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Clustering in neutral ecology

B. Houchmandzadeh[1] and M. Vallade[2]
[1]*Centre National de la Recherche Scientifique (CNRS), Laboratoire de Spectrometrie Physique, BP87, 38402 St-Martin, d'Heres Cedex, France*
[2]*Laboratoire de Spectrometrie Physique, Université Joseph Fourier, BP87, 38402 St.-Martin d' Heres Cedex, France*

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The ''neutral ecology'' model assumes that all organisms in the same trophic level have the same death, duplication, migration and mutation rates and are subjected to a zero sum rule. We show by exact analytical methods that under the assumption of this model, organisms tend to aggregate and form clusters. At dimensions less than or equal to 2, cluster size grows in average and one specie will dominate the whole ecosystem if enough time is allocated. At dimension $d=3$ (or higher), an equilibrium is reached and cluster sizes are distributed as a power law.

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I. INTRODUCTION

In most ecological models the ecosystem under investigation is zero dimensional. This approach may allow for an understanding of some fundamental aspects without dealing with mathematical difficulties associated to spatially extended systems. It is, however, a common observation that living organisms are not distributed homogeneously in nature, but tend (more or less) to aggregate into patches. There is now a fast growing branch of ecology, termed spatial/metapopulation/landscape ecology that is entirely devoted to the investigation of spatial effects [1].

The spatial pattern of biodiversity can be due to several causes such as social and/or nonlinear interactions between one or more species. In classical theories of ecology cited above, the clustering is attributed to spatial variation of environmental conditions (local humidity, exposition to sun, . . .): each species fitness (i.e., growth rate, probability of successful migration and colonization, . . .) is supposed to be a specific function of environmental parameters. Thus, species tend to occupy the spatial niches that allow for the highest fitness (for a review of various flavors of these theories, see [2]).

Another more intrinsic and often neglected source of clustering can be the stochastic noise. Death and duplication of a living organism are *discrete* random processes and can have drastic effects on the distribution of an organism. ''Discrete'' refers to the unit of population change: one. If a cluster of size 10 loses 9 of its individuals, it can be rescued later by the duplication of the remaining one. On the other hand, a cluster of one individual losing one will disappear definitively. Therefore if there is no density dependent effect (such as an increase in the death rate when density increases), big clusters tend to get bigger and small ones tend to vanish. This aggregation phenomenon is a pure discrete effect and cannot be found in continuous models where the population size can change by arbitrary small values. The aggregation of planktons on the ocean surface has recently been proposed to be due to such an effect, where it was also shown that diffusion cannot smoothen the clustering phenomena [3,4].

The assumption of no density dependence is of course rather harsh and of limited applicability: limited resources will ultimately stop further growth of a big aggregate. But looking at a given pattern of biodiversity, one can question what part of it has been caused by intrinsic stochastic noise and what part is due to external effects. In order to evaluate these contributions, Hubbell [5] has proposed a neutral model where all individuals of all species in a given trophic level have the same parameters. There is a density dependent threshold in this model which limits the growth of all species in the same way. Competition between species, subjected to a zero sum rule, is driven by the stochastic noise of death, birth and immigration events. The aim of the model is to provide a null hypothesis to which actual pattern of species distribution can be compared. Despite the apparent simplicity of neutral models, many numerical simulations have shown striking similarity between the prediction of these models and observed patterns of species distribution in nature [6]. Figure 1 shows a two-dimensional numerical simulation of the Hubbell model with snapshots of the ecosystem at various times. Only one specie's population is displayed, and as it can be observed, the initial homogeneous distribution gives rise to a clustered one.

This paper is devoted to the study of clustering in the framework of neutral models. We will first recall Hubbell's model and known results at zero dimension. We will then show by exact analytical computation, that at dimensions $d \leqslant 2$, species tend to aggregate into growing clusters. At $d \geqslant 3$, a stable limit is reached, where cluster sizes are distributed according to a power law.

