Dynamical mechanism for coexistence of dispersing species without trade-offs in spatially extended ecological systems

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Most prior studies on the role of dispersal in the coexistence of competing species have emphasized the need for trade-offs between competitive and colonizing abilities for coexistence. Theoretical studies of the evolution of dispersal recently have revealed an alternative mechanism for the coexistence of species differing solely in dispersal rates in spatially extended systems. We present an analysis and numerical evidence indicating that chaotic synchronism, occurring in an extremely intermittent form, is an important feature of the spatiotemporal variation in fitness required for the coexistence of species without trade-offs.

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I. INTRODUCTION

A central problem in community ecology is to understand the factors that promote or prevent the coexistence of competing species [1–3]. Recent years have seen a growing appreciation of the importance of spatial heterogeneity and dispersal in explaining species coexistence [4]. One familiar mechanism by which dispersal facilitates coexistence at the landscape scale is a trade-off among species between colonizing and competitive abilities [5]. For instance, consider a guild of competitors that utilizes a single limiting resource. In a closed, local habitat patch the species which can persist at the lowest resource level will eventually displace species with higher resource requirements [6]. But if habitat patches are open, and if there are extinctions that empty out patches and are asynchronous among patches, inferior competitors which can disperse sufficiently rapidly may be able to coexist regionally with superior competitors. In effect, rapid dispersal can provide temporary windows of opportunity during which locally inferior species can colonize empty patches and reproduce sufficiently fast to colonize yet other patches, before being excluded by more slowly dispersing but competitively superior species.

Another distinct mechanism of coexistence recently has emerged in theoretical studies of the evolution of dispersal. Without *temporal variation*, spatial heterogeneity alone does not tend to favor the evolution of dispersal [7,8]. Even if the external environment is constant, however, nonlinear population dynamics leading to cycles or chaotic dynamics can produce the appropriate spatiotemporal variation in fitness that favors the evolution of dispersal and, at times, the coexistence of competing species [9,10]. Consider a scenario in which species compete in patches and disperse among them. Within patches, all species are assumed to be equivalent, but species may differ in their rates of movement among patches. It has been found [9,10] that given unstable dynamics, there is often the potential for sustained coexistence of two or more species, differing greatly in dispersal rates. This coexistence is permanent [11], in that each species can increase when it is rare and the other species is in its single-species dynamical attractor. Because species are assumed to behave identically within patches (so that density dependence is experienced uniformly within and among species), there is by definition no trade-off between colonizing and competitive abilities, and so a different mechanism must underlie the observed robust coexistence.

A question of paramount interest is thus the following: what is the dynamical mechanism that permits the coexistence of competing species through dispersal in the absence of trade-offs? Qualitatively, it has been suggested [9] that coexistence arises because the system tends to shift between distinct dynamical behaviors concordant with temporal variation in average dispersal rates. For instance, at high dispersal rates, different habitats tend to become synchronized in their dynamics. This can favor low dispersal, if there is spatial variance in fitness [7]. But as the system evolves towards lower dispersal rates, the dynamics of different patches may become desynchronized, and a selective advantage of dispersal may then emerge.

The aim of this paper is to report our finding that, due to nonlinear dynamics, the temporal synchronization and desynchronization between populations in different habitats in fact occurs through a pattern of on-off intermittency. In particular, say we consider a simple system consisting of two patches and two species. Let N_{T1} and N_{T2} be the total populations in patches 1 and 2, respectively. Then the relative populations of the two patches, defined to be the ratios N_{T1}/K_1 and $N_{T2}/K2$, tend to follow each other, approximately, in long epochs of time (laminar phases or, dynamically, the ''off'' state). (Here, K_j is the carrying capacity of patch j, the population size where local births equal local deaths, so that the local population is stationary when $N_{tj} = K_j$.) The synchronization is, however, interrupted by time periods in which the relative populations deviate rapidly from each other (bursts or the ''on'' state). The deviation occurs randomly in time and typically lasts for a short time period (compared with the average time duration of the laminar phase), after which temporal synchronization between the populations in different patches is restored. We can define the following quantity to characterize the *quality of synchronization*:

$$Q(t) = \frac{N_{T1}(t)}{K_1} - \frac{N_{T2}(t)}{K_2}. \tag{1}$$

The quantity $Q(t)$ exhibits on-off intermittency, a dynamical behavior that has received extensive recent attention [12–14]. We provide numerical support and an analysis for the synchronization and on-off intermittent behaviors in this model. Our analysis suggests that the observed coexistence is unlikely to be a transient behavior. An implication is that intermittently chaotic synchronism may be a fundamental mechanism for the coexistence of competing species in spatially extended ecological systems.

