [63], in our case density means the area of forest divided by total area. One of the problems is that density is difficult to determine because we do not know the total area that the forest can potentially colonize, this has to be estimated introducing more uncertainty in the density. The other problem is that the variance increase in density appears when the system is very close to the transition [54], this practically does not constitute an early warning indicator. An alternative is to analyze the variance of the fluctuations of the largest patch ΔS_{max} : a maximum is attained at the critical point but a significant increase occurs well before the system reaches the threshold [54]. In addition, before the critical fragmentation the skewness of the distribution of ΔS_{max} should be negative, implying that fluctuations below the average are more frequent. We characterized the increase in the variance using quantile regression: if variance is increasing the slopes of upper or/and lower quartiles should be positive or negative.

All statistical analyses were performed using the GNU R version 3.3.0 [64], using code provided by Cosma R. Shalizi for power law with exponential cutoff model and the `powerlaw` package [65] for fitting the other distributions. Image processing was done in MATLAB (Version??). The complete source code for the processing of images and analysis, the patch size data and the figures with each fit (year by region by subregion) is available at figshare <http://dx.doi.org/10.6084/m9.figshare.XXXXX>.

Results

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

parameter α was similar by ± 0.02 to the pure power law. Additionally the patch size where the exponential tail begins is very large, thus we used the power law parameters for this cases (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 [20]. 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, which follows a log-normal distribution. The log-normal and power law are both heavy tailed distributions and difficult to distinguish, but in this case Akaike weights have very high values for log-normal (near 1), meaning that this is the only possible model. In addition, 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 rejected the power law model in fewer 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 (α) and the temporal autocorrelation, there is no significant differences between α for the regions with the biggest (greater than 10^7 km²) forest areas (Figure 1 and Supplementary figure S8). There is also no difference between these regions and smaller ones (Supplementary Table S2 & S3), and all the slopes of α are not different from 0 (Supplementary Table S3). This implies a 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 km² of forest is shown in figure 2. South America tropical and subtropical (SAST1) and North America (NA1) have a higher RS_{max} of more than 60%, and other big regions 40% or less. For regions with less total forest area (Supplementary figure S9 & Table 1), the United Kingdom (EUAS3) has a very low proportion near 1%, while other regions such as New Guinea (OC2) and Malaysia/Kalimantan (OC3) have a very high proportion. SEAS2 (Philippines) is very interesting because it seems to be under 30% until the year 2005, fluctuates in the range 30-60%, and then stays over 60% (supplementary figure S9). This seems to be an example of a transition from an unconnected to connected state, and deserves further in-depth study.

We analyzed the distributions of fluctuations of the largest patch relative to total forest area ΔRS_{max} and fluctuations of the largest patch ΔS_{max} . The model selection for ΔS_{max} results in power law distributions for all regions (Supplementary table S6). The goodness of fit test (GOF) did not reject power laws in any case, but nor could it reject the other models except in a few cases, because of the small number of observations. We found some differences in ΔRS_{max} : Eurasia mainland (EUAS1), New Guinea (OC2), Malaysia (OC3),

