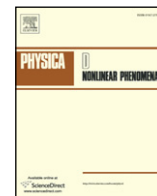




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Spatial organization of vegetation arising from non-local excitation with local inhibition in tropical rainforests

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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.

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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 Kolmogorov equation

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

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

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 ($\text{m}^2 \text{yr}^{-1}$), $\nabla^2 P$ is the Laplacian ($\partial^2 P / \partial x^2 + \partial^2 P / \partial y^2$), 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 $\alpha (\text{yr}^{-1})$ 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:

$$\frac{\partial P}{\partial t} = r \left(1 - \frac{P}{K} \right) P - \alpha P_r - m d P + \alpha \left\{ \int_0^y \int_0^x P_r(x', y') W_d(x', y') dx' dy' \right\} \quad (2)$$

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:

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

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 :

$$\frac{\partial P_r}{\partial t} = P_r \left(r \left(1 - \frac{P_r}{K} \right) - \alpha - m d \right) + P_j H_1(P - S_p) - P_r H_1(S_p - P) \quad (4)$$

$$\frac{\partial P_j}{\partial t} = r \left(1 - \frac{P_j}{K} \right) P_j + \alpha \int_0^y \int_0^x P_r(x', y') W_d(x', y') dx' dy' - m d P_j - P_j H_1(P - S_p) + P_r H_1(S_p - P) \quad (5)$$

$H_1(\dots)$ 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.*

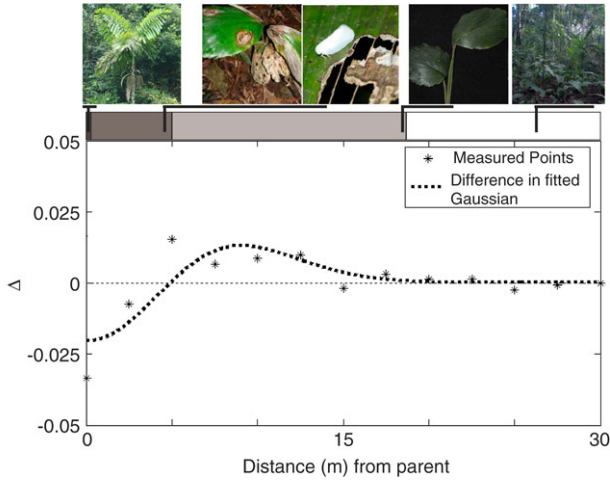


Fig. 1. Sample seedling survival data for *I. deltoidea*, computed as the difference in normalized probabilities (Δ) of seedling dispersal and mortality (due to a number of factors). The line shows the difference between computed mortality and dispersal kernels (assumed to be Gaussian). The zero crossing is consistent with the order of magnitude of the crown diameter and represents the point where seedling recruitment is no longer inhibited by the presence of the mature tree. Photographs show the typical condition of a mature palm, seedlings undergoing high mortality [32], and healthy seedlings that have escaped JC effects [29].

deltoidea, exhibits such behavior, with most mortality associated with insect attack over small spatial scales [32]; while median seed dispersal distances are in the order of 100 m [27]. Although the choice of dispersal and mortality kernels for this study are based phenomenologically on measurements of *I. deltoidea* conducted at CC and LA, the results obtained are generalizable to species exhibiting JC effects [6]. The 9 plots from CC and LA were pooled to derive the survival data shown in Fig. 1 for *I. deltoidea*. This kernel was computed as the difference in probabilities of seedling (not seed) dispersal and mortality. While seed dispersal kernels are not used here, we note that previous studies demonstrate that the dispersal kernels are 'heavy-tailed' and fit similarly well (to within 3.5%) by exponential, Gaussian or the so-called 2Dt kernel shapes [28]. For the seedling data presented in Fig. 1, the critical feature of the dispersal is not the shape of the dispersal kernel itself (we approximate it as Gaussian) but the observation that seed survival is negative within a threshold distance. To model the dispersal of the surviving seeds only, the positive component of the survival kernel is approximated with a gamma distribution shifted a distance R (m) from the parent tree. That is,

$$W_d(r_d) = \frac{r_d^{k-2}}{2\pi} \frac{e^{-\frac{(r_d-R)}{\theta}}}{\theta^k \Gamma(k)}. \quad (6)$$

