

Sustainability without coexistence state in Durrett–Levin hawk–dove model

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Abstract Models that explain the sustainability of an exploiter–victim ecosystem admit, generally, a coexistence state of both species in the well-mixed limit. Even if this state is unstable, the extinction-prone system may acquire stability on spatial domains where different patches oscillate incoherently around the coexistence state. New experiments, however, suggest that a spatially segregated system may be stable even in the absence of such a coexistence state. Here we revisit the hawk–dove (case 3) model of Durrett and Levin, which has been shown to support persistent population for system of interacting particles. It turns out that this model does not admit a (stable or unstable) coexistence state on a single habitat. We analyze the peculiar mechanism that leads to persistence in this case and the role of demographic stochasticity with and without self-interaction, using numerical simulations and exact solutions in the infinite diffusion limit.

Keywords Sustainability · Population dynamics · Demographic stochasticity · Self-interaction · Victim–exploiter systems · Metapopulation

Introduction

The analysis of ecosystems and their stability is done using a variety of modeling techniques. In their landmark paper, Durrett and Levin (DL; Durrett and Levin

1994a) identify four approaches for the modeling. The simplest approach neglects both spatial effects and the discreteness of individuals (demographic stochasticity); thus, the system is described by a set of ordinary differential equations describing the deterministic time evolution of a “density” which is associated with the average number of individuals. The condition for persistence is then associated with the existence of an attractive manifold for the set of ODEs, like an attractive fixed point, limit cycle, or a strange attractor.

If the spatial structure is taken into account but the model is still deterministic (individuals are infinitesimal), one arrives at a system of partial differential equations, which in most cases takes a reaction–diffusion–advection form. Patch models, on the other hand, deal with discrete individuals without spatial structure and are subject to demographic stochasticity. Finally, an interacting particle system (IPS) is a model including both spatial effects and the stochasticity associated with the discreteness of individuals.

When the non-spatial, deterministic system of ODEs supports an attractive coexistence fixed point, the effect of stochasticity that appears in IPSs is relatively well understood. Demographic fluctuations may lead to extinction of the colony, but the chance of extinction decreases exponentially with the number of individuals at the steady state (see e.g., Kamenev and Meerson 2008; Kessler and Shnerb 2007) and references therein. Typically the size of demographic fluctuations scales like $1/\sqrt{N}$, where N is the number of individuals at the steady state. On spatial domains, demographic stochasticity is controlled by the effective N , which depends on both the carrying capacity of a site and the migration rate (Kessler and Shnerb 2008). If the migration among sites is weak, local extinctions may accumulate to yield

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global extinction even on an infinite domain, but at higher dispersal rates, the system is stable (Hanski and Gilpin 1997; Durrett and Levin 1994b; Snyder and Nisbet 2000; Barkham and Hance 1982). Migration, thus, increases the persistence time of a system that admits a stable equilibrium since it suppressed fluctuations and reduces local competition. It may hurt sustainability only in the presence of migration cost, either direct (increased mortality during dispersal; Casagrandi and Gatto 2002, 2006) or indirect (movement from source to sink or, in general, into less favorable habitats; Cantrell and Cosner 2003; Amarasekare 2004; Hastings 1983; Kessler and Sander 2009).

Some deterministic models that do not support a coexistence fixed point still admit other attractive manifolds, like a limit cycle or chaotic attractor (Wilson and Abrams 2005; Abrams and Holt 2002; Armstrong and McGehee 1980). The effect of demographic stochasticity on the extinction rate in these cases is also exponentially small, where now N should be taken as the minimal number of agents along the deterministic trajectory (Kessler and Shnerb 2010; McKane and Newman 2005). This holds unless the stable manifold is “excitable” and the system undergoes long excursions under weak perturbations (Ben Zion et al. 2010).

In this paper, we focus on the other extreme, the case where the deterministic non-spatial system is extinction prone and its sustainability is acquired via the interplay between spatial structure and stochasticity. This possibility was demonstrated by Durrett and Levin in their third, hawk–dove case. Here we intend to analyze this model in detail and reveal the underlying mechanism that leads to persistence. An interesting peculiarity of the DL system is the absence of coexistence manifold. This has to do with the results of some recent experiments that study the effect of spatial structure on sustainability in laboratory microcosms.

As a concrete example, let us focus on the work of Holyoak and Lawler (1996). These authors used a predator–prey pair (*Didinium nasutum* and *Colpidium* cf. *striatum*). In an undivided habitat of 270-mL bottle, one of the species always goes extinct, and this of course is also true in a single 30-mL bottle. However, in a microcosm made of an array of nine 30-mL bottles interconnected by tubes, the system persisted for 130 days (hundreds of generations), after which the experiment ended.

Now let us imagine a similar setup where the rate of migration via the interconnecting tubes is a free parameter (say, one can change the tubes’ radius). If the migration rate is much faster than any other rate in the system, one effectively gets a single large bottle and the system goes extinct. The same is true when the

migration rate is zero, where the microcosm becomes a collection of nine isolated small bottles. Only for intermediate migration rates is persistence possible. The system is thus extinction prone in the well-mixed limit (no attractive fixed point) and acquires stability due to spatial structure. It is hard to imagine that migration cost (e.g., death of individuals caused by their movement, as in Casagrandi and Gatto (2002, 2006)) plays any role for these sub-millimeter protists. As the migration rate increases, the deterministic non-spatial approximation becomes better; thus, the system goes extinct.