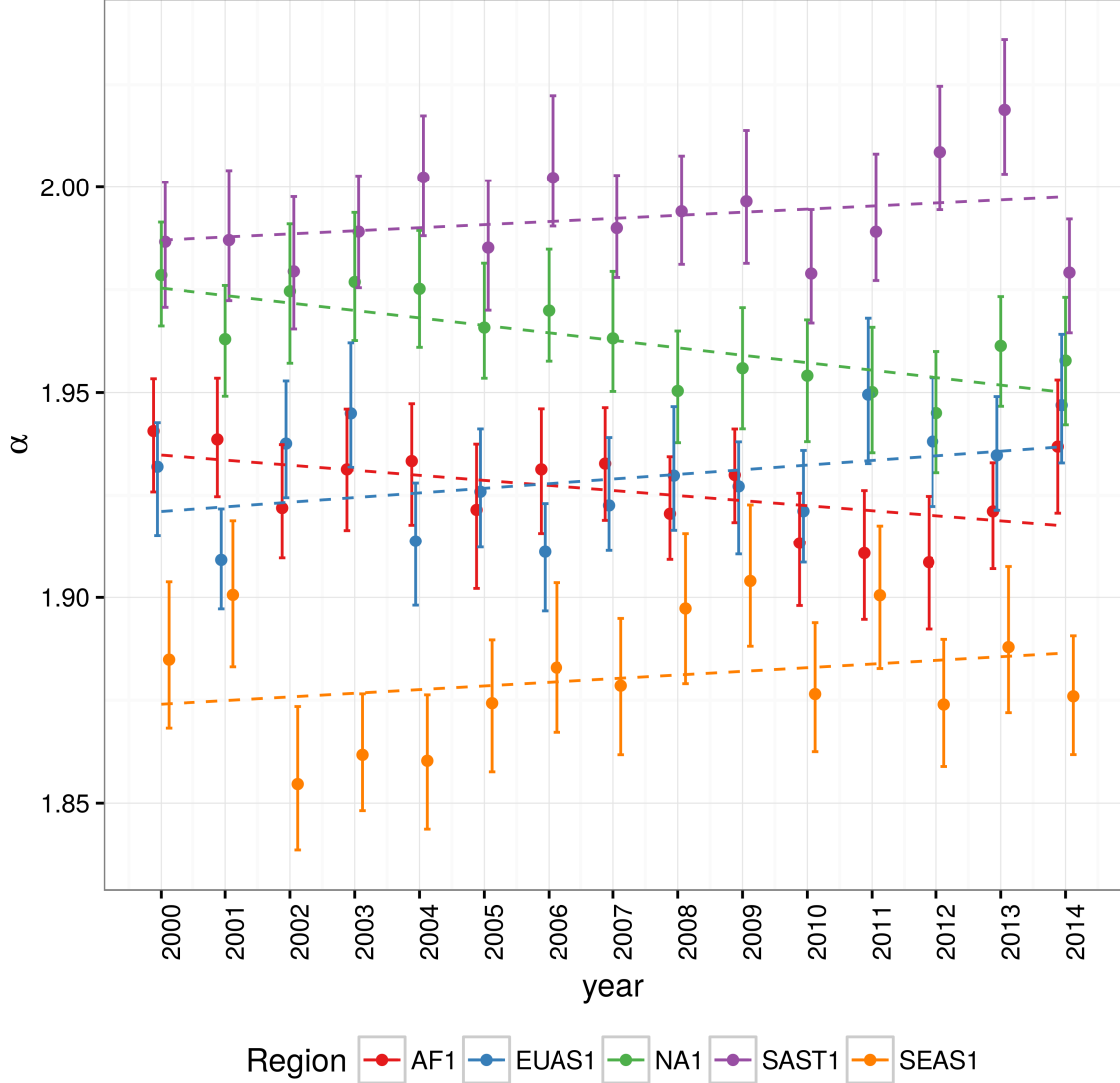


Figure 1: Power law exponents (α) of forest patch distributions for regions with total forest area $> 10^7$ km². Dashed horizontal lines are the fitted generalized least squares linear model, with 95% confidence interval error bars estimated by bootstrap resampling. The regions are AF1: Africa mainland, 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.

