

Emergent spatial patterns of coexistence in species-rich plant communitiesPablo Villegas^{1,*}, Tommaso Gili,¹ and Guido Caldarelli^{2,3,4,5}¹*IMT Institute for Advanced Studies, 55100 Lucca, Italy*²*Department of Molecular Sciences and Nanosystems, Ca' Foscari University of Venice, 30172 Venice, Italy*³*European Centre for Living Technology, 30124 Venice, Italy*⁴*Institute for Complex Systems, Consiglio Nazionale delle Ricerche, UoS Sapienza, 00185 Rome, Italy*⁵*London Institute for Mathematical Sciences, W1K2XF London, United Kingdom* (Received 28 April 2021; revised 31 July 2021; accepted 2 August 2021; published 13 September 2021)

Statistical physics has proved essential to analyze multiagent environments. Motivated by the empirical observation of various nonequilibrium features in Barro Colorado and other ecological systems, we analyze a plant-species abundance model of neutral competition, presenting analytical evidence of scale-invariant plant clusters and nontrivial emergent modular correlations. Such first theoretical confirmation of a scale-invariant region, based on percolation processes, reproduces the key features in natural rainforest ecosystems and can confer the most stable equilibrium for ecosystems with vast biodiversity.

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The stable coexistence of multiple ecological species represents a primary problem in theoretical ecology. Mesoscopic descriptions and agent-based modeling—aiming to elucidate the mechanisms upscaling the response of individuals (trees) to the ecosystem level—have proven that constitutes a multi-scale problem far from being resolved [1–3]. In this respect, the first theoretical problem arising in the study of extensive forests is defining the mechanisms determining the response at the ecosystem level from the individual one (trees) [2]. Usual approaches relying on “mean-field” approximations—e.g., considering multiple interdependent Langevin’s equations to determine individual average density for a single species [4]—indicate that stable coexistence is difficult to reach in large communities. However, they represent a crucial step demonstrating that detailed balance is not fulfilled [5] (even though some analytical treatments are derived under such assumption [6]), making it possible to spontaneously broke the neutral symmetry [4].

We deal with complex aggregates in rainforests where a single species’ presence is generally not expected. Ecosystems with a high diversity level have been addressed so far within the neutral theory (NT) framework of biodiversity [7,8]. Few parameters are enough to describe species abundance distribution (SAD), species-area relationships (SAR), and the main biodiversity indices in tropical forests [8,9]. However, NT does not consider essential features like competition for resources nor how key ecological patterns (spatial tree patterns, SAR, and SAD) are intimately intertwined and scale-dependent, thus neglecting essential space-dependent aspects [8,10].

Adding space-dependent aspects, e.g., through spatially explicit neutral models (SENM), is equally problematic [9]. SENMs have made progress in studying natural ecosystems [11–13] by explaining patterns such as beta-diversity [14] and species–area relationships [12,13]. Nonetheless, they also deal with many significant theoretical challenges concerning their nonspatial formulations [8,15,16].

The interdependence between the emergent spatial patterns—at the mesoscale—and species coexistence has been often overlooked [3], even if their joint action with seed dispersal may be critical to ensure a rich biological diversity [17–19]. In particular, only recent works have emphasized the difficulty of integrating spatial patterns into coexistence theories of species-rich communities, showing how they play an essential role in species coexistence of high diversity plant communities [3].

Some works have recently highlighted the ability of SENM to produce single-species patterns characterized by spatial density correlations and fluctuations in qualitative agreement with field data in the 50 ha tropical forest plot on Barro Colorado Island (BCI) [15,20,21]. In particular, it has been proved the prevalence of tree clumping at small scales together with anomalous spatial density fluctuations [20,22,23]. Nevertheless, the role of dispersion and immigration in maintaining biodiversity richness and their effects in the emergent spatial point patterns remains an open question. Indeed, it still needs to be clarified whether correlations between species operate when competing for space. This is particularly important to describe patterns with characteristic scales (e.g., stripes or Namibian fairy circles [24,25]) or conversely lacking scale (e.g., the low-canopy gaps in BCI [26] or tree canopy clusters across different Kalahari landscapes [27]). Bistability associated with discontinuous transitions has been suggested to play a critical role in regular patterns in arid ecosystems [28] and percolation phenomena to justify the emergence of very broadly distributed vegetation patterns [29]. Therefore, the

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emergence of scale-free clusters in multiagent competitive environments, in concomitance with complex spatial patterns, remains a crucial question to be answered.

