

Biodiversity collapse in a phase transition between neutral and niche communities

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Abstract

The dynamics of ecological communities can be described by two contrasting models: the first assumes that the individuals of all species are identical and do not have competitive interactions. The second assumes that species are different, adapted to particular habitat conditions, and have strong interactions. These represent extremes of a continuum: the neutral and the niche models of community organization. Real communities are actually a mixture of both types of dynamics. Here we study the simplest model of neutral-niche communities where niche dynamics is represented as a competitive hierarchy. The competition intensity is defined as a parameter that modulates the transition between these extremes. We use a stochastic cellular automata to show that there is a phase transition between the neutral and niche model with a spanning patch formed by the most abundant species. We measure the diversity as the Shannon index and the richness as the number of species. The transition implies a sharp fall of species diversity but the richness shows a gentle decline with increasing competitive intensity. As this kind of multi-species critical transition have not been described previously, we suggest new early warning signals: the rate of exponential decay in the patch distribution of the non-dominant species. This rate decreases when the community approaches the critical point and increases when the community crosses it. As an example we apply the early warnings to the Barro Colorado Tropical forest, which as expected, appear to be far from a critical transition. The model shows that the critical point occur at a very low value of competitive intensity. Low values of competitive intensity were also reported for different high diversity real communities suggesting the possibility that these kind of communities are located near the critical point. This transition could happen before habitat destruction or degradation affect the community in response to changes in environmental conditions like the ones produced by climate

1 change or exotic species invasions.

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

3 *keywords:* Continuous critical transitions; Percolation; Neutral-niche communities; spatial stochastic models;

4 Biodiversity collapse

1 Introduction

2 Much effort has been devoted to understanding the mechanisms of community assembly and dynamics. In
3 principle, the emphasis was on deterministic processes based on niche differences between species; the niche
4 theory assumes that different species are regulated by different environmental factors and infer that diversity
5 originates from spatial and temporal environmental heterogeneity (Tilman 1982, Chesson 2000). More
6 recently, the emphasis shifted to stochastic mechanisms in the form of the Neutral Theory of Biodiversity
7 and Biogeography (Hubbell 2001). The neutral theory assumes that individuals of all species are equivalent
8 and it proposes that diversity originates from a balance between immigration, speciation, and extinction.
9 The neutral theory has been proposed as a parsimonious formulation that can provide new insight into the
10 patterns of community assembly (Hubbell 2005), besides this simplification it can predict some community
11 metrics very well (Volkov et al. 2007, Rosindell et al. 2012), mainly the species abundance distribution
12 (SAD).

13 Finally a unified view has arisen that accepts that both kinds of mechanisms are present at the same time and
14 the focus shifted to quantifying the relative importance of these in natural communities (Leibold and McPeck
15 2006, Vergnon et al. 2009, Martorell and Freckleton 2014, Kalyuzhny et al. 2014). The main point is to
16 understand which species level traits are important for community dynamics and which ones are unimportant
17 (Matthews and Whittaker 2014), and this is related to the scale of observation. The problems of pattern and
18 scale are critical in ecology (Levin 1992, Chave 2013), because patterns that seem stochastic at one scale
19 may reveal structure at another scale. The concept of pattern is related to some sort of repetition that our
20 brain can detect, when this pattern repeats at different scales we talk about scale invariance or self-similarity,
21 characterized by power laws. These patterns could be produced by critical phase transitions described by
22 percolation theory (Stauffer and Aharony 1994). This kind of spatial phase transitions were first introduced
23 in ecology in the framework of landscape ecology (Loehle et al. 1996) and habitat fragmentation (Bascompte
24 et al. 1996).

25 Percolation is characterized by the presence of two phases defined by some macroscopic features, e.g. the
26 presence of vegetation or a desert in arid ecosystems (Kéfi et al. 2007). These phases are linked by a critical
27 point where a sudden transition happens and a large spatial pattern emerges. In a two dimensional landscape
28 where each site is connected to the nearest neighbors with some probability p , if you start with a small p
29 there will be some connected sites that form a cluster or patch. When p increases, there is a point at which
30 appears a cluster of sites spanning the entire landscape. This spanning cluster has a self-similar structure
31 and is produced by local interactions (Solé and Bascompte 2006).