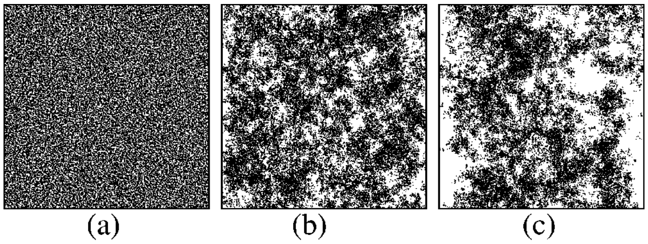

FIG. 1. Numerical simulation of a $d=2$ Hubbell model with $m=0.75$. Only one species (A) distribution is displayed. (a) The initial, homogeneous distribution of A population; (b) at $t=500$; (c) at $t=5000$. The unit of time corresponds to N death and duplication, where N is the total size of the ecosystem.

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II. NEUTRAL ECOLOGY AT $d=0$

The ingredients of Hubbell's model are the following [5]: (i) there is no restriction on the number of species in a given ecosystem; (ii) resources are limited, so the ecosystem can carry only a limited number of individuals, which we will call J; (iii) as soon as an individual of a given species dies, another one (from the same or another species) duplicates instantly; (iv) all individuals have the same death rate and probability of replacing a dead organism by one of their duplicates.

To illustrate rules (ii) and (iii), we can imagine the ecosystem as a tropical rain forest: the competition for space is severe, and as soon as a seed gets free space, it grows (thereby inhibiting the growth of other neighboring seeds). The limiting resource here is the space, and J denotes the number of trees a plot of given area can contain. Rules (ii) and (iii) also imply that at any given time, the number of individuals in the ecosystem is exactly J. Rule (iv) is the neutrality hypothesis, and we will extend it to any other parameter that we will introduce. Note the difference between this model and the logistic one: in the latter, a given species has a preferred population size, whereas in the former model, only the population size of the whole ecosystem is imposed and a given specie can have between 0 and J individuals with no preference.

Let us now recall some of the known results obtained by Hubbell. We will use the continuous time approach instead of the nonoverlapping generations used by Hubbell. We will concentrate on the size n of a given specie, say A, in the ecosystem. The probability per unit time for A to increase its size from n to $n+1$ is the probability of an individual belonging to another specie to die, multiplied by the probability of one individual belonging to A to duplicate

$$W^{+}(n)=\mu(J-n)\frac{n}{J-1}, \tag{1}$$

where μ is the death rate, n is the size of A population and $(J-n)$ is the number of all individuals not belonging to A. The $(J-1)$ factor is due to the fact that when an organism dies, there remain only $(J-1)$ in the ecosystem capable of duplicating.

The same argument applies to the transition rate from n to $n-1$: this is the probability for one A-specie individual to die, and one organism not belonging to A to duplicate

$$W^{-}(n)=\mu n\frac{J-n}{J-1}. \tag{2}$$

One can note that both transition rates are equal and that there is no growth above J or below 0. Also, if a specie becomes dominant $(n=J)$ or extinct $(n=0)$, it will stay so.

Let $P(n,t)$ be the probability of A specie having n individuals at time t. We call n_0 the initial A-population size, i.e., $P(n,0)=\delta_{n,n_0}$. The master equation for P reads

$$\partial_t P(n)=W^{+}(n-1)P(n-1)+W^{-}(n+1)P(n+1) \\ -[W^{+}(n)+W^{-}(n)]P(n). \tag{3}$$

The existence of the two adsorbing states $n=0$ and $n=J$ implies that there is a stable stationary solution centered on these two states: $P(0)=1-n_0/J$, $P(J)=n_0/J$ and $P(0<n<J)=0$ as it can be checked directly on Eq. (3).

Because of the symmetries in transition rates, various moments of the A-population size can be computed without explicitly solving the master equation. The ensemble average reads

$$d\langle n\rangle/dt=\sum_n [W^{+}(n)-W^{-}(n)]P(n,t)=0. \tag{4}$$

Thus the mean population size will remain n_0. The second moment reads

$$d\langle n^2\rangle/dt=\sum_n \{2n[W^{+}(n)-W^{-}(n)]+[W^{+}(n) \\ +W^{-}(n)]\}P(n,t)=\frac{\mu}{J-1}\{-2\langle n^2\rangle+2J\langle n\rangle\}. \tag{5}$$

The variance is thus $\sigma^2(\tau)=\langle n^2\rangle-\langle n\rangle^2=n_0(J-n_0)(1-e^{-2\tau})$ where $\tau=\mu t/(J-1)$ is the rescaled dimensionless time. The probability distribution converges to the stationary one on $\tau\approx 1$ time scale. This is equivalent to stating that in this closed neutral ecosystem, a population either goes extinct or dominant.

