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The role of heterogeneity on the spatiotemporal dynamics of host–parasite metapopulation[☆]

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Abstract

Subpopulations of organisms in different habitat patches may differ from each other in biotic (e.g., inherent growth rate and interaction strength) and abiotic (e.g., climatic and landscape pattern) components. Such heterogeneity can influence the mode and extent of dispersal of individuals among these subpopulations, which, in turn, may regulate their spatiotemporal dynamics. We have modelled a homogeneous metapopulation of the interacting host and parasite system, with closed boundary and dispersal limited to nearest neighbours, using the spatially explicit coupled map lattice approach. We have studied the role of heterogeneity in terms of landscape fragmentation and demographic heterogeneity on the spatiotemporal dynamics. The homogeneous metapopulation shows spatiotemporally synchronous dynamics in the long-term, which is independent of the exact forms of the dispersal function considered commonly. The primary role of both types of heterogeneity is to resist evolution of spatiotemporal synchrony in the lattice, and the dynamics in the metapopulation remains asynchronous for a very long time. Spatiotemporal synchrony in species population may be detrimental to persistence and is a potential problem for conservation biologists. Thus, evolution and maintenance of ecological and demographic diversity in nature seem to aid in species persistence at a metapopulation level.

Keywords: Landscape fragmentation; Asynchrony; Demographic heterogeneity; Coupled map lattice; Dispersal

1. Introduction

In nature, a metapopulation consists of subpopulations having non-identical behavioural and demographic properties, and occupying habitats of variable extent/quality and connectivity. Functional dynamics of those species, which have the capability to induce damage to other species (e.g., a parasite or pathogen), assume larger importance in the metapopulation context. The classical model to study the growth of the interacting host (H) and parasite (P) populations (Nicholson and Bailey, 1935) is inherently unstable and extinct-prone. Some studies (May, 1978; Reeve, 1988), aimed at resolving this stability problem, have considered the effect of environmental variability on persistence of a “population” of sub-populations of these H–P models. These studies considered the statistical aspect of the stability of the H–P dynamics rather than the effects of variable environment on the spatiotemporal pattern formation and dynamics. Later studies (Hassell et al., 1991, 1994; Comins et al., 1992) used the spatially extended models of the H–P

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system and showed that, when individuals are allowed to disperse to neighbouring patches, the ensemble of populations could survive. Though the natural resource heterogeneity has been expressed in terms of patches in these models, however, the distribution of these patches and the biotic (e.g., the growth rate of hosts, or the attack rate of parasites) and abiotic (e.g., climatic factor, landscape quality, etc.) components of the environment are homogeneous.

The influence that local population dynamics with limited dispersal in space exert in inducing global spatiotemporal patterns in metapopulation is of ecological interest (Sinha and Parthasarathy, 1996; Tilman and Karieva, 1997; Parekh et al., 1998). There is some empirical evidence that animal populations fluctuate in synchrony over a large geographical area (Lloyd and May, 1999; Ims and Andreassen, 2000), and some recent studies have given migration as a plausible explanation for such patterns (Ranta et al., 1997; Lande et al., 1999; Paradis et al., 1999; Engen et al., 2002). The importance of spatial synchrony may be different for different interest groups (Earn et al., 1997). For example, spatial synchrony (in a species population) may be a potential problem for local and global persistence of any population and thus are important for conservation biologists (Allen et al., 1993; Bolker and Grenfell, 1996; Heino et al., 1997; Earn et al., 2000). Though there have been discussions in support of the inclusion of habitat patchiness in various population modelling approaches (Lloyd, 1995; Mills and Getz, 1996; Keitt, 1997; Ziv, 1998; Plotnick and Gardner, 2002), little progress has been made to explore the role of different biotic and abiotic factors such as, spatial heterogeneity in habitat quality, connectivity among patches regulating dispersal, and demographic variability among populations, on the long-term spatiotemporal dynamics in metapopulation (Engen et al., 2002). These are important in the present scenario of ongoing destruction and fragmentation of natural landscapes (Moilanen and Hanski, 1998). Our goal, in this paper, is to study a spatially explicit model of the host–parasite metapopulation to address some of these open questions.