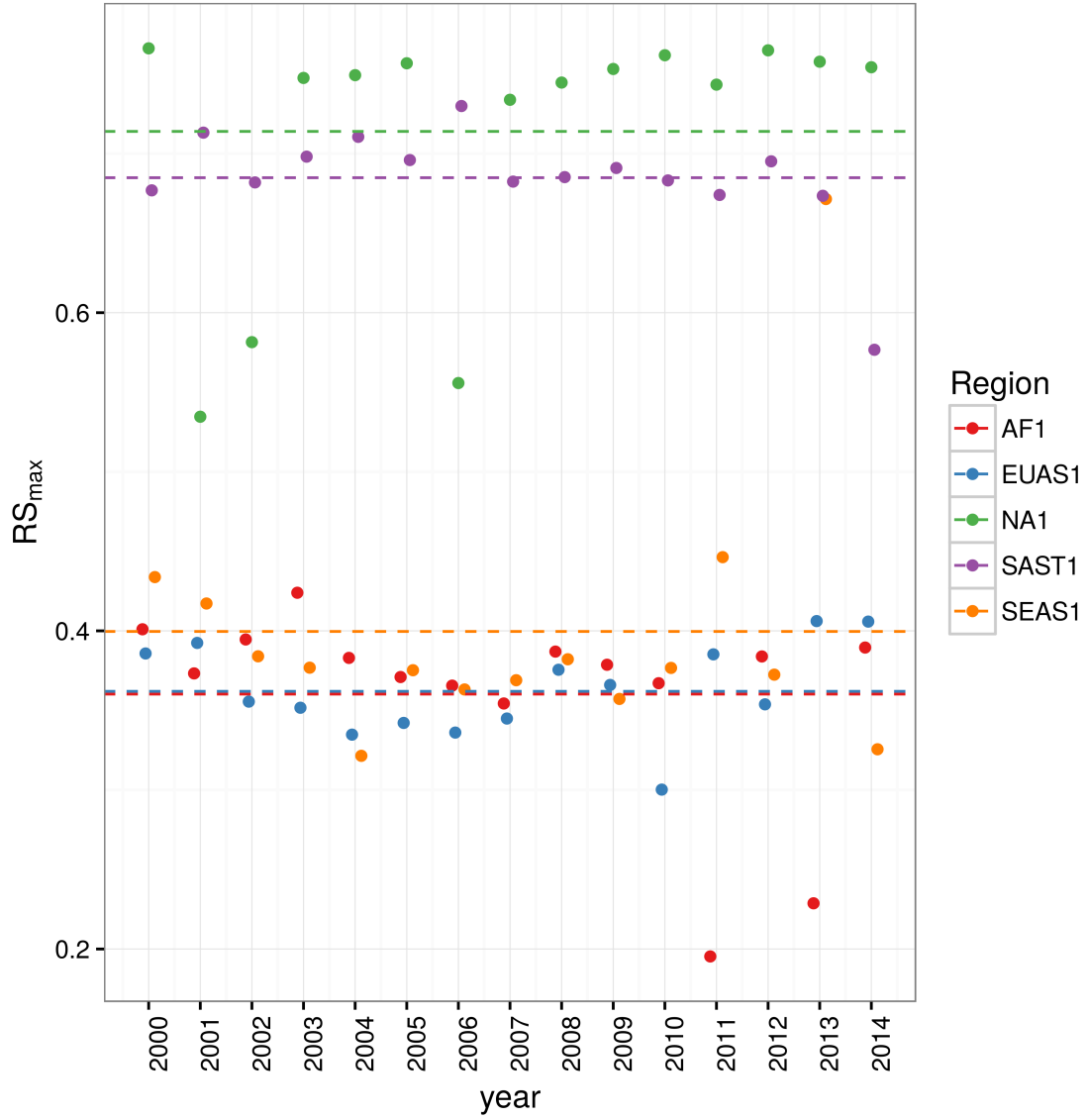


Figure 2: Largest patch proportion relative to total forest area RS_{max} , for regions with total forest area $> 10^7$ km². Dashed lines are averages across time. The regions are AF1: Africa mainland, EUAS1: Eurasia mainland, NA1: North America mainland, SAST1: South America tropical and subtropical, SEAS1: Southeast Asia mainland.

1 New Zealand (OC6, OC8) and Java (OC7) all follow an exponential distribution (Supplementary Table S7).
2 We only considered fluctuations to follow a power law when this distribution was selected for both absolute
3 and relative fluctuations.

4 The animations of the two largest patches (Supplementary data) qualitatively shows the nature of fluctuations
5 and if the state of the forest is connected or not. If the largest patch is always the same patch over time,
6 the forest is probably not fragmented; this happens for regions with RS_{max} of more than 40% such as AF2
7 (Madagascar), NA1 (North America), and OC3 (Malaysia). Moreover these regions maintain always the same
8 largest patch, which could represent a core area for conservation. [TODO: I'd move previous sentence to
9 discussion] In the regions with RS_{max} between 40% and 30% the identity of the largest patch changes could
10 change or stay the same in time. For OC7 (Java) the largest patch changes and for AF1 (Africa mainland) it
11 stays the same, as this is the zone where the critical transition occurs. Only for EUAS1 (Eurasia mainland)
12 did we observe that the two patches largest patches are always the same, implying that this region is probably
13 composed of two independent domains and should be divided in further studies. For regions with RS_{max} less
14 than 30%, the largest patch always changes, e.g. in SAST2 (Cuba) and EUAS3 (United Kingdom), reflecting
15 their fragmented state. In the case of SEAS2 (Philippines) a transition is observed, with the identity of the
16 largest patch first variable, and then constant after 2010.

17 The results of quantile regressions are identical for ΔRS_{max} and ΔS_{max} (supplementary table S4). Among
18 the biggest regions, Africa (AF1) has upper and lower quantiles with significantly negative slopes, but the
19 lower quantile slope is lower, implying that negative fluctuations and variance are increasing (Figure 3).
20 Eurasia mainland (EUAS1) has only the upper quantile significant with a positive slope, suggesting an
21 increase in the variance. North America mainland (NA1) exhibits a significant lower quantile with positive
22 slope, implying decreasing variance. Finally, for mainland Australia, all quantiles are significant, and the
23 slope of the lower quantiles is greater than the upper ones, as variance is decreasing (Supplementary figure
24 S10). These results are summarized in Table 1.

25 The conditions that indicate that a region is near a critical fragmentation threshold are that patch size
26 distributions follow a power law; temporal ΔRS_{max} fluctuations follow a power law; variance of ΔRS_{max} is
27 increasing in time; and skewness is negative. All these conditions were true only for Africa mainland (AF1)
28 and South America tropical & subtropical (SAST1).