The important fact to note is that the evolution equation of the kth moment does not involve any moment higher than k. Therefore moments of arbitrary order can be obtained exactly and without any moment closure approximation. This feature will remain as we will add more and more ingredients to the model.

The ecosystem (termed community) need not be isolated and can receive migrants from an outside pool (metacommunity), which we suppose to be extremely large. The classical picture is that of an island not far from the shore of a continent. Then, when a local individual dies, it can either be replaced by a local or by a migrant one. The probability per unit time for A to increase its size from n to $n+1$ is that one organism not belonging to A dies and is replaced either by a local or migrant A individual. Calling x_A the proportion of As in the metacommunity, and m the probability that the replacement is from migrants (of course, the same for all species) the transition rates read

$$W^{+}(n)=\mu(J-n)\left[(1-m)\frac{n}{J-1}+mx_A\right], \tag{6}$$

$$W^{-}(n)=\mu n\left[(1-m)\frac{J-n}{J-1}+m(1-x_A)\right]. \tag{7}$$

As before, the evolution equation of a moment does not contain higher order ones and can be obtained as in Eqs. (4) and (5). The ensemble average is $\langle n(t)\rangle=(n_0-Jx_A)e^{-\mu m t}+Jx_A$ and converges to its value in the metacommunity. The variance converges to

$$\sigma^2(\infty)=Jx_A(1-x_A)\frac{J-m}{1-2m+mJ}.$$

III. NEUTRAL ECOLOGY AT $d=1$

Until now we have assumed that an individual in the ecosystem can be replaced by any other one. The ecosystem is however spatially extended, and the replacement probability should decrease with the distance between individuals. It is not hard to generalize the formalism developed above: divide the space into patches of J individuals, each patch communicating with the neighboring ones. In this paper we will consider the spatially infinite ecosystem. Physically, the size of a patch is of the order of the average distance to which trees send their seeds. An individual dying in a given patch can then be replaced by the descendant of a local one with probability $(1-m)$, or by a migrant from the immediate neighbor patches with probability m. Transition rates for the patch i to change its A-population size from n_i to $n_i\pm 1$ is an immediate generalization of Eqs. (6) and (7)

$$W^+(n_i)=\mu(J-n_i)\left[(1-m)\frac{n_i}{J-1}+\frac{m}{2J}(n_{i-1}+n_{i+1})\right], \tag{8}$$

$$W^-(n_i)=\mu n_i\left[(1-m)\frac{J-n_i}{J-1}+\frac{m}{2J}(2J-n_{i-1}-n_{i+1})\right]. \tag{9}$$

If there is no migration $(m=0)$, the A population in each patch either goes extinct or dominant. We will see that allowing communication between patches generalizes this tendency: broader and broader ensemble of connected patches will go extinct or dominant together (see Fig. 1).

Various moments (the mean and correlations) can be extracted without major difficulties from the master equation. As before, no moments higher than k is involved in the computation of the kth moment. The average reads

$$(d/d\tau)\langle n_i\rangle=-\langle n_i\rangle+(\langle n_{i-1}\rangle+\langle n_{i+1}\rangle)/2, \tag{10}$$

where $\tau=\mu m t$ is the dimensionless rescaled time. The average thus obeys a simple diffusion equation. Taking homogeneous initial conditions of all patches having exactly n_0 A organism at $t=0$ [i.e., $P(\mathbf{n};t=0)=\Pi_{n_i}\delta_{n_i,n_0}$], we see that the average remains constant.

The equations for the correlations $u_k=\langle n_i n_{i+k}\rangle-\langle n_i\rangle\langle n_{i+k}\rangle$ are less trivial and read

$$(d/d\tau)u_0=-2(1+\alpha)u_0+2(1-\beta)u_1+K, \tag{11}$$

$$(d/d\tau)u_k=-2u_k+u_{k-1}+u_{k+1}\quad (k>0), \tag{12}$$

where $\alpha=(1-m)/m(J-1)$, $\beta=1/J$ and $K=2(\alpha+\beta)n_0(J-n_0)$. Note that because of the homogeneous initial conditions, $u_k(\tau=0)=0$.