The rest of the paper is organized as follows. In Sec. II, we describe the Holt-McPeek model. In Sec. III, we present numerical results for synchronization and on-off intermittency in the model. A physical analysis for the observed intermittent synchronization is given in Sec. IV. A brief discussion is presented in Sec. V.

II. HOLT-McPEEK MODEL

The ecological model of Holt and McPeek [9] describes the population dynamics of two species that disperse in a spatially extended environment defined by two local patches. (The general phenomena illustrated by this model arise in a wide range of spatial models with chaos [15].) Let $N_{ij}(t)$ be the density of species i in patch j at generation t. The local population growth rate, or the realized fitness, of species i in patch j is given by the Ricker equation [16]

$$W_j = \exp\left[r_j \left(1 - \frac{N_{1j} + N_{2j}}{K_j} \right) \right],$$

where r_j is the intrinsic rate of increase at low-population size in patch j, and K_j is the carrying capacity of patch j for both species combined. The model assumes that the growth rate is identical for each species within each patch and that local fitness depends on the total population occurring in each patch. To model dispersal, Holt and McPeek assume that of the total population of species i, a fraction e_i migrate, at each generation, from their natal patch, while the remainder $(1-e_i)$ remain in this patch. The quantity e_i is then the dispersal rate of species i; this quantity differs for each species, though the two species are identical in all other respects. The migratory fraction of the population experiences a mortality rate, or cost of dispersal, of $(1-m)$, leaving only a fraction m of immigrants to compete on equal terms with the resident population. The resulting model assumes that reproduction and density dependence precede dispersal. The census immediately follows dispersal, costs of dispersal for a species are experienced entirely by those individuals that actually disperse, and population densities are sufficiently high so that they can be represented by continuous variables rather than discrete integers. The evolution of the density of species i $(i=1,2)$ is thus given by

$$\begin{aligned} N_{i1}(t+1) &= (1-e_i) W_1[N_{T1}(t)] N_{i1}(t) \\ &\quad + m e_i W_2[N_{T2}(t)] N_{i2}(t), \\ N_{i2}(t+1) &= (1-e_i) W_2[N_{T2}(t)] N_{i2}(t) \\ &\quad + m e_i W_1[N_{T1}(t)] N_{i1}(t). \end{aligned} \tag{2}$$

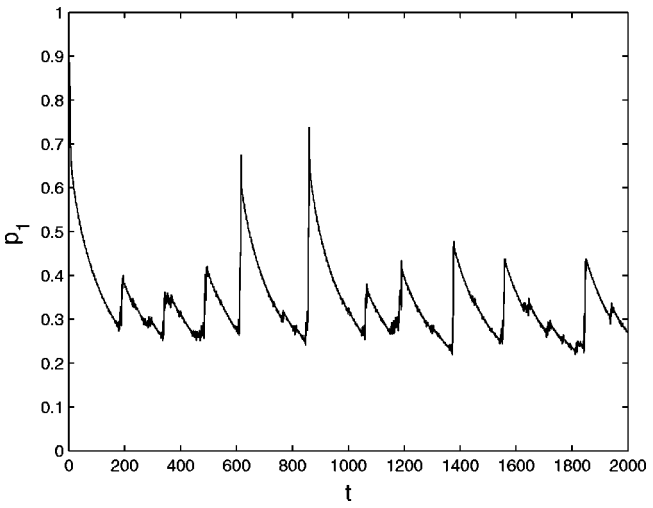

FIG. 1. Time series $P_1(t)$ for the Holt-McPeek model with $r=3.0$, $K_1=100$, $K_2=50$, $e_1=0.5$, $e_2=.01$, and $m=1$.