Here $\theta > 0$ is a scale parameter, $k > 0$ is a shape parameter, $\Gamma(k)$ is the Gamma function of k and r_d indicates radial distance from the parent tree (m). The mean of the distribution μ_d is given by $k\theta$ and the variance σ_d^2 by $k\theta^2$. For the model calculations, k was set to 2 and θ was treated as a single 'control' parameter determining the width of the kernel. The mortality kernel was approximated as a 2D Gaussian distribution with zero mean. The mortality at the center ($r_d = 0$) is set to zero so that trees do not exert mortality effects on themselves. The area of influence of the elevated mortality can be directly altered by changing the variance of the kernel, σ_m .

2.4. Addition of a stochastic component

The influence of light gaps was incorporated into the model by varying growth rate r . Undisturbed sites had $r = 0.01 \text{ yr}^{-1}$ corresponding to low light environments. Based on light gap

frequency analyses at CC 2% of the landscape was randomly disturbed each year. Total biomass (P) in these cells was reduced to zero, and the growth rate increased 100-fold to account for increased light availability. If biomass in the cell had not reached 0.001 K after three years, the growth rate reverted to the low light environment value. Similarly, when biomass in a gap reached maturity the growth rate reverted to the low light environment value. The selection of these disturbance fractions and growth rates are not intended to reproduce a particular field experiment or a study site, but to represent known features of the ecosystems so as to derive general conclusions.

2.5. Limitations of the model

The overriding goal in developing this model was to capture the spatial complexity of JC processes via a simple amendment to the FK equation, minimizing the number of parameters needed to define the model behavior. These simplifications inevitably result in some model limitations. These are primarily associated with the treatment of mature biomass that suffers mortality and declines, and with competitive interactions. The JC-FK model assumes that reproductive biomass that declines to less than S_p should be treated as immature biomass. It is appropriate to assume that such biomass does not reproduce or exert JC effects, but it would be more ecologically reasonable for such biomass to contribute to a "non-reproductive mature biomass pool" which does not experience JC effects or reproduce. In the current formulation the JC effects are assumed to act equivalently for mature-mature interactions and mature-immature interactions. This avoids the necessity of introducing a nonreproductive biomass pool at the expense of forcing mature and immature biomass to conform to the same spatial relationships. Future version of the model could be extended to address these issues.

3. Steady states of the model

This section derives the homogeneous steady states of the JC-FK model and presents their stability to spatial perturbations as determined from numerical simulations.

3.1. Nondimensionalization

The model is nondimensionalized by scaling all biomass terms with the carrying capacity K : $P^* = P/K$, $P_r^* = P_r/K$, $S_p^* = S_p/K$; all temporal terms with the mortality m : $t^* = tm$, $a = r/m$, $b = \alpha/m$, $c = H_1(\dots)/m$; and all spatial terms with σ_m : $x^* = x/\sigma_m$, $y^* = y/\sigma_m$. The spatial kernels are also rescaled by σ_m , and referred to as d^* , W_d^* and W_m^* . The resulting nondimensional equations (in which the $*$ has been dropped for clarity) are given by:

$$\frac{\partial P_r}{\partial t} = a(1 - P_r)P_r - bP_r - dP_r + P_jc(P - S_p) - P_rc(S_p - P) \quad (7)$$

$$\frac{\partial P_j}{\partial t} = a(1 - P_j)P_j + b \int_0^y \int_0^x P_r(x', y') W_d(x', y') dx' dy' - dP_j - P_jc(P - S_p) + P_rc(S_p - P). \quad (8)$$

All further discussion will refer to the nondimensionalized values of P_r , P_j , P and S_p .

3.2. Analysis of the equations

Spatially homogeneous steady states $[P_j^0, P_r^0]$ may be identified by noting that all spatial kernels integrate to 1 under homogeneous

Table 1
Details of the simulations performed, the parameter values (and their variation), and the ICs.