Before going to the details of the solution, let us note a few facts. First, if $m\to 0$, the above equations uncouple, u_0 converges to $n_0(J-n_0)$ for $t\to\infty$ where all other correlations remain 0: patches become independent and in each patch, the population either goes extinct or dominant. To see that, restore the real time t by multiplying Eqs. (11) and (12) by m and let $m\to 0$. Second, for $m\neq 0$, the above equations possess a homogeneous stationary (HS) solution $u_n=n_0(J-n_0)$. This corresponds to specie A invading all the space or going extinct everywhere. Whether the actual solution converges to the HS one is a question of dimension.

To solve Eqs. (11) and (12) let us note that $\mathcal{I}_n(\tau)=\exp(-2\tau)I_n(2\tau)$, where I_n is the modified Bessel function, is a solution of the bulk equations (12) [but not of Eq. (11)]. Therefore we look for solutions of the form (for details, see the Appendix)

$$u_n(\tau)=\int_0^\tau e^{-2s}I_n(2s)f(\tau-s)ds, \tag{13}$$

where f is a function to be determined. One can check by direct differentiation that the above form is a solution of the bulk Eqs. (12) for arbitrary (and reasonably regular) function f. Plugging Eq. (13) into Eq. (11) allows one to find an integral equation for f:

$$f(\tau)=-2\int_0^\tau e^{-2s}[\alpha I_0(2s)+\beta I_1(2s)]f(\tau-s)ds+K. \tag{14}$$

This equation is solved by the usual Laplace transform, and we finally get, for the Laplace transform of correlations,

$$\tilde{u}_n(\omega)=\frac{K}{\omega}\frac{\tilde{\mathcal{I}}_n(\omega)}{1+2\alpha\tilde{\mathcal{I}}_0(\omega)+2\beta\tilde{\mathcal{I}}_1(\omega)} \tag{15}$$

$$=\frac{1}{z^n}\frac{z^2}{(z-1)^2}\frac{K}{z^2+2\alpha z+2\beta-1}, \tag{16}$$

where $\mathcal{I}_n(\tau)=\exp(-2\tau)I_n(2\tau)$, $\tilde{\mathcal{I}}_n(\omega)$ is its Laplace transform and $\omega=z+1/z-2$. The variable z is a shorthand notation to avoid writing complicated combinations of ω and $\sqrt{\omega(\omega+4)}$ on the right hand side of Eq. (16). The validity of Eqs. (15) and (16) can be checked directly on the Laplace transform of Eqs. (11) and (12).

Without computing the inverse Laplace transform we can gather much information from Eq. (16). As $\omega\to 0$, the leading terms in the development of $\tilde{u}_n(\omega)$ read (for $n^2\ll 1/\omega$)

$$\tilde{u}_n(\omega)=n_0(J-n_0)\left[\frac{1}{\omega}-\frac{C+n}{\sqrt{\omega}}\right]+O(1), \tag{17}$$

where C is a constant. This implies that as $\tau\to\infty$, $u_n(\tau)\approx n_0(J-n_0)[1-(C+n)/\sqrt{\pi\tau}]$ for $n^2\ll\tau$. All correlations converge to the *same* stationary value, implying that species aggregate into bigger and bigger clusters.

In $d=1$, the large time approximation of $u_n(\tau)$ can even be extended uniformly to all n (see the Appendix)

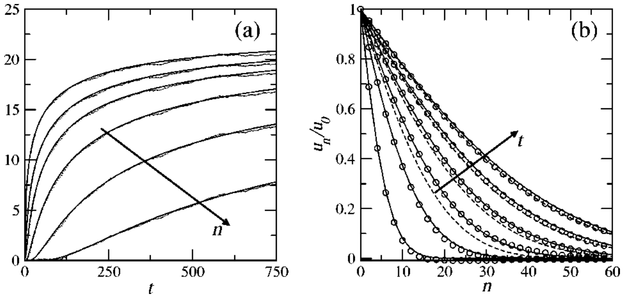

FIG. 2. Numerical simulation and comparison to theoretical results of the $d=1$ neutral model for an ecosystem composed of $N=5\times10^5$ patches of $J=10$ individual where $m=0.75$ and $\mu=2\times10^{-7}$. A maximum of 5×10^{10} death and replacement events have occurred. In both figures, solid lines represent theoretical values and dots are computed from the numerical simulation. (a) Correlations $u_n(t)$ as a function of t for $n=0,2,4,8,16$, and 32. (b) Correlations u_n as a function of their index n and normalized by u_0 for various times $t=21.1\times(1,4,9,16,25,36)$. Dashed curves: long time approximation (18) (only the last four, where time is large enough for this approximation to be valid, are displayed).

$$u_n(\tau)=1-\mathrm{erf}\left(\frac{n}{2\sqrt{t}}\right)-\frac{1-\beta}{\alpha+\beta}\frac{1}{\sqrt{\pi\tau}}\exp\left(-\frac{n^2}{4t}\right), \quad (18)$$

which, of course, reduces to Eq. (17) for $n^2\ll\tau$.