To understand what conditions favor the survival of a dispersing species, in competition with a species nearly stationary in space, Holt and McPeek set $e_2 \gg e_1$ and simulate Eq. (2) for various values of the growth parameters. As an example, using the parameter values $K_1=100$, $K_2=50$, $e_1=0.5$, $e_2=0.01$, $m=1$, and $r_1=r_2=r$, Holt and McPeek find that low r values of 1 and 2.5 produce stable and cyclic dynamics, respectfully. Given population stability, clones with relatively lower dispersal rates (i.e., $e_2=0.01$) displace clones with higher dispersal rates (i.e., $e_1=0.5$). With the high-dispersal clone now extinct, the average dispersal rate of the population is low. In other words, dispersal is disfavored. However, for a higher r value of 3.0, chaotic behavior arises: instead of dying off, the high-dispersal clone now persists and experiences episodic increases in population, as shown in Fig. 1, where the instantaneous fraction of the high-dispersal population,

$$P_1(t) = \frac{N_{11}(t) + N_{12}(t)}{N_{11}(t) + N_{12}(t) + N_{21}(t) + N_{22}(t)},$$

is plotted. Holt and McPeek conclude, based on this observation, that *chaos favors dispersal* in the sense that the highly dispersing species cannot survive unless the growth rates of the patches are sufficiently high to produce chaotic dynamics [9].

Intuitively, the reasons that regular dynamics disfavors while chaotic dynamics favors dispersal can be seen as follows [9]. At sufficiently low intrinsic rates of increases (i.e., low r's), the population settles into a stable equilibrium or a periodic orbit, so dispersers flow from high-K to low-K patches, indirectly increasing fitness in the former while decreasing fitness in the later. As a result, on average, dispersing individuals flow down gradients in fitness, so they have lower fitness than nondispersers. The evolutionarily stable state of the population is zero dispersal. The reasoning also implies that a dispersing species can coexist with a stationary one if the patches have approximately identical values of K. On the other hand, in the case of chaotic dynamics (for high

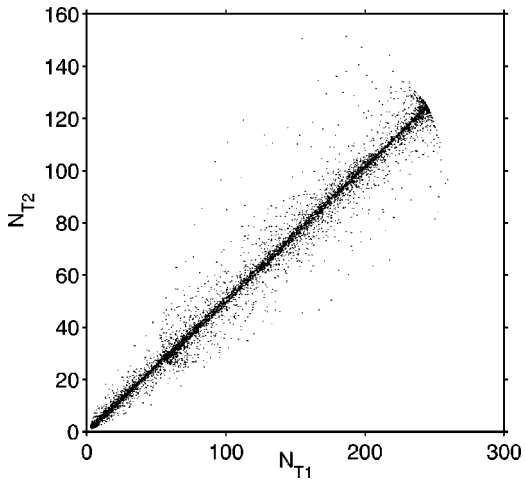

FIG. 2. For $m=1$ in the Holt-McPeek model, Eq. (2): total population of patch 2 ($N_{T2}=N_{12}+N_{22}$) versus total population of patch 1 ($N_{T1}=N_{11}+N_{21}$).

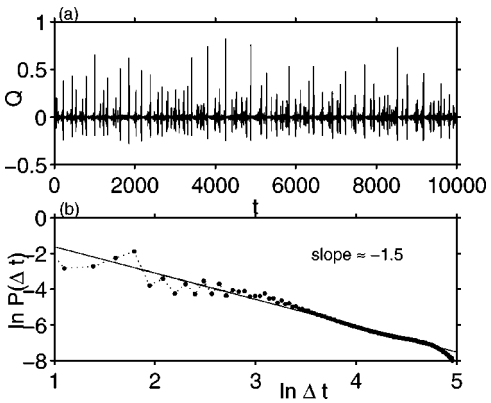

FIG. 3. For $m=1$ in the Holt-McPeek model, Eq. (2): (a) on-off intermittency in $Q(t)$, quality of synchronization; (b) a histogram of the distribution of the laminar phase.

values of r), the instantaneous frequency of the high-dispersal clone generally tends to decrease but with sudden sharp increases occurring at random times. These episodic jumps in the frequency increase the mean dispersal rate, which in turn tends to synchronize the population dynamics in the two patches. Once the patches are synchronized, dispersal becomes disfavored (as with regular dynamics). As the frequency of the high-dispersal clone declines, the patch dynamics becomes progressively uncoupled, the relative fitnesses among patches generated by chaotic dynamics switch in rank order again, providing the conditions in which dispersal is, once again, advantageous.