We propose here such a dynamic regime. For that purpose, we show the existence of a rich phase diagram in the SENM, where bistable effects, clustered patterns, and scale-invariant regions are present. In particular, scale invariance allows many species to live together, maintaining high specific spatial correlations, while the percolating nature of the spatial distribution of the intertwined species reveals a non-trivial emergent modular structure between them. This region constitutes the optimal regime for natural systems of exceedingly high biodiversity to harbor complex behavior, featuring optimal trade-offs between species richness, displaying a non-trivial emerging modular structure, and long-range spatial correlations at the single-species level.

II. SPATIALLY EXPLICIT NEUTRAL MODEL

The investigation presented consists of a careful analysis of the phase diagram in a plant species abundance model’s parameter space. We modeled this data through the SENM [7] or multispecies voter model [11,30] with a particular rule for the species seed dispersal. The SENM dynamics—on a square lattice of size $N = L^2$ —is defined as follows (see also Fig. 1). A random tree gets replaced via (i) speciation processes or immigration, i.e., introducing a new species with probability ν , or (ii) dispersal effects, i.e., selecting another random tree from its neighborhood, with probability $1 - \nu$. For the sake of simplicity, the neighborhood is defined as a square dispersal kernel of size K centered on the gap. The assumptions underlying the model are based on three main aspects: dispersal limitation, demographic fluctuations, and competition between species, which are *a priori* equivalent at the individual level: i.e., they compete for space with identical birth and death rates and dispersal mechanisms [7].

A. Dual representation of the SENM

The simulations of the SENM have been made exploiting its duality with a system of coalescing random walkers [30–32]. This widely used and powerful method has the great advantage of allowing high-speed simulations of independent realizations virtually free from boundary effects as, e.g., those of periodic boundary conditions (typically employed in the model’s forward dynamics). Of course, this procedure can

only be used if one is interested in the static, long-term properties of the model, and, consequently, this duality enables the study of the ergodic properties of the infinite system [32]. In particular, the generation of many sample patterns at the (nonequilibrium) stationary state allows exploration of the statistical ensemble. The dual dynamics of the SENM works as follows (see also Refs. [11,12] for an accurate description of the process): (i) A random walker is placed on each lattice site, and the process proceeds backward in time to reconstruct the ancestry of the species. (ii) With probability $1 - \nu$, a randomly chosen walker is moved—at each discrete (backward) time step—to a different site selected from a squared dispersal kernel of length K (pay particular attention to the possibility of choosing a site outside the sampled domain, since we only observe a portion of the infinite lattice). If the landing site is occupied, then the two walkers coalesce, remove one of them, and trace the coalescing partner. (iii) With probability ν , the random walker is killed. This corresponds—in the forward dynamics—to a speciation or immigration event associated with a new species’ growth. (iv) The simulation finishes when only one walker remains. The complete history of coalescing events, i.e., the tree of coalescences, allows us to trace back the entire genealogical tree of a species up to the speciation event that originated it. In other words: On a dual simulation, once all walkers coalesced or were annihilated, species are assigned to the starting site of each walker, obtaining a possible configuration (i.e., a “snapshot” from the ensemble of possible states) of the SENM [11,12].

Stochasticity and competition (controlled by local abundances) with other species generate, as in mean-field neutral models [8], a nonequilibrium stationary state where the number of species fluctuates around a mean value, depending on ν . Nevertheless, its mean-field counterpart has no order parameter and no formal phase transition depending on ν values [34]. As mentioned above, the evolution of the population density for the most abundant species can be described as a Langevin equation for a two-species voter model [35] in the presence of a small external driving [36,37], the mutation rate, which has been proved to remove the process’ absorbing states [37].

