

The intermediate dispersal principle in spatially explicit metapopulations

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Abstract

Aim of this paper is to assess the fate of metapopulations described by spatially explicit models. To this end, we first present an interacting particle system (IPS) where individuals of a single species compete logistically at the local scale and can move among patches according to various dispersal kernels. As the IPS is a complex stochastic system, it is impossible to determine the persistence–extinction boundaries in any relevant parameter space with analytical methods or numerical continuation techniques. We thus resort to a heuristic method that lets us determine the boundaries as space–time percolation thresholds with a relatively modest computational effort. Such boundaries are qualitatively consistent with those we obtained with spatial implicit modelling. In particular, we find that the intermediate dispersal principle, namely that globally persistent metapopulations correspond to dispersal rates that are neither too low nor too high, turns out to be very robust even in this explicit context. However, the quantification of the boundaries strongly depends upon the number of patches, the dispersal kernels and the border conditions. Finally, we show that there exists a scaling law that relates the number of species lost in a fragmented landscape to the number of patches. Thus, the law allows a rough estimation of the cost of destroying a patch.

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1. Introduction

The process of fragmentation, intended as both the loss of habitat and the breaking apart of it (Fahrig, 2003), is certainly one of the major determinants of extinction for a variety of taxa at the global scale (Tilman et al., 1994; Turner, 1996; Vitousek et al., 1997). Pristine, spatially continuous landscapes are indeed very rare on Earth nowadays (Myers et al., 2000). Thus, it is extremely important to develop methods to assess which populations living in fragmented habitats (metapopulations) are at risk of extinction. These methods must be based on their demographic, behavioral and ecological characteristics and those of the landscape they inhabit.

As we cannot afford to experimentally perform this evaluation by a “wait and see” strategy, we must necessarily resort to models for predictions.

However, the choice of the appropriate metapopulation model is not an easy task. In particular, there are two important choices a theoretical ecologist should make. The first regards the extent to which the habitat can be accurately described at the expense of mathematical complexity. The second deals with the number and type of variables that should be used to model local demography. As summarized by Hanski (1998, see his Fig. 1), there are three qualitatively different choices for the habitat description. The simplest and most theoretical alternative considers an infinite number of equal patches. If the patches are linked by a rain of propagules, this leads to the so-called *spatially implicit* approaches. On the other extreme of the spectrum, one can use a geographical information system to detail the

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biotic and abiotic characteristics of the landscape continuum. Also, more realistic dispersal descriptions can be used, e.g., via dispersal kernels. An intermediate, yet *spatially explicit* approach consists in dividing the landscape into a finite number of patches, each of them possibly being characterized by its area, resource availability and location in space (so that the relative distances among the patches can be explicitly considered). Three qualitatively different alternatives can also be identified for modelling local demography. The simplest one considers only the presence or absence of the species and leads to what we call *boolean* models, because each patch can be in two states (vacant or occupied). Accounting for the exact, discrete number of individuals inhabiting each patch is obviously a much more difficult approach (*discrete* models). Thus, a third alternative is to describe local demography at some intermediate level of complexity (*structured* models), for example by complementing the boolean models with information on how the average and the variance of the abundances in occupied patches change over time (Casagrandi and Gatto, 1999). Many combinations of these different approaches have been used in the past: from the spatially implicit boolean model originally proposed by Levins (1969) to the spatially implicit structured models, like the Markov chains introduced by Chesson (1984) or the PDE's used by Gyllenberg and Hanski (1992); from the spatially explicit boolean models, like presence–absence cellular automata (Molofsky, 1994; Hiebeler, 1997), to the more complex, structured and spatially explicit approaches, such as, for example, coupled maps (Allen et al., 1993; Hastings, 1993; Earn et al., 2000; Yakubu and Castillo-Chavez, 2002) or spatially realistic Levins model (Hanski and Ovaskainen, 2000).

Our past modelling efforts (Casagrandi and Gatto, 1999, 2002a,b) concentrated on discrete models where individuals are accounted for as discrete entities, namely abundance is an integer number. The core of the metapopulation concept and of island biogeography is indeed that each local population is prone to extinction because each habitat patch hosts a finite number of individuals, subject to random demographic events or genetic drift or behavioral disruption. In order to correctly estimate the extinction risk of endangered metapopulations, local population sizes can hardly be approximated by real numbers. This somehow obvious biological consideration causes some mathematical complications. Consider, for example, a spatially implicit approach. Instead of using a single variable $p(t)$ to describe the fraction of occupied patches, as in Levins-like models, one is forced to use an infinite number of variables to consider discrete individuals. By defining $p_i(t)$ as the probability that i individuals (with $i = 0, 1, 2, \dots$) be contained in a patch at time t , it is possible to construct a Markovian model under the

hypothesis that birth and death events take place at the local scale and that dispersal uniformly connects an infinite network of identical patches (Casagrandi and Gatto, 1999). The strength of this discrete model is that it leads naturally to a persistence criterion (Casagrandi and Gatto, 2002a), namely that metapopulation persistence is guaranteed if and only if $E_0 > 1$, where E_0 is the expected number of successful dispersers from a patch begun with one individual and to which immigration is excluded (see also Chesson, 1984, on this). We showed that the condition $E_0 = 1$ corresponds to a transcritical bifurcation of the Markovian model. Since, we provided an analytical way of computing E_0 as a function of the main biological characteristics of the species, it was possible to obtain persistence–extinction boundaries in the space of model parameters. By assuming logistic demography and density-independent dispersal we found that an intermediate level of dispersal is generally required for metapopulation persistence. This result, referred to as *the intermediate dispersal principle* in the present paper, was proved to be very robust to wide changes in the other parameter values. Moreover, if environmental catastrophes and habitat destruction—in terms of either random loss of patches or patch erosion—are introduced into the model, the intermediate dispersal principle still remains valid (see Casagrandi and Gatto, 2002b, for a detailed discussion on the role played by disturbances).