Several different ecological spatial models exhibit critical behavior related to the degree of disturbance (Pascual and Guichard 2005). Some of these models showed robust criticality: a particular kind of criticality discovered for ecological systems, where self-similarity is present for a wide range of parameters and does not necessarily involve drastic changes in the biological variables of interest (Roy and Pascual 2003). This kind of criticality has been documented for arid ecosystems (Solé 2007); here the sudden shift towards a desert condition might occur when rainfall decreases (Scanlon et al. 2007) or also with more intense grazing (Kéfi et al. 2007). The mechanism producing self-similarity is the positive effect produced by local facilitation, the chance of a new seedling to become established is higher near the parent plant.

Another example of an ecosystem exhibiting criticality are savannas, where the transition occurs between tree and grass cover (Abades et al. 2014). In critical phenomena, the transition is produced by the capacity of the system to transmit some signal or information, for example in savannas the proportion of 60% grass 40% trees is linked to the threshold needed for fire to spread. If there is not enough grass to act as a combustible, fire can not spread across the landscape (Staver and Levin 2012). Thus the increase in the proportion of trees, due to a change in environmental conditions, can create positive feedback mechanisms resulting in the encroachment of savanna ecosystems (Abades et al. 2014).

Neutral models can produce species patches with power law distributions without been near a critical state (Houchmandzadeh and Vallade 2003), so the detection of this kind of patterns does not imply a phase transition. Moreover phase transitions are also observed in non-spatial models, some studies detected the presence of a sharp transition between neutral and niche dynamics in spatially implicit models (Chisholm and Pacala 2011) and Fisher et al. (2014) demonstrated the presence of a phase transition for this kind of neutral-niche models.

Here we study a different kind of ecological spatial phase transition that is not related to disturbance or fire: it is the transition between a neutral and a niche community. We used the simplest model of neutral-niche communities where niche dynamics is represented as a competitive hierarchy (Saravia 2015). This spatially explicit model unifies Tilman’s model of hierarchical competition with the classical neutral model using one parameter: competition intensity. This parameter is represented as the probability that one species replaces another and it modulates the transition between the neutral phase and niche phase.

Our first aim is to demonstrate the existence of a spatial phase transition in neutral-niche models, our second objective is to explore the dependence of the critical point with the parameters that are more important for the spatial pattern and to suggest some possible early warnings of the transition. Finally we will apply this new kind of early warnings to the repeated censuses of the Barro Colorado Island 50-ha forest plot in Panama

(BCI).

Methods

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

The spatial stochastic model

This model represents a continuum between hierarchical and neutral model in the same spirit as Gravel et al. (2006), and others (Zhou and Zhang 2008, Chisholm and Pacala 2010). The model is a stochastic cellular automata (CA) or also called an interactive particle system (Durrett and Levin 1994). In these kind of models space is discretized into a grid and only one individual can occupy a particular position. Each position represents an area fixed by the investigator to mimic the real system. Time is continuous so the update of the model is asynchronous. Sites are chosen at random to be updated and to perform one complete time interval cJ sites have to be updated, where c is a constant that describes the overall rate at which transitions are occurring and J is the size of the grid (Durrett and Levin 1994).

We use periodic boundary conditions, which makes the landscape a torus. It means that sites on the top edge of the grid are neighbors of those on the bottom edge, and sites on the right edge are neighbors of those on the left. With this choice we avoid edge effects, this is equivalent to thinking that the grid is embedded in a large community. The size of the community is given by $J = \dim X \times \dim Y$, where $\dim X$ and $\dim Y$ are the dimension of the grid. Thus J is the maximum number of individuals in the simulated area. As in a classical neutral model there is a metacommunity i.e. a regional species pool assumed very large and invariant in ecological time scales (Hubbell 2001). All individuals have the same parameters, unless they should belong to different species (Hubbell 2001), and each species is assigned with a number. There are only two possible differences between species:

- They may have a different frequency X_i in the metacommunity and also different abundances in the local community.