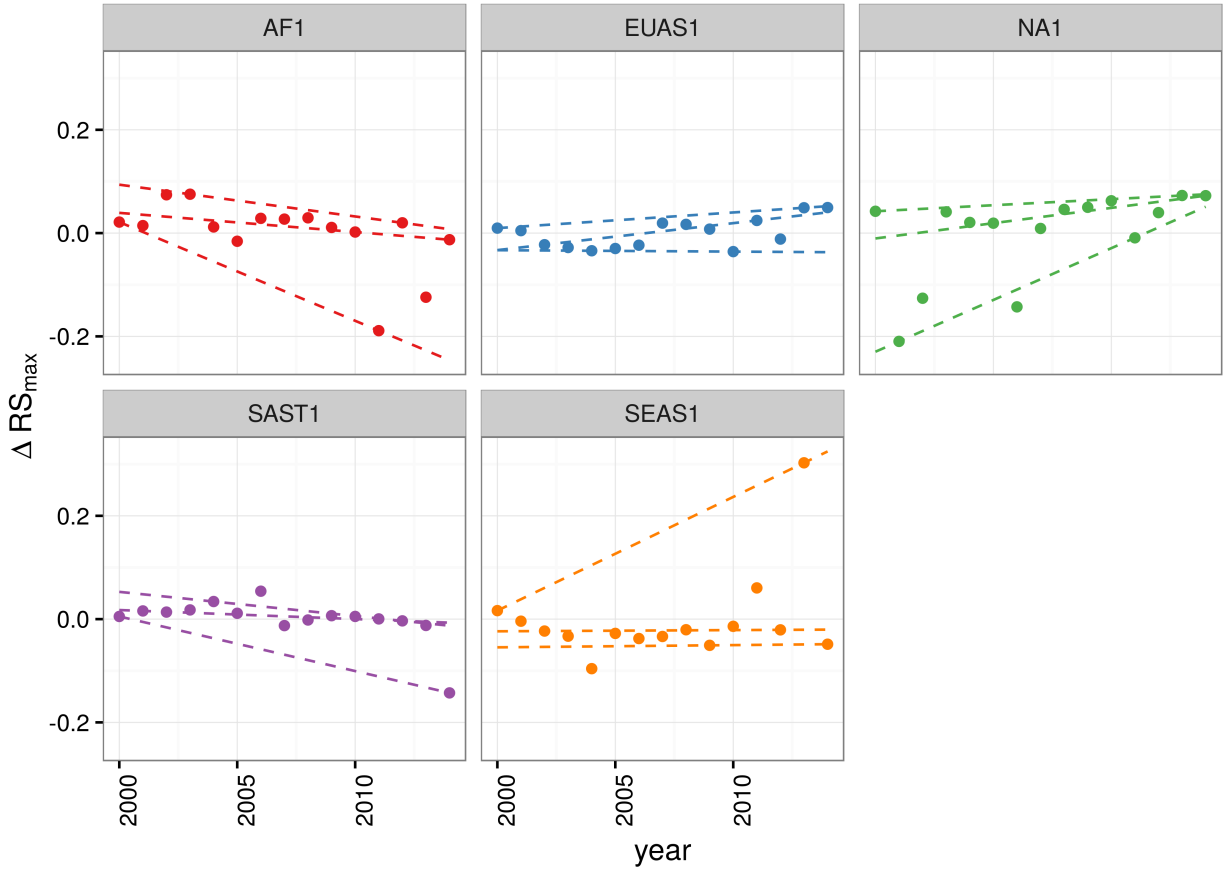


Figure 3: Largest patch fluctuations for regions with total forest area $> 10^7 \text{km}^2$. The patch sizes are relative to the total forest area of the same year. Dashed lines are 90%, 50% and 10% quantile regressions, to show if fluctuations were increasing. The regions are AF1: Africa mainland, 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, ΔRS_{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	ΔRS_{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	ΔRS_{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
3 seven orders of magnitude. These include tropical rainforest, boreal and temperate forest. Power laws have
4 previously been found for several kinds of vegetation, but never at global scales as in this study. Interestingly,
5 Eurasia does not follow a power law, but it is a geographically extended region, consisting of different domains
6 (as we observed in the Supplementary Information animations); the union of two independent power law
7 distributions produces a lognormal distribution [66]. Future studies should split this region into two or more
8 new regions, and test if the underlying distributions are power laws.

9 Several mechanisms have been proposed for power laws: the first is related self organized criticality (SOC),
10 when the system is driven by its internal dynamics to the critical state; this has been suggested mainly for
11 fire-driven forests [21,67]. Real ecosystems do not seem to meet the requirements of SOC dynamics: their
12 dynamics are influenced by external forces, and interactions are non-homogeneous (i.e. vary from place to
13 place) [68]. 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. [35] do not find any such effect,
15 and suggested that other mechanisms produce the power laws patterns observed.

The mechanism suggested by Pueyo et al. [35] 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 forest growth to be a random process at local scales, but it is possible that combinations of factors cancel out to produce seemingly random forest dynamics at large scales. If this is the case the power law exponent should be theoretically near $\alpha = 2.05495$, but this value is outside the confidence interval we found for α (1.898–1.920), and thus other explanations are needed.