However, the question immediately arises whether the principle still holds if spatially realistic metapopulations are considered. In fact, in a very influential paper, Durrett and Levin (1994a) studied the dynamics of two populations in the case of both mutualistic and competitive interactions, with four different mathematical approaches, namely: (a) ODE's with no spatial structure (mean field models); (b) patch models, where discrete individuals group into patches without additional spatial structure; (c) reaction–diffusion models, where infinitesimal individuals are distributed in space; and (d) interacting particle systems (IPSS), where individuals are discrete and space is treated explicitly. The authors' analysis showed that the four approaches do agree in the case of mutualism, but they predict outcomes that are qualitatively very different in the case of competition. For the same parameter settings, for example, there are cases where the spatially explicit approaches lead to the coexistence of both species while, according to the mean field models, one of the two species is doomed to extinction (competitive exclusion). Every theoretical ecologist must then be aware that the results one finds can be more related to the mathematical method used than to the proposed biological problem. For this reason, we will consider a spatially explicit context to verify if the intermediate dispersal principle we found with spatially implicit models is really robust in metapopulation ecology.

When discrete individuals and their interactions in space are explicitly considered, the aptest description is an IPS, a tool that is widely used in different scientific contexts (see Liggett, 1985). An IPS for single-species metapopulations living in a finite lattice of patches is thus presented in the next section. As we discuss in Section 3, defining persistence–extinction boundaries in the parameter space of the IPS is non-trivial. Therefore we suggest a heuristic definition related to percolation theory and propose a technique for evaluating the boundaries. Using the proposed method, we discuss the robustness of the intermediate dispersal principle in Section 4. In the same section, we explore the effect on extinction risk of various dispersal mechanisms and of the dispersal rules at the lattice border. We close the article with a discussion on a potentially important power law emerging from the model analysis. The law shows how the IPS scales to spatially implicit models.

2. An interacting particle system for single-species metapopulations

We assume that the single-species metapopulation is composed by a finite number of subpopulations living in a lattice of identical patches connected by dispersal. For simplicity, the lattice is assumed to be a square grid of $k \times k$ cells. We expressly consider small grids (6×6 – 30×30) because we want to contrast the results of spatially explicit models with those previously obtained via spatially implicit ones, which are based on the assumption of an infinite number of patches. To describe the change in the metapopulation from time t to time $t + \Delta t$, we introduce a $k \times k$ matrix $\mathcal{N}(t)$ whose $z = k^2$ elements $n_{xy}(t)$ represent the number of individuals (particles) inhabiting the patch at row x and column y at time t . The state variables of the particle system can take up only discrete values (i.e. $n_{xy}(t) = 0, 1, 2, \dots$). We can thus clearly define extinction, at both the local scale ($n_{xy}(t) = 0$ for some x and y), and the global scale ($N(t) = \sum_{x=1}^k \sum_{y=1}^k n_{xy}(t) = 0$).

As for the demography, we introduce density dependence at the local scale, namely the death and birth rates in each subpopulation at time t depend on $n_{xy}(t)$. Similarly to what we did in the spatially implicit models (Casagrandi and Gatto, 2002a), we assume that the per-capita birth rate v and the per-capita death rate μ in the unit time satisfy the logistic relationships, i.e.

$$\begin{aligned} v(n_{xy}) - \mu(n_{xy}) &= r \cdot \left(1 - \frac{n_{xy}}{K}\right) \quad \text{and} \\ v(n_{xy}) + \mu(n_{xy}) &= \beta + \gamma \cdot n_{xy}, \end{aligned} \quad (1)$$

where the intrinsic rate of increase r , the carrying capacity K and $\beta > r$ are positive parameters, while γ can possibly be negative. From Eq. (1), under obvious positivity constraints for the rates, we evaluate v and μ

in each cell at any time t depending upon the current local abundance $n_{xy}(t)$ according to the rules

$$v(n_{xy}) = \max\left\{\frac{1}{2} \cdot \left[(\beta + r) - \left(\frac{r}{K} - \gamma\right) \cdot n_{xy}\right], 0\right\}, \quad (2)$$

$$\mu(n_{xy}) = \frac{1}{2} \cdot \left[(\beta - r) + \left(\frac{r}{K} + \gamma\right) \cdot n_{xy}\right]. \quad (3)$$

As in our spatially implicit models, a function $D(n_{xy})$ represents the per-capita probability of dispersal in the unit time. For sake of simplicity, in the sequel the dispersal rate is assumed to be density-independent: $D(n_{xy}) = D$ constant. To further contrast the present approach with the spatially implicit models, we consider not only the case in which the dispersers can move from one patch to any other patch with the same probability $1/k^2$ (*propagule rain* mechanism), but also the case in which dispersal has a restricted spatial range and is confined to nearby cells. More specifically, we explore two other options, namely that a dispersing individual can move with probability $\frac{1}{4}$ to one of the four nearest neighbors (*Von Neumann* rule) or with probability $\frac{1}{8}$ to one of the eight nearest neighbors (*Moore* rule). In addition, since a disperser targeting a specific patch might not be able to colonize it, we multiply the dispersal probability by a parameter called a which represents the colonizing probability of any dispersing organism ($0 \leq a \leq 1$).

As the lattice is finite, we have to specify the dispersal rules at the borders. We consider the three following cases: *periodic* border conditions (the lattice is isomorphic to a torus); *open* borders, i.e. going outside from any border leads to death (this condition will be called *absorbing*); and *closed* borders, i.e. from the border it is possible to move in all directions but outside (this condition will be called *reflecting*). In Fig. 1, we present a sketch of the model lattice in which we

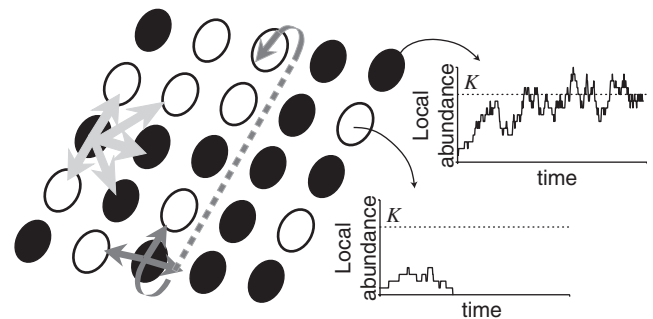


Fig. 1. A sketch of the spatially explicit metapopulation. At any given time step, the patches can be occupied by a positive integer number of individuals (black) or be empty (white). As shown in the two panels, the local dynamics in absence of dispersal is logistic in a stochastic sense. As examples of the possible dispersal mechanisms from occupied patches and border rules, we show the case of the Von Neumann rule on periodic borders (dark gray arrows) and the Moore rule with reflecting borders (light gray arrows).

summarize the assumptions about local dynamics and the various dispersal mechanisms and border conditions used in the present approach.