Similar results have been reported in many recent experiments (Kerr et al. 2002, 2006; Dey and Joshi 2006; Ellner et al. 2001; Molofsky and Ferdy 2005) for both single species, predator–prey, and host–parasitoid dynamics. The results imply that in a *well-mixed* case, i.e., when the migration rate is large enough to wipe out the spatial structure, the population reaches extinction within relatively short time scales. As migration rate decreases, the population density starts to display space (or space–time) modulations, and in this regime, its lifetime peaked. Reducing the migration rate even further, one encounters another extinction regime, where the system effectively segregated to small patches and the “rescue effect” (recolonization of vacant habitat patches) is diminished. The general picture emerging is that of a “sustainability window” at intermediate levels of movement among patches, while the population goes extinct rapidly if the migration rate is too large (Earn et al. 2000) or too small (Mobilier et al. 2006), and the sustainability is peaked at intermediate migration (Ben Zion et al. 2010).

To explain these features, several theoretical frameworks have been suggested (Murdoch et al. 1992; Murdoch and Oaten 1975; Hassell and May 1988; Crowley 1981; Reeve 1990; Jansen and de Roos 2000; Jansen and Sigmund 1998; Janssen 1981; Reichenbach et al. 2007; Abta et al. 2007, 2008; Earn et al. 2000; Earn and Levin 2006; Briggs and Hoopes 2004; Adler 1993; Keeling et al. 2000). All these models assume that the ODEs describing the well-mixed system support an *unstable* coexistence fixed point. As pointed out by Nicholson (1933) and as suggested by almost all the classical models, an inherent feature of this instability is that population overshoot leads to growing oscillations around the steady state. For example, in a predator–prey system at the fixed point, the demographic losses of the prey population due to predation are balanced exactly by reproduction (birth events). Excess predator density will lead to a decrease in the prey population that induces, in turn, a depletion of the predator population. When the predator gets back its steady

state value—after a period of overpredation—the prey density must be in a deficit, so the predator population keep decreasing and so on.

In all the models mentioned above (except of DL), the fact that a well-mixed population is extinction-prone while a spatially segregated community is stable is attributed to these oscillations around the coexistence fixed point. The common feature of all models is the appearance of some mechanism that supports spatial segregation into subdomains that oscillate incoherently; this spatial desynchronization then stabilizes a finite population state. In some cases, the deterministic dynamics itself admits a pattern-forming instability in some range of parameters (Reichenbach et al. 2007; Jansen and de Roos 2000; Jansen and Sigmund 1998; Janssen 1981). In other scenarios, the sustainability is acquired due to the interplay between the deterministic dynamic and the noise (e.g., demographic stochasticity; Abta et al. 2008; Keeling et al. 2000).

Given this general picture, one may expect (at least in experiments, where the effect of external noise is quite weak) the following occurrences: In a well-mixed system, population oscillations grow in time until extinction is reached, while with spatial segregation, the overall occupancy of certain species reaches some finite value and fluctuates only slightly around it. However, examining the results of some new experiments (Kerr et al. 2002, 2006; Holyoak and Lawler 1996), one realizes that the well-mixed system (e.g., the 270-mL bottle mentioned above) flows almost directly to extinction, without any salient oscillations. It seems, thus, that the ODEs for the corresponding deterministic do *not* support an unstable steady state with growing oscillations around it. Accordingly, at least in the context of these systems, one cannot use the decoherence-based mechanisms suggested above: All of them fail in the absence of deterministic oscillations close to an unstable manifold.

In view of this puzzle, it is interesting to reexamine the hawk–dove (case 3) model of DL (Durrett and Levin 1994a). In contrast with other studies, this models does not support any finite population state, either stable or unstable, in the well-mixed phase. Technically, all the trajectories of a single-patch deterministic dynamics end up at extinction and oscillations are prohibited; there are no (stable or unstable) fixed points or limit cycles of any kind. Sustainability, thus, is related to the emergence of a new type of trajectories, due to the combination of spatial structure and the effect of stochasticity. In the following, this mechanism will be analyzed and demonstrated via numerical simulations. The Durrett–Levin system goes extinct without any oscillations when the system admits no spatial structure

but may persist forever as a metapopulation, i.e., on a subdivided habitat.

The model of Durrett and Levin is somewhat special: It assumes no linear term for the growth rate of both species, and the per-capita birth rate is singular at the origin. In most of the population dynamics models (unlike evolutionary game theory models, from which Durrett–Levin have been inspired), at least one species admits a fixed, frequency independent per capita growth rate. Another peculiarity of the model is that it allows for self-interactions; without self interactions, the results change substantially, as will be discussed below.