- Hierarchical competition: species with lower numbers has a probability to replace species with higher numbers as in (Tilman 1994). Thus a species with number 1 have a probability to replace species with number 2 and greater. The species with number 2 can replace species starting from 3. The probability of replacement (ρ) is a parameter, when it is 0 there is no replacement and the model behaves like a neutral model without competitive hierarchy.

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

There are three processes included in the model: death, local dispersal, and migration, starting with an empty site the following events can happen:

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

(2) When the grid is not full, individuals give birth with rate 1 to a new individual that disperses to the neighborhood with a dispersal kernel, here we use an inverse power kernel (Marco et al. 2011):

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

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

(3) Individuals die at a rate μ

(4) When an individual dies, it is replaced by a migrant from metacommunity with probability m and with probability $1 - m$ by an individual from the neighborhood. The neighborhood is established using the dispersal kernel with average distance d . Once the grid is full it stays full, because when an individual dies it is immediately replaced by another. This is called the zero-sum assumption in neutral models.

(5) If the individual does not die it can be replaced by an individual from the metacommunity or neighborhood as in (4), but an individual of species with number k can replace an individual of a species $k + 1$ with probability ρ . Thus a hierarchical ordering of species is established. When this probability is zero, the model behavior becomes neutral.

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>.

1 Percolation and simulations

2 To characterize our model in terms of percolation theory, we need to define an order parameter that depends
3 on an external control or tuning parameter that can be continuously varied. Thus, we defined as tuning
4 parameter the replacement probability ρ , and the order parameter as the probability that a patch of one
5 species connects the landscape, this is called the spanning cluster probability SC_p .

6 In our model, percolation is produced when there is at least one patch of one species that spans from one edge
7 of the system to the opposite edge. To detect species patches we used a modified Hoshen–Kopelman cluster
8 labeling algorithm (Hoshen and Kopelman 1976) with a neighborhood defined by the four nearest sites (Von
9 Neumann neighborhood) available at github <https://github.com/lisaravia/Clusters>. The percolation point is
10 defined as the value of the tuning parameter ρ at which SC_p is 0.5. We used one snapshot of the spatial
11 pattern to make our results more compatible with field studies, hence we measure the patch size distributions
12 after 5000 time iterations (as defined above).

13 The size of the lattice affects the value of the critical point ρ_c at which the transition occurs; in small lattices
14 SC_p is non-zero for values of ρ below the ρ_c , because patches that connect the entire lattice appear only
15 by chance. Therefore, in order to obtain an asymptotic estimate for ρ_c we performed a finite size scaling
16 analysis. For this, we run simulations for different lattice sizes (Side = 100, 150, 256, 512) and obtained
17 asymptotic values by regressing ρ_c against $1/N$, the intercept becomes an estimate for a lattice of infinite
18 size (ρ_c^∞) (Stauffer and Aharony 1994, Sornette 2000).

19 We determined critical points for two different metacommunities: a) One with a logseries species abundance
20 distribution, the most common distribution that fits experimental data (White et al. 2012). With this
21 metacommunity we included a competition-colonization trade-off by arranging species numbers in inverse
22 order as it's frequency X_i in the metacommunity. b) A uniform species distribution, all species have the
23 same probability to colonize the local community, this is analogous to simulating the appearance of a new
24 species by evolution thus the migration parameter m would represent a speciation rate. The values of the m
25 parameter (Table 1) were at least two orders of magnitude higher than realistic speciation rates (Rosindell
26 and Cornell 2009) as it is not our aim to interpret the results in an evolutionary framework, only to show the
27 influence of different metacommunities.