More specifically, the procedure we use to update $n_{xy}(t)$ to $n_{xy}(t + \Delta t)$ for all x 's and y 's is the following:

1. Evaluation of the birth and death rates via the relationships (2)–(3).
2. Computation of transition probabilities. The probability that no event occurs in the patch xy occupied by n_{xy} individuals during the time interval Δt is given by

$$\psi(n_{xy}) = e^{-[v(n_{xy}) + \mu(n_{xy}) + D] \cdot n_{xy} \cdot \Delta t} \quad (4)$$

(see Mangel and Tier, 1993, for details). The probabilities of a birth (p_v), a death (p_μ), or a dispersal event (p_D) are thus, respectively,

$$\begin{aligned} p_v &= \frac{1 - \psi(n_{xy})}{v(n_{xy}) + \mu(n_{xy}) + D} \cdot v(n_{xy}), \\ p_\mu &= \frac{1 - \psi(n_{xy})}{v(n_{xy}) + \mu(n_{xy}) + D} \cdot \mu(n_{xy}), \\ p_D &= \frac{1 - \psi(n_{xy})}{v(n_{xy}) + \mu(n_{xy}) + D} \cdot D. \end{aligned} \quad (5)$$

3. Extraction of a random event according to the probabilities just evaluated.
4. Addition [subtraction] of an individual to [from] the current subpopulation if the event is a birth [death/dispersal].
5. In the case of a dispersal event, the subtraction of an individual from the current subpopulation is then followed by the random choice of a target cell for the dispersing individual, the evaluation of the success during colonization (at random according to colonization probability a) and, if colonization is successful, the eventual addition of an individual to the target subpopulation.

Stochastic simulations can actually be obtained by choosing an initial condition, a time step Δt and a simulation horizon T . The initial condition we will use hereafter is “all the cells contain $K/2$ individuals”, namely we start with intermediate densities in each metapopulation patch. However, we anticipate that other initial conditions, like the rule “all the cells contain one individual” or random initialization, do not significantly impact on the results presented in the following. As for the length of the time step Δt , it must be related to the metapopulation parameters in order to ensure that the process is indeed Poissonian, i.e. events occurring in a cell at any time step are rare. In other words, the probability $\psi(n_{xy})$ of no event occurring during Δt must be high. As a rule of thumb, we have chosen a value of Δt such that $\psi(1) = 0.95$

(see Eq. (4) above), namely $\Delta t = -\log(0.95)/(v(1) + \mu(1) + D)$. Therefore, simulation time steps are adapted to the metapopulation demographic parameters. As for the simulation horizon, we set $T = w\Delta t$ where w is the number of time steps. A reasonable choice could be that of choosing w in the order of thousands (but see the next section).

A typical pattern of the dynamics of the total metapopulation size N that emerges from simulations of the IPS for intermediate values of D well inside the persistence region of the implicit model (see Fig. 3 in Casagrandi and Gatto, 2002a) is shown in Fig. 2. After a short transient (Fig. 2A, thin black line), the total number of individuals keeps oscillating randomly around a constant value, and the oscillations are caused by the lattice being finite and small. Despite this regularity at the global scale, the fluctuations in the subpopulations can be extremely irregular. The gray line in the same panel (Fig. 2A) shows, for example, the dynamics of one of these subpopulations for the same realization of the stochastic process. Because of a sequence of unfortunate events (demographic stochasticity) the last individual inhabiting the patch leaves it at step $w^* = 3666$, and the patch becomes temporarily empty (local extinction). It takes another 400 steps to have a disperser from a nearby patch colonizing that cell

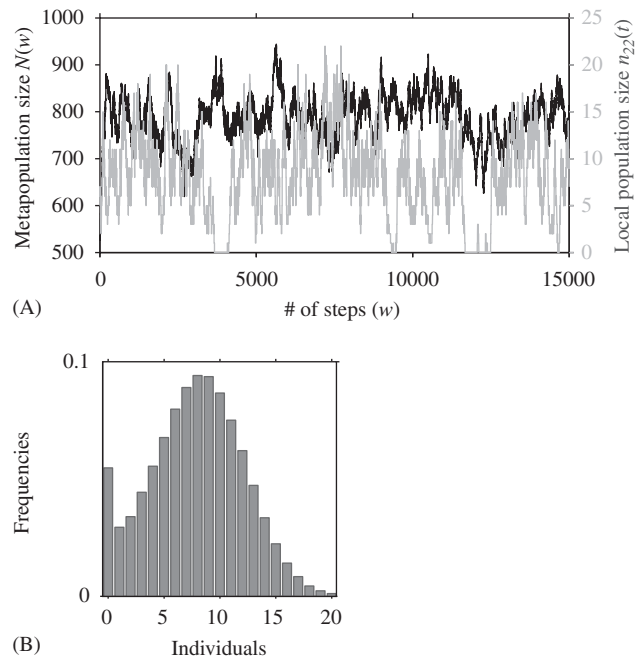


Fig. 2. Results from a single realization of the IPS. We initialized each cell of a 10×10 lattice with $n_{xy}(0) = K/2$ individuals $\forall x, y \in \{1, \dots, 10\}$ and simulated over $w = 15000$ steps. The dispersal mechanism is Von Neumann under periodic border conditions (see text for details). Parameter values are $\beta = 0.2$, $K = 10$, $\gamma = 0.001$, $a = 0.75$, $r = 0.08$, $D = 0.01$. (A) The black line (left axis) represents the metapopulation size $N(w)$ while the gray line (right axis) is the abundance of one of the subpopulations (patch located at row 2, column 2) and (B) the frequency distribution of local abundances.

again. By counting the number of times that any patch is occupied by i individuals ($i = 0, 1, 2, \dots$) at any step during the simulation horizon (with the exception of the initial transient), it is possible to obtain a frequency distribution of local abundances (Fig. 2B). We remark that the shape of this distribution is very similar to the stationary distribution obtained from the spatially implicit model (see again Casagrandi and Gatto, 2002a).

