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 first is the neutral and the later the niche model of communities. Real communities are actually a mixture of both dynamics. Here I 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 cluster formed by the most abundant 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 result to be far from a critical transition. The model shows that the critical point is at a very low value of competitive intensity and the same was reported

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for different high diversity real communities, this suggest the possibility that this kind of communities live 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 change or exotic species invasions.

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

Introduction

Much effort has been devoted to understand the mechanisms of community assembly and dynamics. In principle the emphasis were on deterministic processes based on niche differences between species; the niche theory assumes that different species are regulated by different environmental factors and infer that diversity originates from spatial and temporal environmental heterogeneity [1–3]. More recently the emphasis shifted to stochastic mechanisms in the form of the Neutral theory of Biodiversity and Biogeography [4]. The neutral theory assumes that individuals of all species are equivalent and it proposes that diversity originates from a balance between immigration, speciation, and extinction. Neutral theory has been proposed as a parsimonious formulation that can provide new insight into the patterns of community assembly [5], besides this simplification it can predict some community metrics very well [6,7], mainly the species abundance distribution (SAD).

Finally arises a unified view that accepts that both kinds of mechanisms are present at the same time and tries to quantify the importance of these in natural communities [8–11]. The main point is to understand which species level traits are important for community dynamics and which ones are unimportant [12], and this is related to the scale of observation. The problems of pattern and scale are critical in ecology [13,14], because patterns that seem stochastic at one scale may reveal structure at another scale. The concept of pattern is related to some sort of repetition that our brain can detect, when this pattern repeats at different scales we talk about scale invariance or self-similarity, characterized by power laws. These patterns could be produced by critical phase transitions described by percolation theory [15]. This kind of spatial phase transitions were first introduced in ecology in the framework of landscape ecology [16] and habitat fragmentation [17].

Percolation is characterized by the presence of two phases defined by some macroscopic features, e.g. the presence of vegetation or a desert in arid ecosystems [18]. These phases are linked by a critical point were a sudden transition happens and a large spatial pattern emerges. In a two dimensional landscape where each site is connected to the nearest neighbors with some probability p, if you start with a small p there will be some connected sites that forms a cluster or patch. When you increase p there is a point where appears

a cluster of sites spanning the entire landscape. This spanning cluster has a self-similar structure and is produced by local interactions [19].

Several different ecological spatial models exhibit critical behavior related to the degree of disturbance [20]. 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 involves drastic changes in the biological variables of interest [21]. This kind of criticality has been documented for arid ecosystems [22]; here the sudden shift towards a desert condition might occur when rainfall decrease [23] or also with more intense grazing [18]. 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 [24]. 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 [25]. Thus the increase in the proportion of trees, due to a change in environmental conditions, the can create positive feedback mechanisms resulting in the encroachment of savanna ecosystems [24].

Neutral models can produce species patches with power law distributions without been near a critical state [26], so the detection of this kind of patterns do 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 [27] and Fisher et al. [28] 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, 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 [29]. This spatially explicit model unifies the Tilman's model of hierarchical competition with the classical neutral model using one parameter: the competition intensity. This parameter is represented as the probability that one species replace another and 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 we made simulations, then we analyze early warnings for this critical transition and use the same techniques for BCI plot data. We refer to interested readers to more extensive introductions to percolation theory in an ecological context [Reference 19;Oborny2007].

The spatial stochastic model

This model represent a continuum between hierarchical and neutral model in the same spirit as in [30–32]. The model is a stochastic cellular automata (CA) or also called interactive particle system [33]. 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 [33].

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 can avoid edge effects and is equivalent to thinking that the grid is embedded in a large community. The size of the community is given by $J = dimX$ x $dimY$, where $dimX$ and $dimY$ 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 [4]. All individuals have the same parameters, besides they should belong to different species [4], 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 have a probability to replace species with higher numbers as in [34]. Thus a species with number 1 have a probability to replace species with number

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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 as it's frequency X_i in the metacommunity, 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 four 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 disperse to the neighborhood with a dispersal kernel, here I use an inverse power kernel [35]:

$d(x) = \frac{\alpha-1}{x_{min}} \left(\frac{x}{x_{min}} \right)^{-\alpha}$ with $mean = \frac{\alpha-1}{\alpha-2} x_{min}$ where $\alpha > 1$ 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 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 keeps full, because when an individual dies 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 and 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 is neutral.