A H–P metapopulation is modelled using the coupled map lattice (CML) approach (Kaneko, 1992), where each lattice node represents a single subpopulation of the host–parasite system (Sole et al., 1992a; Parekh and Sinha, 2002) with dispersal occurring to the nearest neighbours. A homogeneous metapopulation has all nodes occupied by identical H–P subpopulations having same demographic parameters and same number of neighbours. Our results show that the long-term dynamics in the homogeneous metapopulation tend to synchronise across space and time with all subpopulations exhibiting the same dynamics at the same phase, irrespective of the two types of dispersal function considered (Sole et al., 1992a; Hassell et al., 1995). Two types of heterogeneity are considered for studying their role on metapopulation dynamics. In the metapopulation context, landscape heterogeneity arising due to fragmentation of habitat, introduces variability in the number of neighbouring subpopulations to which dispersal can take place. Our results show that, even low amount of landscape heterogeneity destroys the spatiotemporal synchrony in dynamics and persistent global spatial pattern is observed. For demographic heterogeneity, subpopulations with phenotypic variability in hosts and parasites (Chesson and Murdoch, 1986; Reeve, 1988; Pascual, 1993; Pascual and Caswell, 1997) are considered, where the host population faces variable risk of parasitism in different patches due to variability in the parasite attack rate. Our results show that this parametric heterogeneity also induces asynchrony in spatiotemporal dynamics that persists for very long time in a non-fragmented metapopulation, even though asymptotically the dynamics may synchronise as is observed for the homogeneous metapopulation. Both demographic and environmental heterogeneity are omnipresent in nature, and our results indicate that even low levels of variability help induce persistent asynchronous spatiotemporal dynamics in metapopulation. Since it is believed that transient dynamics (with a long time scale) in discrete time ecological systems may be more relevant than their asymptotic behaviour (Hastings and Higgins, 1994), evolution and maintenance of heterogeneity in nature is indicative of the positive role that habitat and phenotypic diversity may play in species survival.

2. Models and methods

2.1. The host–parasite model

The modified H–P model (Sole et al., 1992a) is given by

$$\begin{aligned} H_{t+1} &= f(H_t, P_t) = \mu H_t(1 - H_t)\exp[-\beta P_t],\\ P_{t+1} &= g(H_t, P_t) = H_t(1 - \exp[-\beta P_t]) \end{aligned} \qquad (1)$$

Here H_t and P_t are the sizes of the host and parasite (or, parasitoid) population at generation t respectively. In the absence of parasite, the host has logistic growth function and can exhibit a variety of dynamics, from equilibrium to chaos through period-doubling bifurcations, with increasing intrinsic reproductive rate μ (May, 1976). The parasite grows only in presence of the host. The searching efficiency of the parasite to attack the host is represented by β, and $\exp[-\beta P_t]$ is the fraction of the host population that escapes parasitism. Fig. 1 shows the long-term population dynamics of the H–P system for different parasite searching efficiency, β, when the intrinsic growth rate of the host is chaotic, i.e., $\mu = 4$. The bifurcation diagrams (Fig. 1a and b) show that increasing β can lead to a variety of population dynamics of the host and parasite. At very low values of β (<1.67), the parasite does not survive and the host dynamics remains chaotic. Beyond a threshold β, both the host and parasite exhibit equilibrium dynamics and the parasite population increase reducing the host population size with increasing β. At higher β, the dynamics becomes complex and the population exhibits quasi-periodic to chaotic dynamics through higher period oscillations. The time series of the host population showing quasi-periodic dynamics for $\beta = 4$ and chaotic dynamics for $\beta = 5$ are shown in Fig. 1c and d.