In view of these unique properties of the model, it should be stressed that we are not trying to relate it directly to empirical results or to claim that it should be considered as the only reasonable model in population dynamics. The aim of this paper is to analyze the stability mechanism of the hawk–dove case and to explain how spatial sustainability may emerge, in principle, without oscillation in the well-mixed limit. We do suggest that similar mechanism may manifest itself in other systems, including those admitting frequency-independent growth rate term.

In the following section, we will survey the properties of the hawk–dove model in its deterministic limit, showing that it is indeed extinction prone and that no coexistence manifold exists, neither stable nor unstable. In the third section, the spatial deterministic version and the stochastic patch model dynamics are shown to go extinct also, so the only scenario that will yield persistent population is the IPS, as already argued by DL. In “[Neighborhood interactions and self-interactions](#)” section, the infinite diffusion limit is analyzed with and without self-interaction, and finally, we conclude with a short discussion.

The hawk–dove model and its deterministic dynamics

The model of Durrett and Levin incorporates elements from the evolutionary game theory with “traditional” victim–exploiter dynamics. It describes the interaction between two species or two strategies, “hawks” and “doves”. When two agents interact, the profits, or the losses to an individual, are given by the payoff matrix:

	<i>H</i>	<i>D</i>
<i>H</i>	<i>a</i>	<i>b</i>
<i>D</i>	<i>c</i>	<i>d</i>

For example, when two hawks encounter each other, any of them “wins” or “loses” *a*, while upon interaction between hawk and dove, the hawk gets *b* and the dove

acquires c . Specifically for DL case 3, the parameters chosen and used hereon were $a = -0.6$, $b = 0.9$, $c = -0.9$, and $d = 0.7$. This payoff matrix resembles the situation known as the prisoner's dilemma: If the players have to choose together a strategy, it will be better for both to play dove. This state, however, is not a Nash equilibrium (i.e., is not evolutionary stable) as in such a case it is beneficial for a single player to switch to the hawk strategy. The only ESS is for both players to play hawk.

The model does not allow, though, for individuals to use rational reasoning and to switch strategies. Instead, the fitness, or the fecundity, of agents is determined by their payoff. If the system is well mixed and contains H hawks and D doves (H and D are integers), the total payoff for, say, a hawk is proportional to its chance to play against another hawk (this chance is the fraction of the hawks in the population, $H/(H + D)$) multiplied by the payoff a plus the corresponding term for the case of encountering a dove, i.e.,

$$\begin{aligned} \text{hawk payoff} &= aH/(H + D) + bD/(H + D) \\ \text{dove payoff} &= cH/(H + D) + dD/(H + D). \end{aligned} \quad (1)$$

To get the deterministic dynamics of the system, neglecting the effects of demographic stochasticity, one replaces the integers H and D by the hawk density u and the dove density v . The well-mixed deterministic dynamics is given by the pair of nonlinear equations:

$$\begin{aligned} \frac{du}{dt} &= u \left(\frac{au}{u+v} + \frac{bv}{u+v} - \kappa(u+v) \right) \\ \frac{dv}{dt} &= v \left(\frac{cu}{u+v} + \frac{dv}{u+v} - \kappa(u+v) \right), \end{aligned} \quad (2)$$

where the κ term sets an upper bound for the size of the population, i.e., its carrying capacity.

Unlike evolutionary games, where the population size is kept fixed and a successful strategy dominates the population, here the total number of agents changes along time. While the basic interactions of this hawk–dove case are very similar to those that appear in a predator–prey model, Durrett and Levin have pointed out that the dynamics described by Eq. 2 leads inevitably to the extinction of both species: The hawks “consume” the doves then went extinct in the absence of food. This feature is demonstrated in Fig. 1, where the flow lines that correspond to the time evolution (Eq. 2) are plotted in the u, v plane.

One may wonder if the phase portrait contains also an unstable fixed point. The almost periodic trajectory in the lower-left corner of Fig. 1 seems to encircle such a point. In fact there is no coexistence fixed point. The best way to realize that is to look at the u nullcline

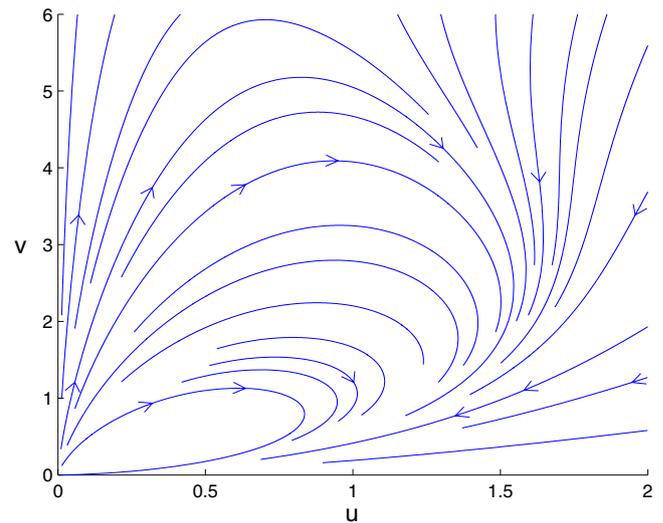


Fig. 1 Flowlines of the deterministic dynamics that correspond to Eq. 2. The values of the parameters are $a = -0.6$, $b = 0.9$, $c = -0.9$, and $d = 0.7$. Here $\kappa = 0.08$

of this model, shown in Fig. 2. Along this line, $\kappa(u + v)^2 = au + bv$; plugging this into the equation for v one finds that, for these model parameters, \dot{v} is negative along the u nullcline. The u and the v nullclines never cross each other: All trajectories cross the v nullcline rightward and the u nullcline downward; thus, all trajectories eventually are “trapped” below the u -cline and reach zero asymptotically along the line $v = Au^{c/a}$, where A is an arbitrary constant. The deterministic dynamics is thus extinction prone with no oscillations. The overzealous predators exploit their prey and then