The third mechanism suggested as the cause of pervasive power laws in patch size distribution was facilitation [43,44]: a patch surrounded by forest will have a smaller probability of been deforested or degraded than an isolated patch. We hypothesize that models that include facilitation could explain the patterns observed here. The model of Scanlon et al. [39] represented the dynamics of savanna trees includes a global constraint (mean rainfall), a local facilitation mechanism, and two states (tree/non-tree), producing power laws across a rainfall gradient without the need for 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, and exhibited deviations from power laws at high grazing pressures [38]. The values of the power law exponent α obtained for this model are dependent on the intensity of facilitation, when facilitation is more intense the exponent is higher but the maximal values they obtained were still lower than the ones we observed. The interesting point is that the value of the exponent is dependent on the parameters, thus the observed α might be obtained with some parameter combination. Kefi et al. [38] proposed that a deviation in power law behavior with the form of an exponential decay or cut-off could be a signal of a critical transition. At the continental scales studied here, we did not observe exponential cut-offs, but we do observed other signals of a transition, this confirms that different mechanisms could produce different spatial patterns near the transition and that early warnings based only on spatial patterns are not universal for all the systems [49,69].

It has been suggested that a combination of spatial and temporal indicators could more reliably detect critical transitions [69]. In this study, 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 the skewness of the fluctuations. Each one of these is not a strong individual predictor, but their combination 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 met the five criteria and thus seem to be near a critical fragmentation threshold. This means that the combined influence of human pressures and climate forcings might trigger all the undesired effects of fragmentation in these extended areas. A small but continuous increase in forest loss could produce a biodiversity collapse [29], and this threshold effect has been observed in different kind of models, experimental microcosms [70], field studies [71,72] and food webs [73]. Of 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 [74]. The region of South America tropical forest has a RS_{max} of more than 60% suggesting that the fragmentation transition is approaching but not yet started.

When habitat is reduced species population will decline proportionally; this can happens even when the habitat fragments retain connectivity. As habitat reduction continues, the critical threshold is approached and connectivity will have large fluctuations [75]. This could trigger several synergistic effects: populations fluctuations and the possibility of extinctions will rise, increasing patch isolation and decreasing connectivity [75]. This positive feedback mechanism will be enhanced when the fragmentation threshold is reached, resulting in the loss of most habitat specialist species at a landscape scale [71]. 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 that its existence is questionable [75]. Fragmentation is by definition a local process that at some point produces emergent phenomena over the entire landscape, even if the area considered is infinite [76]. In addition, after a region's fragmentation threshold connectivity decreases, there is still a large and internally well connected patch that can maintain sensitive species [72]. What is the time needed for these large patches to become fragmented, and pose a real danger of extinction to a myriad of sensitive species? If the forest is already in a fragmented state, a second critical transition could happen, this is called the desertification transition [54]. Considering the actual trends of habitat loss, and studying the dynamics of non-forest patches—instead of the forest patches as we did here—the risk of this kind of transition could be estimated. The simple models proposed previously 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 [50]. Regions that are in an unconnected state require large efforts to recover a connected state, but regions that are near a transition could be easily pushed to a connected state; feedbacks due to facilitation mechanisms might help to maintain this state.

It will be possible that these thresholds will sum up and produce a cascading effect to reach a planetary tipping point [4], if the dynamics of all the regions have strong connectivity. From the patterns of the fractal dimension of the biggest regions there seems to be no evidence of this coupling, and the largest patch time series also show at most a weak coupling. Only if the regions with more importance to the biosphere suffer a collapse, as maybe Africa and South America tropical forest, the coupling via atmospheric system feedback could effectively influence all other regions probably in a short time frame. Maybe too short to be offset by evolutionary responses, and that will produce an effective biodiversity collapse in all the biosphere.

The way that these regions could be strongly coupled is by a strong feedback with the climate system [24]. That could be produced. One would be linked by a strong one, we should extend the effects of these changes to know how it will feedback on global land-atmosphere processes that affect climate change. [TODO: could use a stronger finish - specific recommendations?]

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/doi/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: 1–9. Available: <http://advances.sciencemag.org/content/1/2/e1500052.abstract>.

6. Mitchell MGE, Suarez-Castro AF, Martinez-Harms M, Maron M, McAlpine C, et al. (2015) Reframing landscape fragmentation's effects on ecosystem services. *Trends in Ecology & Evolution* 30: 190–198. Available: <http://www.sciencedirect.com/science/article/pii/S0169534715000233>.

7. 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>.

8. 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>.

9. 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>.

10. 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.html>.

11. 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>.

12. 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>.

13. 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.

14. 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>.