2.2. The host–parasite metapopulation model

The closed boundary H–P metapopulation is modelled using the CML formalism where the landscape is described by a one-dimensional (1D) or two-dimensional (2D) lattice with zero flux boundary conditions. Each site in the lattice is occupied by a H–P subpopulation given by Eq. (1) whose individuals are capable of dispersing to the m neighbouring sites. This mesoscopic formalism gives a better description, compared to the coarse-grained partial differential equation approach, in the metapopulation context as the subpopulations are spatially localised and the species have temporally discrete growth and dispersal.

Migration/dispersal of individuals between neighbouring subpopulations in the CML formalism is modelled using the discretised Laplacian operator for the diffusion (as in reaction diffusion systems). The mode of dispersal of individuals can be of different types depending on the life history of the species. In ecological literature, primarily two schemes have been used for modelling dispersal between sites in the CML. The “intra-generation” dispersal, termed as *Type I* here, considers the growth process and dispersal to occur simultaneously (Sole et al., 1992a,b; Sole and Valls,

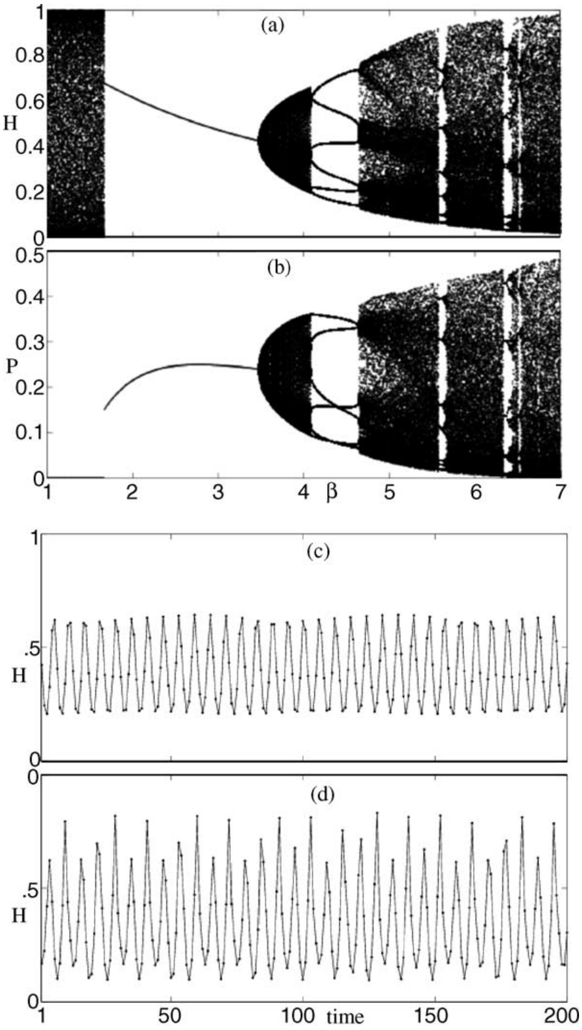

Fig. 1. Dynamics exhibited by a single host–parasite population. Bifurcation diagrams of the (a) host and (b) parasite populations with increasing searching efficiency of the parasite, β. Time series of the host showing (c) quasi-periodic dynamics for $\beta = 4$, and (d) chaotic dynamics for $\beta = 5$.

1992; Bascomte and Sole, 1994), which is unrealistic for discrete generation populations. The size of the H–P subpopulation at the site (j,k) in a 2D lattice following *Type I* dispersal is given by

$$\begin{aligned} H_{t+1}(j,k) = f(H_t, P_t) + \frac{d1}{m}\{&H_t(j-1,k) \\ &+ H_t(j+1,k) + H_t(j,k-1) \\ &+ H_t(j,k+1) - m(H_t(j,k))\} \end{aligned} \tag{2a}$$

$$\begin{aligned} P_{t+1}(j,k) = g(H_t, P_t) + \frac{d2}{m}\{&P_t(j-1,k) \\ &+ P_t(j+1,k) + P_t(j,k-1) \\ &+ P_t(j,k+1) - m(P_t(j,k))\} \end{aligned} \tag{2b}$$

Except for the no-flux boundary sites, $m = 4$ here. The dispersal coefficients of the host and the parasite are $d1$ and $d2$ respectively.