28 All simulations started with an empty lattice that is colonized by migrants mimicking the assembly of a
29 new community. For each parameter combination we performed 30 simulations. Thus, we calculate the
30 SC_p as the number of times we observed a spanning cluster divided by the number of simulations. The
31 range of parameters used were compatible with published results in tropical forest (Condit et al. 2002,

Etienne 2007, Anand and Langille 2010), It was suggested that fat-tail dispersal kernels give more realistic results (Rosindell and Cornell 2009, Seri et al. 2012) so we used an inverse power law distribution with an exponents always greater than two—so the mean exists (Table 1). The parameter ρ is varied across all the range between 0 and 1 to determine the critical point, in the region where we suspect the ρ_c will be located (near 0) the steps were very small (0.0001) and greater (0.1) in the region where we don't expect the ρ_c . The analysis of the model output were done in the R statistical language (R Core Team 2015) and the scripts are available at github <https://github.com/lisaravia/CriticalTransition> and figshare <http://dx.doi.org/10.6084/m9.figshare.2007537>.

We calculated the sensitivity of the critical point for infinite lattices (ρ_c^∞) varying three parameters of the model, one at a time: the migration m , the dispersal distance and the number of species in the metacommunity. To change the dispersal distance we vary the power exponent of the dispersal kernel α . The range of parameters we used is described in table 1. We used as a base the first row of the table, so if we vary m , the other parameters are fixed at $\alpha = 2.04$ and the metacommunity number of species to 64.

Communities and early warnings signals

To compare communities change near and far from the ρ_c we measured the species abundance distribution (SAD) and calculated the rank abundance diagrams (RAD). These diagrams are equivalent to cumulative distributions and thus are a robust way to visualize the SAD without losing information (Newman 2005). We also calculated richness (S) and the Shannon diversity index (H) for each simulation.

The patch size distribution has been suggested as an early warnings for ecological transitions (Kéfi et al. 2014), although a more in-depth study is necessary to reliably identify early warnings we present these as a first step in this new kind of models. The difference with previous models of phase transition in ecology (Kéfi et al. 2011), is that they have one or two species patches and we have from 16 to 256 different species. We already know that the patch size distributions of species in neutral models follow a power law (Houchmandzadeh and Vallade 2003), although we added a competitive interaction to the neutral model we expect that the patch size distribution follows a power law ($f(x) = x^{-\alpha}$) or due to the finite size of the simulations a power law with exponential cutoff ($f(x) = x^{-\alpha}e^{-\lambda x}$) (Pueyo 2011, Weerman et al. 2012). As an alternative model we fitted an exponential distribution ($f(x) = e^{-\lambda x}$). Near the critical point, and after it, we have a species with a continuous patch that spans all over the area: the spanning species. Thus we fitted the patch distribution of the spanning species and the distribution of all other species aggregated. Before the critical point we do not have a spanning species thus we fitted the patch distribution of the species that has the biggest patch

1 and also the distribution of all other species excluding the one that has the biggest patch.

2 For each of these species or set of species, we fitted the mentioned 3 discrete distributions using maximum
3 likelihood methods (Clauset et al. 2009). After that we calculated the Akaike information criteria corrected
4 for small samples (AIC_c), to select the best model (Burnham and Anderson 2002, Burnham et al. 2011).
5 To characterize the variation of fitted parameters against ρ , we used quantile regression (Cade and Noon
6 2003). All the analysis were made using the R statistical language (R Core Team 2015), the fitting of patch
7 distributions was made using mainly the package `poweRlaw` (Gillespie 2015) and quantile regressions with R
8 package `quantreg` (Koenker 2013).

9 We measured the patch size distribution from simulations in a range of ρ from neutral to niche communities,
10 using a smaller set than the ones we used to estimate the critical point: $\rho=\{0.0000, 0.0005, 0.0010, 0.0020,$
11 $0.0030, 0.004, 0.005, 0.01\}$, the other parameters were from the first row of table 1 and a *Side* of 256 sites.
12 The simulations run up to time 5000 and then we collected the patches every 40 time intervals for 400 time
13 intervals more each. In some simulations the spanning cluster occupies a great proportion of the landscape in
14 consequence very few patches remain to estimate a distribution. We only fitted a model when there are at
15 least 20 patches and 5 different patch sizes.

