

1 **Biodiversity collapse and early warning indicators in a spatial phase**  
2 **transition between neutral and niche communities**

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## 1 Abstract

2 The dynamics of ecological communities have been described by neutral and niche theories that are now  
3 increasingly integrated into unified models. It is known that a critical transition exists between these two  
4 states, but the spatial aspect of this transition has not been studied. Our aim is to study the spatial aspect of  
5 the transition and propose early warning signals to detect it. We used a stochastic, spatially explicit model  
6 that spans a continuum from neutral to niche communities, and is driven by the intensity of hierarchical  
7 competition. The transition is indicated by the emergence of a large patch formed by one species that  
8 connects the whole area. The properties of this patch can be used as early warning indicators of a critical  
9 transition. If competition intensity increases beyond the critical point, our model shows a sudden decrease of  
10 the Shannon diversity index and a gentle decline in species richness. The critical point occurs at a very low  
11 value of competitive intensity, with the rate of migration from the metacommunity greatly influencing the  
12 position of this critical point. As an example, we apply our new method of early warning indicators to the  
13 Barro Colorado Tropical forest, which, as expected, appears to be far from a critical transition. Low values of  
14 competitive intensity were also reported by previous studies for different high-diversity real communities,  
15 suggesting that these communities are located before the critical point. A small increase of competitive  
16 interactions could push them across the transition, however, to a state in which diversity is much lower.  
17 Thus this new early warnings indicator could be used to monitor high diversity ecosystems that are still  
18 undisturbed.

19 *Short title:* A spatial phase transition between neutral and niche communities

20 *keywords:* Continuous critical transitions; Percolation; Neutral-niche communities; spatial stochastic models;  
21 Biodiversity collapse

## 1 Introduction

2 Much effort has been devoted to understanding the mechanisms of community assembly and dynamics.  
3 Classical studies emphasized deterministic processes based on niche differences between species; niche theory  
4 assumes that different species are regulated by various environmental factors and infer that diversity originates  
5 from spatial and temporal environmental heterogeneity (Tilman 1982, Chesson 2000). More recently, the  
6 emphasis has shifted to stochastic mechanisms in the form of the Neutral Theory of Biodiversity and  
7 Biogeography (Hubbell 2001). The neutral theory assumes that individuals of all species are functionally  
8 equivalent, and proposes that diversity originates from a balance between immigration, speciation, and  
9 extinction. The neutral theory has been proposed as a parsimonious formulation that can provide new insight  
10 into the patterns of community assembly (Hubbell 2005). In spite of its simplicity, the theory can predict some  
11 community metrics very well, like the species abundance distribution (SAD) (Volkov et al. 2007, Rosindell  
12 et al. 2012), beta-diversity (Condit et al. 2002) and species-area relationships (Rosindell and Cornell 2009,  
13 O'Dwyer and Green 2010).

14 The neutral theory has generated a great deal of controversy, mainly due to its equivalence assumption (Chave  
15 2004, Clark 2012). One way to resolve this is to understand that at a local scale, niche differences between  
16 species seem to be important for community dynamics, but at broader scales differences in specific traits are  
17 not essential to predict community patterns (Chave 2004, Matthews and Whittaker 2014). Finally, a unified  
18 view has arisen that accepts that both kinds of mechanisms are present at the same time, shifting the focus  
19 to quantifying the relative importance of these in natural communities (Gravel et al. 2006, Zhou and Zhang  
20 2008, Vergnon et al. 2009, Jabot and Chave 2011, Martorell and Freckleton 2014, Kalyuzhny et al. 2014).

21 The problems of pattern and scale are critical in ecology (Levin 1992, Chave 2013), because patterns that  
22 seem stochastic at one scale may reveal structure at another scale. The concept of pattern is related to  
23 some sort of repetition that our brain can detect; when this pattern occurs at different scales we talk about  
24 scale invariance or self-similarity, characterized by power laws. These patterns could be produced by critical  
25 phase transitions described by percolation theory (Stauffer and Aharony 1994). These kinds of spatial phase  
26 transitions were first introduced in ecology in the framework of landscape ecology (Loehle et al. 1996) and  
27 habitat fragmentation (Bascompte and Solé 1996).

28 Percolation is characterized by the presence of two phases defined by some macroscopic features, such as the  
29 presence or absence of vegetation in arid ecosystems (Kéfi et al. 2007). These phases are linked by a critical  
30 point where a sudden transition happens and a large spatial pattern emerges. To illustrate the mechanism  
31 behind a phase transition, we define first a two-dimensional landscape composed by a grid of sites. Each site

1 is connected to its four nearest neighbors with probability  $p$ . If  $p$  is small there will be only a few connected  
2 sites that form clusters. When  $p$  increases, the clusters become larger because each site is connected with  
3 higher probability to its neighbors. Finally, there is one value of  $p$  at which a single cluster spans the entire  
4 landscape. This spanning cluster has a self-similar structure and is produced by local interactions (Solé and  
5 Bascompte 2006). The clusters are usually called ‘patches’ in the ecological literature, and here we continue  
6 to use patches to refer to the clusters that connect through their four nearest neighbors.

7 Several different ecological spatial models exhibit critical behavior related to the degree of disturbance  
8 (Pascual and Guichard 2005). Some of these models show robust criticality, a particular kind of criticality for  
9 ecological systems, in which self-similarity is present for a wide range of parameters and does not necessarily  
10 involve drastic changes in the biological variables of interest (Roy and Pascual 2003). This kind of criticality  
11 has been suggested for arid ecosystems (Solé 2007), in which a sudden shift towards desert conditions might  
12 occur when rainfall decreases (Scanlon et al. 2007) or also with more intense grazing (Kéfi et al. 2007). The  
13 mechanism producing self-similarity is the positive effect produced by local facilitation, e.g. the establishment  
14 of a new seedling is more likely near the parent plant. Another example of an ecosystem exhibiting criticality  
15 are savannas, where the transition occurs between tree and grass cover (Abades et al. 2014). In critical  
16 phenomena, the transition is produced by the capacity of the system to transmit some signal or information.  
17 In savannas, when the proportion of grass approaches a 60%, fire can spread across the landscape; conversely,  
18 if there is less grass to act as a fuel, fire cannot spread (Staver and Levin 2012). Thus an increase in the  
19 proportion of trees, due to a change in environmental conditions, can create positive feedback mechanisms  
20 resulting in the encroachment of savanna ecosystems (Abades et al. 2014).

21 The self-similar structure of the spanning patch is characterized by a power law patch size distribution, but  
22 neutral models can produce power law patch distributions without being near a critical state (Houchmandzadeh  
23 and Vallade 2003), so the detection of these kind of patterns does not imply a phase transition. Moreover,  
24 sudden changes between neutral and niche dynamics have been described for non-spatial models (Zhou and  
25 Zhang 2008, Chisholm and Pacala 2011, Kalyuzhny et al. 2014), and Fisher et al. (2014) demonstrated the  
26 presence of a phase transition for neutral-niche models. However, the spatial properties and consequences of  
27 this transition have not been studied.

28 Here we study the phase transition between neutral and niche dynamics from a spatial point of view by  
29 applying methods of percolation theory. We will use a spatially explicit neutral model where niche dynamics  
30 is represented as a competitive hierarchy (Saravia 2015). Our first objective is to demonstrate the existence  
31 of the phase transition in our spatial neutral-niche model triggered by competition intensity; we show that  
32 the phase transition is determined by the geometric characteristics of the species patches, and that the niche

1 state that emerges after the critical point has lower species diversity and richness. Our second objective  
2 is to define early warning indicators based on the dynamics of patches. Finally, we apply our new early  
3 warning indicators to the repeated censuses of a 50-ha forest dynamics plot of Barro Colorado Island (BCI)  
4 in Panama.

## 5 **Methods**

6 First, we define the spatial explicit neutral-hierarchical model; then we explain how we characterized its  
7 critical behavior in terms of percolation theory and how simulations were performed. We analyze early  
8 warnings for this critical transition and apply the same techniques for BCI plot data. We refer interested  
9 readers to more extensive introductions to percolation theory in an ecological context (Solé and Bascompte  
10 2006, Oborny et al. 2007).