The biologically meaningful "inter-generation" dispersal, termed as *Type II*, has two consecutive discrete growth generations separated by an event of dispersal of individuals to the neighbouring sites (Hassell et al., 1991, 1994; Rohani and Miramontes, 1995; Ruxton and Rohani, 1996; Heino et al., 1997; Savill et al., 1997). The post-dispersal host (H'_t) and parasite (P'_t) population sizes at site (j,k) are

$$\begin{aligned} H'_t(j,k) = (1-d1)H_t(j,k) + \frac{d1}{m}\{&H_t(j-1,k) \\ &+ H_t(j+1,k) + H_t(j,k-1) \\ &+ H_t(j,k+1)\} \end{aligned} \tag{3a}$$

$$\begin{aligned} P'_t(j,k) = (1-d2)P_t(j,k) + \frac{d2}{m}\{&P_t(j-1,k) \\ &+ P_t(j+1,k) + P_t(j,k-1) \\ &+ P_t(j,k+1)\} \end{aligned} \tag{3b}$$

where H_t and P_t are the pre-dispersal host and parasite densities in generation t. These dispersed adults reproduce locally at the site according to Eq. (1) and population sizes H_{t+1} and P_{t+1} at the next generation are given by

$$H_{t+1}(j,k) = f(H'_t, P'_t) \tag{3c}$$

$$P_{t+1}(j,k) = g(H'_t, P'_t) \tag{3d}$$

In a homogeneous metapopulation, all sites are occupied by subpopulations that have the same population parameters μ and β. Comparison of the dispersal terms in Eq. (2a)–(2b) and Eq. (3a)–(3d) shows that in *Type II* dispersal the phenomena of growth and dispersal are two independent procedures carried out successively leading to sequential repetition of the two processes. Thus *Type I* dispersal is linear, whereas Type II entails non-linear transformations (Kaneko and Tsuda, 2000).

Two types of heterogeneity have been considered in the model metapopulation. *Landscape heterogeneity* is simulated in lattices where certain fraction of the total sites is randomly chosen to be "vacant" (no population growth or dispersal here) in the beginning of simulation. This leads to subpopulations in sites that do not have the same neighbourhood. *Demographic heterogeneity* is introduced by randomly choosing some sites in a homogeneous metapopulation to have parasite subpopulations with different searching efficiencies (β). For simulations, metapopulation lattices of size $L = 50$ (one dimensional) and $L \times L = 50 \times 50$ (two-dimensional) are considered. The initial host and parasite populations are chosen randomly from $0.3 < H_0(j,k), P_0(j,k) < 0.4$. In the case of host, all sites except the vacant sites are seeded initially, but parasite population is distributed only to few randomly selected sites (e.g., 10 pairs of j and k). We have studied the long-term host–parasite distribution on a large number of lattices by varying the initial random parasite distribution, and considered up to 10^8 generations (after discarding the initial 5000 generations) for making inferences.

3. Results

3.1. Dynamics of the homogeneous metapopulation

Both 1D (Fig. 2A) and 2D (Fig. 2B) homogeneous H–P metapopulations are studied to find if the Type I and Type II dispersals have any differential effect on the spatiotemporal dynamics. Fig. 2A shows the space–time plot for 20 generations (after discarding transients) of the host for the two types of dispersal to the two nearest neighbours. It is clear that all subpopulations are synchronised in phase to exhibit identical dynamics in host (and parasite) population across the landscape for both types of dispersal.