Finally, the inverse Laplace transform (see the Appendix) gives the explicit and exact time dependent correlations

$$u_n(\tau)=e^{-2\tau}\sum_{k=1}^{\infty}a_kI_{n+k}(2\tau), \quad (19)$$

where

$$a_k=2n_0(J-n_0)\left[1-\frac{1}{2}(z_1^k+z_2^k)-\frac{1-\beta}{z_1-z_2}(z_1^k-z_2^k)\right]$$

and $z_{1,2}$ are the roots of $z^2+2\alpha z+2\beta-1=0$. Figure 2 shows correlations computed from a numerical simulation of the neutral model at one dimension and its comparison to the theoretical expressions Eq. (18) and Eq. (19), where only the 16th first terms of the series (19) have been computed.

IV. NEUTRAL ECOLOGY AT HIGHER DIMENSIONS

A one dimensional ecosystem can be one along the shore of an island or the bed of a river. Most often however, ecosystems are two dimensional. As the explicit Laplace transforms of products of Bessel functions are not known, we cannot exhibit an analytical form for correlations as in Eq. (19). But the limit for large time, and its important implication on whether clustering occurs or not are not hard to come by. Expressions (8), (9) and (11), (12) easily generalize to higher dimension, where the summation has to be taken over all the neighbors in the d-dimensional space. The solution of the correlation equations can then be sought in the same manner as above as an integral equation. At $d=2$, we have, for the Laplace transform of correlations,

$$\tilde{u}_{m,n}(\omega)=\frac{K}{\omega}\frac{\tilde{\mathcal{I}}_{m,n}(\omega)}{1+2\alpha\tilde{\mathcal{I}}_{0,0}(\omega)+2\beta\tilde{\mathcal{I}}_{0,1}(\omega)}, \quad (20)$$

where $\mathcal{I}_{m,n}(\tau)=\exp(-2\tau)I_m(\tau)I_n(\tau)$ and $\tilde{\mathcal{I}}_{m,n}(\omega)$ is its Laplace transform. For large time, $\mathcal{I}_{m,n}(\tau)\sim1/\tau$ and therefore $\tilde{\mathcal{I}}_{m,n}(\omega)$ diverges logarithmically as $\omega\to0$. The leading terms in the development of the correlations are

$$\tilde{u}_{m,n}(\omega)\approx n_0(J-n_0)\left[\frac{1}{\omega}+\frac{C+\log r}{\omega\log\omega}\right], \quad (21)$$

where $r^2=m^2+n^2>0$ and $r^2\ll1/\omega$. For $m=n=0$, the above expression is of the form $(1/\omega)(1+C'/\log\omega)$ (see the Appendix). Thus, as $\tau\to\infty$, $u_{m,n}(\tau)\approx n_0(J-n_0)[1+(C+\log r)/\log\tau]$ (for $r^2\ll\tau$). Again, as in the $d=1$ case, all correlations converge to the *same* value for large times: The clustering occurs also at two dimension, but on a much slower (logarithmic) pace. The $d=2$ clustering is illustrated in Fig. 1.

The clustering phenomenon at $d=3$ is different and reaches an equilibrium. To be precise, at three dimension, following the same line of arguments as above, we have

$$\tilde{u}_{m,n,p}(\omega)=\frac{K}{\omega}\frac{\tilde{\mathcal{I}}_{m,n,p}(\omega)}{1+2\alpha\tilde{\mathcal{I}}_{0,0,0}(\omega)+2\beta\tilde{\mathcal{I}}_{0,0,1}(\omega)},$$

where $\mathcal{I}_{m,n,p}(\tau)=\exp(-2\tau)I_m(2\tau/3)I_n(2\tau/3)I_p(2\tau/3)$.