### 11 **The spatial stochastic model**

12 This model represents a continuum between a neutral model and a niche model of hierarchical competition, in  
13 the same spirit as Gravel et al. (2006), and others (Zhou and Zhang 2008, Chisholm and Pacala 2010). The  
14 model is a stochastic cellular automaton (CA), also called an interactive particle system (Durrett and Levin  
15 1994). In these models space is discretized into a grid and only one individual can occupy a particular position.  
16 Each position represents an area fixed by the investigator to mimic the real system. Time is continuous, so  
17 the update of the model is asynchronous. Sites are selected at random and to perform one complete time  
18 interval  $J$  sites have to be updated, where  $J$  is the size of the grid (Durrett and Levin 1994). The units of  
19 the grid are arbitrary but for using parameters compatible with field studies we choose a side of 1 meter.

20 We use periodic boundary conditions, which makes the landscape a torus: sites on the top edge of the grid are  
21 neighbors of those on the bottom edge, and sites on the right edge are neighbors of those on the left. With  
22 this choice we avoid edge effects, this is equivalent to treating the grid as embedded in a large community.  
23 The size of the community is given by  $J = \text{dim}X \times \text{dim}Y$ , where  $\text{dim}X$  and  $\text{dim}Y$  are the dimensions of the  
24 grid. Thus  $J$  is the maximum number of individuals in the simulated area. As in a classical neutral model,  
25 there is a metacommunity, i.e. a regional species pool assumed to be very large and invariant in ecological  
26 time scales (Hubbell 2001). All individuals have the same parameters, unless they belong to different species  
27 (Hubbell 2001), and each species is assigned an indicator number that is used to define a competitive hierarchy.  
28 There are only two possible differences between species:

- 1 • They may have a different frequency  $X_i$  in the metacommunity and also different abundances in the  
2 local community.
- 3 • Hierarchical competition: species with lower numbers have a probability of replacing species with higher  
4 numbers as in (Tilman 1994). Thus a species with number 1 has a probability of replacing species with  
5 number 2 and greater. The species with number 2 can replace species starting from 3. The probability  
6 of replacement ( $\rho$ ) is a parameter; when it is 0, there is no replacement and the model behaves like  
7 a neutral model without competitive hierarchy. The parameter  $\rho$  is also referred as the intensity of  
8 competition, because when  $\rho = 1$  the intensity will be maximal: whenever two individuals of different  
9 species meet there will be a competitive displacement. When  $\rho$  is lower, this will not happen in all  
10 encounters, and the intensity of competition will decrease.

11 The colonization-competition and other possible trade-offs are not explicitly included in the model. However,  
12 a colonization-competition trade-off can be established if species numbering is arranged in inverse order to its  
13 frequency  $X_i$  in the metacommunity. If colonization-competition trade-off is included, the most competitive  
14 species (with number 1) will have the lowest migration rate and the less competitive will have the highest  
15 migration rate.

16 There are four processes included in the model: death, local dispersal, migration, and competition. After  
17 setting initial conditions the following events can happen:

18 (A) If the selected site is empty:

19 (1) With probability  $m$  an individual of a species  $i$  can migrate from the metacommunity, at a rate  
20 proportional to its frequency  $X_i$  in the metacommunity.

21 (2) With probability  $1-m$  the site could be occupied by a new individual that disperses to the  
22 neighborhood with a dispersal kernel. Here we use an inverse power kernel with average distance  $d$   
23 (Marco et al. 2011):

$$24 \quad d(x) = \frac{\alpha-1}{x_{min}} \left( \frac{x}{x_{min}} \right)^{-\alpha} \quad \text{with } mean = \frac{\alpha-1}{\alpha-2} x_{min} \quad \text{where } \alpha > 1 \text{ and } x \geq x_{min}.$$

25 where  $d(x)$  is the probability that an individual disperses a distance  $x$  from the parent. In all cases we  
26 used  $x_{min} = 1$ .

27 (B) If the selected site is not empty:

28 (3) Individuals die at a rate  $\mu$

29 (4) When an individual dies, it is replaced by a migrant from metacommunity with probability  $m$  and

1 with probability  $1 - m$  by an individual from the neighborhood as in (1) and (2). Once the grid is  
2 full it stays full, because when an individual dies it is immediately replaced by another. This is  
3 called the zero-sum assumption in neutral models.

4 (5) Surviving individuals can be replaced by individuals from the metacommunity or neighborhood as  
5 in (4) based on the competitive hierarchy where an individual of species  $k$  can only replace an  
6 individual of species  $k + 1$  with probability  $\rho$ . Thus a hierarchical ordering of species is established.  
7 When this probability is zero, the model behavior becomes neutral.

8 In the simulations, the events are evaluated in the order specified by its numbers. The parameter  $m$  has  
9 the same meaning as in the spatially implicit neutral model, but there are two fundamental differences: a)  
10 individuals that disperse by the edges of the lattice produce the same effect as  $m$ , and therefore as local  
11 dispersion already accounts for part of migration, the values of  $m$  are lower for our spatially explicit model;  
12 b) individuals who colonize the grid due to  $m$  do so in random positions, disrupting the patch structure  
13 produced by local dispersion.

14 The model was developed using the C++ programming language and its source code is available at <https://github.com/lasaravia/neutral> and figshare <http://dx.doi.org/10.6084/m9.figshare.969692>.

## 16 Percolation and simulations

17 To characterize our model in terms of percolation theory, we need to define an order parameter that depends  
18 on a tuning parameter (describing an external control) that can be continuously varied. We defined the  
19 tuning parameter as the replacement probability  $\rho$ , and the order parameter as the probability that a patch  
20 of one species connects the landscape, called the spanning cluster probability  $SC_p$ . Percolation is produced  
21 when a spanning cluster is present, meaning that there is at least one patch of one species that spans from  
22 one edge of the system to the opposite edge. We calculated the patches for all species using a modified  
23 Hoshen–Kopelman cluster labeling algorithm (Hoshen and Kopelman 1976) with a neighborhood defined by  
24 the four nearest sites (Von Neumann neighborhood) available at <https://github.com/lasaravia/Clusters>. A  
25 method to obtain the percolation point is to estimate the value of the tuning parameter  $\rho$  at which  $SC_p$  is 0.5  
26 (Ziff and Newman 2002). To obtain  $SC_p$  we measure the frequency of simulations where a spanning cluster  
27 appears. We used one snapshot of the spatial pattern to make our results more compatible with field studies;  
28 hence we measure the patch size distributions after the model reach a steady state between 5000 and 30000  
29 time intervals (as defined above). We checked that the model reached a steady state by a series of preliminary  
30 simulations using the same range of parameters as for the experiment. We calculated the average Shannon

1 diversity index ( $H$ ) of the last 1000 time steps for runs with different total time (3000,5000,10000,20000 and  
2 30000 time steps). Then we compared the values of the average  $H$  for consecutive total times (3000 vs 5000,  
3 5000 vs 10000,) and we observed if the last  $H$  range was similar to the previous. If the range keeps constant,  
4 we take the minimum time as the steady state simulation time. We also checked the steady state by visually  
5 inspecting the  $H$  time series.

6 The size of the lattice affects the value of the critical point  $\rho_c$  at which the transition occurs; in small lattices  
7  $SC_p$  is non-zero for values of  $\rho$  below the critical point  $\rho_c$ , this means that patches that connect the entire  
8 lattice appear by chance. Therefore, to obtain an asymptotic estimate for  $\rho_c$  we performed a finite size  
9 scaling analysis. For this, we run simulations for different lattice sizes (Side = 128, 192, 256) and obtained  
10 asymptotic values by regressing  $\rho_c$  against  $1/Side^2$ ; the intercept becomes an estimate for a lattice of infinite  
11 size, denoted by  $\rho_c^\infty$  (Stauffer and Aharony 1994, Sornette 2000).