Running stochastic simulations ten thousand times under the same settings (i.e. parameter values, time horizon and initial conditions) as those of Fig. 2 provides us with information regarding the risk of extinction within the chosen time horizon T . The light gray area of Fig. 3 represents the maximum variation of the metapopulation size N at each time step t over the 10 000 simulations: while the total abundance can peak up to almost reach the total carrying capacity of the metapopulation ($K \cdot k^2$), it never falls down to extremely low values. We can thus provisionally conclude that the settings of Fig. 2 describe a persistent metapopulation, although we might wonder whether this would still hold true if we considered a longer time horizon. A clear conclusion can also be reached with the parameter values that give rise to the dark gray area in Fig. 3: over the chosen time horizon the population always becomes extinct, so we can conclude that the risk of extinction is 100%. However, there are a lot of parameter combinations for which the results are more equivocal: in the same figure we show that for a third parameter choice the metapopulation can sometimes persist and sometimes become extinct over the chosen time horizon. Of course, this possible outcome is very well-known and well-described in the literature dealing with Population Viability Analysis (Boyce, 1992; Reed et al., 2002), where a wide range of indices are introduced to evaluate extinction risk and estimate extinction time. However, this outcome is worth being

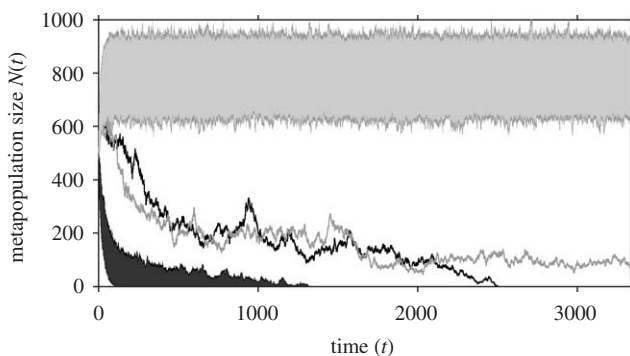


Fig. 3. Risk of metapopulation extinction within a fixed time horizon T for three different parameter settings: the metapopulation never [always] becomes extinct over 10 000 realizations (light [dark] gray area) for $D = 0.01$ [$D = 0.3$]. Two realizations with $r = 0.03$ and $D = 0.005$ give rise to opposite results (intermediate gray lines). All other parameters as in Fig. 2.

contrasted with the behavior of the spatially implicit model. In that case the judgment (persistent vs. extinct) was instead very clear, as the boundary between extinction and persistence was given by the condition $E_0 = 1$. If the metapopulation parameters satisfied the condition $E_0 > 1$ (persistence) the frequency of empty patches (which coincided with the probability that a single patch be empty by the law of large numbers) never went to 1; the opposite was implied by the extinction condition ($E_0 < 1$). We remind the reader that E_0 can be calculated as (see Casagrandi and Gatto, 2002a)

$$E_0 = \sum_{j=1}^{\infty} a \frac{D(j)}{(\mu(j) + D(j))} \cdot \frac{v(1) \cdot v(2) \cdot \dots \cdot v(j-1)}{(\mu(1) + D(1)) \cdot \dots \cdot (\mu(j-1) + D(j-1))}.$$

Given this premise, we may wonder whether comparing persistence–extinction boundaries of spatially implicit models with those of spatially explicit ones is a well-posed problem. In fact, we may definitely doubt that it makes sense to define persistence–extinction boundaries for the IPS we described above. In the next section we will show that this is still possible in a heuristic sense, provided we correctly choose the time horizon over which we define a metapopulation as being persistent or extinct.

3. Persistence–extinction boundaries in the spatially explicit model

From the theoretical viewpoint, the IPS described in the previous section is just a Markov chain. Each state of the chain is identified by an ordered string of k^2 integer numbers, each of which represents the abundance of organisms in each cell. Metapopulation extinction coincides with the state represented by the string of all 0's. General properties of Markov chains can be invoked to explain the model dynamics. The main point is that the IPS consists of two equivalence classes: the null string and the set of all other strings. The null string is a recurrent and absorbing state, i.e. if the Markov chain reaches the extinction state, it will stay there forever. The second property is that extinction is not only a recurrent state, but it is the only recurrent state, all other states being transient: because of density dependence, the birth rates in each cell vanish for large n_{xy} 's and consequently the Markov chain will sooner or later reach the null state, whatever the initial conditions (Karlin, 1966). Therefore, if we consider an infinite time horizon, all metapopulations are bound to extinction. How is it possible, then, to define persistence–extinction boundaries? The fact is that the mean time to extinction may be very long, actually so astronomically long that in

these cases we can regard the metapopulation as persistent from an ecological viewpoint. Thus, if we want to evaluate the persistence–extinction boundaries for real metapopulations we have to consider the stochastic process over an “appropriate” time horizon. Unfortunately, it is hard to tell which horizon is appropriate, since, to our knowledge, no results are available on the average time to extinction of multiple stochastic logistic processes coupled by dispersal.

However, more detailed theoretical results are available for models simpler than the IPS we consider here. In particular, there are many studies concerning two somehow dual situations: the finite contact process (see Durrett, 1992, for a review) and the stochastic logistic model (Nåsell, 2001). In the finite contact process there is a finite number of cells each of which cannot contain more than one individual: each individual can die at a rate μ or send an offspring to a nearby cell at a rate λ . The offspring dies if the nearby cell is already occupied. Conversely, in the stochastic logistic model there is just one cell inhabited by an integer (>1) number of individuals that reproduce and die according to relationships of the kind (2)–(3). The IPS we propose is an extension of both in that it is a spatially explicit dispersal model (like the contact process), but more than one individual can locally interact with others (as in the logistic model).

For the finite contact process it has been shown (see, for example, Durrett and Levin, 1994b) that the expected extinction time is of the order of $(1/\mu)\exp(ck^2)$, with $c > 0$, if the corresponding contact process on an infinite lattice survives. We remind the reader that the infinite contact process survives, i.e. extinction is not reached with probability one from any other state, if and only if the ratio $R_0 = \lambda/\mu$ of the dispersal to the death rate exceeds a certain threshold θ (see, e.g. Durrett and Levin, 1994b; Schinazi, 1999). In fact, the infinite contact process can be regarded as a model of percolation in space–time (Neuhauser, 2001): beyond the threshold the system percolates and this implies the process survival and the population persistence. It is to be remarked that θ must be larger than one, namely the occurrence of percolation requires a natality rate λ that is strictly larger than the local mortality rate μ . It has been shown that in the finite contact process the constant c increases with R_0 and vanishes at the survival threshold θ . This result guarantees that even for small values of the lattice size k the average extinction time of a finite contact process is much longer than the average time to local extinction $1/\mu$ whenever the corresponding infinite contact process survives ($R_0 > \theta$). On the contrary, the average extinction time is comparable to the time to local extinction if $R_0 < \theta$. Therefore, we can define a finite contact process as persistent whenever it persists on a time-scale that is finite, but much longer than $1/\mu$.