Based on their numerical observations, Holt and McPeek argue that there are two qualitatively distinct states in the system dynamics.

(i) The populations in the two patches tend to be synchronized when the frequency of the high-dispersal clone (p_1) is large because there is a strong coupling between the two patches. In this nearly synchronized state, dispersal becomes disadvantageous, leading to a decrease in p_1 and, hence, over time the patch dynamics becomes progressively decoupled.

(ii) As a consequence of the reduced coupling strength, the approximate synchronization state can no longer be maintained, so the patch populations become desynchronized and dispersal becomes advantageous again, thereby pushing the system towards synchronization.

This scenario, synchronization $\rightarrow$ desynchronization $\rightarrow$ synchronization $\rightarrow \cdots$, with random time intervals between stages of desynchronization, is a characteristic dynamical pattern of on-off intermittency.

III. SYNCHRONIZATION AND ON-OFF INTERMITTENCY

To provide numerical support for this synchronization and desynchronization scenario, we regard the two patches in Eq. (2) as two coupled systems and examine the total populations in both patches: $N_{T1}=N_{11}+N_{21}$ and $N_{T2}=N_{12}+N_{22}$. Figure 2 plots N_{T1} versus N_{T2} for $K_1=100$, $K_2=50$, $e_1=0.5$, $e_2=0.01$, $m=1$, and $r_1=r_2=3.0$. We see that the population dynamics is apparently chaotic, and the instantaneous values of N_{T1}/K_1 and N_{T2}/K_2 change between 0 and some constant on the order of unity (in contrast to the case of regular dynamics, say, a stable equilibrium, where these values tend to unity). More interestingly, we observe that the trajectory points tend to lie in the vicinity of the line defined by $\mathcal{L}$: $N_{T1}/K_1=N_{T2}/K_2$, with occasional bursts away from it. The line $\mathcal{L}$ can thus be considered as the synchronization manifold of Eq. (2) in a general sense, as there is no direct synchronization between the corresponding dynamical variables in the two patches. Such ''indirect'' synchronization is a special form of *generalized synchronization* [17]. We also find that, when the trajectory wanders near $\mathcal{L}$, the frequency $p_1(t)$ of the high-dispersal species tends to be large, indicating a strong instantaneous coupling between the two patches. As $p_1(t)$ declines, the patches become desynchronized, and the trajectory moves away from the line $\mathcal{L}$. We observe that a movement from peak to valley on $p_1(t)$ corresponds to a burst of the trajectory off the synchronization line $\mathcal{L}$. After a desynchronization burst, conditions are favorable for the invasion of the high-dispersal species, leading to an increase in p_1 and, consequently, to generalized synchronization again. Thus, the time trace of $Q(t)$ [Eq. (1)] exhibits an intermittent behavior, as shown in Fig. 3(a). We see that most of the time, Q remains close to zero, signifying synchronization, but the synchronization state is interspersed with occasional bursts away from it. The pattern in Fig. 3(a) is thus typical of on-off intermittency. The laminar phase, or the time interval Δt between successive bursts in the time series, apparently exhibits an algebraic distribution for small values of Δt and an exponential tail for large values of Δt, as shown in Fig. 3(b). To obtain Fig. 3(b), we set a threshold Q_{th} (quite arbitrarily) and accumulate the time intervals between the successive bursts through Q_{th} in $Q(t)$. The distribution so obtained generally does not depend on choices of Q_{th}, insofar as it is chosen so that a bursting behavior is meaningful. In the range of approximately algebraic behavior, we observe that the slope of the distribution is about -1.5. The behaviors shown in Figs. 2, 3(a), and 3(b) appear to be typical for Eq. (2) as they occur in wide regions in parameter space, as we have observed by systematically examining the two-

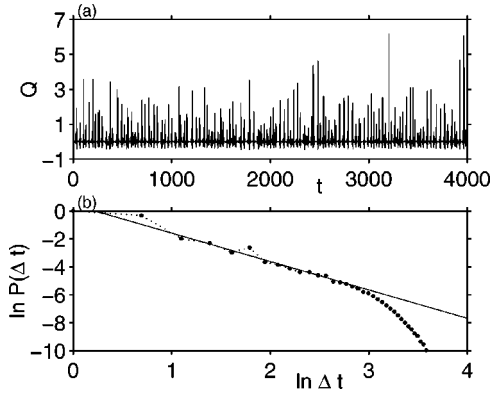

FIG. 4. For $m=0.8$ in the Holt-McPeek model, Eq. (2): (a) on-off intermittency in $Q(t)$, quality of synchronization; (b) a histogram of the distribution of the laminar phase.

dimensional parameter plane (e_1,e_2) for several values of r and m.