15. 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>.

16. 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>.

17. 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>.

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

19. Solé RV, Bascompte J (2006) *Self-organization in complex ecosystems*. New Jersey, USA.: Princeton

- 1 University Press. Available: <http://books.google.com.ar/books?id=v4gpGH6Gv68C>.
- 2 20. Stauffer D, Aharony A (1994) Introduction To Percolation Theory. London: Taylor & Francis.
- 3 21. Zinck RD, Grimm V (2009) Unifying wildfire models from ecology and statistical physics. The American
4 naturalist 174: E170–85. Available: <http://www.ncbi.nlm.nih.gov/pubmed/19799499>.
- 5 22. Ochoa-Quintero JM, Gardner TA, Rosa I, de Barros Ferraz SF, Sutherland WJ (2015) Thresholds of
6 species loss in Amazonian deforestation frontier landscapes. Conservation Biology 29: 440–451. Available:
7 <http://onlinelibrary.wiley.com/doi/10.1111/cobi.12446/abstract>.
- 8 23. Leibold MA, Norberg J (2004) Biodiversity in metacommunities: Plankton as complex adaptive systems?
9 Limnology and Oceanography 49: 1278–1289. Available: http://www.aslo.org/lo/pdf/vol{_}49/issue{_}4{_}part{_}2/
- 10 24. Lenton TM, Williams HTP (2013) On the origin of planetary-scale tipping points. Trends in Ecology &
11 Evolution 28: 380–382. Available: <http://www.sciencedirect.com/science/article/pii/S0169534713001456>.
- 12 25. Bonan GB (2008) Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests.
13 Science 320: 1444–1449. Available: <http://www.sciencemag.org/content/320/5882/1444.abstract>.
- 14 26. Solé RV, Bartumeus F, Gamarra JGP (2005) Gap percolation in rainforests. Oikos 110: 177–185.
15 Available: <http://onlinelibrary.wiley.com/doi/10.1111/j.0030-1299.2005.13843.x/abstract>.
- 16 27. He F, Hubbell S (2003) Percolation Theory for the Distribution and Abundance of Species. Physical
17 Review Letters 91: 198103. Available: <http://link.aps.org/doi/10.1103/PhysRevLett.91.198103>.
- 18 28. Bascompte J, Solé RV, Sole RV (1996) Habitat fragmentation and extinction thresholds in spatially explicit
19 models. Journal of Animal Ecology 65: 465–473. Available: <http://www.jstor.org/discover/10.2307/5781?uid=3737512{\\&}u>
- 20 29. Solé RV, Alonso D, Saldaña J (2004) Habitat fragmentation and biodiversity collapse in neutral com-
21 munities. Ecological Complexity 1: 65–75. Available: [http://www.sciencedirect.com/science/article/pii/](http://www.sciencedirect.com/science/article/pii/S1476945X03000084)
22 [S1476945X03000084](http://www.sciencedirect.com/science/article/pii/S1476945X03000084).
- 23 30. Loehle C, Li B-L, Sundell RC (1996) Forest spread and phase transitions at forest-prairie ecotones in
24 Kansas, U.S.A. Landscape Ecology 11: 225–235.
- 25 31. Naito AT, Cairns DM (2015) Patterns of shrub expansion in Alaskan arctic river corridors suggest phase
26 transition. Ecology and Evolution 5: 87–101. Available: <http://dx.doi.org/10.1002/ece3.1341>.
- 27 32. Dai L, Vorselen D, Korolev KS, Gore J (2012) Generic Indicators for Loss of Resilience Before a Tipping
28 Point Leading to Population Collapse. Science 336: 1175–1177. Available: <http://www.sciencemag.org/>

content/336/6085/1175.abstract.

33. Hastings A, Wysham DB (2010) Regime shifts in ecological systems can occur with no warning. *Ecology Letters* 13: 464–472. Available: <http://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2010.01439.x/abstract>.

34. Boettiger C, Hastings A (2012) Quantifying limits to detection of early warning for critical transitions. *Journal of The Royal Society Interface* 9: 2527–2539. doi:10.1098/rsif.2012.0125.

35. Pueyo S, de Alencastro Graça PML, Barbosa RI, Cots R, Cardona E, et al. (2010) Testing for criticality in ecosystem dynamics: the case of Amazonian rainforest and savanna fire. *Ecology Letters* 13: 793–802. Available: <http://dx.doi.org/10.1111/j.1461-0248.2010.01497.x>.

36. Zhang JY, Wang Y, Zhao X, Xie G, Zhang T (2005) Grassland recovery by protection from grazing in a semi-arid sandy region of northern China. *New Zealand Journal of Agricultural Research* 48: 277–284. Available: <http://dx.doi.org/10.1080/00288233.2005.9513657>.