As for the stochastic logistic model, according to Nåsell (2001) its study goes back to Feller (1939); however, approximations for the mean time to extinction have been determined only recently (Nåsell, 1996; Andersson and Djehiche, 1998; Nåsell, 2001; Ovaskainen, 2001). In particular, Nåsell (2001) showed that the mean time to extinction starting from quasi-stationarity (that is, the distribution of local abundance conditional on non-extinction) increases exponentially with the carrying capacity K and scales as $1/r$ if the corresponding deterministic model corresponds to a viable population, namely if $r = v(0) - \mu(0) > 0$. We remind the reader that in the deterministic logistic model the time constant associated with the carrying capacity (the equilibrium for the system) is exactly $1/r$. Nåsell's (2001) result guarantees that even for small values of K the average extinction time of a stochastic logistic population is much longer than $1/r$ whenever the corresponding deterministic population survives ($v(0)/\mu(0) > 1$). If we did not know the condition for persistence ($v(0)/\mu(0) > 1$), we could establish it empirically by running several simulations for each value of v/μ over a time horizon that is much longer than $1/r$, while recording the number of times the population becomes extinct. For $v(0)/\mu(0) > 1$ the percentage of extinctions is very low.

Although theoretical results for the IPS we consider in the present paper are not available, the model can be seen as a spatially explicit version of the logistic process or, alternatively, as a logistic version of the contact process. Thus, we can guess from the properties we just stated that quite likely there should be a boundary of the parameter space along which there is percolation in the IPS from extinction to persistence. Along this boundary the mean time to global extinction switches from being relatively short to being much longer than the mean time to local extinction, which can be measured in units of $1/r$. Stated otherwise, if we consider a time horizon T much larger than the time to local extinction, yet not astronomical, the probability e_T of global extinction within time T should rapidly change from 1 to less than 1 along the boundary. In fact, this is actually what occurs, as shown in Fig. 4, where we evaluate the frequency \widehat{e}_T of extinctions out of 1000 realizations over a time horizon $T = 100/r$ as a function of the intrinsic rate of increase r . The frequency $\widehat{e}_{100/r}$ rapidly decreases from 1 to 0 while increasing r by only 10% of its value. By contrast, the number of successful colonizers E_0 , which is the most relevant indicator for persistence in the corresponding spatially implicit model with discrete individuals increases very smoothly with r . Note that persistence of the IPS requires values of E_0 well above unity (see again Fig. 4, right axis). This result is somehow similar to the condition that R_0 must be well above unity in the contact process. However, in the contact process there is a threshold θ , such that the

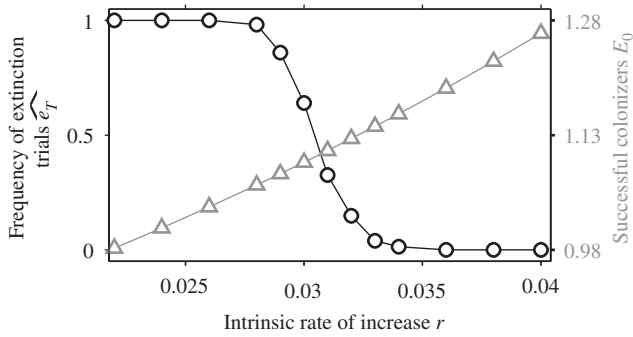


Fig. 4. The frequency \widehat{e}_T of extinctions out of one thousand realizations (circles, left axis) as a function of the intrinsic rate of increase r . We use a 10×10 lattice and we simulate the IPS over a time horizon $T = 100/r$. Each of the open triangles (right axis) represents the number of successful colonizers E_0 evaluated with the Markovian model described in Casagrandi and Gatto (2002a). Parameter values as in Fig. 2, except for $D = 0.065$.

condition $R_0 > \theta > 1$ guarantees percolation in space–time from extinction to persistence. Instead, it looks like there is no such a threshold for E_0 in the IPS: in fact, our calculations show that E_0 is not constant along the persistence–extinction boundaries. Thus, there must be determinants other than E_0 alone that cause extinction in space-explicit metapopulations with discrete individuals and finite number of patches.

We can then heuristically conclude that, in order to identify the persistence–extinction manifold in a more-than-one-dimensional parameter space, one can in principle use the following procedure:

- Set up a grid in the parameter space of the model.
- For each node of the grid run several stochastic simulations starting from given initial conditions for a number w of time steps, such that $T = w\Delta t$ is much larger than $1/r$.
- Record the number of times the realizations of the birth–death–dispersal process result in a persistent metapopulation ($N(T) > 0$) or in global extinction ($N(\tilde{t}) = 0$ with $\tilde{t} \leq T$).
- Estimate the extinction risk e_T of the metapopulation as the frequency \widehat{e}_T of extinctions evaluated from the set of realizations. For example, repeating ten 10000 times the simulation of Fig. 3 characterized by $r = 0.03$, for which $T = 100/r \cong 3333$, one obtains 4455 extinctions. Thus a reasonable extinction risk for that parameter setting can be 0.4455.
- By establishing a risk threshold below which the metapopulation is considered to be persistent it is finally possible to find out what we term *persistence–extinction boundary*.

Of course, deciding which threshold value is the most appropriate in the metapopulation context is debatable.

A risk of extinction in the order of 20%, for example, can be considered as very low by a real-estate developer or be seen as unacceptably high by a conservation biologist. From an ecological perspective, though, we think that it is more convenient to select parameter values such that \widehat{e}_T is small ($\leq 10\%$).