Of particular importance to the problem of the coexistence is the parameter m, the fraction of the dispersing population that can compete with the resident population [$(1-m)$ is the cost of dispersal]. If m is too small or the cost of dispersal is too high, then generally the dispersing species will be extinct. We find in numerical experiments that, insofar as chaos is present, the minimum values of m for coexistence can be as low as 0.3. Figures 4(a) and 4(b) show, for $m=0.8$, the apparent on-off intermittent behavior in $Q(t)$ and the distribution of the corresponding laminar phases, respectively. There is still a range of Δt in which the distribution appears algebraic, followed by an exponential tail. The algebraic exponent [18] is approximately -2.

IV. PHYSICAL THEORY

We now provide an analytic argument for synchronization and on-off intermittency that permit the high-dispersing species to persist. To construct a simple model amenable to analysis, we consider the extreme case where the coexisting species is almost stationary, in that its dispersal rate is close to zero. The presence of this species affects the fitness of the high-dispersing species in local patches, and the magnitude of this effect varies with the density of the stationary species. For the high-dispersing species, the existence of the stationary species, with time varying population densities in the patches, may be viewed heuristically as comparable to imposing time-dependent disturbances on the carrying capacities of the patches. This line of thought leads to the following heuristic model describing the population densities $N_1(t)$ and $N_2(t)$ of the high-dispersing species alone:

$$N_1(t+1)=(1-e)W_1[N_1(t)]N_1(t)+meW_2[N_2(t)]N_2(t),$$
$$N_2(t+1)=(1-e)W_2[N_2(t)]N_2(t)+meW_1[N_1(t)]N_1(t), \tag{3}$$

where the growth dynamics in the two patches are given by $W_1=e^{r[1-N_1(t)/K_1(t)]}$ and $W_2=e^{r[1-N_2(t)/K_2(t)]}$ with time-dependent carrying capacities $K_1(t)$ and $K_2(t)$. Numerical studies of Eq. (3) reveal patterns with essentially identical characteristics to the full model (e.g., Figs. 2 and 3). In the following, we consider two situations in turn: (1) where the patch environments are identical and (2) where the patches are nonidentical.

A. Identical patches

In this case, we have $K_1(t)=K_2(t)=K(t)$. Introducing two new variables $u(t)=\frac{1}{2}[N_1(t)+N_2(t)]/K(t)$ and $v(t)=\frac{1}{2}[N_1(t)-N_2(t)]/K(t)$, we see that the synchronization state (manifold) is given by $v=0$. In the vicinity of the synchronization manifold, $v\approx 0$, so we have $e^{\pm rv(t)}\approx 1\pm rv(t)$. In the (u,v) variables, Eq. (3) becomes

$$u(t+1)=A\exp\{r[1-u(t)]\}u(t),$$
$$v(t+1)=B\exp\{r[1-u(t)]\}[1-ru(t)]v(t), \tag{4}$$

where $A=1-e+me$ and $B=1-e-me$ are constants. We see that (1) $u(t)$ is governed by a simple growth model which exhibits chaos and (2) $u(t)$ provides a driving to the $v(t)$ subsystem. The synchronization manifold $v=0$ is invariant under Eq. (4) and, hence, perfect synchronization $v=0$ can be achieved if it is transversely stable. The transverse stability of $v=0$ can be determined by the following: $\Lambda_T=\int B\exp[r(1-u)](1-ru)\rho(u)du$, where $\rho(u)$ is the invariant density of the chaotic driving variable u. If $\Lambda_T<0$, asymptotically we have $v(t)\to 0$ (stable synchronization). However, if $\Lambda_T\gtrsim 0$, $v(t)$ exhibits on-off intermittency, which can be understood by analyzing the behavior of Λ_T computed at finite times for an ensemble of initial conditions, as follows. Suppose we distribute a large number of initial conditions with $v\approx 0$, compute $\Lambda_T(t)$ for each trajectory at time t, and then construct the histogram of these finite-time exponents. Typically, the histogram is centered at $\Lambda_T\gtrsim 0$ with a width that is proportional to $1/\sqrt{t}$. Thus, at any finite time, the distribution of $\Lambda_T(t)$ will have a tail on the negative side, indicating that some trajectories actually experience attraction towards $v=0$. By ergodicity of the chaotic variable $u(t)$, we see that a single trajectory, while it is in general repelled from $v=0$, will experience episodes of time intervals during which it is actually attracted towards $v=0$. Thus, what typically is observed is that the trajectory tends to stay near $v=0$ with bursts away from it at random times, signifying on-off intermittency [19].