We propose an order parameter capturing essential spatial properties of abundant species: (i) the ability to fill all the available space, i.e., to percolate in space, and (ii) exhibit high conspecific correlations and clustering, i.e., compact clusters. Thus, the collective state can be quantified through the percolation strength concerning the most abundant species, defined as the average size of the largest cluster, $\langle S_M \rangle$, normalized to its total number of trees N_i , $P_\infty^{(1)} = \frac{\langle S_M \rangle}{N_i}$ (alternatively, the total system size can be considered, thereby defining P_∞ but without altering the results, see Supplemental Material I [33]). Consequently, in an environment characterized by monodominance, both values P_∞ and $P_\infty^{(1)}$ are expected to be high, while they can differ in megadiverse ecosystems, e.g., if an individual species can generate compact clusters without spatial percolation at large scales.

III. RESULTS

We have performed a detailed computational study of the SENM—exploiting its duality with coalescing random walks [30–32]—depending on both the specific values of K

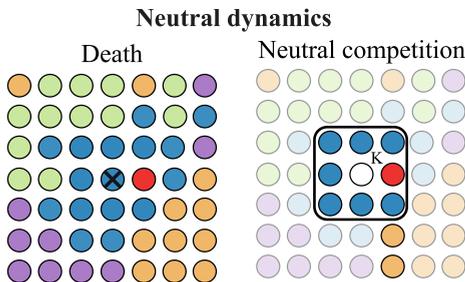


FIG. 1. Sketch of the neutral dynamics. A place is selected, and the tree dies, being replaced by (a) seed dispersal from a kernel K or (b) immigration or speciation with a small probability ν .