12 We determined critical points for two different metacommunities: a) One with a logseries species abundance  
13 distribution, the most common distribution that fits experimental data (White et al. 2012). With this  
14 metacommunity we included a competition-colonization trade-off by arranging species numbers in inverse  
15 order as it is frequency  $X_i$  in the metacommunity. b) A uniform species distribution, in which all species  
16 have the same probability of colonizing the local community. The parameter  $m$  represents a long-distance  
17 dispersal event from the metacommunity but can also be interpreted as a speciation parameter (Chave 2004,  
18 Rosindell and Cornell 2009). The values of the  $m$  parameter (Table 1) were at least two orders of magnitude  
19 higher than realistic speciation rates (Rosindell and Cornell 2009) as it is not our aim to interpret the results  
20 in an evolutionary framework, only to show the influence of different metacommunities.

21 The parameters used were compatible with published results from tropical forests, but we do not intend to  
22 encompass all the possibilities: the number of species in the metacommunity was between 16 and 320, and  
23 the mean dispersal distance was between 13-53 meters (Condit et al. 2002, Anand and Langille 2010). It has  
24 been suggested that fat-tail dispersal kernels give more realistic results (Rosindell and Cornell 2009, Seri  
25 et al. 2012) so we used an inverse power law distribution with exponents always greater than two (Table  
26 1). The parameter  $m$  has a range from 0.0001 to 0.01; note that the spatially explicit parameters do not  
27 have the same values than the parameters estimated for the spatially implicit model. We used the formulas  
28 from Etienne & Rosindell (2011) to calculate the equivalence of spatially explicit parameters with the neutral  
29 theory spatially implicit parameters  $\theta$  and  $I$  (Appendix Table S1). The range of the parameter  $m$  is similar  
30 to the one used in other studies of neutral spatially explicit models (May et al. 2015).

31 The parameter  $\rho$  is varied across all the range between 0 and 1 to determine the critical point. In the region

1 where we suspected the  $\rho_c$  to be located (near 0), the steps were very small (0.0001), and greater (0.1) in  
2 regions unlikely to include  $\rho_c$ . To calculate the value of  $\rho_c$  at which  $SC_p = 0.5$  we interpolate linearly from  
3 the four values of  $\rho$  that have the nearest values of  $SC_p$  to 0.5.

4 All simulations started with a lattice filled with individuals at random positions, following the same abundance  
5 distribution as the metacommunity. For each parameter combination we performed 50 simulations. Thus,  
6 we calculated the  $SC_p$  as the number of times we observed a spanning cluster divided by the number  
7 of simulations. The analysis of the model output was done in the R statistical language (R Core Team  
8 2015) and the scripts are available at GitHub <https://github.com/lisaravia/CriticalTransition> and figshare  
9 <http://dx.doi.org/10.6084/m9.figshare.2007537>.

10 We estimated the critical point using a wide range of parameters to test that the transition is not confined  
11 to a small region in the parameter space. In addition, we analyzed changes in the critical point to give us  
12 an idea of the sensitivity of the simulated communities to changes in the intensity of competition. This  
13 could be used to compare the predictions of the model with the behavior of real communities where a change  
14 in the competitive intensity has been documented. We analyzed the critical point for infinite lattices ( $\rho_c^\infty$ )  
15 varying three parameters of the model, one at a time: the migration  $m$ , the dispersal distance, and the  
16 number of species in the metacommunity. The parameter  $\mu$  was fixed at 0.2, a higher mortality rate than  
17 observed for tropical forests, but because of the zero-sum assumption the only effect of this is to increase the  
18 turnover rate of species and thus reduce the time needed to reach a steady-state of the model. To change the  
19 dispersal distance we varied the power exponent of the dispersal kernel  $\alpha$  (Table 1). We used as a baseline  
20 the parameters listed in the first row of table 1, so if we vary  $m$ , the other parameters are fixed at  $\alpha = 2.04$   
21 and the metacommunity number of species to 320.

Side	Species	$\mu$	$\alpha$ (mean dist.)	$m$
128	320	0.2	2.04 (26.6)	0.0001
192	64		2.08 (13.3)	0.001
256	16		2.02 (53.3)	0.01

Table 1: Parameters values used in the simulations of the neutral-hierarchical model. Side is the size of the side of the simulation grid. The parameter  $\mu$  is the mortality rate;  $\alpha$  is the exponent of the inverse power law dispersal kernel, between brackets is the mean dispersal distance; and  $m$  is the migration from the metacommunity. The units of the simulation grid and dispersal are in meters to make them comparable with field values.

## 1 Communities and early warnings signals

2 To compare community changes near and far from the critical point  $\rho_c$  we calculated the species abundance  
 3 distribution (SAD) and the rank abundance distribution (RAD). RADs are equivalent to cumulative distribu-  
 4 tions and thus are a robust way to visualize the SAD without losing information (Newman 2005, Etienne and  
 5 Rosindell 2011). We also calculated richness as the number of species ( $S$ ), and the Shannon diversity index:  
 6  $H = -\sum_{i=1}^S p_i \ln(p_i)$ , where  $p_i$  is the relative abundance of each species.

7 At the critical point there is a species with a large patch that dominates the landscape: the spanning species,  
 8 the species with the largest patch ( $S_{max}$ ). Before the critical point, the system is in a subcritical state, and  
 9 the species with the largest patch could be the spanning species. After the critical point, the system is in  
 10 a supercritical state and most of the landscape is occupied by the spanning species. The fraction of the  
 11 cover of the largest patch ( $S_{max}$ ) can be used as an index to determine if the system is in a subcritical or  
 12 supercritical state. The  $S_{max}$  is calculated as the size of the largest patch divided by the area of the system.  
 13 If we are working with natural systems the total area might not be precisely calculated; i.e. if we included a  
 14 non-habitable area we will overestimate the total area, and the  $S_{max}$  will be underestimated. Thus, we also

1 divided the largest patch area by the total area occupied by the species, as this represents the proportion of  
2 the largest patch to the total area occupied by the same species  $RS_{max}$ . The  $S_{max}$  and  $RS_{max}$  are useful  
3 qualitative indices that can be used to detect if the system is in a subcritical or supercritical state, but do  
4 not tell us if the system is near or far from the critical transition.

5 The closeness of the critical transition can be evaluated using the temporal fluctuations of  $S_{max}$  (Corrado et  
6 al. 2014). We calculate the  $S_{max}$  fluctuations around the mean  $\Delta S_{max} = S_{max}(t) - \langle S_{max} \rangle$ , and  $\Delta RS_{max}$   
7 using the same formula but with  $RS_{max}$ . The variance of the fluctuations of the largest patch  $\Delta S_{max}$  reaches  
8 a maximum at the critical point but a significant increase occurs well before the system reaches the critical  
9 point (Corrado et al. 2014). Also, before the critical point, when the skewness of the distribution of  $\Delta S_{max}$   
10 and  $\Delta RS_{max}$  should be negative, because fluctuations below the average are more frequent (Corrado et al.  
11 2014). We calculated the fluctuations using the last 50 points of the time series with the same length and a  
12 similar range of  $\rho$  as the ones used for the estimation of the critical point. We classified them as before, near  
13 and after the critical point, and for each  $\rho$  we performed ten repetitions.

14 For spatial systems with patch structures another possible early warning indicator of the transition is the  
15 distribution of patch sizes or clusters (Kéfi et al. 2014). From percolation theory we expect that the  
16 distribution of the species with the largest or spanning patch should be a power law ( $f(x) = x^{-\alpha}$ ) or a power  
17 law with exponential cutoff ( $f(x) = x^{-\alpha} e^{-\lambda x}$ ) (Stauffer and Aharony 1994, Pueyo 2011, Weerman et al.  
18 2012). Besides that, we already know that the patch size distributions of species in spatially explicit neutral  
19 models follow a power law corresponding to the subcritical part of our model (Houchmandzadeh and Vallade  
20 2003, Campos et al. 2013). Thus the power law distribution of patch sizes should be present from  $\rho = 0$  to  
21 near after the critical point  $\rho_c$ . As an alternative model we fitted an exponential distribution ( $f(x) = e^{-\lambda x}$ ).  
22 As is usual in percolation studies we excluded the spanning patch from the estimation (Stauffer and Aharony  
23 1994). Before the critical point we may not have a spanning species and thus we fitted the patch distribution  
24 of the species that has the largest patch.