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

Percolation and simulations

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

In our model percolation is produced when there is at least one patch of one species that spans from one edge of the system to the opposite edge. To detect species patches we used a modified Hoshen–Kopelman cluster labeling algorithm [36] with a neighborhood defined by the four nearest sites (Von Neumann neighborhood) available at github https://github.com/lsaravia/Clusters. The percolation point is defined as the value of the tunning parameter ρ at which SC_p is 0.5 and the patch size distributions were measured after 5000 time iterations. We used one snapshot of the spatial pattern to make our results more compatible with field studies.

The size of the lattice affects the value of the critical point ρ_c at which the transition occurs; in small lattices SC_p is non-zero for values of ρ below the ρ_c, because patches that connect the entire lattice appears only by chance. Therefore, in order to obtain an asymptotic estimate for ρ_c we performed a finite size scaling analysis. For this, we run simulations for different lattice sizes (Side = 100, 150, 256, 512) and obtained asymptotic values by regressing ρ_c against $1/N$, the intercept becomes an estimate for a lattice of infinite size (ρ_c^∞)[15,37].

We determined critical points for two different metacommunities: a) One with a logseries species abundance distribution, the most common distribution that fits experimental data [38]. With this metacommunity we included a competition-colonization trade-off by arranging species numbers in inverse order as it's frequency X_i in the metacommunity. b) A uniform species distribution, all species have the same probability to colonize the local community, this is analogous to simulate the apparition of a new species by evolution thus the migration parameter m would represent an speciation rate. The values of the m parameter (Table 1) were at least two orders of magnitude higher than realist speciation rates [39] as is not our aim to interpret the results in an evolutionary framework, only to show the influence of different metacommunities.

All simulations started with an empty lattice that is colonized by migrants mimicking the assembly of a new community, for each parameter combination we made 30 simulations. Thus we calculate the SC_p as the number of times we observed a spanning cluster divided by the number of simulations. The range of parameters used were compatible with published results in tropical forest [40–42], It was suggested that fat-tail dispersal kernels give more realistic results [39,43] so we used an inverse power law distribution with an

exponents always greater than two—so the mean exist (Table 1). The parameter ρ is varied in 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 were we don't expect the ρ_c. The analysis of the model output were done in the R statistical statistical language [44] and the scripts are available at github https://github.com/lsaravia/CriticalTransition and figshare http://dx.doi.org/10.6084/m9.figshare.XXXXXX.

We calculated the sensitivity of 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 on the metacommunity. To change the dispersal distance we vary the power exponent of the dispersal kernel α. The range of parameters we used is 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 equal 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 [45]. 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 [46], besides 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 [47], 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 [26], besides we added to the neutral model a competitive interaction 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 ($f(x) = x^{-\alpha}e^{-\lambda x}$)[48,49]. 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 don not have a spanning species thus we fitted the patch distribution of the species that has the biggest patch and also the distribution of all other species excluding the one that has the biggest patch.

For each of these species or set of species, we fitted the mentioned 3 discrete distributions using maximum likelihood methods [50]. After that we calculated the Akaike information criteria corrected for small samples (AIC_c), to select the best model [51,52]. To characterize the variation of fitted parameters against ρ, we

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used quantile regression [53]. All the analysis were made using the R statistical language [44], the fitting of patch distributions was made using mainly the package poweRlaw [54] and quantile regressions with package quantreg [55].

We measured the patch size distribution from simulations in a range of ρ from neutral to niche communities, using a smaller set than the ones we used to estimate the critical point: ρ={0.0000, 0.0005, 0.0010, 0.0020, 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. The simulations run up to time 5000 and them we collected the patches every 40 time intervals for 400 time intervals more each. In some simulations the spanning cluster occupies a great proportion of the landscape in consequence very few patches remains to estimate a distribution. We only fitted a model when there are at least 20 patches and 5 different patch sizes.

Application of early warnings to BCI forest data

The Barro Colorado Island forest plot is a 50 hectare rectangle (1000 m x 500 m) of tropical forest located at Panama and managed by the Smithsonian Tropical Research Institute [56]. In this plot all individuals $\geq$ 1cm dbh of free standing woody tree species have been measured and identified. Since the first census at 1982-1983, there was a second census in 1985, and then each five years, there are seven publicly available censuses. We will estimate the species patch distributions for each year to check if there is a tendency.