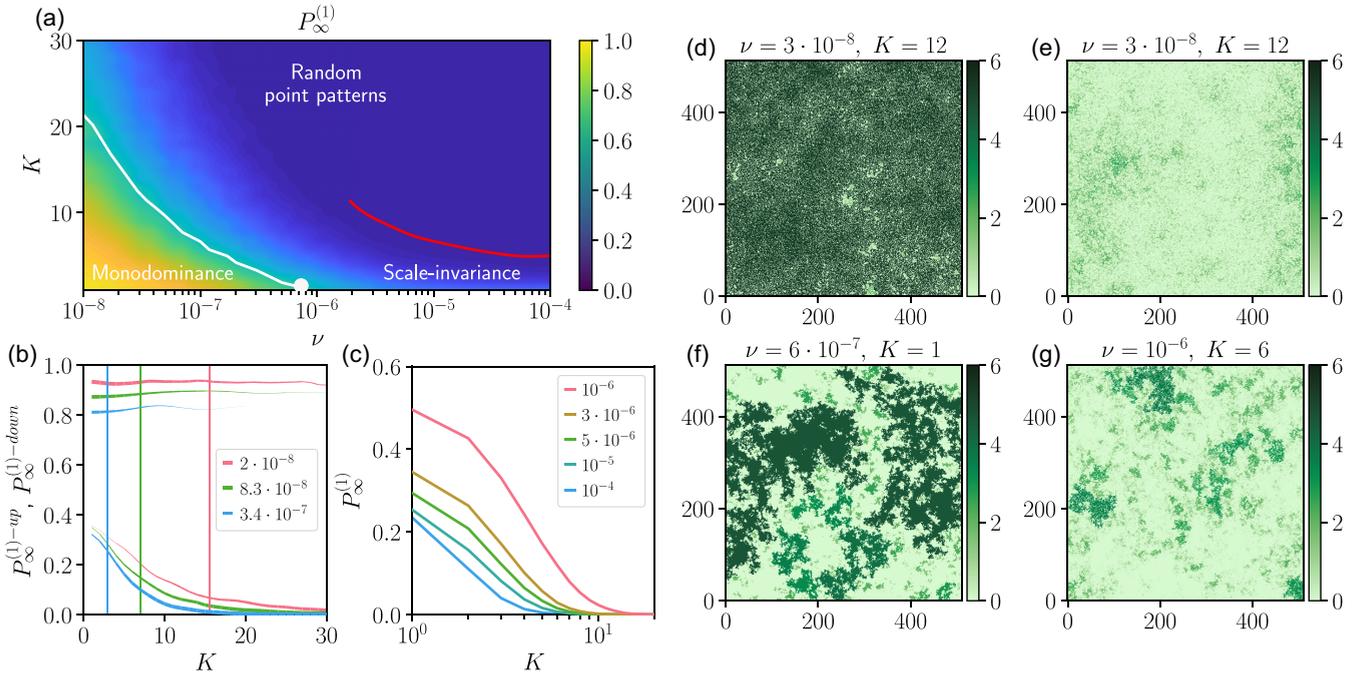


FIG. 2. (a) Phase diagram for the most abundant species. Colors represent the intensity of the percolation strength, $P_\infty^{(1)}$, at the single-species level. White line (involving bistability, which vanishes at the white point) divides monodominant states, i.e., where more than 50% of the tree canopy comprises a single tree species, to coexistence between a small number of species. Redline shows the estimated limit of the scale-invariant regime. Nonhomogeneous random point patterns emerge for large dispersal kernels (bluish regions). (b) $P_\infty^{(1)} > 0.5$ and $P_\infty^{(1)} < 0.5$ vs K for different values of ν (see legend). The size of each branch is proportional to its relative probability. Vertical solid lines show the Maxwell point for each case. (c) $P_\infty^{(1)}$ vs K for different values of ν (see legend) in the scale-invariant regime, characterized by nonvanishing values of $P_\infty^{(1)}$ (see Supplemental Material 2 [33]). [(d)–(g)] Clusters of vegetation for the most abundant species accounting for the following: [(d) and (e)] Two different realizations in the monodominant regime for high and low values of $P_\infty^{(1)}$, (f) the region when bistability disappears and (g) the scale-invariant regime. Color intensity reflects the logarithm of the cluster size. Simulations have been averaged over 10^3 runs on a lattice of size $N = 512^2$.

and ν , and averaged over many different and independent realizations, in order to obtain a highly accurate phase diagram, needed for forthcoming analyses. Our results reveal the bistable nature of the dynamical system for low values of ν [as reflected in Fig. 2(b), with two different branches for $P_\infty^{(1)} > 0.5$ and $P_\infty^{(1)} < 0.5$], together with a very rich phase diagram [see Fig. 2(a)]. Figure 2(a) illustrates the existence of different types of emergent spatial point patterns (see also Supplemental Material 1 [33] for different multispecies spatial distributions): Poisson-like noncorrelated random patterns (for large dispersal kernels, in the upper part of the diagram, showing an exponentially increasing number of species as ν grows), monodominance (in the lower left part of the diagram) and a vast region of scale-invariant spatial patterns for local-dispersal kernels (lower-right part).

In the monodominance regime, the boundary between states [white line in Fig. 2(a)] corresponds to the so-called *Maxwell point*, where both the monodominant and spatially diffused states are equally stable. We also computed the probability distribution \mathcal{P} of $P_\infty^{(1)}$ and used it to determine the stationary scalar potential $V_1 = -\log \mathcal{P}[P_\infty^{(1)}]$. The effective potential exhibits an explicit bistable nature, with a characteristic deep minimum close to the origin—as stochastic systems with multiplicative or demographic noise generally do [38,39]—for low values of ν and large dispersal distances, K (see Supplemental Material 1 [33]). Observe that—where

bistability exists—the maximum is not a singularity just because $\nu > 0$ prevents a pure monodominant (absorbing) state from existing. The Maxwell’s point displacement is also revealed through extensive computational analyses of the entire system [see Fig. 2(b)]: Bistability finally vanishes for large-enough values of ν at low dispersal distances (see the white point in Fig. 2(a) and effective potentials in Supplemental Material 1 [33]).

Once bistability disappears, nontrivial clusters of vegetation are still present for local-dispersal kernels [see Fig. 2(f) and Fig. 2(g)], characterized by nonvanishing values of $P_\infty^{(1)}$ [see Fig. 2(c)]. To determine the size of contiguous clusters, we describe the distribution of cluster sizes within the von-Neumann neighborhood, i.e., four immediate neighbors without diagonals. Figure 3(a) and Fig. 3(b) show the distribution of cluster sizes for the scale-invariant regime, showing a scale-free behavior, $P(s) \sim s^{-\tau}$, spanning across many decades and characterized by a variable exponent, which depends on the dispersal kernel (see Supplemental Material 2 [33] for an extensive analysis in terms of ν). More specifically, one can fit exponent values ranging from $\tau = 1.9$ to $\tau = 2.5$ (fully compatible with percolation critical exponents [40,41]). The cluster size distribution becomes exponential for large-enough values of the dispersal kernel. Moreover, the system obeys finite-size scaling [as observed at criticality, see Fig. 3(b)] when the immigration probability is properly