Using the previous method for systematically exploring a parameter space is however a time-consuming task. Just to give an idea of the high computational effort required to evaluate the extinction risk as proposed above, the 10000 simulations just mentioned have required a few hours of intensive computations on a dedicated workstation. Even if one grids the parameter space very coarsely and reduces the number of simulations, the time required for the analysis is enormous. To overcome this problem is not difficult, however, if we realize that there are regions of the parameter space where we can establish persistence or extinction with a very high confidence without running so many simulations. In fact, to this end we can use a sequential probability ratio test (SPRT, see Hoel, 1971) where we contrast an extinction hypothesis H_0 (extinction probability $e_T = \xi_0$) against a persistence hypothesis H_1 ($e_T = \xi_1 < \xi_0$). The SPRT requires also that one sets acceptable thresholds for the hypothesis testing errors, which can be of two types: the type I error ε_I , which represents the probability of rejecting H_0 when it is true, and the type II error ε_{II} , which is the probability of accepting H_0 when it is false. After m simulations that result in d_m persistent populations, one has simply to evaluate the likelihood ratio

$$\chi = \frac{(1 - \xi_1)^{d_m} \cdot \xi_1^{m-d_m}}{(1 - \xi_0)^{d_m} \cdot \xi_0^{m-d_m}}.$$

It is then possible to decide trial after trial if H_0 holds [$\chi \leq \varepsilon_{II}/(1 - \varepsilon_I)$] or H_1 holds [$\chi \geq (1 - \varepsilon_{II})/\varepsilon_I$], or another realization of the process is needed. In this way, only a minimum number of simulations has to be run, namely the one required to reach a decision with a given degree of confidence. Although, one does not a priori know the exact number of simulations that must be run, (but some estimates of the average number of runs are possible, see again Hoel, 1971, for details) it is intuitive that for parameter values well within the extinction [persistence] region only a few simulations are required to establish that H_0 [H_1] holds. It is only in the proximity of the persistence–extinction boundary that the number of simulations can be quite large. We will see that using the SPRT allowed us to keep the computational effort within reasonable limits. As we do not want to risk underestimating the extinction region, we will safely use the values $\xi_0 = 0.2$ and $\xi_1 = 0$ for the alternative hypotheses and the values $\varepsilon_I = 0.05$ and $\varepsilon_{II} = 0.1$ for the errors.

4. Results

Although there are several parameters in the model, we restrict our attention to r , the main parameter describing local demography, and D , the main parameter describing the connection among patches. We fix the other parameters and find the persistence–extinction boundary in the plane (D, r) . The boundaries for the IPS, evaluated according to the method described in the previous section, are presented in Fig. 5 together with the frontier obtained with the spatially implicitly model (Casagrandi and Gatto, 2002a). Technically, for any fixed value D^* of the dispersal we searched for the growth rates $r^* = r^*(D^*)$ that discriminated between extinction (H_0 is true) and persistence (H_1 is true) using a bisection method. In order to mitigate the random effects, we decided to replicate this procedure ten times and to average the results (standard deviations for each boundary point are shown as error bars in Fig. 5B). Before discussing the quantitative differences between the curves of Fig. 5 obtained under different assumptions for the dispersal mechanism and border conditions, it is important to emphasize that the intermediate dispersal principle found with the spatially implicit model—i.e. that too low or too high dispersal rates are detrimental to metapopulation persistence—still holds for the spatially explicit IPS. This equivalence might seem obvious to the casual reader who is however reminded that obtaining contradictory results between explicit and implicit spatial models for the same phenomenon can be the rule rather than the exception in population dynamics (Durrett and Levin, 1994a).

More specifically, in panel A of Fig. 5 we present the effect of different dispersal kernels on the persistence–extinction boundary of a rather large metapopulation, inhabiting a 30×30 lattice. As expected, larger extinction regions are obtained, *ceteris paribus*, with shorter dispersal distances (we remind the reader that extinction occurs below the boundary). It is interesting to notice that for a population with a rather large number of patches the boundary corresponding to the propagule rain dispersal mechanism is very close, even quantitatively, to the bifurcation curve of the spatially implicit model ($E_0 = 1$, dotted line). The effects of the border conditions are shown in panel B of Fig. 5 for a quite small metapopulation, living in a 6×6 lattice, in which we use the Von Neumann dispersal rule. Absorbing borders correspond to the largest extinction region. In fact, the probability for an individual to move out of the suitable metapopulation habitat is greater than with the other two border conditions. Less evident is the reason why the persistence region obtained with reflecting borders is smaller than the one calculated with periodic border conditions. The simplest explanation is that the latter case implies the destruction of the spatial correlations between local abundances of adjacent