To see the mathematical difference below and above the critical dimension 2, we should journey back and forth to Laplace space. The solutions at all dimensions are of the same form $\tilde{\mathcal{I}}_{\mathbf{n}}(\omega)/\tilde{\mathcal{I}}_{\mathbf{0}}(\omega)$. At d dimension, the leading term in $\mathcal{I}_{\mathbf{n}}(t)$ for large times is $\sim t^{-d/2}$, and is independent of **n**. This, At $d\leqslant2$, implies the divergence of $\tilde{\mathcal{I}}_{\mathbf{n}}(\omega)$ for $\omega\to0$ with a leading term *independent* of **n**. The leading term in the development of $u_{\mathbf{n}}$ therefore will also be independent of **n** and all correlations converge to the same value.

At $d=3$, for large time, $I_{m,n,p}(\tau)\sim\tau^{-3/2}$: its Laplace transform $\tilde{\mathcal{I}}_{m,n,p}(\omega)$ does not diverge anymore for $\omega\to0$. The development of the correlations reads

$$\tilde{u}_{m,n,p}(\omega)=\frac{C_{m,n,p}}{\omega}+O(1)$$

and thus the leading term *depends* on the index. For large times, correlations converge to a *nonhomogeneous* stationary solution: $u_{m,n,p}(t=\infty)=C_{m,n,p}$ where

$$C_{m,n,p}=Cte\int_0^{\infty}\mathcal{I}_{m,n,p}(t)dt. \quad (22)$$

Moreover, it is not difficult to show (see the Appendix) that for large r (where $r^2=m^2+n^2+p^2$), $C_{m,n,p}\sim1/r$. Because of this slow $1/r$ decrease in correlations, no characteristic cluster length scale can be defined at equilibrium. The absence of characteristic length scale means that when looking at various scales of the ecosystem (by using different magnifications), one will always see the same picture or alternatively, one will not be able to determine the magnification used by simply looking at a picture. If we represent one specie by black and all others by white, a big cluster of black will be seen filled with smaller clusters of white, themselves filled with smaller clusters of black and so on. This is for example the classical picture of power law domain size distribution at the critical point in a second order phase transition.

V. CONCLUDING REMARKS

Let us summarize the main results of this paper. Begin with an ecosystem where various species are dispersed homogeneously and allow them to evolve according to the neutral, zero-sum rules exposed above. Each species will then tend to self-organize into clusters, and the size of these clusters will grow with time, as $\sqrt{t}$ in the one dimensional case (such as an ecosystem along the bed of a river) and as $\log t$ in the two dimensional one. If enough time is allocated, one specie's cluster will eventually reach the size of the system and this specie will dominate the whole ecosystem. There is no need to invoke inter and/or intra species social interactions between individuals; the stochasticity of birth and death events is enough to provoke clusterization. Note that this does not mean that social interactions in real ecosystems do not exist or do not provoke organization into clusters, but only that their importance has to be compared to clustering due to stochasticity. Note also the consequence of this model for the relative importance of aggregation in $d=1$ compared to $d=2$. In the former one, aggregates grow much faster than in the latter. This implies that $d=1$ ecosystems will be much more likely to be dominated by a single specie than $d=2$ ones.

The case of $d=3$ systems is different. Let us first note that these kinds of ecosystems are not common. They certainly do not exist for terrestrial species, and even marine species such as fish tend to remain within a layer of small thickness compared to their horizontal expansion. In $d=3$, species will also tend to self-organize into clusters, but no one will become dominant. An equilibrium will be reached where big clusters break into small ones and small ones fuse to form bigger ones. Note however that the difference between $d=2$ and $d=3$ is due to our hypothesis of spatially infinite system. If the system is finite, even a $d=3$ system will be dominated by a single specie if enough time is allocated. The qualitative difference between dimensions $\leqslant 2$ and >2 is not an unusual feature in problems related to diffusion: the probability for a Brownian particle to come back to the origin is $\neq 0$ at $d\leqslant 2$ and zero otherwise.

Two phenomena, however, will limit the large time behavior of this model and the complete dominance by one specie at $d<3$. The first hypothesis of the neutral model is that environmental parameters do not change over time. This assumption can be reasonable for short (on geological scale) period of time. But we know that there are global changes like glaciation periods where environmental parameters do change in radical ways. The time scale for these global changes will put a cutoff for large time behavior of the neutral model.