25 We measured the patch size distribution from simulations in a range of  $\rho$  from neutral to niche communities,  
26 using a smaller set than the ones we used to estimate the critical point:  $\rho = \{0.0000, 0.0001, 0.0002, 0.0003,$   
27  $0.0005, 0.0010, 0.01\}$ , the other parameters were from the first row of table 1 and a *Side* of 512 sites. We  
28 performed 30 simulations that run near the steady-state time, and then collected the patch sizes of all  
29 species. In some simulations, the spanning cluster occupies a considerable proportion of the landscape, and  
30 in consequence very few patches remain to estimate a distribution. We only fitted a model when there are at  
31 least 20 patches and five different patch sizes.

1 We fitted the mentioned discrete distributions using maximum likelihood methods (Clauset et al. 2009),  
2 and then calculated the Akaike information criteria corrected for small samples ( $AIC_c$ ) to select the best  
3 model (Burnham and Anderson 2002, Burnham et al. 2011). All analyses were performed using the R  
4 statistical language (R Core Team 2015). The fitting was made using code provided by Cosma R. Shalizi  
5 for the power law with exponential cutoff and the package `powerLaw` for the other distributions (Gillespie  
6 2015). The complete source code for statistical analysis and the outputs of the model is available at GitHub  
7 <https://github.com/lSaravia/CriticalTransition> and figshare <http://dx.doi.org/10.6084/m9.figshare.2007537>.

## 8 **Application of early warnings to BCI forest data**

9 The Barro Colorado Island forest plot is a 50 hectare rectangle (1000 m x 500 m) of tropical forest located  
10 in Panama and managed by the Smithsonian Tropical Research Institute (Condit 1998). In this plot, all  
11 individuals  $\geq 1$  cm diameter at breast height (dbh) of free standing woody tree species have been measured  
12 and identified. Since the first census at 1982-1983, there was a second census in 1985, and then every five  
13 years; to date there are seven publicly available censuses. We estimate the patch distributions of each species  
14 for each census to apply the same set of early warning used for the model to check if there is any evidence of  
15 a critical transition. To estimate the patch distribution we first discretized the positions of the trees to fit  
16 them in a lattice. After that, we estimated largest patch statistics and fit the patch size distributions models  
17 for each year. To check for a tendency in the fitted parameters we performed a median regression.

18 To estimate the patch distribution we need to choose a length scale to make the discretization. If we intend  
19 to fit all the individuals of all species on a different site the scale should be around 0.10 m for this plot, as  
20 the plot is 1000m x 500 m, resulting in a lattice of 10000x5000 sites with a great proportion of empty places.  
21 This will lead to a majority of isolated sites with almost no patches. If we use a bigger scale e.g. of 0.5 m,  
22 more than one individual of possibly different species may occupy some of the sites; in these cases, we have  
23 to decide which one will occupy the site. We establish that the one with greater dbh, no matter the species,  
24 will be the one that occupies the site, thus favoring more mature individuals.

25 In this process, we have to find the scale that gives us the maximum occupation of the lattice without losing  
26 the species structure of the community. Our criteria to stop enlarging the scale is that the species abundance  
27 distribution (SAD) of the discretized lattice should not be statistically different from the original SAD. To  
28 test this we use the Anderson-Darling statistic with a randomization procedure using the R package `kSamples`  
29 (Scholz and Zhu 2015); this statistic has proven powerful to detect different kinds of communities using SAD  
30 (Saravia 2015). With this procedure we obtained a scale of 1 m, and thus used a lattice of 1000x500 sites.

## 1 Results

2 We observed a typical pattern of a second order continuous phase transition (Figure 1) which means that at  
3 the critical point  $\rho_c$  one species percolates through the lattice: a mono-specific patch spreads from side to  
4 side, which is called the spanning patch or spanning cluster. As expected from percolation theory (Stauffer  
5 and Aharony 1994, Sornette 2000) the probability of a spanning cluster ( $SC_p$ ) is greater than 0 for  $\rho < \rho_c$  and  
6 small lattice sizes, for bigger lattice sizes  $SC_p$  is 0 for  $\rho < \rho_c$  and jumps quickly to 1 for  $\rho > \rho_c$ ; this clearly  
7 defines the two phases or states of the system. These two phases can be detected by analyzing the largest  
8 patch relative to the total area  $S_{max}$  before the critical point  $\rho < \rho_c$  is in the range 0.002-0.15, and after the  
9 critical point  $\rho > \rho_c$  is greater than 0.92. The largest patch relative to the total species' area  $RS_{max}$  has the  
10 same behavior, with a range of 0.009-0.23 before, and greater than 0.96 after, the critical point (Appendix  
11 Figure S1 and Table S2).

12 The critical point  $\rho_c^\infty$  is the value of the intensity of competition where the phase transition occurs at infinite  
13 lattices, obtained from the finite-size scaling analysis. The actual values for finite-size lattices may vary,  
14 but we observed that in general, the transition happened at very low  $\rho$  values (Appendix Table 3). That  
15 means that low levels of competition are needed for a phase change, and this produces a sharply decrease in  
16 Shannon diversity. This is observed for both logseries and uniform metacommunities. The values for  $\rho_c^\infty$  are  
17 very similar for logseries and uniform metacommunities.

18 We analyzed how the critical point changes varying model parameters, and thus the validity of our findings  
19 is restricted to these ranges (Table 1). Most of the  $\rho_c^\infty$  values fall in the range 0.0002-0.0003 (Appendix  
20 Table S3). Taking into account the standard error (Appendix Table S3), we conclude that there is not much  
21 variation of  $\rho_c^\infty$  with regard to dispersal distance, number of species in the metacommunity, or the type of  
22 the metacommunity. The migration parameter  $m$ , instead, produced a variation in  $\rho_c^\infty$  from around 0.0003  
23 to 0.006. When  $m$  is bigger there is more influence of the metacommunity on the local community. This is  
24 because the migration process adds individuals in the local community with the same species proportion  
25 than the metacommunity, favoring the less competitive species in both types of metacommunities simulated.  
26 Additionally, the individuals that migrate from the metacommunity have random positions and thus mix  
27 into the local community and break the species patches. The combined effect is to make the  $\rho_c^\infty$  higher. The  
28 effect becomes important when  $m = 0.01$ , which results in the biggest  $\rho_c^\infty$  (approximately 0.006, an order of  
29 magnitude greater than all the other cases) (Appendix Table S3).

30 When the competitive intensity surpasses the critical point ( $\rho_c$ ), the space left by the spanning species  
31 decreases quickly, so the Shannon diversity ( $H$ ) collapses, but some individuals can escape the competitive