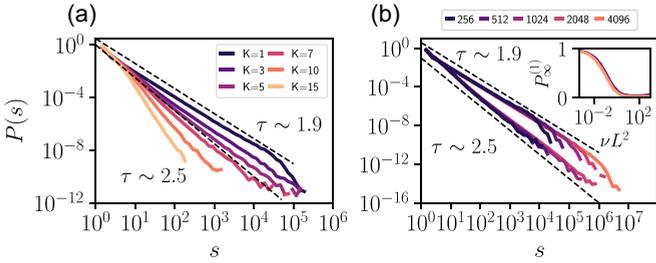


FIG. 3. Cluster sizes for the most abundant species. (a) Cluster-size distributions for $\nu = 5 \times 10^{-6}$, $L = 512$ for different dispersal kernels. The system exhibits power-law-distributed cluster sizes with continuously varying exponents. Black dashed lines are guides to the eye. (b) Finite-size scaling analysis of the cluster size distribution for two kernel values ($K = 1$, upper curves, and $K = 5$, lower curves) and different system sizes (see legend) for a fixed value $\nu L^2 = 2.62$. Inset: Scaling collapse of $P_\infty^{(1)}$ vs ν for different system sizes and $K = 3$. Simulations are averaged over 2×10^3 realizations.

rescaled by a factor νL^2 [see Fig. 3(c) and Supplemental Material 2 [33] for different kernel sizes].

Thus far, we have described the phase space in terms of the most abundant species’ properties. However, intricate interactions among species exist in complex environments, and non-trivial interactions are expected to emerge across space [42]. These empirical facts motivated us to perform additional analysis of our theory, in which interspecific correlations are considered. To do that, we define a protocol to analyze spatial cor-

relations between species. Given N points off different species in an area A , divide the area A in cells, e.g., squares of side ℓ , and denote with $n_i^j(x)$ the number of points for each species in the cell-centered in x . Once this procedure has been done for all species, we computed the averaged Pearson’s correlation coefficient between species i and j along with all the boxes. Therefore, the intertwined spatial relationships between species—for a given scale ℓ —can be mapped into a correlation matrix between them [as illustrated in Figs. 4(a)–4(c)].

On the one hand, Pearson’s correlation matrices between species have been computed for different dispersal kernels. For ease of comparison with empirical results, we selected a specific system size ($N = 512^2$) showing a mean value of 300 species (see Supplemental Material 3 [33]). Correlation matrices of the top two hundred species exhibit a clear non-trivial modular structure for local dispersal kernels [$K = 5$, see Fig. 4(a)], much more diffuse for large dispersal kernels [$K = 25$ see Fig. 4(b)]. Besides that, correlations between species in BCI—at the macroscale, i.e., fixing box sizes of $\ell = 50$ m—exhibit a nontrivial modular structure between species [see Fig. 4(c)].

On the other hand, null correlation matrices have been generated to assess the modular structure’s validity. To do so, we generated null matrices with the same row (or column) sum values as those for the original matrix, using the standard configuration model [43]. Thus, the conservation of the variance—for each node—of the original correlation matrix remains ensured. We want to point out that this approach is entirely analogous to the configuration model for networks,