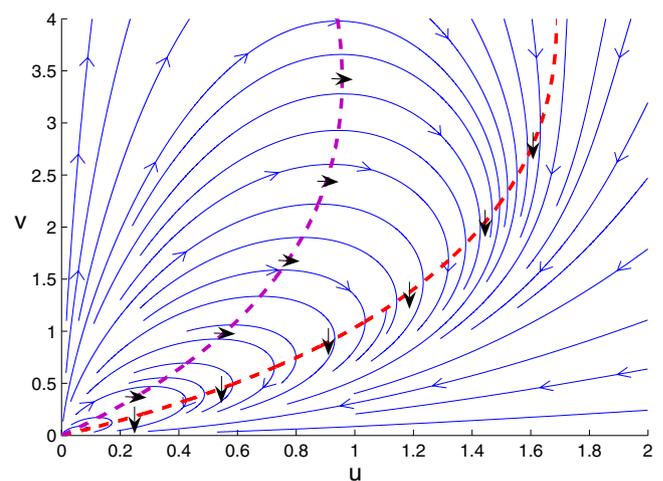


Fig. 2 Same as Fig. 1, where now the u and v nullclines are plotted. The trajectories must cross the u nullcline vertically downward and the v nullcline horizontally rightward; any trajectory that is trapped below the u -cline flows to zero. The only fixed point, where nullclines intersect each other, is at the origin

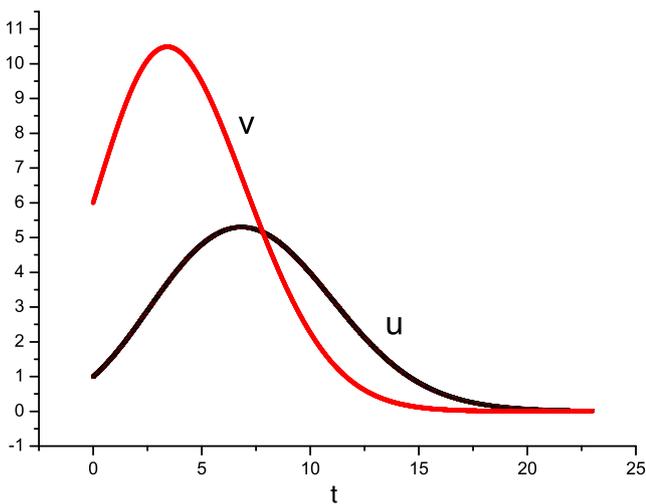


Fig. 3 The time development of the predator density u and the prey density v governed by the deterministic rate Eq. 2. There are no oscillations and both populations flow, after a short transient, toward extinction

go extinct. Figure 3 depicts the time evolution of population densities, where indeed no oscillations occur.

Demographic stochasticity, persistence, and the effect of enrichment

As pointed out by Durrett and Levin, spatial structure per se is not a cure for the system considered here. Figure 4 demonstrates what happens if different spatial patches are connected by density independent migration (diffusion) of the populations. The deterministic equations for a one-dimensional array of patches are:

$$\begin{aligned} \frac{du_m(t)}{dt} &= \mu(-2u_m + u_{m+1} + u_{m-1}) \\ &\quad + u_m \left(\frac{au_m}{u_m + v_m} + \frac{bv_m}{u_m + v_m} - \kappa(u_m + v_m) \right) \\ \frac{dv_m(t)}{dt} &= \mu(-2v_m + v_{m+1} + v_{m-1}) \\ &\quad + v_m \left(\frac{cu_m}{u_m + v_m} + \frac{dv_m}{u_m + v_m} - \kappa(u_m + v_m) \right). \end{aligned} \tag{3}$$

where u_m (v_m) is the hawk (dove) density on the m -th patch and μ is the strength of migration. For the simulation presented below, periodic boundary conditions are assumed.

From Fig. 2, it is clear that an isolated patch below the u -cline may escape extinction if certain external perturbation takes it to a point above this line. If the initial conditions of the spatial system are not uniform,

migration may provisionally supply such a perturbation; thus, a certain patch may take another “round” in the u, v -plane, as depicted in Fig. 4. This behavior, however, is only a transient; in the long run, the system synchronizes since migration negates spatial gradients. In its coherent phase, the system follows a single-patch trajectory to global extinction. Unlike (Reichenbach et al. 2007; Jansen and de Roos 2000; Jansen and Sigmund 1998; Janssen 1981), there is no instability that leads to the formation of permanent spatial pattern in the deterministic (noise free) limit of this hawk–dove model.