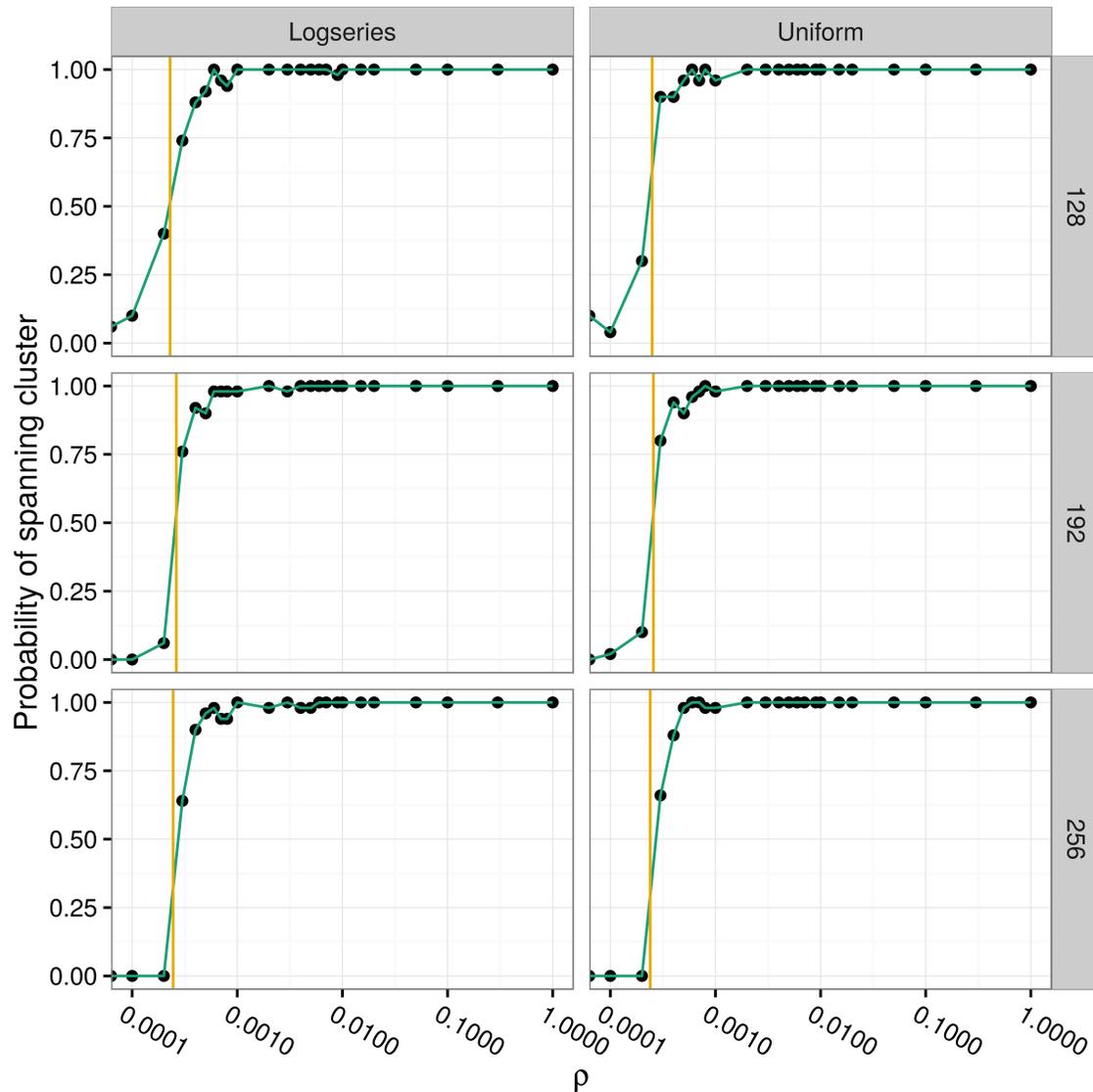


Figure 1: Probability of Spanning cluster for a spatial neutral/niche model as a function of the intensity of competition  $\rho$ . When the competition intensity  $\rho$  is near zero the community is at the neutral phase, the vertical line is the critical point and after it the community is in the niche phase. The columns represent two different metacommunity types: Logseries, a metacommunity with logseries species abundance distribution (SAD); Uniform, a metacommunity with a uniform SAD. The columns represent the side of the simulation lattice, the total size is  $side^2$ . The critical point was determined as the point where the spanning probability is 0.5, the other parameters used were  $m=0.0001$ , dispersal distance = 26.66

1 displacement and thus richness ( $S$ ) shows a more gentle fall (Figure 2). The same kind of patterns of  $H$   
2 and  $S$  are observed with all the range of parameters of table 1; the only difference is the value of  $\rho_c$  and  
3 the absolute values of  $H$  and  $S$ . After the critical point a spanning patch appears (Figure 3) that occupies  
4 a great portion of the landscape. The number of species is almost the same, and  $H$  drops quickly. The  
5 effect of the competition-colonization trade-off can be observed in the logseries metacommunities: before the  
6 critical point there is a small increase in  $H$  and also in  $S$ . This is because in the long term, the average SAD  
7 from a neutral community will tend to match the metacommunity SAD, for  $m > 0$  (Houchmandzadeh and  
8 Vallade 2003). Thus a small degree of competition lowers the density of species with high colonization rate,  
9 which were the most abundant, and raises  $H$  before the critical point. The effect of the trade-off can also  
10 be observed in  $S$ , by the same mechanism there is a small increase in  $S$  before the  $\rho_c$  (Figure 2). Logseries  
11 communities also have fewer species than uniform communities because in the neutral phase poor colonizers  
12 have small populations and extinguish due to stochasticity. Comparing logseries with uniform communities  
13 at the same  $\rho_c$ , they always have fewer species.

14 The differences between logseries and uniform communities also appear in the RADs (Appendix figure 2).  
15 Before the critical point, logseries communities have a convex shape reflecting that abundances of species  
16 with ranks from 10-30 have a slightly higher frequency than uniform communities. Species with ranks more  
17 than 40, which are rare species, have in contrast a more uniform frequency than do logseries communities.  
18 After the critical point the curvature is inverted (becomes concave) for both kind of communities. The change  
19 observed in RADs is more gradual than the observed in  $H$  or in the  $S_{max}$  and  $RS_{max}$ .

20 The largest patch fluctuations  $\Delta S_{max}$  showed a much greater variance near the critical point than before  
21 or after (Figure 4A), and the same pattern is observed for  $\Delta RS_{max}$  (Appendix figure S6). The skewness  
22 of  $\Delta S_{max}$  have a positive value before the critical transition and a negative value after it, but it can have  
23 both positive or negative values when the critical transition is happening (Figure 4B). This means that these  
24 indicators should be combined to obtain an evaluation of the closeness to the critical point. If we observe a  
25 low value of  $S_{max}$  or  $RS_{max}$  then we know that the system is before the critical point, but if  $\Delta S_{max}$  shows  
26 an increase and skewness becomes negative we can conclude that the system is about to suffer a critical  
27 transition.

28 The fits of patch size distributions showed that the most frequent best model—with lower  $AIC_c$ —was the  
29 power law with exponential cutoff (54%). The pure power law was found best in 21% of the cases and the  
30 exponential model was never the best (Appendix Table S4). The rest of the cases (25%) correspond to  
31 simulations with  $\rho$  greater than  $\rho_c$ , in which one big spanning patch exists and there are few other patches of  
32 the same species, so a distribution model can not be fitted following the criteria stated in the Methods.