To analyze the patch distribution of BCI plot we first discretized the positions of the trees to fit them in a lattice, in each position only one individual of a particular species can be present, this is the same assumption that we made for the model above. We have to choose a length scale to make the discretization, if we want to fit all the individuals of all species in a different site the scale would be around 0.10 m for the BCI, but that would result in an big lattice of 10000x5000 sites with a great proportion of empty sites, this will result in a majority of isolated sites with almost no patches. When we use a bigger scale of 0.5 m more than 1 individual of possibly different species get in some of the sites, so we have to choose which one will be the winner. We establish that the one with greater diameter at breast height (dbh) no matter the species will be the one that occupies the site, thus we are favoring the more mature individuals.

We have to find the scale that give us the maximal occupation of the lattice without loosing the species structure of the community. Then the criteria to stop enlarging the scale is that the species abundance distribution (SAD) of the discretized lattice has not to be statistically different from the original SAD. To test this we use the Anderson-Darling statistic with a randomization procedure using the R package kSamples [???], this statistic has been proved powerful to detect different kinds of communities [29]. Using

this procedure we obtained a scale of 1 m, thus we used a lattice of 1000x500 sites. After that we apply the same methods described in the previous section for each year, and to check if there is any tendency in the parameters we used median regression—equivalent to the 0.5 quantile.

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 [15,37] 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 logseries metacommunity, and 0.34-0.36 for uniform metacommunity. This suggest that communities with a species patch around these areas are candidates to 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 (H) communities than purely neutral ones. This is because in the long term the SAD from a neutral community will match the metacommunity SAD [26], 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 4). 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 began 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 raises, the number of species keep constant until we reach ρ=0.1. This explain 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 suggest a method to find communities were 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 5). 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 5). 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 (Online appendix Table 2). The number of species in the metacommunity have 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, and this is buffered by the effect of the competition-colonization trade-off present in logseries communities. Finally dispersal distance have 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 [46]. 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 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 for some the tendency is weak and non-significative at 5% level in near 60% of the cases (Appendix Table 4 and appendix Figure 1), The λs are also non-significative in near 60% 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 2). The most clear and consistent patterns are observed for the patches of other species

1   clumped, which have for λ only 1 case non-significative (8%) but for α also have 58% of cases non-significative

2   (appendix table 4). Before the critical point the λ have a negative slope and after the critical point have

3   a positive slope, we also observed that the median of λ reaches a minimum right after the critical point

4   (ρ_c between 0.0011-0.0013). Thus the slope of λ could be used as an indicator of the critical point. If the

5   community is approaching the critical point the slope will be negative and if it is past the critical point the

6   slope will be positive.

7   For BCI data we found that there is no spanning patch, the relatively small scale we chose for discretization

8   produced small patches so the biggest patch have in average a size of 0.006 % of the lattice. The best models

9   were the power law with exponential cutoff for the biggest patch species, and the power law for the other

10 species, but in this last group the power law with exponential cutoff is also a plausible model because the

11 differences in AIC_c are around 2, and the fitted power exponents are the same (up to two decimals). Thus

12 we regress the parameter λ against year to detect any tendency that would indicate an approaching or a

13 moving away from a critical point. The slopes we obtained were all non-significative (Appendix table 5) thus

14 there is no indication that the BCI is near a critical point.

Discussion

16 We described for the first time a spatial phase transition between neutral and niche ecological communities.

17 The power laws of patch sizes distributions observed in this model are not only produced at the critical point

18 but are present over the whole range of the control parameter ρ. There are some ecological models that

19 display this kind of behavior and it has been termed robust criticality, because of the permanence of scaling

20 laws [20]. These previous models all included some kind of disturbances or stress, and with the increase in

21 disturbance levels an increase in the exponential decay (λ) of patch sizes is observed. This increase can be

22 the result of a switch from a power law to a power law with exponential cutoff model [47], or by an increase

23 of (λ) in the power law with exponential cutoff model [48]. In our model model the competition intensity

24 ρ can play the same role of stress; a very small degree of competition produce a critical transition from a

25 neutral phase to a niche phase, and the most competitive species invades a great portion of the landscape.

26 The sequence of an increasing λ when the critical point is approached is not observed in our model but a

27 decrease of it when the system goes towards the critical point, and then an increase. This coincides with

28 theoretical predictions from percolation theory [15], at the critical point the exponential decay in the patch

29 distribution vanishes and the patch distribution becomes a pure power-law. We did not observe the pure

30 power-law because the size of the simulations is finite, but as λ becomes very small the power-law and

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power-law with exponential cutoff become almost identical.