We proceed to examine the effects of discreteness. Instead of integrating numerically equations like Eq. 2 or 3, an agent-based numerical procedure is implemented to treat the stochastic dynamics of individual agents on each patch.

Our simulation technique is a generalization of the Gillespie algorithm (Gillespie 1977), adjusted to spatially segregated population. The numbers of hawks and doves on the m -th site are integers denoted by H_m and D_m correspondingly. Given the distribution of individuals at certain time t , the rates of all possible processes are identified. For example, μH_m is total rate of emigration of hawks from the m -th site, while $(aH_m + bD_m)/(D_m + H_m)$ is the total birth rate (if positive) or death rate (if negative) for hawks at this site.

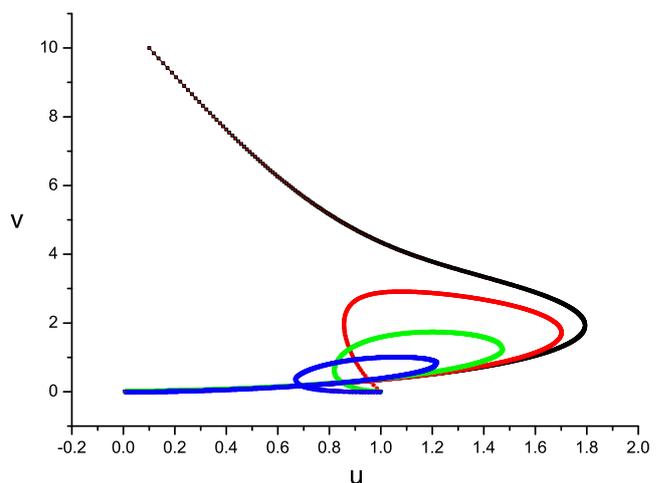


Fig. 4 Hawks vs. doves densities obtained from Euler integration of the deterministic equations (Eq. 3) for a system of ten patches with periodic boundary conditions, $\mu = 1$ and $\kappa = 0.02$. The black line is the trajectory followed by a single patch initiated at $u = 0.1, v = 10$, while the other lines show the path followed by three other patches, all with initial population $u = 1, v = 0.0001$. An isolated patch goes monotonically to extinction from these initial conditions. In the spatial system, instead, the migration from the high population patch causes the flow line of these three patches to cross the u -nullcline, but this is only a transient and the whole system finally went extinct

An elementary Monte Carlo cycle starts with a full list of all rates for all possible events at all sites. An event is then picked randomly by tossing a weighted coin between all possibilities. If this event is, for example, a birth of a dove on the m -th site, the number of doves on that site grows by one unit; the time counter is moved forward according to the Gillespie procedure and the table of event rates is updated before the next elementary step takes place.

Figure 5 demonstrates that discreteness by itself (patch model) is not a stabilizing factor. When the system is well mixed or almost well mixed, the stochastic trajectories either follows the deterministic one or reaches extinction even faster.

The system may survive (Durrett and Levin 1994a) due to the combination of discreteness-induced noise and spatial segregation. If the population on a certain patch goes extinct, it may happen that two doves, but no hawk, will arrive from a neighboring, already active, site. In such a case, the dove population grows on the recolonized patch and reaches a steady state quite fast, then waits for the arrival of an immigrant hawk. If the timescale for recolonization of this kind is smaller than the time to extinction of a single patch, the whole system stays alive. Large spatial systems, thus, do support persisting densities as exemplified in Fig. 6.

This mechanism cannot work in the deterministic limit, or otherwise when the number of animals on a patch is very large (small κ). In such a case, the

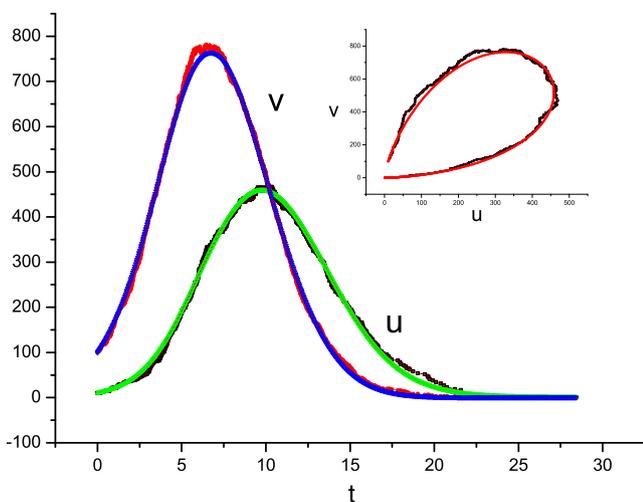


Fig. 5 Dynamics of a single-patch stochastic scenario for $\kappa = 0.0002$. The results of the stochastic process (agent-based simulation, *dots*) are shown together with the deterministic prediction (*lines*) for the same initial conditions. The *main figure* shows the dove and the hawk populations vs. time, and the *inset* is the phase portrait. The stochastic system follows, more or less, the deterministic predictions