Trial	Question	Parameters	Values	Output parameters	Initial conditions
1.	Nonlinear dynamics of JC model	$a = r/m$ r_d/σ_m σ_d/σ_m	0.5, 0.75, 1, 1.5 2, 4, 5, 10 4, 2, 1, 0.5, 0.1 0.1, 0.25, 0.5, 1, 2	Steady state biomass distribution	Random points (mature biomass) perturbation about 0.8 K
2.	Qualitative comparison with field data	r m r_d σ_m σ_d	0.32 yr ⁻¹ 0.5 yr ⁻¹ 4 m 3 m 15 m	Biomass distribution c.f. 33 yr of field sampling	Measured locations of mature trees
3.	Couple to stochastic light gaps	r m r_d σ_m σ_d	0.01 – 1 yr ⁻¹ 1 yr ⁻¹ 10 m 10 m 10 m	Biomass distribution at 20, 100 and 700 yr. Total biomass evolution	Random points (mature biomass)

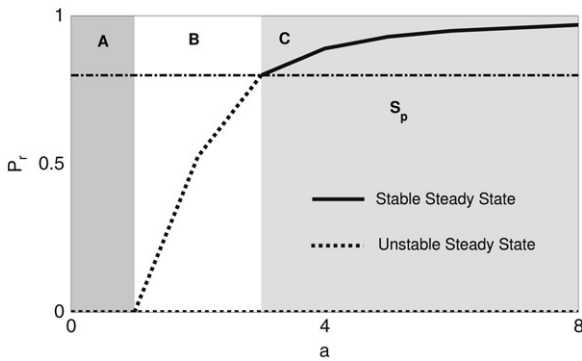


Fig. 2. Bifurcation diagram and phase plane for the steady states of the FK-JC model. (A) shows the bifurcation in stability of the states as determined by the condition of P_r . (B) shows a phase plane for a situation where a stable steady state exists but is precluded from forming because it lies below the threshold for maturity.

conditions. There are then two possibilities to consider, the first being that the homogeneous steady state does not include reproductive biomass. In this situation, all terms referring to P_r (including the spatial mortality d) drop out of the evolution equation for P_j . Provided that $P_j^o < S_p$, there is no conversion of immature biomass to mature biomass and the evolution equation for P_j collapses to the logistic equation. The two well-known steady states of this equation are $P_j^o = 0, K$, where the zero steady state is unstable. However it is necessary that $S_p < K$. Hence the second possibility is the steady state $P_r^o > 0$ and $P_j \neq K$. Under these conditions $P - S_p > 0$, allowing the simplification of the equations to:

$$0 = a(1 - P_r^o)P_r^o - bP_r^o - P_r^o + P_j^oc(> 0) \quad (9)$$

$$0 = a(1 - P_j^o)P_j^o + bP_r^o - P_j^o - P_j^oc(> 0). \quad (10)$$

Solving these functions simultaneously yields

$$P_r^o = \frac{P_j^o(a(P_j^o - 1) + 1 + c(> 0))}{b} \quad (11)$$

while P_j^o is defined by the solution of:

$$0 = \frac{1}{b} (P_j^o (b^2 (1 + a(P_j^o + 1)) - b(a - 1) (1 + c + a(P_j^o - 1)) + a(1 + c + a(P_j^o - 1))^2 P_j^o)). \quad (12)$$

Although analytical solutions of Eq. (12) for (P_r^o, P_j^o) exist they are not readily rendered in closed form. Instead the general solution behavior was elucidated by fixing b and $c(> 0) = 1$ and