16 **Application of early warnings to BCI forest data**

17 The Barro Colorado Island forest plot is a 50 hectare rectangle (1000 m x 500 m) of tropical forest located
18 at Panama and managed by the Smithsonian Tropical Research Institute (Condit 1998). In this plot all
19 individuals ≥ 1 cm diameter at breast height (dbh) of free standing woody tree species have been measured
20 and identified. Since the first census at 1982-1983, there was a second census in 1985, and then each five
21 years, there are seven publicly available censuses. We will estimate the species patch distributions for each
22 year to check if there is a tendency.

23 To analyze the patch distribution of BCI plot we first discretized the positions of the trees to fit them in a
24 lattice (Appendix 1). After that we fit the same models that we described above to the patch size distributions
25 for each year. To check for a tendency in the fitted parameters we quantil regressions but only with the 0.5
26 quantile (median) because we have a smaller n.

Results

We observed a typical pattern of a second order continuous phase transition (Figure 1) which means that at the critical point ρ_c one species percolates through the lattice: a mono-specific patch spreads from side to side, this patch is called the spanning patch or spanning cluster. As expected from percolation theory (Stauffer and Aharony 1994, Sornette 2000) the probability of a spanning cluster (SC_p) is greater than 0 for $\rho < \rho_c$ and small lattice sizes, for bigger lattice sizes SC_p is 0 for $\rho < \rho_c$ and jumps quickly to 1 for $\rho > \rho_c$ and this clearly define the two phases. Consequently the critical point for smaller lattices is lower than for bigger lattices (Table 2). The size of the spanning cluster is between 0.28-0.37 in proportion of the lattice for a logseries metacommunity, and 0.34-0.36 for a uniform metacommunity. Communities with a species patch around these areas could be near a critical point.

When the competitive intensity surpasses the critical point, the space left by the spanning species quickly diminish so the Shannon diversity (H) collapses (Figure 2), but some individuals can escape the competitive displacement thus richness shows a more gentle fall (Figure 3). We can observe the effect of the competition-colonization trade-off in the logseries metacommunities: a very small degree of competition produces more diverse communities than purely neutral ones. This is because in the long term the SAD from a neutral community will match the metacommunity SAD (Houchmandzadeh and Vallade 2003), thus a small degree of competition lowers the density of colonizers and raises H before the critical point. The effect of the trade-off also can be observed in richness, logseries communities have in general less species and the decrease in richness is slower than with uniform communities (Figure 3).

The differences between logseries and uniform communities are also observed looking at the RADs (Figure S1). Before the critical point logseries communities have the effect of the trade-off: neutral ones ($\rho = 0$) have a greater negative slope and less species, then the slope is more flat (ρ around 0.0005), and approaching the critical point it begins to fall again but the shape of the RADs are different, the curvature is inverted. For uniform communities, the shape of the RAD is constant while the dominance of competitive species rises, the number of species keep constant until we reach $\rho=0.1$. This explains why we observed a sharp drop in H and a gentle decrease in S when we raise ρ . The change in the RAD with ρ also suggests a method to identify communities where the trade-offs are important or not.

The critical point is the value of the intensity of competition where the phase transition occurs ρ_c . We observed that in general the transition happened at very low ρ values (Figure S2). That means that low levels of competition are needed to change the phase and sharply decrease diversity, this is observed for both logseries and uniform metacommunities. The effect of the colonization-competition trade-off in communities

with logseries metacommunities is to slightly increase ρ_c^∞ . Thus logseries communities can have slightly higher levels of competition than uniform communities before the transition to the niche phase.

We analyzed how the critical point changes varying model parameters in ranges suggested by previous studies, thus the validity of our findings is restricted to these ranges (Table 1). The migration parameter m had the widest range and the biggest relative influence (0.9) on the critical point ρ_c^∞ (Appendix Table 2). When m is greater we have more influence of the metacommunity on the local community, this lowers the effect of competition intensity and makes the ρ_c^∞ higher (Figure S2). The effect becomes important when $m = 0.016$ which results in the biggest ρ_c^∞ , approximately 0.01 which is an order of magnitude greater than all the other cases (Appendix Table 2). The number of species in the metacommunity has a strong influence on ρ_c^∞ and we observed different relative responses for logseries (0.29) and uniform (0.39) metacommunities. For higher number of species in the metacommunity we obtained higher ρ_c^∞ , this means that when we have less species the effect of competition is stronger, the community changes from the neutral to niche phase earlier. The competition-colonization trade-off, present in logseries communities, diminish the influences of competition so the variation in ρ_c^∞ is smaller (Appendix Table 2). Finally dispersal distance has a weak effect in the range we used (relative variation of 0.1).