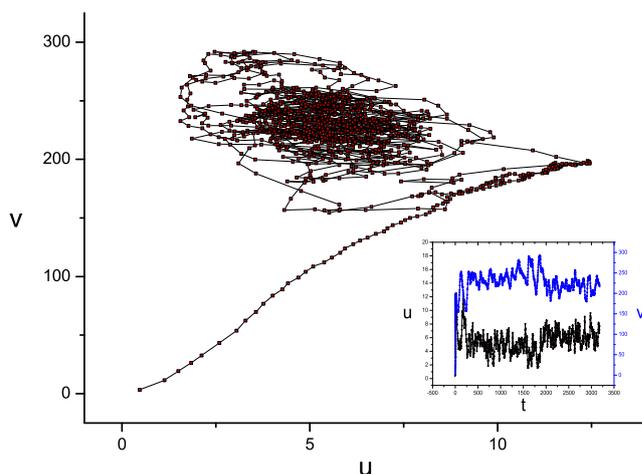


Fig. 6 Phase space trajectory of the total population on 100 patch system, with $\kappa = 0.002$ and $\mu = 0.01$. The average density (number of individuals per site) of hawks (u) and dove (v) is plotted in the u, v -plane (*main*) and for each species vs. time (*inset*). For this set of parameters, the hawk–dove system reaches some equilibrium density with slight perturbations attributed to demographic stochasticity, but none of the species goes extinct

immigration into an empty patch involves almost necessarily both doves and hawks, and the system follows its deterministic dynamics. This surprising feature of the model is emphasized in Fig. 7. Here the lifetime of the metapopulation (time until extinction in the non-sustainable phase) is plotted against the parameter κ that dictates the carrying capacity of a single patch. The fact that large κ (small number of particles per patch) corresponds to shorter lifetimes is sort of trivial—strong demographic stochasticity is known to lead to extinction as the system is trapped into the empty (absorbing) state (Mobilia et al. 2006; Durrett and Levin 1994b; Snyder and Nisbet 2000; Barkham and Hance 1982). The nonmonotonic dependence of the lifetime on κ implies that large number of agents at each patch is also dangerous, as under weak stochasticity the time evolution is governed by the deterministic dynamics that leads to extinction. The maximum persistence regime corresponds to *intermediate* stochasticity, not too small or too large.

This phenomenon may be considered as a strong version of Rosenzweig’s “paradox of enrichment” (Gilpin and Rosenzweig 1972): Here even the increase of carrying capacity for both the victim and the exploiter may lead to extinction since it reduces the relative importance of stochasticity. It is interesting to note that a similar effect has been pointed out by Tilman (1982) for deterministic, competitive exclusion systems, where coexistence occurs in intermediate levels of food supply.

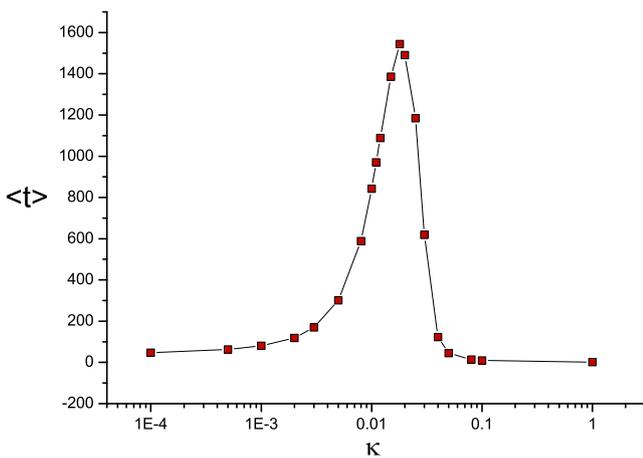


Fig. 7 Time to extinction of spatially extended hawk–dove system (an array of ten patches connected by migration, $\mu = 1$) as a function of κ . Here the size of the system is too small to allow for a real steady state; the average time to extinction $\langle t \rangle$ is plotted vs. κ . The carrying capacity of a site (the maximal number of individuals on a site) is proportional to $1/\kappa$. When the carrying capacity is large (small κ), the system follows its deterministic trajectories and the lifetime is small. When κ is too large, the number of individuals on each site is small and stochasticity leads to local extinctions that accumulate to yield global death. For intermediate values of local carrying capacity, the system reaches its maximal sustainability, as the demographic stochasticity is strong enough to perturb the deterministic flow to extinction, yet too weak to induce high rate of local extinctions. *Squares* represent the results obtained from exact simulations, and the *line* connecting them is just an interpolation to guide the eye

Neighborhood interactions and self-interactions

In relating the analysis presented so far to the original Durrett–Levin hawk–dove model (case 3), two issues must be discussed. First, our system differs from the original model in the definition of the “interaction range” between agents. DL have considered the case where an agent at a certain spatial location interacts not only with members of its local community but also with all agents in some neighborhood of its local habitat. Our analysis allows only for local interactions, but this reflects only the difference in the partition of area into patches: We consider all animals within the interaction range as a single patch. The strong migration (well-mixed) limit is the same in both cases, so up to the rescaling of the inverse carrying capacity parameter κ and the migration rate μ the two modeling approaches are the same.