treating a as a control parameter. A plot of the resulting bifurcation diagram in terms of P_r and a is shown in Fig. 2. Three states occur in this plot. (A) the unstable no-biomass solution; (B) a stable solution which exists provided $a > \approx 2$ but where $P_r^o < S_p$; (C) the same stable solution curve where now $P_r^o > S_p$. Regime A is unstable to any perturbation, while regime C is stable to all perturbations. Regime B merits further discussion. In this regime the system stabilizes at $P = S_p$. If $P > S_p$ the mature biomass attempts to evolve to the steady state, but in doing so loses biomass and becomes non-reproductive. If $P < S_p$ then the system attempts to evolve to K and in doing so gains mass and again crosses S_p . The ecological interpretation of this state is that the minimum biomass needed for reproduction generates such large competitive effects that the system cannot reach the homogeneous steady state. This state is stable to homogeneous perturbations, but unstable to spatially variable perturbations. The first bifurcation of the system is observed at the point where $P_r^o = S_p$. As the control parameter $a(=r/m)$ is tuned beyond this point the patterned solution continuously increases in amplitude and wavelength.

4. Methods

Details of the model runs are presented in Table 1 along with the research question targeted by each simulation. Steady homogeneous states of the JC-FK model were identified and the stability to random spatial perturbations tested numerically. States were explored as temporal and spatial control parameters were varied. For all simulations, α was set to 4×10^{-4} yr⁻¹, and simulations were all run for 500 yr. Transient behavior was examined over a shorter “generational” timescale of 33 yr using initial conditions drawn from the location of mature trees on one of the plots at CC. The results were compared to the locations of saplings and seedlings recorded in the field, to assess the “realism” of model performance in a qualitative sense. The deterministic JC-FK model was also coupled to the stochastic appearance of light gaps over various timescales. Numerical calculations were performed using an Euler forward difference scheme with a spatial discretization of 5 m($dx = dy$), and a time-step of 0.004 yr. For the JC-FK equations, all convolutions between the biomass and spatial kernels were performed in the Fourier domain using a fast Fourier transform algorithm [33]. Initial conditions (ICs) included point conditions (a random initialization of 1% of the domain with mature trees) and random perturbations about a homogeneous biomass density at S_p (set to 0.8 K).

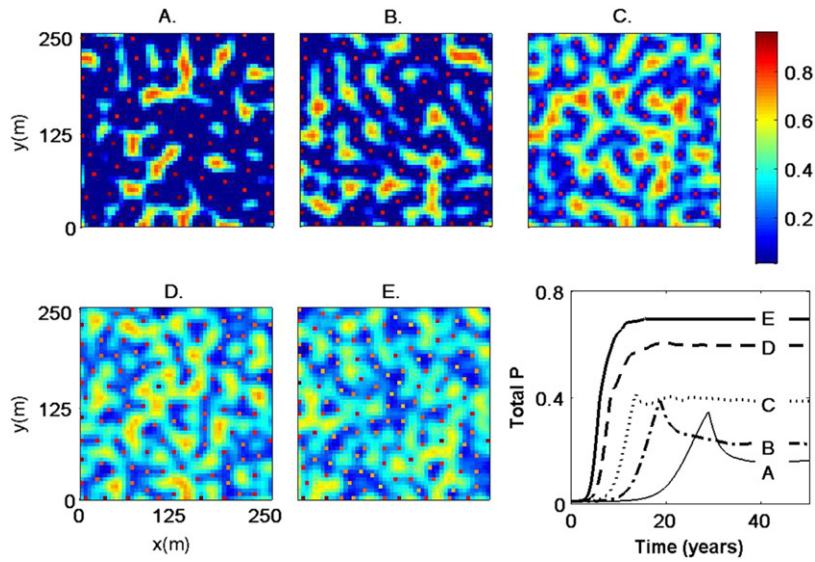


Fig. 3. As $a = r/m$ is increased from 0.5 (panel A) through 0.75 (B), 1 (C), 1.5 (D) to 2 (E), the spacing between mature trees becomes denser, and the overall biomass increases (bottom-right panel). Isolated “spots” of high biomass represent reproductive trees, while larger patches of lower biomass represent areas of recruiting juveniles. With increasing a , the ratio of immature to mature biomass increases, and the biomass dynamics resembles logistic growth behavior. The biomass density shown is normalized by the carrying capacity of the entire (250 m \times 250 m) domain.