37. Allington GRH, Valone TJ (2010) Reversal of desertification: The role of physical and chemical soil properties. *Journal of Arid Environments* 74: 973–977. Available: <http://dx.doi.org/10.1016/j.jaridenv.2009.12.005>.

38. Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, et al. (2007) Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449: 213–217. Available: <http://dx.doi.org/10.1038/nature06111> <http://www.nature.com/nature/journal/v449/n7159/abs/nature06111.html>.

39. Scanlon TM, Caylor KK, Levin SA, Rodriguez-iturbe I (2007) Positive feedbacks promote power-law clustering of Kalahari vegetation. *Nature* 449: 209–212. doi:10.1038/nature06060.

40. Vandermeer J, Perfecto I, Philpott SM (2008) Clusters of ant colonies and robust criticality in a tropical agroecosystem. *Nature* 451: 457–460. doi:10.1038/nature06477.

41. Saravia LA, Giorgi A, Momo F (2012) Multifractal growth in periphyton communities. *Oikos* 121: 1810–1820. Available: <http://doi.wiley.com/10.1111/j.1600-0706.2011.20423.x>.

42. Dal Bello M, Maggi E, Rindi L, Capocchi A, Fontanini D, et al. (2014) Multifractal spatial distribution of epilithic microphytobenthos on a Mediterranean rocky shore. *Oikos* 124: 477–485. Available: <http://onlinelibrary.wiley.com/doi/10.1111/oik.01503/abstract>.

43. Manor A, Shnerb NM (2008) Origin of pareto-like spatial distributions in ecosystems. *Physical Review Letters* 101: 268104. Available: <http://link.aps.org/doi/10.1103/PhysRevLett.101.268104>.

44. Irvine MA, Bull JC, Keeling MJ (2016) Aggregation dynamics explain vegetation patch-size distributions.

- 1 Theoretical Population Biology 108: 70–74. Available: [http://www.sciencedirect.com/science/article/pii/](http://www.sciencedirect.com/science/article/pii/S0040580915001239)
2 S0040580915001239.
- 3 45. Bulleri F, Bruno JF, Benedetti-ecchi L (2008) Beyond Competition: Incorporating Posi-
4 tive Interactions between Species to Predict Ecosystem Invasibility. PLoS Biology 6: 1136–1140.
5 doi:10.1371/journal.pbio.0060162.
- 6 46. DiMiceli C, Carroll M, Sohlberg R, Huang C, Hansen M, et al. (2015) Annual Global Automated
7 MODIS Vegetation Continuous Fields (MOD44B) at 250 m Spatial Resolution for Data Years Beginning
8 Day 65, 2000 - 2014, Collection 051 Percent Tree Cover, University of Maryland, College Park, MD, USA.
9 Available: https://lpdaac.usgs.gov/dataset{_}discovery/modis/modis{_}products{_}table/mod44b.
- 10 47. Sexton JO, Noojipady P, Song X-P, Feng M, Song D-X, et al. (2015) Conservation pol-
11 icy and the measurement of forests. Nature Climate Change advance on: 192–196. Available:
12 <http://www.nature.com/nclimate/journal/vaop/ncurrent/full/nclimate2816.html> <http://dx.doi.org/10.1038/nclimate2816>
13 <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-information)
14 information.
- 15 48. Belward AS (1996) The IGBP-DIS Global 1 Km Land Cover Data Set “DISCover”: Proposal and Imple-
16 mentation Plans : Report of the Land Recover Working Group of IGBP-DIS. IGBP-DIS Office. Available:
17 <https://books.google.com.ar/books?id=qixsNAAACAAJ>.
- 18 49. Weerman EJ, Van Belzen J, Rietkerk M, Temmerman S, Kéfi S, et al. (2012) Changes in diatom
19 patch-size distribution and degradation in a spatially self-organized intertidal mudflat ecosystem. Ecology
20 93: 608–618. Available: <http://www.esajournals.org/doi/abs/10.1890/11-0625.1>.
- 21 50. Oborny B, Szabó G, Meszéna G (2007) Survival of species in patchy landscapes: percolation in space
22 and time. In: Scaling biodiversity. Cambridge University Press. pp. 409–440. Available: [http://dx.doi.org/](http://dx.doi.org/10.1017/CBO9780511814938.022)
23 10.1017/CBO9780511814938.022.
- 24 51. Gastner MT, Oborny B, Zimmermann DK, Pruessner G (2009) Transition from Connected to Fragmented
25 Vegetation across an Environmental Gradient: Scaling Laws in Ecotone Geometry. The American Naturalist
26 174: E23–E39. Available: <http://www.jstor.org/stable/10.1086/599292>.
- 27 52. Ódor G (2004) Universality classes in nonequilibrium lattice systems. Reviews of Modern Physics 76:
28 663–724. Available: <http://link.aps.org/doi/10.1103/RevModPhys.76.663>.
- 29 53. 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>.
54. 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>.
55. 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>.
56. 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>.
57. Efron B, Tibshirani RJ (1994) *An Introduction to the Bootstrap*. New York: Taylor & Francis. Available: <https://books.google.es/books?id=gLpIUxRntoC>.
58. Burnham K, Anderson DR (2002) *Model selection and multi-model inference: A practical information-theoretic approach*. 2nd. New York: Springer-Verlag.
59. Klaus A, Yu S, Plenz D (2011) Statistical analyses support power law distributions found in neuronal avalanches. *PloS one* 6: e19779. Available: <http://dx.plos.org/10.1371/journal.pone.0019779>.
60. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) *nlme: Linear and Nonlinear Mixed Effects Models*. Available: <http://cran.r-project.org/package=nlme>.
61. Gardner RH, Urban DL (2007) Neutral models for testing landscape hypotheses. *Landscape Ecology* 22: 15–29. Available: <http://dx.doi.org/10.1007/s10980-006-9011-4> <http://www.springerlink.com/content/2vq21v4v78461506/>.
62. Keitt TH, Urban DL, Milne BT (1997) Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1: 4. Available: <http://www.ecologyandsociety.org/vol1/iss1/art4/>.
63. Benedetti-Cecchi L, Tamburello L, Maggi E, Bulleri F (2015) Experimental Perturbations Modify the Performance of Early Warning Indicators of Regime Shift. *Current biology* 25: 1867–1872. doi:10.1016/j.cub.2015.05.035.
64. R Core Team (2015) *R: A Language and Environment for Statistical Computing*. Available: <http://www.r-project.org/>.
65. Gillespie CS (2015) Fitting Heavy Tailed Distributions: The powerLaw Package. *Journal of Statistical Software* 64: 1–16. Available: <http://www.jstatsoft.org/v64/i02/>.
66. Rooij MMJW van, Nash B, Rajaraman S, Holden JG (2013) *A Fractal Approach to Dynamic Inference*