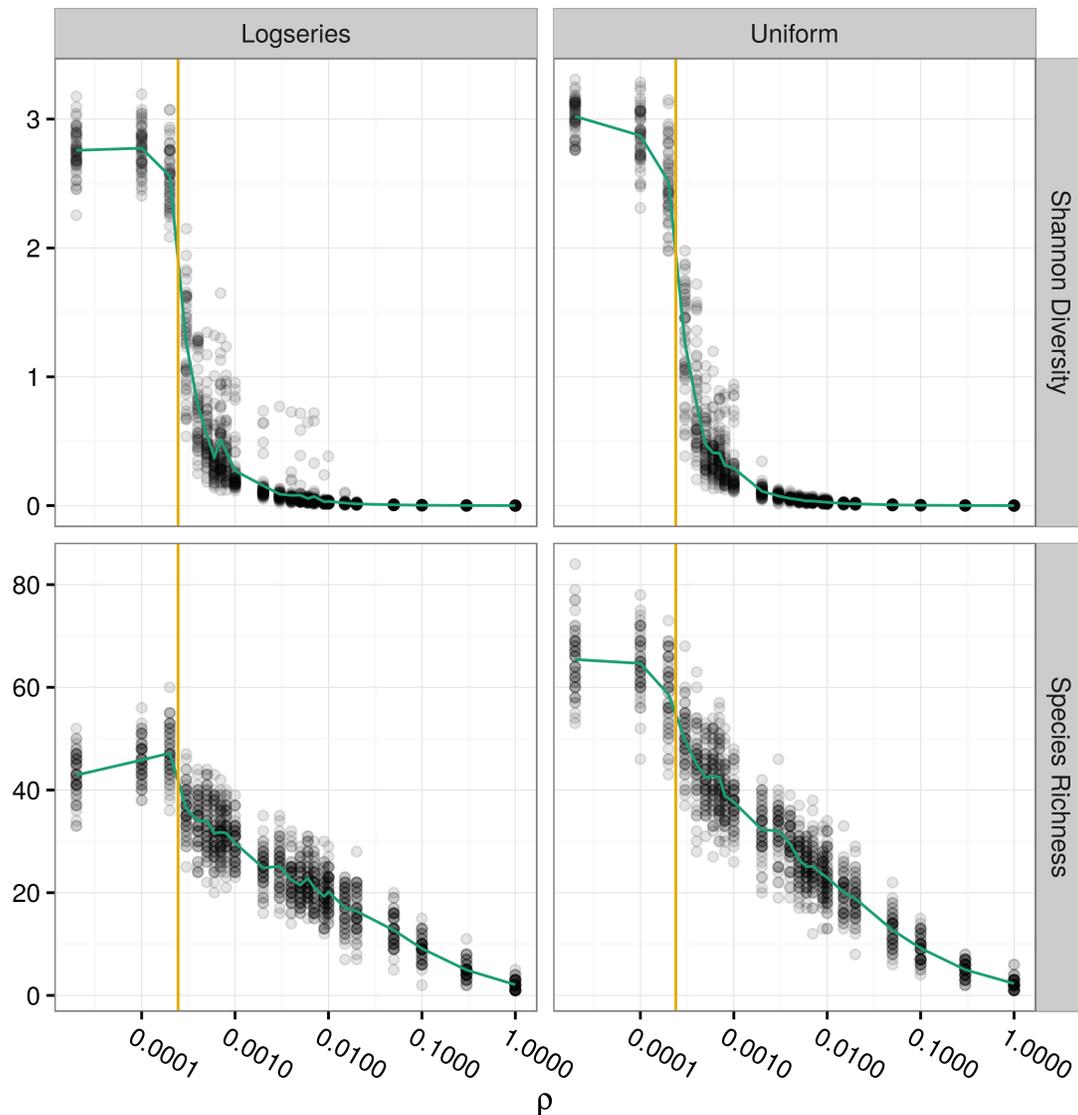


Figure 2: Shannon diversity index and species richness for a spatial neutral/niche model as a function of the intensity of competition  $\rho$ . When the competition intensity  $\rho$  is near zero the community is at the neutral phase, the vertical line is the critical point and after it the community is in the niche phase. Columns represent metacommunity types: Logseries is a metacommunity with logseries species abundance distribution (SAD), and the Uniform metacommunity have a uniform SAD, both with 320 species. Rows represent different Shannon Diversity and richness. Points are independent simulations of the model. The leftmost value of  $\rho = 0$  has been shifted to allow its representation in logarithmic axes. Other parameters used were side of the simulation lattice 256 sites,  $m=0.0001$ , dispersal distance = 26.66.

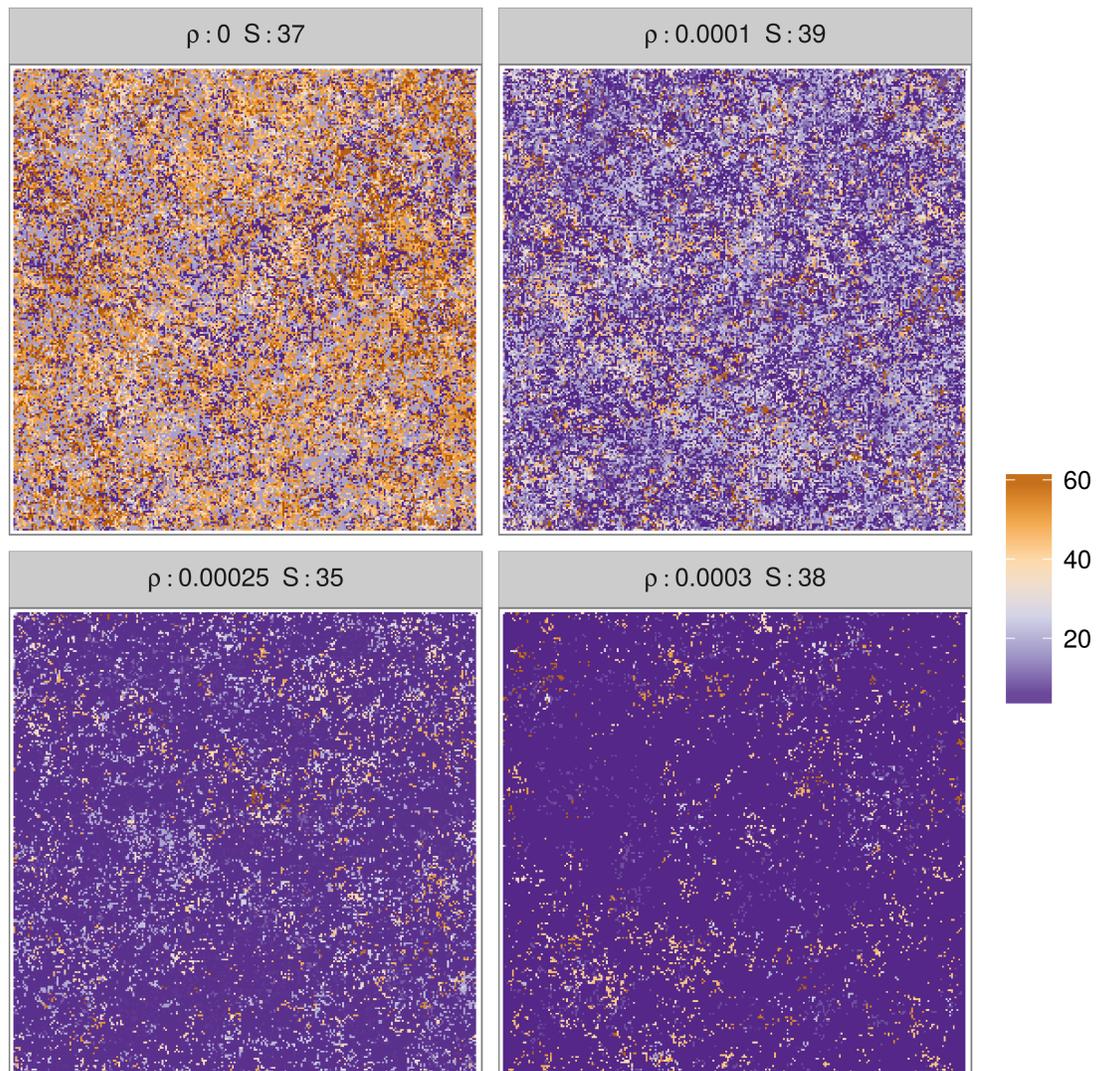


Figure 3: Spatial pattern for species before and after the critical points. The intensity of competition  $\rho$  determines if the community is in a neutral or niche phase, for  $\rho = 0$  &  $\rho = 0.0001$  the communities are neutral and for greater  $\rho$  they surpassed the critical point and a spanning patch appears. The letter S in the labels represent the number of species, and the colors specified in the legend are the different species. The parameters used here were: side of the simulation lattice 256 sites, migration  $m=0.0001$ , dispersal distance = 26.66, and a uniform metacommunity with 64 species.

1 Patch size distributions have been used to detect the closeness of the critical point when the spatial patterns  
2 are non-periodic or irregular as here (Kéfi et al. 2014). Two kinds of patterns have been suggested as early  
3 warnings of a critical transition: a switch from a power law to a power law with exponential cutoff (Kéfi et al.  
4 2007, 2011); and an increase of the  $\lambda$  parameter—assuming that the power law with exponential cutoff is a  
5 plausible model for all the cases (Pueyo 2011). We did not find evidence of a switch between power law and  
6 power law with exponential cutoff when the system approaches the critical point, as the power law with cutoff  
7 always had a greater percentage, except when  $\rho$  was far from the critical point and only a few simulations  
8 could be fitted (Appendix figure S3). The exponent ( $\alpha$ ) of both models showed a decreasing tendency when  
9 the critical point is approached, but there was a substantial amount of variability which makes the use of  
10  $\alpha$  dangerous as an early warning (Figure S4). The exponential decay rate parameter ( $\lambda$ ) also exhibited  
11 a tendency to decrease when the critical point is approached (Figure S5), and there was a high degree of  
12 scattering. Thus these two indicators should be used with care and in combination with the previous ones.  
13 The calculation of early warnings for the BCI data showed the following values for the mean  $S_{max}=0.00008$ ,  
14 the mean  $RS_{max}=0.04$ , the variances  $\Delta S_{max}=1.3e-10$  and  $\Delta RS_{max}=0.0014$ ; all of these were low values that  
15 situate the BCI before the critical point. The skewness of  $\Delta S_{max}=0.52$  was positive, and for  $\Delta RS_{max}=-0.36$   
16 was negative. In all the years the best model for the patch size distributions was the power law with  
17 exponential cutoff, and the exponent  $\alpha$  and the decay rate  $\lambda$  showed a decreasing pattern (Appendix figure  
18 S7 & S8).