In the 2D metapopulations, 100 simulations were performed for each type of dispersal with random

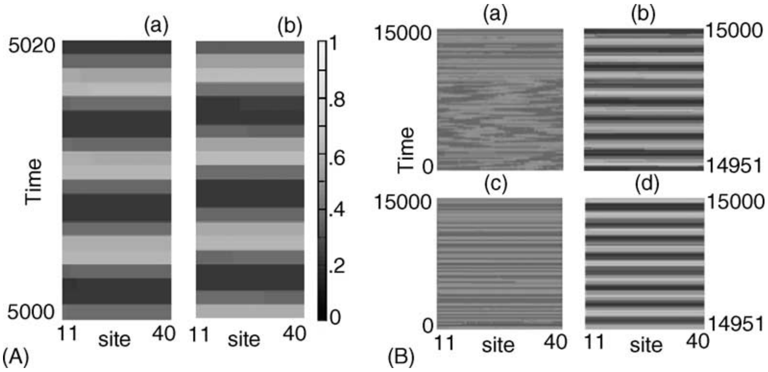

Fig. 2. (A) The long-term space–time plot for the host on sites 11–40 in a 1D H–P metapopulation with (a) Type I, and (b) Type II dispersal. The grey scale indicates the host population size at each site. $\mu = 4.0$, $\beta = 4.0$, $d1 = 0.2$, $d2 = 0.1$. (B) Spatiotemporal dynamics of host populations in sites 11–40 of the middle row in a 2D H–P metapopulation. The left panels show the variation in population size for 15 000 generations, and the right panels are for the last 50 generations when the dispersal is—(a) and (b) Type I; (c) and (d) Type II. Parameters are—$\mu = 4.0$, $\beta = 4.0$, $d1 = 0.2$, $d2 = 0.1$.

variation in the initial parasite distribution. Both dispersal schemes showed primarily synchronised lattices, but in few cases it was asynchronous and showed spatial structures. The time evolution of the host subpopulations, in the 25th row of a synchronised 2D lattice, is compared in Fig. 2B for both types of dispersals. Though there is difference in the time taken for populations to reach synchrony in the two dispersal schemes (Fig. 2B (a and c)), the long-term behaviour is the same in both cases (Fig. 2B (b and d) and Column 1 of Table 1). Fig. 3a shows the commonly observed spatially synchronised 2D lattice for the host, and Fig. 3b is an example of the rare asynchronous lattice with stable spiral pattern for Type I dispersal. In the few cases where the dynamics was asynchronous, there was slight difference for the two dispersal schemes—fully grown spirals for Type I and broken spirals for Type II dispersal. Though rare in occurrence, these spatiotemporal patterns were very persistent in time. This is also clear from Fig. 4 where, even after 10^5 generations, 13 out of 200 lattices remained asynchronous in their spatiotemporal dynamics for the 0% vacancy case. Thus, the homogeneous H–P metapopulation primarily exhibit coherent spatiotemporal dynamics irrespective of the type of dispersal considered.

There are many mechanisms for spatial pattern formation in non-equilibrium systems (Cross and Hohenberg, 1993). In continuous Reaction Diffusion systems, spatial patterns arise due to Turing instabilities (Turing, 1952; Murray, 1989) when the inhibitor species diffuse faster than the activator species. The mechanism of spatial pattern formation in excitable media has been applied to many biochemical and biological processes such as, Belousov–Zhabotinsky reactions, Slime Mould aggregation, and cardiac rhythm (Keener and Sneyd, 1998). The evolution of spiral wave like pattern is generic in spatially extended systems where local oscillatory dynamics is coupled to diffusion. In a small lattice with no-flux boundary conditions (as the one used here) the spatial pattern is unlikely to be stable over long time as during the evolution of the host and parasite population many such spirals are formed in space, which generally disappear when the tip touches the boundary or by annihilation of two spirals. However, a few of the spirals within the lattice tend to stabilise. In larger lattices more spirals are observed and many take longer to disappear also. It has been shown by

Table 1
Comparison between the two types of dispersals on the synchronicity of the long-term ($t = 10^5$) spatiotemporal dynamics in metapopulations

Dispersal type	Homogeneous lattice	Vacancy	
		5%	10%
Type I	93	7	0
Type II	71	8	1

One hundred cases of random initial parasite distribution (at 10 sites) are studied for each dispersal type.