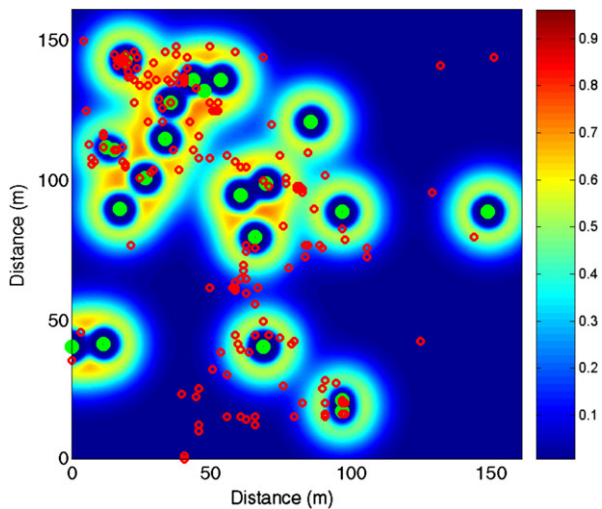


Fig. 4. Comparison between model calculations of normalized biomass (color-map) and field data (red circles). The model calculations are initialized with the fruiting trees (here identified by green circles) measured since 1974, and seedlings are predicted after a 33-year simulation showing current seedling recruitment at Cocha Cashu Biological Station. Approximately 75% of the seedlings identified in the field are located in areas where the model predicted immature biomass would exceed 1% of carrying capacity. The remaining seedlings are either located at long distances from the fruiting trees and are likely to have been introduced to the site by long distance dispersal, or are located in close proximity to the parent tree, suggesting that the JC effect was not completely effective in preventing establishment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Results and discussion

5.1. Determinants of spatial organization

The spatially organized steady state is structured around an irregular lattice of mature trees. Immature biomass is suppressed around these trees and increases with distance from mature trees. The spacing of mature trees is controlled by a minimum separation distance proportional to σ_m and a , perturbed randomly by the ICs and the dispersal parameters. Systematic variation of the dispersal behavior for fixed mortality and ICs did not change the structure

of the steady state (as measured by the minimum separation distance between mature trees). The intensity of the signal of spatial organization was set by a , with the weakest intensity near the bifurcation, and increasing as a declined (Fig. 3). The model results partially support the JC hypothesis prediction that mature trees should become regularly spaced at long timescales. Regular spacing was not precisely produced. The spatial density of trees remained well below that predicted by a circle packing analysis, generally between 18 and 50% of the maximum possible density $\left(\frac{\sqrt{3}\pi}{6}\right)$ for the domains used. The lack of regularity indicates multiple degrees of freedom in the model system and is the source of the apparently arbitrary relationship between the spatial organization and the ICs and dispersal terms. The minimal sensitivity to the dispersal parameters results from the use of continuous distributions to represent the biomass dispersal. Provided the tails of the mortality kernel decay faster than those of the dispersal kernel, “escape” as predicted in the JC Hypothesis always occurs. The use of continuous dispersal kernels accords well with field observations [11,25], which suggest that for animal dispersed species (such as *I. deltoidea*) some proportion of seed is usually conveyed substantial distances from the parent tree and escape almost always occurs.

5.2. Comparison with field data and timescales

The deterministic model was run over a 33-year period using initial conditions from a 33 year experiment conducted at the CC research station for *I. deltoidea*. The results were compared to field data indicating the position of adult trees and seedlings at the end of this 33-year period. Approximately 75% of the seedlings recorded in the field were located in sites that the model predicted would be occupied by biomass (Fig. 4). The seedling locations that were not well explained by the deterministic model arose through one of two mechanisms: they either fell too close to the parent tree, indicating that the JC effect had not prevented establishment at those sites, or they were located remotely from fruiting trees and presumably either occurred due to seed dispersal from trees outside the boundary of the surveyed area or were the result of animal dispersal from distant plants, an effect that this model did not directly parameterize. At intergenerational