The second, more subtle issue is the possibility of self-interactions. In the original DL work, as well as in other studies of evolutionary games on spatial domains (Nowak and May 1992), agents were allowed to interact with themselves. This implies that the number of hawks,

say, that interact with a specific hawk is given by the total number of hawks in its neighborhood including this predator itself. As pointed out by Soares and Martinez (2006), this assumption makes sense when each cell of the lattice represents a whole group of individuals interacting among themselves and with other groups as well. With self-interaction, DL showed that the system does support an attractive fixed point in the hydrodynamic limit, a result that has been proven mathematically by Perrut (2000). If, on the other hand, any agent in the game is considered as an individual animal, self-interactions should be avoided. As DL have pointed out, the payoff functions on a site with H hawks and D dove, then take the form,

$$\begin{aligned} \text{hawk payoff} &= a(H - 1)/(H + D - 1) + b D/(H + D - 1) \\ \text{dove payoff} &= cH/(H + D - 1) + d(D - 1)/(H + D - 1). \end{aligned} \tag{4}$$

For a site with no hawk/dove agents, the corresponding payoff for the absent species is defined to be zero (when DL considered the case with no self-interaction, they have added a linear growth term that reflects the reproduction rate of a single hawk/dove. With such a term, the system of ODEs admit a stable manifold, so we have omitted it here).

Given these payoffs, the well-mixed dynamics (on a single site when the corrections due to demographic stochasticity are neglected) is given by

$$\begin{aligned} \frac{du}{dt} &= u \left(\frac{a(u - 1)}{u + v - 1} + \frac{bv}{u + v - 1} - \kappa(u + v - 1) \right) \\ \frac{dv}{dt} &= v \left(\frac{cu}{u + v - 1} + \frac{d(v - 1)}{u + v - 1} - \kappa(u + v - 1) \right). \end{aligned} \tag{5}$$

To compare Eqs. 2 and 5, the phase space trajectories of Eq. 5 are presented in Fig. 8, together with the u and v nullclines. One observes that the general picture is similar: No trajectory crosses the v nullcline leftward or the u nullcline upward, so all the deterministic flows end up at the same point. This point, however, is not the origin but $(0,1)$, i.e., it is the state where the population admits only a single hawk and no dove, in which the dynamics halts.

What happens for the stochastic, spatially segregated system? Let us start by considering the infinite diffusion limit, i.e., the case where the migration rate is so fast that any agent moves into a new random location between two interaction events. Durrett and Levin have developed a mathematical procedure that yields an exact effective deterministic description of the time

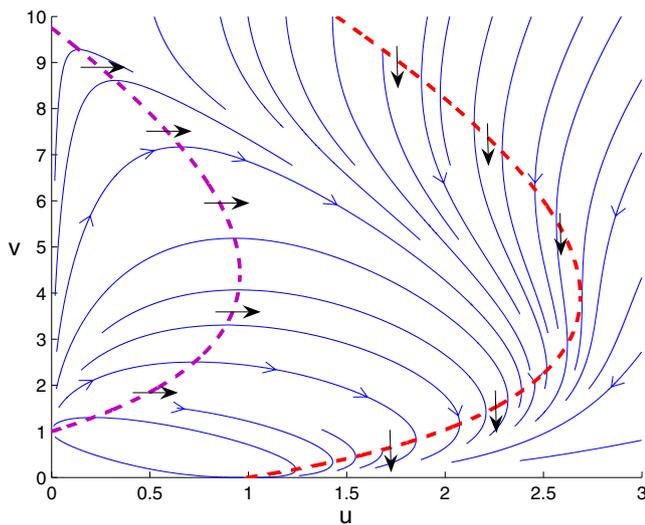


Fig. 8 Phase portrait of a few trajectories of Case 3 without self-interaction (Eq. 5). The dashed lines are the u and the v nullclines

evolution of the average total population. If the average number of hawks/doves per site ($\mathbb{E}[H]$ and $\mathbb{E}[D]$) is given at time t , the chance to find H hawks, say, on a specific site is given by a Poissonian distribution with average $\mathbb{E}[H]$ and the same, mutatis mutandis, holds for the doves. Any payoff term, thus, should be replaced by its average with respect to these two Poissonian distributions. This procedure, the Durrett–Levin transform, has been analyzed in detail by Cantrell and Cosner (2004). It yields exact deterministic equations for the time evolution of the average densities in the limit of infinite number of patches (no correlations between subpopulations) and infinite migration rate.

As noted already by Cantrell and Cosner (2004), in the infinite diffusion limit, there is a difference between the self-interacting and the non-self-interacting scenarios. In the self-interacting case considered originally by Durrett and Levin (1994a), the resulting time evolution for the average densities supports a stable fixed point, while without self-interaction, the system is still extinction prone. In fact, applying the DL transform to Eq. 5, one finds that all constants a, b, c and d are multiplied by the same factor $1 - e^{-s}$, where $s = \mathbb{E}[H] + \mathbb{E}[D]$; thus, the structure of the phase portrait is the same as in Fig. 2 and the only difference is a global rescaling of time. The infinite diffusion limit of DL case 3 without self-interaction is thus again extinction prone. Intuitively, in the infinite diffusion limit, each agent “feels” the average effect of rapidly changing environment; thus, the effective deterministic equations are not affected by the discreteness of individuals. With self-interaction, the situation is different, as the agent

interacts with itself on each patch; thus, its effective environment is different.

