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Spatial organization of vegetation arising from non-local excitation with local inhibition in tropical rainforests

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ABSTRACT

The Janzen–Connell (JC) effect, which hypothesizes that recruitment and growth of seedlings is positively correlated to the distance from the parent tree, is shown to generate highly organized vegetation biomass spatial patterns when coupled to a revised Fisher–Kolmogorov (FK) equation. Spatial organization arises through a novel mechanism of non-local activation and local inhibition. Over a single generation, the revised FK model calculations predict a "hen and chicks" dynamic pattern with mature trees surrounded by new seedlings growing at characteristic spatial distances in agreement with field data. Over longer timescales, the importance of stochastic dynamics, such as those associated with randomly occurring light gaps, increase thereby causing a substantial deviation between predictions from the deterministic FK model and its stochastic counterpart derived to account for such random disturbances. At still longer timescales, however, statistical measures of the spatial organization, specifically the spatial density of mature trees and their minimum spacing, converge between these two model representations.

1. Introduction

The Fisher–Kolmogorov (FK) equation is a basis for much of the field of mathematical biology, describing the growth of a population that also moves in space [31]. A number of recent theoretical studies have examined the potential for the FK equation to generate spatial patterning when non-local competition terms are included [1–4]. These studies suggested that non-local factors are important drivers of population dynamics, particularly spatial patterning of bacterial colonies. A macroscopic complement to these studies is found in the non-local activation of tree seedling recruitment, as is postulated to occur due to the "Janzen-Connell" (JC) effect [5]. The JC hypothesis proposes that predation of dispersed seed and young seedlings of rainforest species is negatively correlated to the distance of dispersal of the seed from the parent tree. An 'expansive' interpretation of the JC effect is adopted here including distance dependence arising from plant pathogens, predators, mechanical damage induced by animals, and other mortality factors that are strongly localized near the parent tree. This expansive JC effect is thought to be important in the maintenance of rainforest biodiversity, and is hypothesized to have the following consequences:

- For seeds to survive, they must be dispersed sufficiently far from the parent tree to "escape" the localized area where mortality factors are elevated;
- Seedlings primarily establish beyond some minimum threshold distance from the parent tree, resulting in a spatial pattern of a mature tree(s) surrounded by seedlings at a distance (referred to as a "hen and chicks" pattern) in the short term.

The expansive view of the JC hypothesis and its effects on spatial organization of tropical forests remains a topic of active research in the ecological literature [6–12]. Numerical studies have examined the implications of the JC effect on species richness and establishment [13,14], but the potential for the FK equation (or its variants) to generate spatial patterns when subjected to the JC constraints remains largely unexplored, and is the subject of this study. Field data suggest that spatial organization varies with the timescale considered. Between generations, a parent tree may be found surrounded by seedlings at some characteristic distance (the "hen and chicks" arrangement). At longer, intergenerational, timescales trees may be situated apparently at random across the landscape (the "random cohorts" arrangement). Many sources of stochasticity lead to random cohort arrangements, but the formation of light gaps is likely to have particular importance. Light gaps greatly accelerate growth and determine sites where seedlings can mature. Motivated by field observations and

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theoretical developments in pattern formation via the FK equation, three inter-related research questions frame the study objectives:

1. What are the dynamics predicted when the JC effects are imposed on an FK model? Can bifurcations with ecological relevance be identified? How can spatially organized states be characterized?
2. How do the transient phases for such a model compare to a generational record of field data documenting tree and seedling locations? If stochasticity (e.g. light gap generation) is incorporated into the model, are the underlying dynamics preserved?
3. What is the implication of the spatial organization on upscaling biomass growth subject to JC effects?

This study addresses these questions using model results guided by field data collected at the Cocha Cashu Biological Station in the Manu National Park (CC), and at the Los Amigos Biological Station (LA), both located within Madre de Dios, Peru. Descriptions of the CC and LA field sites, their climate, and their vegetation can be found elsewhere [15–18]. The field data collected at these two sites consist of fruiting tree locations, seed rain, seed and seedling mortality and seedling locations. Data from one plot, which documents locations of the fruiting trees and their seedlings over a 33-year period (from 1974 to 2007), are used in initializing the model calculations. Ecological parameters collected for *Iriartea deltoidea*, one of the most dominant tree species in wet lowland and premontane tropical forests of western Amazonia [19,20] and the Choc- and Central American region [21,22] are employed in the model calculations. This choice of case study provides a robust application of the model, since the very abundance of *I. deltoidea* suggests that JC effects are likely to be less pronounced than in the case of other, less abundant species. Like many rain forest palm species, *I. deltoidea* is animal dispersed, shade-tolerant, and can be found in all size classes within the sub-canopy or in gaps [23–25]. Trees were recorded as being reproductive only if they were observed to bear fruit, or if evidence of past fruiting was observed.