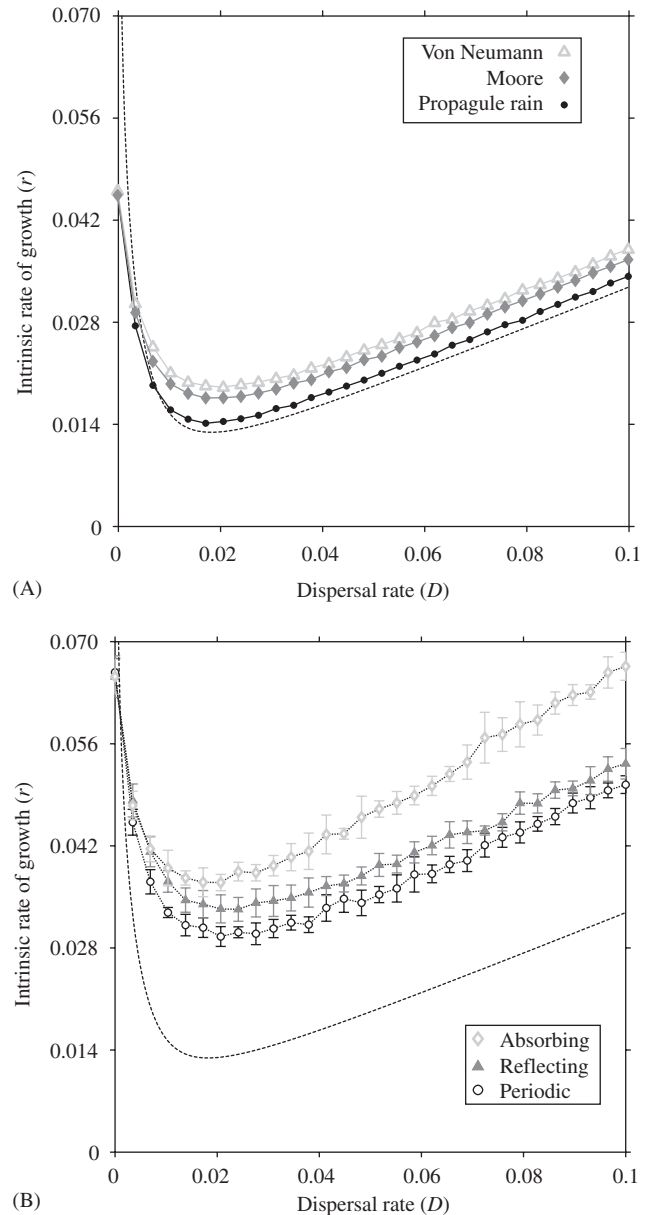


Fig. 5. Persistence–extinction boundaries of the IPS in parameter space (D, r) . The area above the boundaries indicates metapopulation persistence. The algorithm used to obtain the boundaries for the IPS is the Sequential Probability Ratio Test described in the text. As a reference, the boundary obtained via the criterion $E_0 = 1$ with the Markovian model is also plotted (dots). (A) The effect of three different dispersal mechanisms (Von Neumann, Moore and Propagule rain) on the persistence–extinction boundary in a 30×30 IPS with periodic borders. (B) The effect of the border conditions (absorbing, reflecting and periodic) on the persistence–extinction boundary of a 6×6 IPS with Von Neumann dispersal. All other parameters as in Fig. 2.

subpopulations at the borders, a factor that enhances persistence.

Apart from a modelling viewpoint, the results presented here need proper interpretation in ecological terms. In particular, the meaning and significance of the extinction and persistence regions must be clarified.

Each of the points in parameter space (D , r) can be viewed as a particular species living in the fragmented landscape under study. Fig. 5 can be viewed as a summary of the possible loss of biodiversity of the community being analysed, but a few remarks are necessary to correctly understand it. First of all, the fate of each species is considered independently of that of the others (we remind the reader that we deal here with single species metapopulation models). Therefore, the species being assessed for the risk of extinction must have weak trophic and/or competitive interactions among them. Moreover, note that the persistence–extinction boundary is obtained for species that have the same K , β and a . Thus, the analysis holds for a community of species characterized by (a) comparable carrying capacities (for instance, because they have similar body sizes for which the allometric relationships with K are well documented, e.g. in Peters, 1983); (b) similar variances of the birth and death processes at the local scale (such a variance does indeed correlate with $v_0 + \mu_0 = \beta$, see Lande et al., 2003 for details); (c) similar colonizing ability (for instance, because the species belong to the same taxonomic group).

Examples that satisfy these conditions may be provided by guilds of birds or amphibians inhabiting a certain geographic area with rather distinct trophic niches and similar body sizes. If we assume that D and r are more or less uniformly distributed within the guild, the area of the extinction region of Fig. 5 is an indicator of the number of species doomed to extinction in a fragmented habitat. Our analysis makes it possible to identify the main underlying cause of extinction for every endangered species. This is clarified in Fig. 6. Species belonging to the black area would be driven anyway to extinction by low reproduction rate or by demographic stochasticity (Casagrandi and Gatto, 1999, 2002a). Instead, the species included in the gray area P of Fig. 6 are condemned because the landscape is composed by a finite number $z = k^2$ of patches. Their fate is correctly assessed by our model because we consider a more realistic, spatially explicit description of the habitat (the “explicit space” effect) instead of the typical Levins-like assumption of an infinite network of identical patches. Of course, all other conditions being equal, the species characterized by short dispersal distances are expected to be at disadvantage compared to those that can disperse farther. Such a dispersal kernel effect, which determines the extinction for the species whose parameters are in region P' of Fig. 6, can however be weak (region P' is rather small), especially when the metapopulation is composed by just a few patches. In contrast, conditions at the lattice borders can play an important role. The so-called “edge effect” (Saunders et al., 1991) can be very detrimental to the species persistence, particularly for small lattices: species lost because of border effect have parameters

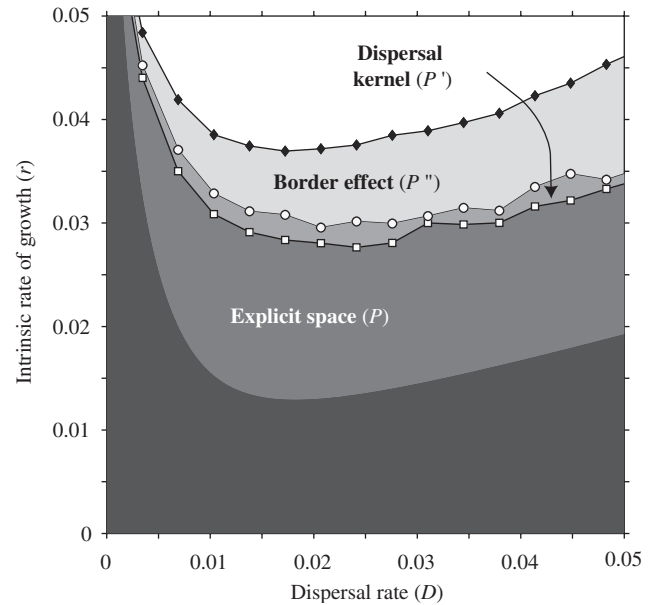


Fig. 6. The underlying ecological causes of extinction for different metapopulation species in a hypothetical habitat composed by 6×6 patches. The line separating the black region from the dark gray region is the boundary $E_0 = 1$ from the spatially implicit model. All other lines are obtained with the IPS under different dispersal mechanisms and border rules: propagule rain and periodic border conditions (white squares), Von Neumann dispersal and periodic border conditions (white circles), Von Neumann dispersal and absorbing border conditions (black diamonds). Unspecified parameter values as in Fig. 5.

belonging to region P'' which is indeed rather large in Fig. 6.