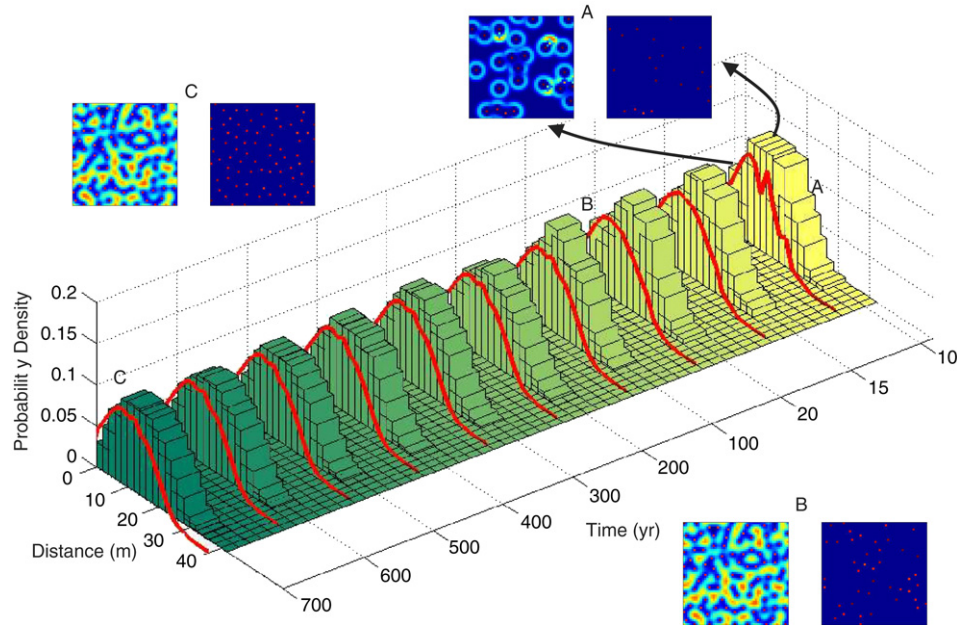


Fig. 5. Evolution of the probability density function (pdf) of separation distances between mature trees as a function of time. Solid bars represent the pdf for the stochastic light gap model and the red lines the pdf for the continuous model. Initially (10–20 yr) the influence of initial conditions dominates. After approximately 100 yr the continuous model reaches a steady state which is quite different from that of the light gap model which is dominated by stochastic effects for ≈ 400 yr. Eventually, after ≈ 500 yr the effects of the JC in structuring the locations of mature trees become the dominant signal in the pdf. The model condition is illustrated after 10, 100 and 700 yr in panels A–C. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

timescales, the predicted “hen and chicks” pattern was a good description of the majority of biomass movement. Similarly, over a generational timescale, the predictions of the deterministic model provided a good indication of where biomass would establish in the stochastic light gap model (Fig. 5). Adding stochasticity to the model, however, retarded biomass migration through space. The dynamics effectively remained “frozen” by the stochasticity in conditions approximating point ICs. Over intermediate timescales, this resulted in a pronounced divergence between the stochastic and deterministic models largely associated with the discrepancy in the time taken for the plant population to disperse throughout the spatial domain. After 100 yr, the stochastic model predicted the existence of only 45% of the number of mature trees predicted by the deterministic model at a steady state, and the difference between the empirical probability density functions (pdfs) of the pair-wise spacing between mature trees were significant at the 1% confidence level ($p = 0.0045$) as determined by the Kolmogorov Smirnov (KS) test. Over longer timescales (400 yr and greater), the distribution of mature biomass in the stochastic model qualitatively resembled that of the steady state deterministic model. Equivalent minimum separation distances ($\approx 1.82\sigma_m$) were observed in each case, the number of mature trees agreed to within 10%, and the differences between the pdfs of mature tree distributions were not significant ($p = 0.62$) via the KS test. The results suggest that in the presence of ‘exogenous’ stochasticity (such as gap formation), the minimum separation distance between fruiting trees remains an appropriate measure of the impact of the JC effect.