The patch size distributions have been used to detect the closeness of the critical point when the spatial patterns are non periodic or irregular as in our case (Kéfi et al. 2014). In our simulations the most frequent best model—with lower AIC_c —was the power law with exponential cutoff (70%), the pure power law was found best in 8% of the cases and the exponential model never was found to be the best model (Appendix Table 3). The rest of the cases (22%) correspond to simulations with ρ greater than ρ_c where one big spanning patch exist and there are few other patches of the same species, so a distribution model can not be fitted following the criteria we stated in methods. Thus we adopted as a possible indicators of the phase transition the parameters of the power law with exponential cutoff model: α the power exponent and λ the exponential decay rate. We fitted quantil regressions using three quantiles: 0.25, 0.50 and 0.75.

For the biggest patch and the spanning species α has an increasing tendency but slopes are non-significative at 5% level in near 60% of the cases (Appendix Table 4 and appendix Figure S3), The λ 's slopes are also non-significant in nearly 60% of cases and do not have consistent patterns for all the cases: a decreasing pattern for logseries communities; for uniform communities most abundant species have negative slopes and spanning species have positive slopes (Appendix Figure S4). The most clear and consistent patterns are observed for the patches of other species clumped, which have for λ only 1 case was non-significant (8%) but for α also had 58% of cases non-significant (Appendix table 4). Before the critical point the λ have a negative slope and after the critical point have a positive slope, we also observed that the median of λ reaches

1 a minimum right after the critical point (ρ_c between 0.0011-0.0013). Thus the slope of λ could be used as an
2 indicator of the critical point. If the community is approaching the critical point the slope will be negative
3 and if it is past the critical point the slope will be positive.

4 For BCI data we found that there is no spanning patch, the relatively small scale we chose for discretization
5 produced small patches so the biggest patch have in average a size of 0.006 % of the lattice. The best models
6 were the power law with exponential cutoff for the biggest patch species, and the power law for the other
7 species, but in this last group the power law with exponential cutoff is also a plausible model because the
8 differences in AIC_c are around 2, and the fitted power exponents are the same (up to two decimals). Thus
9 we regressed the parameter λ against year to detect any tendency that would indicate an approaching or a
10 moving away from a critical point. The slopes we obtained were all non-significant (Appendix table 5) thus
11 there is no indication that the BCI is near a critical point.

12 Discussion

13 We described for the first time a spatial phase transition between neutral and niche ecological communities.
14 The power laws of patch size distributions observed in this model are not only produced at the critical point
15 but are present over the whole range of the control parameter ρ . There are some ecological models that
16 display this kind of behavior and it has been termed robust criticality, because of the permanence of scaling
17 laws (Pascual and Guichard 2005). These previous models all included some kind of disturbances or stress,
18 and with the increase in disturbance levels an increase in the exponential decay (λ) of patch sizes is observed.
19 This increase can be the result of a switch from a power law to a power law with exponential cutoff model
20 (Kéfi et al. 2011), or by an increase of λ in the power law with exponential cutoff model (Weerman et al.
21 2012). In our model model, the competition intensity ρ can play the same role as stress; a very small degree
22 of competition produce a critical transition from a neutral phase to a niche phase, and the most competitive
23 species invades a great portion of the landscape.

24 The sequence of an increasing λ when the critical point is approached is not observed in our model but
25 a decrease of it when the system goes towards the critical point, and then an increase. This coincides
26 with theoretical predictions from percolation theory (Stauffer and Aharony 1994), at the critical point the
27 exponential decay in the patch distribution vanishes and the patch distribution becomes a pure power-law.
28 We did not observe the pure power-law because the size of the simulations is finite, but as λ becomes very
29 small the power-law and power-law with exponential cutoff become almost identical.