The number $z = k^2$ of suitable habitat patches influences the number of persistent metapopulations in a given landscape. Obviously, the higher z the higher the chance of persistence. For instance, contrast the boundary of panel 5A obtained with Von Neumann dispersal rules on a periodic lattice composed by $z = 900$ patches with the boundary of panel 5B obtained under the same settings, but $z = 36$. The area of the region comprised between the actual persistence boundary and the space-implicit model boundary is much larger in the latter case. Let $A(z)$ be this area in a lattice with z patches. One may ask, then, if there exists any scaling law that relates the area A (which is an indicator of the species lost in a finite landscape) with the lattice size z . Intriguingly, the answer is positive at least for small z 's. The quantity we use to show that such a scaling does exist is the normalized $A(z)$, that is $A^*(z) = A(z)/A_{tot}$ where A_{tot} is the total area of the parameter space under consideration. Since r cannot exceed β for biological reasons (as $\mu(0)$ in Eq. (3) must be nonnegative), we restricted our analysis to a square parametric region where r and D both vary between $10^{-2}\beta$ and β . Note that, from an ecological viewpoint, $A^*(z)$ is important as it represents the proportion of species that are lost

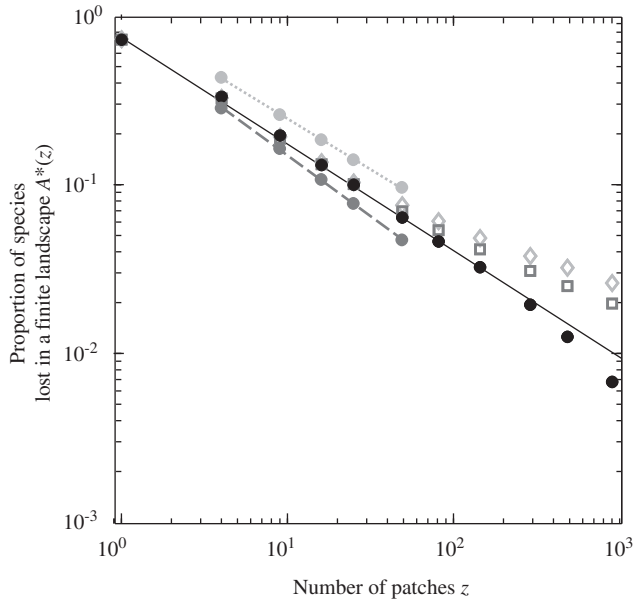


Fig. 7. The proportion of species $A^*(z)$ that are lost because the landscape is composed by less than infinite fragments is plotted against the number of patches z (bilogarithmic scale). We show the three cases with periodic border conditions of propagule rain (black circles), Moore (squares) and Von Neumann (diamonds) dispersal. The solid line is the least-squares fit to the propagule rain data for small z 's; its equation is $A^*(z) \cong 0.74z^{-0.65}$. Parameter values as in Fig. 5. The dotted and dashed lines, whose exponents are -0.60 and -0.72 , respectively, are obtained with the same settings as above but $K = 8$ and 12 .

because the habitat is composed by z patches, and not by an infinite network of patches as in spatially implicit modelling. Fig. 7 makes evident that, regardless of the details concerning the dispersal mechanism, $A^*(z)$ can indeed be very satisfactorily approximated by a power law $A^*(z) = A^*(1)z^{-c}$ for relatively small z 's (at least up to $z = 11^2 = 121$ in our example). Deviations from the scaling law for larger z 's have different convexity depending upon the fact that dispersal operates as a propagule rain or with a dispersal kernel. However, A^* is relatively small ($< 10\%$) for these large z 's. The power law describing how A^* scales with z obviously depends also on parameter values other than r and D . However, those perturbations do not dramatically change the overall picture. In particular, changes in K , as shown in Fig. 7, have a relatively slight influence on the slope c of the scaling law.

5. Conclusion

In this paper, we introduce an interacting particle system (IPS) to discuss the fate of single species metapopulations. At the local scale, demography is assumed to be logistic in a stochastic sense. The individuals, counted as integer numbers, are supposed to

move at random with a density-independent temporal rate D among the equal patches that compose the landscape (a square lattice) according to various rules, characterized by different dispersal distances and border mechanisms.

In our previous studies, which dealt with space-implicit models described by differential equations, we discussed the conditions for metapopulation persistence through analytic criteria (Casagrandi and Gatto, 2002a) or numerical continuation techniques for bifurcations (Casagrandi and Gatto, 2002b). Here, the nature of the model we use leads us to introduce a heuristic method, based on a sequential probability ratio test, to determine the persistence–extinction boundaries as space–time percolation thresholds in any relevant parameter space of the model. The manifolds obtained with that method show that the intermediate dispersal principle is robust to the introduction of explicit space into the model metapopulations.

As an important bridge between the spatially implicit and explicit approaches, we find that there exists a power law

$$A^* \propto z^{-c} \text{ with } c < 1 \tag{6}$$

which relates the proportion of species that can be lost in a habitat composed by few fragments to the number of remaining patches. There are some practical implications of the power law. Suppose we want to salvage some species by restoring patches of habitat that were destroyed. Let A_∞^* be the fraction of species that would be lost even in an infinite network of patches, represented by the area below the persistence–extinction boundary $E_0 = 1$ of the spatially implicit model. Then the fraction A_{pers}^* of species persisting as metapopulations in finite habitats with z patches is given by

$$A_{pers}^*(z) = 1 - A_\infty^* - A^*(z)$$

The advantage of adding a new patch can be roughly estimated as the increase of the fraction of persisting metapopulations, namely $A_{pers}^*(z+1) - A_{pers}^*(z) = A^*(z) - A^*(z+1)$. For not too small z 's, this advantage can be further approximated with the derivative

$$\frac{dA_{pers}^*}{dz} = -\frac{dA^*}{dz} \propto cz^{-(c+1)}.$$

As it is intuitive, the effectiveness in terms of the proportion of salvaged species is much stronger for small than for large z 's. However, the previous relationship suggests that it decreases less than the inverse of the square of the number of patches.

Seen from the opposite viewpoint, the power law (6) also allows the evaluation of the ecological cost of destroying a patch, i.e. $A_{pers}^*(z) - A_{pers}^*(z-1)$. For instance, we evaluate that for metapopulations with each patch holding 10 individuals, the loss of one patch at $z = 5$ would cost the loss of about 4% of the total

number of species, at $z = 10$ the loss of about 1% and at $z = 15$ the loss of about 0.6%. In a scenario where the fragmentation and the subsequent loss of habitat fragments due to landscape destruction is increasing at impressive temporal rates, it is certainly important to give at least some very rough estimate of how many species are going to be condemned by the action of man on the structure of our earth landscapes. As pointed out by Tilman et al. (1994), the majority of extinctions will not occur immediately, but rather a long time after habitat loss. In our approach we select the appropriate time-scale on which fragmented population can be considered as persistent in the long run. Obviously, more realistic descriptions of ecosystem functioning and structure should be considered to draw conclusions for specific cases. Ours is a first step towards establishing a correct methodology with which we can evaluate the “extinction debt” faced by our planet.

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