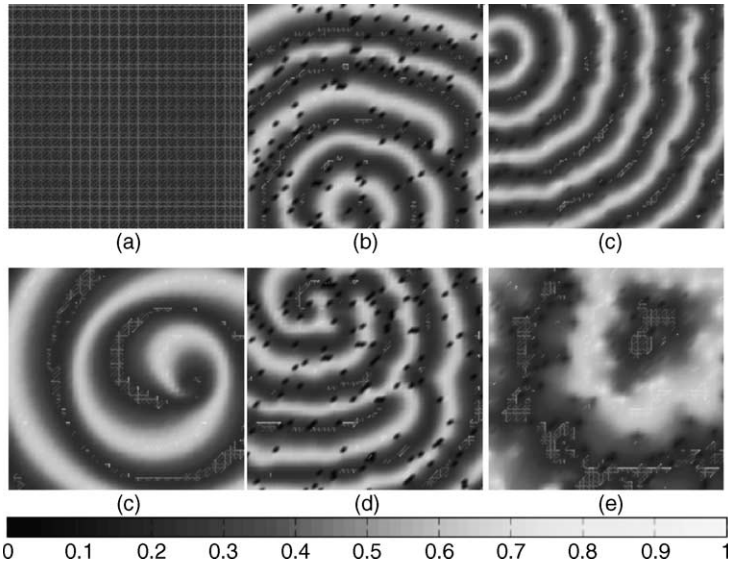

Fig. 3. Spatial abundance pattern in the host populations in a 2D H–P metapopulation, with Type I dispersal, at $t = 25\,000$. The parameters are $d1 = 0.2$, $d2 = 0.1$, $\mu = 4$, and $\beta = 4.0$. Homogeneous lattice: (a) synchronised dynamics and (b) spiral pattern; (c) and (d) landscape heterogeneity (5% vacant sites); (e) and (f) parametric heterogeneity (5% sites have $\beta = 5$) shows asynchronous spiral pattern.

Earn et al. (2000) that if the local dynamics of the spatially extended system (e.g., CML) is equilibrium, periodic or quasi-periodic, then it can show spatial synchrony. For local chaotic dynamics spatial turbulence is expected and our results, with homogeneous metapopulation, also show similar results.

The dispersal coefficients have important role in spatial pattern formation. In a recent paper (Bjornstad and Bascompte, 2001) have succinctly shown the role of the dispersal coefficients in the formation of different types of spatial patterns in another model of the host–parasite CML. The difference in the host and parasite dispersals can induce "lags" or "leads" in one of the populations that help in setting up of spiral like spatial structures. In the long run and in a small lattice with zero-flux boundary most of these patterns tend to disappear as shown by our results. The two types of dispersal are expected to show slight variation in the spatial pattern as Type II amplifies the initial fluctuations (intrinsic "noise" (Shnerb et al., 2000)) in two steps and larger number of spatial structures are observed in the homogeneous case as seen in Table 1.