1 When the increase of λ starts we already have a biodiversity collapse, thus the pattern that can be used to
2 detect the closeness to the collapse is the decrease in λ observed for the patches of all species excluding the
3 one with the biggest patch. The existence of a patch of one dominant species that covers nearly 30% of the
4 area can also suggest that the system is near the critical point. This patch that extends from side to side
5 of the system —also called the spanning cluster— has a variable size depending on the size of the system
6 (from 28% to 38%). Thus it can not be used alone as an early warning, the size of the biggest mono-specific
7 patch should be used in conjunction with the decrease of λ , if the size of the biggest patch is around 10% the
8 system might not be close to the critical point, but if its size is around 30% or more the probability that the
9 system is near a critical transition is greater.

10 We calculated λ for the patch distribution of the Barro Colorado Island in Panama (BCI), the method could
11 be applied because the power-law with exponential cutoff is a plausible model for the patch distributions. We
12 did not find any tendency with time in λ and the biggest mono-specific patches are very small, although we
13 may be underestimating these sizes. There are contradicting results about the BCI regarding if it is in a
14 steady-state, some point out BCI as been in non-equilibrium state (Fort and Inchausti 2013) and another
15 suggests that it is in a steady state (Azaele et al. 2006). We found that λ is not changing with time, this is
16 compatible with a steady-state of the forest, moreover the forest seems not to be close —until now—to a
17 critical point.

18 A commonly used pattern to characterize ecological communities is the species abundance distribution, that
19 we used in the form of rank abundance diagrams (RAD). We found that there is a change in the RAD when
20 the critical point is approached but these changes are small and will probably go undetected (Saravia 2015).
21 The shape of the RAD is highly dependent on the metacommunity, which is difficult to estimate as a baseline,
22 thus there is no RAD characteristic of a community near the critical point. The species richness and Shannon
23 diversity of the community are both resumed versions of the species abundance distribution. Richness keeps
24 fluctuating around a more or less constant value when the community goes through the critical transition.
25 Shannon diversity depend on the metacommunity and on the existence of trade-off: in some cases it increases
26 before the critical point and in other cases starts to decrease. Thus these two indices can be misleading
27 indicators of the proximity of a critical transition.

28 In any case the use of several indicators is recommended (Kéfi et al. 2014), the indicators developed in
29 this study have the advantage of combining the spatial and temporal information thus they should be more
30 robust than indicators based in only one kind of information (Martín et al. 2015). Other kinds of early
31 warnings signals developed for spatial systems like spatial variance or autocorrelation should be adapted for
32 multispecific communities and a detailed study comparing all of them should be done.

Percolation transitions like the one observed in this model are second order or continuous critical transitions. This means that unless the system becomes degraded and changes its internal dynamics, these transitions are reversible. Much of the ecological literature was dedicated to study of other kinds of transitions: first order or discontinuous transitions that produce hysteresis —also called regime shifts—and rely on the understanding of deterministic equations (Solé and Bascompte 2006). These kinds of transitions are practically irreversible but in real ecosystems the presence of noise and spatial heterogeneities can convert irreversible transitions into second order transitions (Martín et al. 2015), this enhances the importance of second order phase transitions like the ones detected here.

A recently published model related the savanna-forest transition to a phase transition between persistent species in a neutral model without including any niche effect (Abades et al. 2014). The spanning cluster that appears at the critical point is theoretically infinite (Stauffer and Aharony 1994, Sornette 2000). But percolation is studied in finite systems as a consequence, in small lattices the spanning cluster has a positive probability to appear. In our model, we observed the apparition of a spanning cluster in the neutral phase only at the smallest lattice sizes (100-150 sites), but a spanning cluster never appears at greater sizes. Thus we did not observe a critical transition for neutral communities, this is in contrast with Abades et al. (2014) who reported a critical phase transition for a neutral model using a lattice with sides from 10 to 100. In both cases the same order parameter was used —the probability of a spanning cluster— but we used a different control parameter. They used the proportion of sites with a stable population of a given species as a control parameter. It seems that their results are related to static percolation, not to the neutral model. In static percolation occupied sites are located at random in a lattice and there is no time dependence or change, when the proportion of occupied sites reach a threshold percolation is observed. This is analogous to Abades et al. procedure, so they obtained percolation because they varied the proportion of occupied sites (and the populations within these sites were stable), not as a result of the use of a neutral model.