5.3. Ecological implications

The evolution of the total biomass in the domain was tracked for all model realizations. Near the bifurcation, the biomass growth closely approximated the sigmoidal curve typical of logistic growth (Fig. 3). Once this state became unstable, however, the impact of spatial organization was to reduce the total biomass at steady state and to introduce additional peaks into its time evolution. The time

evolution of the biomass depended upon the ICs and dispersion parameters. The stochastic model generated lower steady state biomass values than the corresponding deterministic model. Large-scale models of biomass evolution must use averaging techniques, such as an assumption of lumped logistic growth, to scale up over localized spatial dynamics. Caution is needed when upscaling over non-linear dynamics such as those predicted by the JC effect, because the lumped biomass evolution does not always conform to simple predictions such as logistic growth. Near the bifurcation ($a \approx 4.5$ for $S_p = 0.8$), the deviation from logistic growth as predicted by the FK equation is minimal, but as the degree of spatial organization increases, and particularly when stochasticity is added there are large departures from logistic growth. The JC effect depresses the steady state biomass, introduces multiple temporal peaks and, in the stochastic case, random fluctuations. As an alternative to simple logistic upscaling, approaches incorporating the role of the mature trees as the determinants of spatial organization should be considered. Under such a framework, estimates of likely spacing between mature trees could be obtained from measurements of mortality kernels, combined with the packing density predictions (in the range of 18 to 50% of dense circular packing) and estimates of the immature and mature biomass associated with a mature fruiting tree as a means of upscaling over these spatially variable parameters. Mature tree separation distances in this model are strongly determined by σ_m , so that ultimately the spatial density of mature trees for a given species is also a function of σ_m . In ecological terms, expansion of the zone of elevated mortality results in a declining abundance of mature trees, a finding supported by data at CC suggesting that adult abundance scales inversely with the typical distance between recruiting seedlings and the nearest adult tree [30]. If σ_m has a role in controlling abundance at the single species level it may also impact diversity and coexistence of multiple species, particularly as multiple species tend to exhibit varying length scales of seedling mortality. The implications of multiple species exhibiting multiple spatial controls merits further theoretical examination.

6. Conclusions and future work

This work was motivated by three questions relating to the dynamics, timescales and upscaling considerations engendered when incorporating JC effects into models of forest biomass, which we have been able to address to at least a preliminary level of detail using the simple JC–FK equation. JC effects alter the steady states of the FK equation by generating a regime in which the minimum biomass required for reproduction exerts a high degree of competitive pressure, a state unstable to spatial perturbations. The forest has a stable, spatially organized state where mature trees are situated at a minimum distance from each other and determine the concentration of immature biomass in their vicinity. This supports the prediction that a defined length scale exists governing the distribution of mature trees and confirms the concept that seeds must “escape” the zone of higher mortality if the species is to propagate in space. The model findings suggest that the JC parameters, particularly σ_m , help to determine species abundance by governing the density of reproductive trees. The implications of these findings deserve further investigation, particularly in considering the interaction of multiple species. The transient phases of the model compared well to field data and supported the hypothesis of local inhibition and non-local activation over short timescales. The model did not account for long distance dispersal, and through adopting continuous representations of seed dispersal and mortality, was unable to reproduce the findings of a small number of seedlings surviving close to the canopy of mature trees. Finally this work found significant upscaling implications relating to the spatial distribution of reproductive individuals. Where JC effects strongly impact the distribution of a species, estimates of carrying capacity based on resource availability may well over-estimate steady-state biomass. σ_m is identified as a strong determinant of the spatial distribution of areas of high biomass, and thus abundance and spatially upscaled biomass density. Extensions of the current model to differentiate competitive processes between mature and immature biomass, and to address the effects of mortality on mature biomass, can be made relatively simply and may help to account for the presence of fruiting trees within close proximity of each other in the field. Further characterization of the spacing of mature trees over sufficiently large areas in tropical rainforests is needed to critically evaluate model results relating to spatial organization in rainforests. Advances in remote sensing and the use of novel species specific indicators (such as synchronous flowering, which can be readily observed in aerial photography) are starting to provide appropriate datasets to enable more rigorous tests of the predictions of the JC–FK and other spatially explicit biomass models.

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