Another phenomenon which controls the long term behavior of an ecosystem is mutation. Mutations give rise to the appearance of new species and provoke the extinction of the old ones. As noticed by Hubbell, they can be easily included in the neutral model by assuming a unique mutation rate for all individuals in the ecosystem (whatever the specie to which they belong). Let us call ν the probability for the recently duplicated individual to be of a new specie. Then, for example, the rate $W^{+}(n)$ in Eq. (1) has to be multiplied by $(1-\nu)$. All the methods and results of this article can be generalized to take into account mutations. The main result is that the average will decrease uniformly: $\langle n(t)\rangle = n_0\exp(-\nu t)$: when $\nu\neq 0$, the state $n=J$ is not an adsorbing one anymore, as new species can appear even if one has already taken over the whole ecosystem. Correlations (or at least their Laplace transform) in spatially extended system can be computed in the same way. For example, at one dimensions, correlations read

$$u_n(t)=e^{-2\tau}\sum_{k=1}^{\infty} b_k I_{n+k}(2(1-\nu)\tau)$$

and converge to 0 for large time [as $\exp(-\nu\tau)$]. The mutation probability is however very small (in the context of neutral models for tropical forests it has been estimated to $\sim 10^{-11}$ [7]). Therefore its effect on the result of the preceding sections is again to put a cut off for large times. It is beyond the aim of this paper to study the effect of mutations. The equilibrium β diversity (the probability for two individuals at distance x to be of the same species) has been computed elegantly [8,9]. As ν is extremely small, it is not clear, however if such an equilibrium can be reached before a period of global change.

In conclusion, we have shown that in the ecological neutral model proposed by Hubbell, species form aggregates which in average grow with time. The model we have treated is *discrete* (for individuals) and *spatial*. Both of these aspects, despite their tremendous importance, are often neglected in ecological modeling [10]. One of the reasons behind this neglect is the difficulty of getting exact results from these kind of models, even when approximation schemes like moments closure [11] are used. The Hubbell model possesses the particular beauty of allowing the computation of any moment without the invocation of moments of higher order.

Since its apparition, the Hubbell model has stimulated a heated debate both on the validity of its hypotheses [12,13] and its accuracy to describe field data [5,14]. One aim of this article is to provide ecologists with analytical tools helping to evaluate various aspects of this model.

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APPENDIX: MATHEMATICAL DETAILS

(*a*) *Solving the correlation equations.* The integral method we used in Sec. III to solve the correlation equations is a variation of matrix exponentiation. The solution of the linear system $d\mathbf{u}/dt=(A+B)\mathbf{u}+\mathbf{K}$ involves the matrix $\exp(A+B)t$. In our case, A is the tridiagonal diffusion matrix and B is the (almost everywhere) hollow matrix $B_{0,0}=-2\alpha$, $B_{0,1}=-2\beta$ and $B_{m,n}=0$ for all other indexes. The exponential of the sum of two matrices (whether they commute or not) is given by

$$e^{(A+B)t}=e^{At}+\int_0^t e^{A(t-s)}Be^{(A+B)s}ds.$$

This is known in quantum mechanics as the Dyson formula. As $\exp At$ can be computed exactly and B is nearly empty, the components of $\exp(A+B)t$ can be shown to obey integral equations of the type (14). One then has to perform some matrix vector multiplication to obtain the correlations. The integral method we have used is a more compact version of this matrix exponentiation, especially when working with dimensions higher than one.

(*b*) *Large time behavior of correlations.* The large time behavior of correlations can be deduced from the limiting form of the Laplace transform as explained in the text. In order to derive the amplitude of convergence speed, i.e., the numerical coefficient in front of $1/\sqrt{t}$ or $1/\log t$ and its dependence on n, we have to perform some more calculations.