Using an spatially implicit model Fisher & Metha (2014) described a phase transition between a neutral and niche communities. They used a stochastic Lotka-Volterra model for niche communities where neutral dynamics was added as Gaussian noise. Their mechanism is similar to ours but generalized to different kinds of interactions. Their model predicts that under stress a community will suffer a biodiversity collapse produced by a shift towards neutrality. This means that disturbed less diverse communities should have neutral dynamics. This prediction is contrary to most of the models and experimental data that suggest that niche dynamics dominate low-diversity communities while neutral dynamics will be more common in high diversity communities (Chisholm and Pacala 2011). Our results are in accordance with this last prediction: the critical point ρ_c is lower for low diversity communities. This implies that they are more sensitive to

1 changes in environmental conditions, a small change can make them to shift to a niche phase.

2 The results our model and similar works in spatially implicit models implies that most ecosystems will exhibit
3 patterns of diversity that are either strongly niche-structured or indistinguishable from neutral (Chisholm and
4 Pacala 2011, Fisher and Mehta 2014). Anyway there is another option, several field studies have demonstrated
5 that weak interactions are a general phenomenon for species rich communities (Martorell and Freckleton
6 2014, Volkov et al. (2009)) which is also observed for natural food webs (Wootton and Emmerson 2005), so it
7 is possible that these communities live near the critical point between neutrality and niche. This suggests
8 the existence of a mechanism similar to critical self organization as hypothesized by Solé et al. (???) called
9 self-organized instability. In this general mechanism the immigration of new species increase diversity and
10 connectivity, we argue that it also might increase interaction strength; this will happen until the critical point
11 is reached and then diversity diminishes. Thus, only communities with weak interactions can maintain high
12 diversity in the long term. The mechanisms included in this model are generic, the only differences between
13 species are their competitive ability and their frequency in the metacommunity. The habitat is homogeneous
14 so niche partition mechanisms are not included but the final effect could be the same at the end: the lowering
15 of the intensity of interactions.

16 Habitat fragmentation produce more isolated communities (Haddad et al. 2015), where less effective space is
17 available to species thus disregarding the effect of the spatial pattern of habitat destruction this is equivalent
18 to a community composed of less sites. Then it is probable than fragmentation shifts the critical point to
19 lower values making the communities more sensitive to environmental changes. At the same time these
20 communities would have a stronger niche effect and a high probability of biodiversity collapse. As we have
21 previously mentioned, the distribution of habitable and non-habitable sites produced by fragmentation could
22 result in percolation and critical phenomena. The interplay between these two critical transitions can be
23 more complex than was previously thought (Oborny et al. 2007). Thus the combination of these two critical
24 phenomena should be thoroughly studied, also the extension to different kinds of interactions including food
25 webs, mutualistic communities and intransitive competition (Soliveres et al. 2015) is a fundamental next step,
26 but great care should be given to the method of simulating the interaction coefficients to recreate realistic
27 communities (Rohr et al. 2014).

28 The novelty of this critical transition is that it occurs before that produced by habitat loss, deforestation,
29 land use changes, increased grazing, fragmentation, etc., and it only needs a change in the environmental
30 conditions that changes the strength of the interaction between species. This also could be produced if habitat
31 connectivity and species that previously did not interact have the possibility to compete, in the same line an
32 invading species could produce the same effect and trigger a phase transition in a formerly neutral community.

A great portion of biosphere’s ecosystems are under the pressures produced by human-induced activities, but human activities also produce global-scale forcings —like climate change—that can reach relatively pristine ecosystems although they are not under a direct influence of human activities (Barnosky et al. 2012). This kind of changes can be represented by the phase transition described here before the ecosystem is under a direct degradation, and the detection of this kind of transition could be used as a signal to detect a global state shift in the biosphere.

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