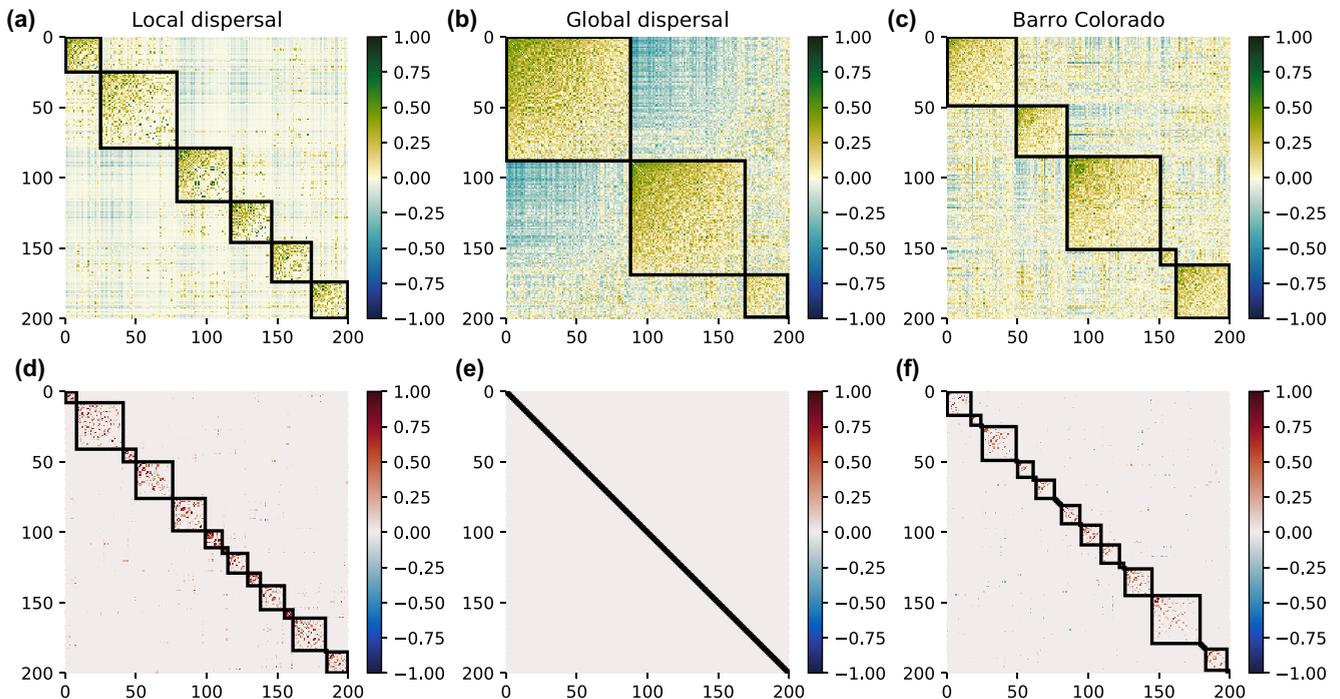


FIG. 4. Interspecific correlations Pearson’s correlation matrix between species i and j considering the 200 more abundant species in (a) SENM with local dispersal kernel ($K = 5$, $\nu = 9.2 \times 10^{-5}$, $L = 512$, $\ell = 32$), (b) SENM with long-distance dispersal ($K = 25$, $\nu = 3.7 \times 10^{-5}$, $L = 512$, $\ell = 32$), and (c) BCI ($\ell = 50$ m). Configurational model for (d) SENM with local dispersal kernel, (e) SENM with long-distance dispersal, and (f) BCI. Reorganization in modules is done through the standard Louvain method over the matrix of positive correlations.

which preserves the row sum of the adjacency matrix (i.e., degree of each node) [43–45]. Figure 4(d) shows that for local dispersal kernels (within the scale-invariant regime), modularity emerges as a robust feature of the system, while for large dispersal kernels (that is, uncorrelated spatial patterns), modularity disappears [see Fig. 4(e)]. For the actual case of BCI [Fig. 4(f)], we have also confirmed the modular structure’s robustness between species.

Additional analyses of our theory have been done to test the replication ability of diverse empirical facts in Barro Colorado. We computed, for the most abundant species, the pair correlation function, $g(r)$, and the spatial density fluctuations, $\delta_r n$, along with the associated SAD. Both quantities have been recently argued to be key to draw conclusions about spatial point patterns [20].