- and Distribution Analysis. *Frontiers in Physiology* 4. Available: http://www.frontiersin.org/fractal{_}physiology/10.3389/f
67. Hantson S, Pueyo S, Chuvieco E (2015) Global fire size distribution is driven by human impact and
climate. *Global Ecology and Biogeography* 24: 77–86. Available: <http://dx.doi.org/10.1111/geb.12246>.
68. Solé RV, Alonso D, McKane A (2002) Self-organized instability in complex ecosystems. *Philosophical transactions of the Royal Society of London Series B* 357: 667–681. Available: <http://rstb.royalsocietypublishing.org/content/357/1421/667>.
69. Kéfi S, Guttal V, Brock WA, Carpenter SR, Ellison AM, et al. (2014) Early Warning Signals of
Ecological Transitions: Methods for Spatial Patterns. *PLoS ONE* 9: e92097. Available: <http://dx.doi.org/10.1371/journal.pone.0092097>.
70. Starzomski BM, Srivastava DS (2007) Landscape geometry determines community response to disturbance. *Oikos* 116: 690–699. doi:10.1111/j.2006.0030-1299.15547.x.
71. Pardini R, Bueno A de A, Gardner TA, Prado PI, Metzger JP (2010) Beyond the Fragmentation
Threshold Hypothesis: Regime Shifts in Biodiversity Across Fragmented Landscapes. *PLoS ONE* 5: e13666.
Available: <http://dx.doi.org/10.1371/journal.pone.0013666>.
72. Martensen AC, Ribeiro MC, Banks-Leite C, Prado PI, Metzger JP (2012) Associations of Forest Cover,
Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance. *Conservation Biology* 26: 1100–1111. Available: <http://onlinelibrary.wiley.com/doi/10.1111/j.1523-1739.2012.01940.x/abstract>.
73. Martinson HM, Fagan WF, Denno RF (2012) Critical patch sizes for food-web modules. *Ecology* 93: 1779–1786. Available: <http://dx.doi.org/10.1890/11-1497.1>.
74. Staver AC, Archibald S, Levin SA (2011) The Global Extent and Determinants of Savanna and Forest as
Alternative Biome States. *Science* 334: 230–232. Available: <http://www.sciencemag.org/content/334/6053/230>.
75. Brook BW, Ellis EC, Perring MP, Mackay AW, Blomqvist L (2013) Does the terrestrial biosphere have
planetary tipping points? *Trends in Ecology & Evolution*. Available: <http://www.sciencedirect.com/science/article/pii/S0169534713000335>.
76. Oborny B, Meszéna G, Szabó G (2005) Dynamics of Populations on the Verge of Extinction. *Oikos* 109: 291–296. Available: <http://www.jstor.org/stable/3548746>.