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

We calculated λ for the patch distribution of the Barro Colorado Island in Panama (BCI), the method could be applied because the power-law with exponential cutoff is a plausible model for the patch distributions. We did not find any tendency with time in λ and the biggest mono-specific patches are very small, besides we may by underestimating these sizes. There are contradicting studies about the BCI regarding if it is in a steady-state, based in fitting different theoretical models some point out BCI as been in non-equilibrium state [57] and another points that it is in a steady state [58]. We found that λ is not changing with time, this is compatible with a steady-state of the forest, moreover the forest seems not to be close —by now—to a critical point.

A commonly used pattern to characterize ecological communities is the species abundance distribution, that we used in the form of rank abundance diagrams (RAD). We found that there is a change in the RAD when the critical point is approached but these changes are small and will probably go undetected [29]. The shape of the RAD is highly dependent on the metacommunity, which is difficult to estimate as a baseline, thus there is no RAD characteristic of a community near the critical point. The species richness and Shannon diversity of the community are both resumed versions of the species abundance distribution. Richness keeps fluctuating around a more or less constant value when the community goes through the critical transition. Shannon diversity depend on the metacommunity and on the existence of trade-off: in some cases increases before the critical point and in other cases starts to decrease. Thus these two indices can be a misleading indicators of the proximity of a critical transition.

In any case the use of several indicators is recommended [46], the indicators developed in this study have the advantage of combining the spatial and temporal information thus they should be more robust than indicators based in only one kind of information [59]. Other kinds of early warnings signals developed for spatial systems like spatial variance or autocorrelation should be adapted for multispecific communities and a

detailed study comparing all of them should be done.

The transition observed in this model is a second order or continuous critical transition, unless the system becomes degraded and change its internal dynamics, this transitions are reversible. Much of the ecological literature was dedicated to study other kinds transitions, mostly first order or discontinuous transitions that produce hysteresis —also called regime shifts—and rely on the understanding of deterministic equations [19]. 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 [59], 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 [24]. The spanning cluster that at the critical point is theoretical infinite [15,37]. But percolation is studied in finite systems as a consequence, in small lattices the spanning cluster have 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. [24] that 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 the use of neutral model.

Using an spatially implicit model Fisher & Metha [28] described a phase transition between a neutral and niche communities. The they used a stochastic Lokta-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 [27]. Our results are in accordance with this last prediction: the critical point ρ_c is lower for low diversity communities this means that they are more sensitive to changes in environmental conditions, a small change can make them to shift to a niche phase.

The results our model and similar works in spatially implicit models implies that most ecosystems will exhibit patterns of diversity that are either strongly niche-structured or indistinguishable from neutral [27,28]. Anyway there is another option, several field studies have demonstrated that weak interactions is general phenomenon for species rich communities [9] which is also observed for natural food webs [61], so it is possible that these communities live near the critical point between neutrality and niche. This suggest the existence of a mechanism similar to critical self organization as hypothesized by Solé et al. [62] called self-organized instability. In this general mechanism the immigration of new species increase diversity and connectivity, we argue that it also might increase interaction strength; this will happen until the critical point is reached and then diversity diminish. Thus only the communities with weak interactions can maintain high diversity in the long term. The mechanism included in this model are generic, the only differences between species are its competitive ability and its frequency in the metacommunity, the habitat is homogeneous so niche partition mechanisms are not included but the final effect could be the same at the end: the lowering of the intensity of interactions.

Habitat fragmentation produce more isolated communities [63] where less effective space is available to species thus disregarding the effect of the spatial pattern of habitat destruction this is equivalent to a community composed of less sites. Then it is probable than fragmentation shift the critical value to lower values making the communities more sensitive to environmental changes, at the same time these communities would have a stronger niche effect and a high probability of biodiversity collapse. As we previously mention, the distribution of habitable and non-habitable sites produced by fragmentation could result per se in percolation and critical phenomena. The interplay between these two critical transitions can be more complex than previously was thought [64]. Thus the combination of these two critical phenomena should be thoroughly studied, also the extension to different kinds of interactions including food webs, mutualistic communities and intransitive competition [65] is a fundamental next step, but great care should be given to the method of simulate the interaction coefficients to recreate realistic communities [Rohr2014].

The novelty of this critical transition is that it occurs previously than the produced by habitat loss, deforestation, land use changes, increased grazing, fragmentation, etc., and it only needs a change in the environmental conditions that change the strength of the interaction between species. This also could be produced if habitat connectivity and species that previously did not interact have the possibility to compete, in the same line an 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 —as climate change—that can reach relatively pristine ecosystems besides they are not under a direct influence of human activities [66].

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 this could be used as a signal to detect a global state shift in the biosphere.

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