In $d=1$, expression (16) can be used directly to compute the limit for $\omega\to 0$ [we will omit the factor $n_0(J-n_0)$]

$$\tilde{u}_n(\omega)\approx\frac{1}{\omega}\left[1-\frac{1-\beta}{\alpha+\beta}\sqrt{\omega}\right]\exp(-n\sqrt{\omega}). \tag{A1}$$

The inverse Laplace transform of this expression is known and gives expression (18). This method cannot be extended to $d=2$ where the exact Laplace transform of $\mathcal{I}_{m,n}(\tau)$ is not known. But we can note that $\mathcal{I}_n(\tau)$ is the solution of the discrete diffusion equation, the continuous version of which is

$$\partial_t c=\Delta c+\delta(r)\delta(t).$$

So for large τ (when the diffusion front has progressed enough and the importance of spatial discreteness is negligible) a very good approximation for $\mathcal{I}_n(\tau)$ is

$$\frac{1}{2\sqrt{\pi\tau}}\exp(-n^2/4\tau),$$

which possesses the Laplace transform $\exp(-n\sqrt{\omega})/2\sqrt{\omega}$. In fact, we could have plugged this expression directly into Eq. (15) to obtain Eq. (A1).

This method can be generalized to $d=2$. For $r^2=m^2+n^2\neq 0$, we have $\mathcal{I}_{m,n}(\tau)\approx\exp(-r^2/2\tau)/2\pi\tau$ which can be Laplace transformed to $\tilde{\mathcal{I}}_{m,n}(\omega)=K_0(r\sqrt{2\omega})$ where K_0 is the modified Bessel function. For $r=0$, $\tilde{\mathcal{I}}_{0,0}(\omega)$ can be computed explicitly and reads $2Ek(4/(2+\omega)^2)/\pi(\omega+2)$ where $Ek(m)$ is the complete elliptic integral of the first kind. The limiting form of these expressions for $\omega\to 0$ is $\tilde{\mathcal{I}}_{0,0}(\omega)\approx(-1/\pi)\log(\omega/16)$, and $\tilde{\mathcal{I}}_{m,n}(\omega)\approx\tilde{\mathcal{I}}_{0,0}(\omega)-\log(\zeta r)$ where ζ is a numerical factor (≈ 1.78) and $r\ll 1/\sqrt{\omega}$. Plugging these into Eq. (20) gives the result (21).

(*c*) *Computing the exact inverse Laplace transform of correlations.* The Laplace transform of $\mathcal{I}_n(t)=\exp(-2t)I_n(2t)$ is $\tilde{\mathcal{I}}_n(\omega)=(1/z^n)z/(z^2-1)$, where $\omega=z+1/z-2$ is the Joukowski transform. The expression (15) for the correlations can be developed in Laurent series:

$$\tilde{u}_n(\omega)=\frac{1}{z^n}\frac{z}{z^2-1}\sum_{k=1}^{\infty}\frac{a_k}{z^k}$$

and thus, $u_n(t)$ is a sum of Bessel functions times an exponential as proposed in Eq. (19). Alternatively, expression (19) can be plugged directly into Eqs. (11) and (12) and the coefficients a_k computed through the recurrence relation $a_1=K$, $a_2=2(1-\alpha)K$ and $a_{k+1}=-2\alpha a_k-(2\beta-1)a_{k-1}+2K$. This recurrence relation is a consequence of relations between Bessel functions and their derivatives. The inverse Laplace transform can also be computed directly, if one uses the generating functions of modified Bessel functions: $\exp(z\cos\theta)=I_0(z)+2\Sigma_{k=1}I_k(z)\cos(k\theta)$. All these methods are, of course, equivalent.

(*d*) *Power law decrease in correlations at $d=3$.* As a shorthand demonstration, we can notice that the function

$$\mathcal{C}_{m,n,p}(\tau)=K\int_0^{\tau}\mathcal{I}_{m,n,p}(s)ds$$

is the solution of the discrete diffusion equation with a source at the origin, i.e., the three dimensional equivalent of Eqs. (11) and (12) where $\alpha=\beta=0$ and $K\neq 0$ (for more details, see [4]). The continuous version of diffusion equation with pointlike source is written as

$$\partial_t c=\Delta c+K\delta(\mathbf{r}). \tag{A2}$$

The stationary solution (reached for $t\to\infty$) of the above equation obviously decreases as $1/r$. Thus, $C_{m,n,p}=\mathcal{C}_{m,n,p}(\infty)\sim 1/r$. We have also checked numerically the validity of $1/r$ decrease over three decades.

We should make a remark here. At one or two dimensions, the solution of the diffusion equation with a source at the origin *diverges* (as $\sqrt{t}$ and $\log t$). α and β act in Eqs. (11) and (12) as singular perturbations, killing all divergences. At $d=3$, there is no more divergence of the solution, and α and β act as regular perturbations.

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