The pair correlation function, $g(r) = \frac{1}{N\rho_0 2\pi r} \sum_{i,j} \delta(r - r_{ij})$, quantifies the average density of trees at distance r from any individual tree, normalized by the mean density of vegetation (ρ_0). For a completely random distribution of points, one expects a flat pair correlation function, $g(r) = 1$, by definition. Conversely, values above 1 denote clumping, i.e., tree clustering, which has been generically found in rainforests [22], while values below 1 indicate anticorrelations. Spatial density fluctuations are based on the same methodology used to build the Pearson’s correlation matrix, but measure the root-mean square deviations at the single-species level, $\delta_r n = [\langle n_r^2(\mathbf{x}) \rangle - \langle n_r(\mathbf{x}) \rangle^2]^{1/2}$, where $\langle [\dots] \rangle$ indicates the average over all cells. Generically, $\delta_r n \propto \langle n_r \rangle^\gamma$, where γ ranges in $1/2 \leq \gamma \leq 1$. Values of $\gamma > 1/2$ are expected to indicate long correlations, a hallmark of out-of-equilibrium systems, and/or the presence of anomalous spatial heterogeneities [46,47]. Finally, species-abundance distribution involves all species in a community, ranked from most to least abundant.

Figure 5(a) shows the species abundance distribution for different dispersal kernels in the SENM using the isoline $n_s \simeq 300$ species for qualitative comparison with actual data of Barro Colorado Island. There is a good qualitative agreement between the empirical data and the simulated spatial patterns for intermediate values of the dispersal kernel (ranging from $K = 3$ to $K = 10$). Figures 5(b) and 5(c) show the spatial correlations and spatial density fluctuations for different values of the dispersal kernel, K , in the scale-invariant regime (see Supplemental Material 4 [33] for further analyses depending on ν and Ref. [20] for additional explanations). For high values of the dispersal kernel, K , and independently of the immigration probability, ν , the pair correlation function is almost 1, thus suggesting a random distribution of points in the available space. However, for local dispersal kernels in the scale-invariant regime, $g(r) > 1$ values at small distances, together with nontrivial scaling of density fluctuations at all scales, provide evidence of clumping and confirm our previous findings.

In summary, high clustering levels at short scales emerge only at the scale-invariant regime, together with anomalous density fluctuations at all scales and fully compatible species abundance distributions of species regarding current BCI data. Both quantities’ joint assessment justifies the nontrivial emergent correlations among species and suggests the qualitative agreement of BCI data with the scale-invariant regime [20].

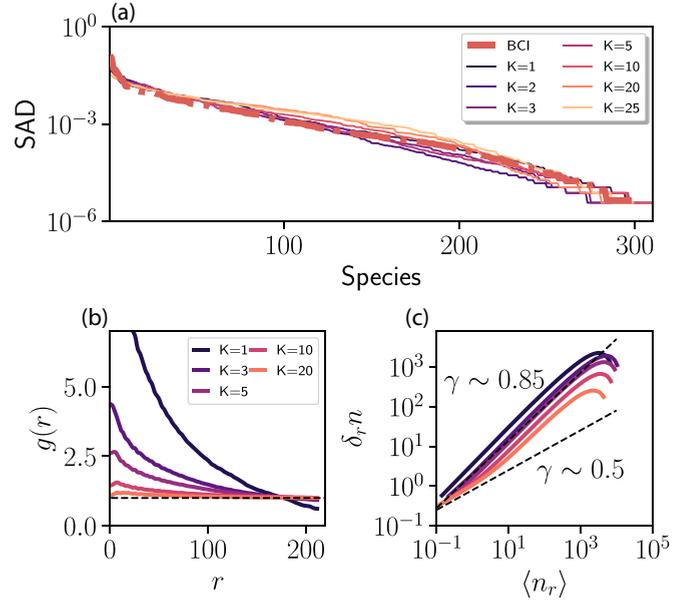


FIG. 5. Spatial correlations and fluctuations. (a) Species abundance curves for different selected realizations of the SENM and different kernel sizes (see legend) along the isoline with $n_s = 300$ species, together with the actual rank abundance of the last census of BCI (red dot-dashed line). (b) Pair correlation function, $g(r)$, vs distance for $\nu = 10^{-4}$ and different dispersal kernels, K (see legend) for the most abundant species. Black dashed line corresponds to the result for an utterly homogeneous distribution. (c) Spatial density fluctuations for the most abundant species for $\nu = 10^{-4}$ and different dispersal kernels, K . Dashed black lines display Taylor’s law exponents $\gamma = 1/2$ (corresponding to a homogeneous random process), and $\gamma \approx 0.85$ (for the sake of comparison with the observed value in BCI [20]). Curves have been averaged over 10^2 realizations in a system of size $N = 512^2$.