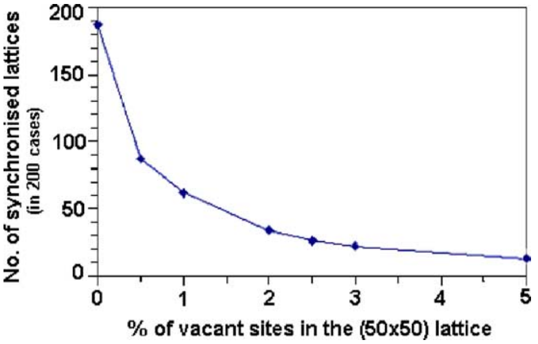

Fig. 4. Effect of increasing number of vacant sites on the long-term ($t = 10^5$) spatiotemporal pattern of the H–P metapopulation. At each vacancy level, 200 different vacancy patterns in the lattice landscape are studied. Parameters are $d1 = 0.004$, $d2 = 0.8$, $\mu = 4$, and $\beta = 4.0$.

3.2. Dynamics of the heterogeneous metapopulation

3.2.1. Landscape heterogeneity

Heterogeneity in the landscape is simulated by randomly introducing vacant sites in which the host and parasite species do not grow or disperse. Due to this heterogeneity of the landscape, different subpopulations on the lattice may have different number of interactive neighbours. The average effect of increasing landscape inhomogeneity (i.e., increasing vacancy in the lattice) on the spatiotemporal synchronicity of the metapopulation dynamics is shown in Fig. 4. Increasing amount of fragmentation in landscape clearly results in decrease in synchrony in the spatiotemporal dynamics. Only 12 or 13 uninhabitable sites (0.5% vacancy) lead to asynchrony in more than 50% of the metapopulations. At 5% vacancy level, only 13 out of 200 cases showed synchronisation in dynamics—a complete reversal of the homogeneous lattice situation where only 13 cases showed asynchronous behaviour! Table 1 also shows that the probability of having synchronisation in spatiotemporal dynamics in the metapopulation decreases rapidly with increasing extent of random vacancy, irrespective of the type of dispersal. The spatial abundance pattern of the host in metapopulations with landscape heterogeneity are shown in Fig. 3c and d for the same initial conditions and time as shown in Fig. 3a and b for the homogeneous lattice. In both cases, the lattices show persistent asynchronous dynamics indicating that fragmentation of landscape introduces asynchrony in spatiotemporal dynamics in metapopulations.

Though not shown here, but the parasite population in the lattice follows similar long-term patterns as the host but with phase lags. As the parasites disperse in the lattice from the few initial sites during the simulation, the host–parasite interactions give rise to localised variations in the populations (depending on the dispersal rates). In the long-term the parasite population also shows synchronous/asynchronous spatial dynamics similar to the host, with the host and parasite population sizes varying between 0.2–0.7 and 0.1–0.35 respectively, for the parameter values chosen.

3.2.2. *Parametric heterogeneity*

For incorporating parametric heterogeneity, a fixed percentage of the total sites (subpopulations) in a homogeneous H–P metapopulation are randomly selected to have parasites with higher searching efficiency ($\beta = 5$) than the parasites in the other sites ($\beta = 4$). Fig. 3e and f shows the two homogeneous landscapes as in (Fig. 3a and b), except that 125 (i.e., 5%) randomly chosen sites have parasite subpopulations with $\beta = 5$. This heterogeneity in parasite behaviour has a startling effect on the spatiotemporal dynamics of the metapopulation. Fig. 3e and f show that parametric heterogeneity resists spatiotemporal synchrony in the homogeneous metapopulation and spatial structures persist for very long time. Thus, our results show that introduction of any heterogeneity such as, fragmentation of landscape, or inhomogeneous distribution in demographic parameters, can lead to asynchrony in spatiotemporal dynamics in the host–parasite metapopulations.

The existence of spatial heterogeneities (landscape or parametric) can lead to different types of local anisotropies that act as “defects/disorders” inducing synchronisation failure in lattices. For example, a vacant site can be a quenched disorder and can act to “pin” the core of the spiral making it robust and decreasing the frequency of spiral annihilation. This increases the possibility of spatial asynchrony even in small lattices where the spirals tend to persist for longer time. Parametric inhomogeneity induces difference in the local dynamics between neighbouring sites thereby inducing spatial asynchrony in pattern. This acts like phase defect and hence the induced pattern is also different than the ones induced by quenched vacancies where the structured spirals get pinned easily and multi-arm spirals are also observed (Holden et al., 1991).