## 19 Discussion

20 We have described, to our knowledge for the first time, a spatial phase transition between neutral and niche  
21 ecological communities. The power laws of patch size distributions observed in this model are not only  
22 produced at the critical point but are present over the whole range of the control parameter  $\rho$ . This broad  
23 range of power law behavior is characteristic of non-equilibrium phase transitions (Ódor 2004) and can also  
24 be produced by spatial heterogeneity (Martín et al. 2015). Some ecological models display this kind of  
25 behavior, and it has been termed ‘robust criticality’ because of the permanence of the scaling laws (Pascual  
26 and Guichard 2005). These models all include disturbances or stress, and with the increase in disturbance  
27 levels an increase in the exponential decay ( $\lambda$ ) of patch sizes is observed. This increase can be the result of a  
28 switch from a power law to a power law with exponential cutoff model (Kéfi et al. 2011) or by an increment  
29 of  $\lambda$  in the power law with exponential cutoff model (Weerman et al. 2012).

30 The most important parameter influencing the value of the critical point is the migration from the meta-

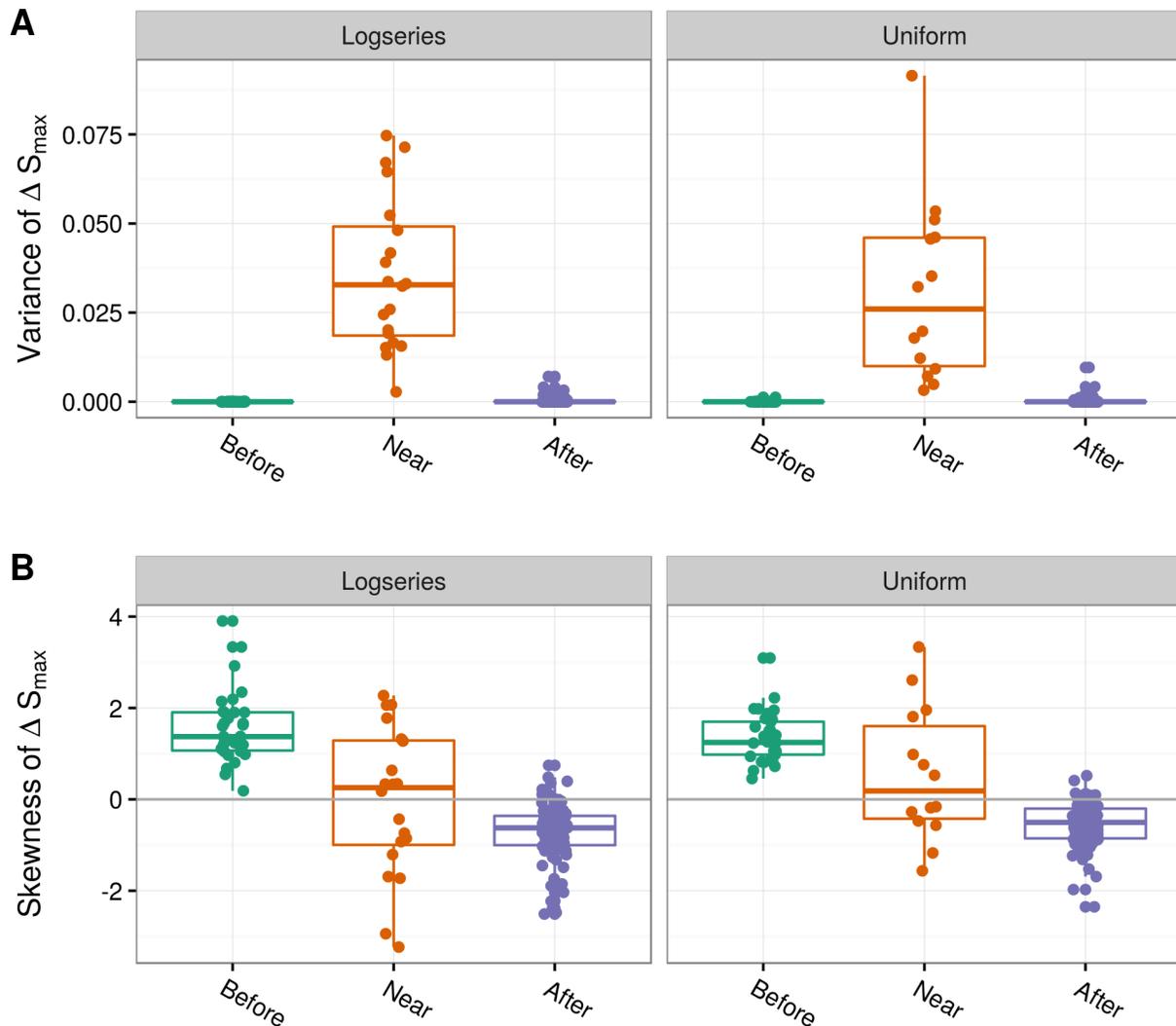


Figure 4: Early warnings indicators for the critical transition between neutral and niche communities. A) The variance of temporal fluctuations of the largest patch relative to the total area  $\Delta S_{max}$ . B) Skewness of the temporal fluctuations of the largest patch relative to the total area  $\Delta S_{max}$ . We simulated communities in the same time span than the simulations to determine the critical point—typically around 20000 time steps—we take the last 5000 and measure the patch sizes each 100 time steps. The communities that did not have a spanning patch were classified as “Before” the critical point, with a range of  $\rho : 0 - 0.0004$ . The communities that present a spanning patch in all the times are measured as “After” the critical point, with  $\rho : 0.0004 - 1$ . The communities where the spanning patch appears and disappears were classified as “Near” the critical point, with  $\rho : 0.0002 - 0.0004$ . We made 10 simulations for each  $\rho$  and two metacommunity types: “Logseries” species abundance distribution (SAD) and “Uniform” SAD. Metacommunities have 320 species, the size of the grid was  $256 \times 256$  sites, migration from metacommunity was 0.0001, dispersal distance=26.66.

1 community  $m$ . It was previously observed that immigration is crucial for maintaining diversity in spatial  
2 competition models (Loreau and Mouquet 1999) and neutral models (Hubbell 2001). If there is no immigration  
3 ( $m = 0$ ) eventually only one species will dominate the local community (Hubbell 2001), a consequence of the  
4 finite size of the local community (Solé et al. 2004); we observed this effect for low values of  $m$  and smaller  
5 sizes of the lattice. Thus it is clear that a higher  $m$  will produce a community more resistant to competitive  
6 replacement. In our model,  $m$  represents the probability of a long-distance dispersal event that happens at  
7 random in the simulation area. Thus, high values of  $m$  will break the local patch structure, and can disrupt  
8 the spanning patch, producing an increase in the critical point.

9 In our simulations, the competition intensity  $\rho$  can play the same role as stress: a very small degree of  
10 competition produces a critical transition from a neutral phase to a niche phase, and the most competitive  
11 species invades a great portion of the landscape. The sequence of an increasing  $\lambda$  when the critical point is  
12 approached is not observed in our model, but rather a decrease, when the system goes towards the critical  
13 point, and then an increase. This coincides with theoretical predictions from percolation theory (Stauffer and  
14 Aharony 1994): at the critical point, the exponential decay in the patch distribution vanishes, and the patch  
15 distribution becomes closer to a pure power law.

16 We observed a decrease of  $\lambda$  but also a decrease of the power law exponent  $\alpha$  when the system is approaching  
17 the critical point  $\rho_c$ , and both reach a minimum after it. Thus the pattern that can be used to detect if we  
18 are approaching the critical point and the biodiversity collapse is the decrease in  $\lambda$  and  $\alpha$ , but as there is a  
19 wide variability in both parameters, it is possible that we will not observe this decrease in some systems that  
20 are nonetheless heading to the critical point.