IV. DISCUSSION AND CONCLUSIONS

Neutral interpretations have revealed to be helpful in the comprehension of a large variety of social and biological scenarios: propagation of memes [48], microbiome evolution [49], microbial communities [50], tumor evolution across cancer types [51], causal avalanches in up-states of cortex functioning [52], or the stem cell renewal of the intestinal epithelium [53], to name but a few.

Limited diffusion is expected to play a crucial role in ecological systems. For example, common species are expected to be small seeded, whereas large-seeded species are consistently rare. However, abundance and seed dispersal do not seem to show a direct relationship [54], but there exists evidence of how plants can modify the seed dispersal range to enhance survival [55]. One could expect spatial effects to be relevant for local diffusion of seeds (far from mean-field behavior, with fluctuations playing an important role [1,56]), while for large dispersal range, results are expected to be closer to the mean-field case. In particular, a key challenge is to test predictions based on disperser behavior against field data [57].

Despite many efforts on shedding light on how NT can qualitatively explain several patterns observed in ecosystems

[8], only some works have contributed to show the ability of its spatially explicit counterpart to reproduce beta-diversity [14] and species-area relationships [12,13].

Here we proposed scrutinizing a richer, though a still simple model of spatial neutral competition, including the dispersal of seeds [11,12]. In particular, it exhibits different types of characteristic regimes (i.e., spatial point patterns), as revealed by analyzing the system's order parameter on changing seed dispersal and immigration parameters. There is a region of bistability (which exhibits monodominance or uncorrelated point patterns among a small number of species) and a scale-invariant region (shifting to uncorrelated patterns for large dispersal kernels). Meticulous computational analyses allowed us to uncover that, in the scale-invariant regime, scale-free distributed clusters of vegetation emerge, with exponents compatible with percolation transitions [34,40,41].

From a global perspective, we have made progress in developing a theoretical framework connecting spatial neutral models (subject to demographic fluctuations), ecological networks, and critical transitions, a key challenge to understand the crucial interplay between ecological dynamics and species interactions [8,9]. In particular, we showed that SENMs are susceptible to reproduce most of the main features observed experimentally in natural rainforests: (i) The species abundance distribution, (ii) high level of clustering at short scales [22], (iii) nontrivial spatial density fluctuations for local dispersal kernels [20], (iv) a modular-like Pearson's correlation matrix between species in the scale-invariant regime, (v) the emergence of scale-free distribution of clusters previously reported in Kalahari woodlands or tree-canopy gaps in BCI [26,27], and (vi) to generate the specific spatial patterns leading to the coexistence mechanism of multiple species also existing in natural rainforests [3].

Let us emphasize that we have not explored niche effects, which are fundamental to explain interspecific competitions [58]. In particular, niche effects as, e.g., competition for diverse limiting resources, response to environmental changes, (co-)evolution of pairs of species (e.g., predator-prey, host-

parasite, etc.), among others, can naturally lead to modular interactions between species [59,60]. However, NT omits limiting resources or asymmetric interactions by making the radical assumption of species equivalence (limited dispersal and speciation alone have proven only partially to explain beta-diversity in tropical forests [61]). The emergent modular structure—despite its complexity—reflects only intermittent spatial competition effects (i.e., correlations) changing over time and cannot explain bona fide biological interactions among species. Indeed, without seeking to propose any claim of neutrality for actual data, we have chosen this approach just for the sake of simplicity, agreeing with the standard overview: “*niche and neutral models are in reality two ends of a continuum with the truth most likely in the middle*” [58]. Quenched and temporal disorder and more sophisticated competition mechanisms (e.g., amensalism and competition for resources) accounting for niche effects, habitat structure (e.g., the emergence of clustering in semiarid ecosystems [27]), and species differences will be analyzed in future work.

However, even if the SENM studied here is exceedingly simple to be a realistic model of a complex ecological landscape, it can provide us with insight into the basic dynamical mechanisms needed to generate its complex dynamical features, paving the way to the long term goal of constructing a statistical-mechanics of rainforests. Furthermore, we propose a novel, powerful and easy-to-use method for building networks in multiagent dynamic systems. We also believe that our approach can open the door to novel research lines in the context of bacterial communities or the spreading of opinion dynamics.

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