4. Discussion

Since homogeneity in both neighbourhood and behavioural parameters among the subpopulations in a metapopulation does not capture the patchiness of the real world, the primary concern of this paper is to address the role of realistic ecological and behavioural features such as, landscape and demographic heterogeneity, in the spatiotemporal dynamics of H–P metapopulation. Our results show that, in a homogeneous metapopulation, host and parasites in all sites tend to synchronise their population dynamics in both space and time and the population sizes vary perfectly in phase. We have done simulations with a large range of parameter values—for the host growth rate “μ”, parasite searching efficiency “β”, and dispersal rates $d1$ and $d2$. Our study, along with others (Earn et al., 2000), shows that all parameters that lead to local equilibrium, periodic and quasi-periodic dynamics (see Fig. 1), the CML dynamics is predominantly synchronised. The effect of the dispersal coefficients on the spatiotemporal patterns in the homogeneous HP CML is similar to what was obtained by Sole et al. (1992a, 1992b), though longer temporal evolution in small lattices with no-flux boundary conditions leads to eventual synchronisation in larger $d1$–$d2$ parameter space. Our results show that this synchrony is broken leading to persistent spatial patterns on introduction of both spatial and parametric heterogeneity.

Increasing heterogeneity in the metapopulation, both in terms of fragmented landscape and demographic variability in the life history parameters of the interacting species, increases asynchrony in spatiotemporal dynamics in the metapopulation. There is a large literature on modelling different aspects of habitat fragmentation using different approaches (e.g., see Hanski and Ovaskainen, 2000). Our results show that the dynamical effect of loss or alteration of connectivity among subpopulations due to landscape fragmentation not only resist synchronisation in the population dynamics across the landscape, they also reinforce the self-organisation of the spatial patterns of hosts and parasites allowing this asynchrony to persist for long time (e.g., 10^8 generations). Such a transient phase for extended period can be more meaningful in reality, even though synchronisation may be the asymptotic dynamics in the metapopulation (Hastings and Higgins, 1994). We have shown that even in a homogeneous landscape, demographic heterogeneity, in terms of phenotypic difference in parasite populations with variability in their attack rate, induce asynchrony in metapopulation dynamics, which persists for very long time.

In this paper we have shown the effect of small amount of landscape heterogeneity on the metapopulation dynamics. The important problem of habitat loss, which is a threat to biodiversity happens with increasing vacancies (landscape heterogeneity). Our preliminary studies show that increased landscape fragmentation leads to isolated population patches that consist of one or more subpopulations. These patches do show within patch synchrony in dynamics though phase difference persists between the patches. Smaller patches increase in number as percentage of vacant sites is increased, and hence risk of extinction also increases. This fragmentation of habitat and reduction in inhabitable sites can also have complex effects on the species persistence in the long run because of other ecological factors that are not considered in this simple model.

Spatial coherence (synchrony) in population dynamics has been implicated to be dangerous for species conservation (Earn et al., 2000), as it increases the risk of extinction under both local and global environmental disturbances (Allen et al., 1993). Asynchronous fluctuations among the subpopulations distributed over a geographical region is supposed to help in persistence of a metapopulation (Ruxton, 1994; Heino et al., 1997; Lloyd and May, 1999). Our theoretical results on evolution and maintenance of spatiotemporal asynchrony in population size in a metapopulation due to heterogeneity in landscape and demographic/behavioural variability in subpopulations is significant, because both are present in real ecological situations. In other words, our theoretical results show that heterogeneity in space and phenotypic diversity in species clearly reduce the risk of population extinction, thereby indicating that ecological and demographic heterogeneity may have indirect adaptive value.

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