2. The model

2.1. The Fisher Kolmorogov equation

The FK equation couples logistic growth of total biomass density (P, kg m^{-2}) to diffusive movement via:

$$\frac{\partial P}{\partial t} = r\left(1 - \frac{P}{K}\right)P + D\nabla^2 P \tag{1}$$

where r is an intrinsic growth rate (yr^{-1}), K is the carrying capacity expressed in terms of biomass density (kg m^{-2}), t is time (yr), D is a diffusion coefficient (m^2 yr^{-1}), $\nabla^2 P_T$ is the Laplacian $\left(\partial^2 P/\partial x^2 + \partial^2 P/\partial y^2\right)$, and x and y are planar Cartesian coordinates (m).

2.2. The modified Fisher–Kolmogorov (FK) equation

To account for JC effects on biomass organization in space and time requires three modifications to the original FK equation. Firstly diffusive biomass movement is replaced by a non-local dispersion term to ensure that the dispersing seeds can "escape" the zone of elevated mortality and to account for non-local seed dispersal. This is achieved by replacing the Laplacian term in the FK equation with a convolution between a dispersal kernel and the reproductive biomass. The kernel prescribes a probability distribution of the location of dispersed seed about a reproducing tree. At every timestep, a proportion α(yr^{-1}) of the reproductive biomass (designated P_r) is converted to seed and dispersed according to this kernel.

Secondly, a spatially varying mortality term is added, in the form of a kernel convolved with P_r, which accounts for both the JC effect and spatial competition between mature trees. A continuous equation describing the evolution of the total biomass P is then given by:

$$\begin{aligned}\frac{\partial P}{\partial t} &= r\left(1 - \frac{P}{K}\right)P - \alpha P_r - mdP \\ &\quad + \alpha\left\{\int_0^y \int_0^x P_r\left(x', y'\right) W_d\left(x', y'\right) \mathrm{d}x'\mathrm{d}y'\right\}\end{aligned} \tag{2}$$

where W_d is the dimensionless dispersal kernel (defined below), m is the maximum mortality rate (yr^{-1}), x' and $y'(m)$ are dummy space variables and d is the dimensionless and spatially variable intensity of mortality. d is set to a maximum of unity through the normalization:

$$d = \frac{\int_0^y \int_0^x P_r\left(x', y'\right) W_m\left(x', y'\right) \mathrm{d}x'\mathrm{d}y'}{\max\left(\int_0^y \int_0^x P_r\left(x', y'\right) W_m\left(x', y'\right) \mathrm{d}x'\mathrm{d}y'\right)} \tag{3}$$

where W_m is the dimensionless mortality kernel defined below.

Thirdly, the model must be able to discriminate between reproductive biomass P_r and non-reproductive biomass (designated P_j) generated by seed dispersal. Typically tropical species reach a reproductive age after several decades (for instance the species considered here, *I. deltoidea*, reaches maturity after approximately 20 yr [25]). In this model, a simplifying assumption is made that the reproductive condition of the biomass at a site can be interpreted as a minimum "biomass for reproduction", so that biomass is defined as reproductive if it exceeds a threshold S_p. A decline in biomass below S_p results in the biomass being classified as non-reproductive. Thus the continuous equation for P may be split into reproductive and non-reproductive components such that $P = P_r + P_j$, with separate evolution equations written for P_r and P_j:

$$\begin{aligned}\frac{\partial P_r}{\partial t} &= P_r\left(r\left(1 - \frac{P_r}{K}\right) - \alpha - md\right) \\ &\quad + P_j H_1\left(P - S_p\right) - P_r H_1\left(Sp - P\right)\end{aligned} \tag{4}$$

$$\begin{aligned}\frac{\partial P_j}{\partial t} &= r\left(1 - \frac{P_j}{K}\right)P_j + \alpha\int_0^y \int_0^x P_r\left(x', y'\right) W_d\left(x', y'\right) \mathrm{d}x'\mathrm{d}y' \\ &\quad - mdP_j - P_j H_1\left(P - S_p\right) + P_r H_1\left(S_p - P\right)\end{aligned} \tag{5}$$

$H_1(\ldots)$ represents the Heaviside unit step function defined such that $H_1(0) = 1$ with dimensions of t^{-1}. It controls the classification of biomass at a site as either reproductive or juvenile, preventing a nonsensical co-location of multiple trees at a site. The construction used has assumed equivalent competitive relationships between two mature trees as between a mature tree and immature plants. This is adopted as a simplifying assumption, commonly employed in other theoretical treatments of the JC effect [26], and could be refined as an extension of the current model. Hereafter, the system of Eqs. (2)–(5) is referred to as the JC modified FK equation, or JC–FK. Note that spatial processes operate on both the growth (due to seed dispersal) and mortality (due to JC effects) of the P_j equation, but only spatial mortality (due to competition) is included in the P_r equation.

2.3. The kernels

The recruitment pattern displayed by a species is a function of both its dispersal behavior and the spatial dynamics of the agents causing mortality, and JC recruitment has been shown to result when mortality agents are most active at short spatial scales but seed dispersal is long-range [6]. The case study addressed here, *I.*