21 A commonly used pattern to characterize ecological communities is the species abundance distribution, which  
22 we used in the form of rank abundance distributions (RAD). It was demonstrated that neutral and niche  
23 mechanisms could produce the same RAD (Volkov et al. 2005, Chisholm and Pacala 2010), so it might not  
24 be useful for determining the proximity to the critical point. We found that there is a change in the RAD  
25 when the critical point is approached but these changes are small and will probably go undetected (Saravia  
26 2015). The shape of the RAD is highly dependent on the metacommunity, which is difficult to estimate as  
27 a baseline, and thus there is no RAD characteristic of a community near the critical point. Richness and  
28 Shannon diversity may have a small increment, or start to decrease, when the community goes through the  
29 critical transition; both depend on the metacommunity and on the existence of trade-off. Thus these two  
30 indices can be misleading indicators of the proximity of a critical transition.

31 The existence of the two phases or states of the system can be characterized by the size of the largest patch

1 in proportion to the size of the area of the system  $S_{max}$ , and with the size of the largest patch in proportion  
2 to the total species' area  $RS_{max}$ . If we are analyzing regions with non-habitable areas that cannot be easily  
3 detected but are included in the total area, the  $S_{max}$  could be relatively low and give a false impression  
4 that the system is in a neutral phase. Thus  $RS_{max}$  is a more robust indicator of the phase state.

5 The analysis of the fluctuations in the largest patch is a relatively new early warning indicator that was  
6 proposed for a patch model representing desertification (Kéfi et al. 2007), and it has not yet been applied to  
7 existing observational data on desertification processes. We present here the first analysis of fluctuations of  
8  $S_{max}$  and  $RS_{max}$  for a multi-species model. These indicators combine both spatial and temporal information  
9 and were the most robust early warning indicator from the set we analyzed. Moreover, these indicators were  
10 easier to estimate than parameters of patch size models. As they are based only on geometrical properties of  
11 patches (percolation) that happen in a wide array of models (Solé et al. 2004, Oborny et al. 2007, Gastner et  
12 al. 2009, Bonachela et al. 2012, Abades et al. 2014), they have the potential to be used as generic indicators  
13 that can be applied to most spatial ecological systems. Analyzing the largest patch (either with only one  
14 snapshot of the spatial distribution, i.e. the proportions ( $S_{max} / RS_{max}$ ), or the fluctuations) is a promising  
15 avenue to obtain warnings of sudden changes in ecosystems.

16 We calculated all the early warnings for the species patch distribution of the Barro Colorado Island at Panama  
17 (BCI). First using the relative size of the largest patch,  $S_{max}$  or  $RS_{max}$ , we identified that the BCI is most  
18 probably in a neutral phase, as suggested by other studies (Jabot and Chave 2011, Seri et al. 2012). The  
19 variance of the fluctuations is also very small which indicates us that BCI is not near a critical transition of  
20 this kind. The Skewness of  $RS_{max}$  and the decrease of the power law exponent  $\alpha$  and the decay parameter  $\lambda$   
21 of the patch size distribution are also compatible with a system far from the transition thus we concluded  
22 that the forest seems not to be close —until now—to a critical point.

23 Percolation transitions are second order or continuous critical transitions. This means that unless the system  
24 becomes degraded and changes its internal dynamics, these transitions are reversible. Much of the ecological  
25 literature is dedicated to studying first order or discontinuous transitions that produce hysteresis—also  
26 called regime shifts—that rely on the understanding of deterministic equations (Solé and Bascompte 2006).  
27 These kinds of transitions are practically irreversible, but in real ecosystems the presence of noise and  
28 spatial heterogeneities can convert irreversible transitions into second order transitions (Martín et al. 2015),  
29 enhancing the importance of second order phase transitions such as the ones shown here.

30 Using a spatially implicit model Fisher & Metha (2014) described a phase transition between neutral and  
31 niche communities. They used a stochastic Lotka-Volterra model for niche communities where neutral

1 dynamics was added as Gaussian noise. Their mechanism is similar to ours but not restricted to hierarchical  
2 competition. This suggests that our results can be extended to a broad kind of competitive interactions that  
3 are present in real ecosystems (Soliveres et al. 2015). A generalized stochastic interaction model can be  
4 defined in which species could have different colonization, mortality and interactions (Sole et al. 2002), a  
5 model in which transitive or intransitive competition, and even predation, could be included. The average  
6 of interaction coefficients is analogous to the intensity of competition  $\rho$  used here, and we expect that if  
7 vary the average interaction from low to high we will observe the same kind of phase transition described  
8 here. The Fisher & Metha model predicts that under stress a community will suffer a biodiversity collapse  
9 produced by a shift towards neutrality. This means that disturbed, less-diverse communities should have  
10 neutral dynamics. This prediction is contrary to most of the models and experimental data that suggest  
11 that niche dynamics dominate low-diversity communities while neutral dynamics will be more common in  
12 high diversity communities (Chisholm and Pacala 2011). Our results are in agreement with with this last  
13 prediction: when the system shift from the neutral phase to the niche phase the reduction in richness and  
14 diversity is produced.

15 Our results imply that most ecosystems will exhibit patterns of diversity that are either strongly niche-  
16 structured or indistinguishable from neutral (Chisholm and Pacala 2011, Fisher and Mehta 2014). Several  
17 field studies have demonstrated that weak interactions are a general phenomenon for species-rich communities  
18 (Volkov et al. 2009, Martorell and Freckleton 2014) and are also observed for natural food webs (Wootton  
19 and Emmerson 2005), so it is possible that these communities live near the critical point between neutrality  
20 and niche. This suggests the existence of a mechanism similar to critical self-organization as hypothesized by  
21 Solé et al. (2002) called self-organized instability. In this general mechanism, the immigration of new species  
22 increases diversity and connectivity. We argue that it also increases average interaction strength—because  
23 if there is an increase in connectivity there has to be some interaction. This will happen only until the  
24 critical point is reached, and then diversity diminishes; thus only communities with weak interactions can  
25 maintain high diversity in the long term. This agrees with some new theoretical developments that state  
26 that the number of interactions (connectivity) and average interaction strength determine the conditions  
27 for coexistence (Grilli et al. 2017). The mechanisms included in this model are generic, with the only  
28 differences between species being their competitive ability and frequency in the metacommunity. The habitat  
29 is homogeneous so niche partition mechanisms are not included but the final effect could be the same at the  
30 end: the lowering of the intensity of interactions.

31 Habitat fragmentation produces more isolated communities (Haddad et al. 2015), where less space is  
32 available to species; this is equivalent to a community composed of fewer sites. Then it is probable that

1 fragmentation shifts the critical point to lower values, making the communities more sensitive to environmental  
2 changes. At the same time, these communities would have a stronger niche effect and a high probability  
3 of biodiversity collapse. This effect has been observed in tropical communities affected by fragmentation,  
4 with local extinctions mediated by niche-based competitive interactions (Bregman et al. 2015). As we have  
5 previously mentioned, the distribution of habitable and non-habitable sites produced by fragmentation could  
6 result in percolation and critical phenomena that are different from those described here (Saravia et al. 2016).  
7 The interplay between these two critical transitions can be more complex than previously thought (Oborny  
8 et al. 2007), and thus the combination of these two critical phenomena should be thoroughly studied. A  
9 fundamental next step is to extend this work to different kinds of interactions, including food webs, mutualistic  
10 communities and intransitive competition (Soliveres et al. 2015).

11 The novelty of this critical transition is that it occurs before transitions produced by habitat loss, deforestation,  
12 land use changes, increased grazing, or fragmentation, and only needs a change in the environmental conditions  
13 that alters the strength of the interaction between species. This also could be produced if species that  
14 previously did not interact have the possibility to compete, e.g. an invading species could trigger a phase  
15 transition in a formerly neutral community. A significant portion of the biosphere's ecosystems are under  
16 pressures generated by human activities, but human activities also produce global-scale forcings—like climate  
17 change—that can reach relatively pristine ecosystems (Barnosky et al. 2012). These kinds of changes can  
18 be represented by the phase transition described here, even before the ecosystem is directly degraded the  
19 methods developed here could be applied to detect a state shift.

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