B. Nonidentical patches

In this case, the new variables are given by $u(t)=\frac{1}{2}[N_1(t)/K_1(t)+N_2(t)/K_2(t)]$ and $v(t)=\frac{1}{2}[N_1(t)/K_1(t)-N_2(t)/K_2(t)]$. For $v\approx 0$, we obtain, to first order in $v(t)$, the following:

$$u(t+1)\approx e^{r(1-u(t)}\{[A_+-(A_--1+e)rv(t)]u(t)-(A_--1+e)v(t)\},$$
$$v(t+1)\approx e^{r(1-u(t)}\{B_+[1-ru(t)]v(t)-(B_--1+e)u(t)\} \tag{5}$$

where the quantities A_+, A_-, B_+, and B_- are time dependent and are given by $A_\pm(t)=1-e+me[K_1(t)^2 \pm K_2(t)^2]/[2K_1(t)K_2(t)]$ and $B_\pm(t)=1-e-me[K_1(t)^2 \pm K_2(t)^2]/[2K_1(t)K_2(t)]$. Due to the difference in the patch environment, we see that $v=0$ is no longer invariant under the dynamics. Thus, we can expect only approximate synchronization ($v\approx 0$) to occur, as illustrated in Fig. 2, where the synchronization state is apparently broadened about $v=0$ (or $Q=0$). Comparing with Eq. (4), we can regard the term $(B_- -1+e)u(t)$ in the v equation in Eq. (5) as a random noise term. As a result, even in parameter regimes where the synchronization state is asymptotically stable, the noiselike term can cause desynchronization and induce on-off intermittency. Thus, for a realistic system such as Eq. (2), we expect approximate chaotic synchronization to occur only in an intermittent way and on-off intermittency to be persistent. We suggest that on-off intermittency may be a widespread phenomenon in spatially extended ecological systems with locally chaotic dynamics.

V. DISCUSSION

The fundamental dynamics in spatially extended ecological systems relies on dispersal, which provides the interaction among species in the spatially extended environment. It is thus of paramount importance to understand under what conditions dispersal favors species coexistence. It has been shown [7,8] that spatial heterogeneity in abundance alone is unable to select for dispersal. To favor dispersal, some temporal heterogeneity must also be present. Many previous theoretical treatments [20] have assumed that external environmental variation supplies the required driving force to create temporal variation in fitness. However, in view of the ubiquity of nonlinearity in ecological systems, it is reasonable that nonlinear population dynamics leading to cycles or chaotic behaviors can produce the appropriate temporal variation in fitness that favors the evolution of dispersal [9,10].

The main contributions of our work are twofold: (1) we provide analysis and evidence that chaotic dynamics in spatially coupled ecological models can indeed provide the spatiotemporal variation in fitness that is necessary for the coexistence of dispersing species; and (2) we show that under fairly general settings, the spatiotemporal variation in fitness leads to on-off intermittency, with respect to the approximate synchronization of the relative patch populations. As such, we expect synchronization and on-off intermittency to be common in spatially extended ecological systems.

ACKNOWLEDGEMENT

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[14] In ecology, it has recently been observed that on-off intermittency describes the dynamics of many natural populations, where variable periods of time at low rarity alternate with sudden outbreaks. The intermittency can arise from different models of competition, where coexistence arises because of a local storage effect [P. L. Chesson, *Community Ecology* (Harper and Row, New York, 1986)]. However, we here demonstrate that on-off intermittency characterizes a competition model where coexistence arises from *dispersal* among patches.
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