Still, for intermediate migration rates (far from that limit, when the rate of migration is comparable with the interaction rates), the system without self-interactions does admit sustained population densities, as demonstrated in Fig. 9.

Note that the infinite diffusion limit considered here differs, formally, from the hydrodynamic limit studied before (Durrett and Levin 1994a; Perrut 2000). For the sake of concreteness, let us assume an array of patches where the typical number of agents in a patch is N_0 , the rate in which agents hop to a neighboring patch is τ , and the distance between patches is ℓ . Formally, our infinite diffusion limit is attained by taking τ to zero while keeping all other parameters fixed; thus, the diffusion constant $D = \ell^2/\tau$ diverges. The hydrodynamic limit is taken by rescaling both τ and ℓ such that D is fixed. However, in both cases, the typical number of particles on a patch, N_0 , holds fixed, since the reaction rates are kept at their original values. In general, one can define an “effective patch”, say, as the average number of patches an agent visits before being involved in a single reaction (this is indeed the “Kuramoto length” (Kuramoto 1973) considered in the theory of stochastic chemical reactions). For both limits mentioned above, the total number of agents on such an effective patch diverges; thus, they both are equivalent to the infinite $N(\equiv N_0\ell_{eff})$ limit considered by Kessler and Shnerb (2008).

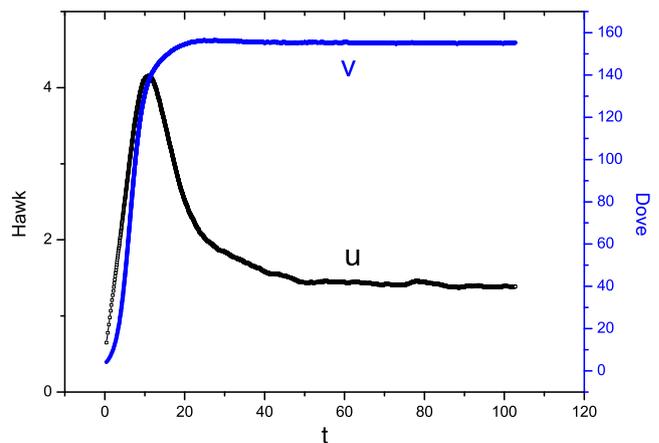


Fig. 9 Time evolution of hawk (u) densities and dove (v) density in an individual-based model without self-interaction. The lines reflect the development of the average population on a 10,000 patches array, with $\kappa = 0.002$ and $\mu = 0.002$. For this set of parameters, the hawk–dove system reaches some equilibrium density with slight perturbations attributed to demographic stochasticity, but none of the species goes extinct

Discussion

The theoretical understanding of ecosystems must involve some strong simplifying assumptions, aimed to reduce the tremendous complexity of the actual dynamics. In the study of metapopulation persistence, many researchers are using the stochastic patch occupancy models (SPOM; Hanski 1999; Etienne et al. 2004; Moilanen 2004; Moilanen and Hanski 1998) as a paradigmatic framework. These models assume that each habitat patch is either occupied or empty, i.e., that the timescale in which the population reaches its local carrying capacity is relatively small. Neglecting the details of the in-site dynamics, the theory is then focused on extinction and recolonization events. Decoherence among local habitats is implicitly assumed in these models since they treat the local extinctions as independent random events.

It is quite easy to verify the presence of a certain species on an island, and it is much harder to obtain the actual number of individuals. Thus, the use of SPOMs is invited when typical datasets gathered from field studies are analyzed.

In laboratory experiments, like those mentioned above, the situation is different. The effects of external perturbations and the variations between different patches are both small, and the monitoring of local population size is pretty good. This situation allows one to examine carefully the inter-patch dynamics and in particular to try to understand the mechanisms that induce decoherence among patches, thus allowing for rescue and preventing a global extinction.

The ability of demographic stochasticity to stabilize extinction-prone dynamics on spatial domains has been already considered in recent works (Abta et al. 2007, 2008). As explained above, the peculiarity of Durrett–Levin’s hawk–dove model (case 3) lies in the absence of any steady-state coexistence solution, either stable or unstable. In previous models, the spatial structure allows for desynchronization among patches and stabilizes the (otherwise unstable) fixed point or a manifold around it. Here the stabilization mechanism on spatial domains involves the crossing of the u -cline resulting from the discreteness of the moving individuals.

As noted above, DL model is somewhat special as a model of population dynamics. Inspired by game theory, it allows only frequency-dependent birth/death rates; thus, it is hard to imagine that this model actually describes the dynamics of populations in the experiments of Kerr et al. (2002, 2006) and Holyoak and Lawler (1996). Our work calls for more detailed examination of the experimental systems, to see if it

is possible that indeed some very strong Allee effect appears such that the frequency independent reaction rates are negligible, and in parallel, it suggests to search for other, more traditional population dynamics models that may support persistence without coexistence.

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