Beneficial role of noise in promoting species diversity through stochastic resonance

Ying-Cheng Lai

Department of Electrical Engineering, Arizona State University, Tempe, Arizona 85287, USA
(Received 6 May 2005; revised manuscript received 13 July 2005; published 18 October 2005)

There is an increasing recognition that patterns in species diversity cannot be understood without reference to nonequilibrial or unstable dynamics. Recently, through a realistic ecological model that involves dispersal, we have addressed the positive role of noise in promoting species coexistence [Phys. Rev. Lett. **94**, 038102 (2005)]. Here we present a physical theory to account for the main scaling law responsible for this phenomenon.

One of the most amazing and beautiful aspects of nature is species diversity. Understanding factors that promote diversity is both of fundamental importance and of general interest. A key to diversity is species coexistence. Thus, one approach to addressing the diversity problem is to study how species, inferior or superior in terms of their competitiveness, are able to coexist in a common environment [1–4]. Due to the relative difficulty to conduct experimental studies, theoretical analyses and computational modeling have become an important tool to address the species coexistence problem. In this regard, models based on nonlinear dynamics have become increasingly important [5] due to the fundamental role played by nonlinear dynamics in ecological systems [6]. A class of computationally tractable models consists of two species (one inferior and another superior) in a spatially extended, patchy environment with fixed resources [5]. Understanding how the inferior species can coexist with the superior one can provide basic insights into the coexistence problem [5,7]. Previous works suggested that the dispersal of the inferior species is essential for its competitive survival and unstable dynamics such as chaos can greatly facilitate the survival and hence coexistence. Recently, we have addressed the role played by noise in promoting species coexistence [8]. In particular, we have demonstrated that noise can enhance the intermittency in the synchronization between patch populations. As a result, some properly defined measure of the degree of coexistence can be optimized by noise, similar to stochastic resonance [9–12]. The purpose of this Brief Report is to complement Ref. [8] by presenting a physical theory for the main scaling law that implies this phenomenon.

The beneficial role of background noise in physical systems [10,11] has been appreciated, particularly since the discovery of stochastic resonance [9]. The effect of noise on ecological system was first addressed by Vilar and Solé [12], where the interplay between noise and periodic modulations was studied in the classical Lotka-Volterra model that describes symmetric, two-species competition in a single environment. The authors found that noise can change the system dynamics characteristically and can enhance coexistence through stochastic resonance. Since the Lotka-Volterra model does not take into account space, the authors studied an idealized coupled-map lattice system and demonstrated that noise can affect the spatial pattern in population density. As we will see, our model differs from the Lotka-Volterra model in that space and species dispersal are essential for the population dynamics. Another feature of our model is that it was constructed based on realistic ecological considerations [5] and, hence, it is also distinct from idealized coupled-map lattice models. Dynamically, the key factor promoting coexistence in our model is unstable dynamics—e.g., chaos. The interplay between chaos and noise can enhance the degree of coexistence [8].

We shall be interested in how an inferior species may coexist with a superior one in a patchy environment. In order to survive in the closed environment where a superior and competitive species is present, the inferior species must move (or disperse) fast relative to the motion of the superior species. Another necessary condition for coexistence is spatiotemporal heterogeneity in the environment because, in a homogeneous environment, the superior species usually dominates [4]. It was shown by Holt and McPeek [5] that temporal irregularity in the dispersing dynamics *alone* can play the role of spatiotemporal heterogeneity and, in fact, chaotic dynamics is sufficient for dispersal to be favored. They obtained this important result by studying an ecologically realistic, two-species, and two-patch model. More detailed examination of this model revealed [7] that the chaotic dynamics is in fact an intermittent, temporally synchronous type of dynamics. In particular, if one examines the total populations in the two patches relative to their respective carrying capacities, one finds that the populations tend to synchronize with each other in various time intervals, with occasional, relatively fast phases of desynchronization. In a synchronous state, dispersal is disfavored, while it is favored during the desynchronization episodes. Thus, the more frequently desynchronizations occur, the more likely and robust that the inferior species is able to survive and coexist with the superior one. We have shown [8] that the presence of noise can enhance the occurrence of the desynchronization events by reducing the average time between these events. As a result, the average relative frequency of the dispersing species increases with noise. A maximal degree of coexistence, as characterized by equal frequencies of the two competing species, can be achieved for an optimal level of noise (stochastic resonance).

We consider the Holt-McPeek model [5]. Let $N_{ij}(t)$ be the population of clone i in patch j at generation t. The realized fitness (the local population growth rate) of clone i in patch j is given by

$$W_{ij}(t) = \exp[r_{ij}(1 - N_{Tj}(t)/K_j)], \qquad (1)$$

where r_{ij} is the intrinsic rate of increase of clone i at low-population size in patch j, $N_{Tj}(t) = N_{1j}(t) + N_{2j}(t)$ is the total population in patch j, and K_j is its carrying capacity. Realistically, in the same patch the intrinsic growth rates for different clones are approximately the same [5]. We thus write $r_{1j} = r_{2j} = r_j$ and $W_{ij} = W_j(t)$. Dispersal is modeled by assuming that, of the total population of clone i, a fraction e_i migrate at each generation from their natal patch, while the remainder $(1 - e_i)$ remain in this patch. The key parameter that distinguishes one clone from another is then e_i, the dispersal rate of clone i. There is a cost of dispersal, since the migratory fraction of the population experiences a mortality rate, which can be conveniently modeled by the parameter $(1 - m)$. That is, only a fraction m of immigrants compete on equal terms with the resident population. To have a model feasible for computation and analysis, the following ecologically realistic assumptions were also made [5]: (1) reproduction and density dependence precede dispersal, (2) the census immediately follows dispersal, (3) costs of dispersal for a clone are experienced entirely by those individuals that actually disperse, and (4) population densities are sufficiently high so that they can be treated as continuous variables rather than discrete integers. The resulted model can be written as a four-dimensional, discrete-time, noninvertible map [5]:

$$N_{11}(t+1) = (1 - e_1)W_1[N_{t1}(t)]N_{11}(t) + me_1 W_2[N_{t2}(t)]N_{12}(t),$$

$$N_{12}(t+1) = (1 - e_1)W_2[N_{t2}(t)]N_{12}(t) + me_1 W_1[N_{t1}(t)]N_{11}(t),$$

$$N_{21}(t+1) = (1 - e_2)W_1[N_{t1}(t)]N_{21}(t) + me_2 W_2[N_{t2}(t)]N_{22}(t),$$

$$N_{22}(t+1) = (1 - e_2)W_2[N_{t2}(t)]N_{22}(t) + me_2 W_1[N_{t1}(t)]N_{21}(t).$$
$$\qquad (2)$$

The effect of small, *additive* noise on a reduced, two-dimensional Holt-McPeek model [7] has been considered [13] in terms of the dynamical phenomenon of bubbling [14]. The ecological meaning of additive noise is, however, not clear. Realistically, random fluctuations in the environment would ultimately affect the resource required for population dynamics. It is thus reasonable to assume that the carrying capacities of the patches fluctuate randomly about some nomial values: $K_j(t) = \bar{K}_j + \epsilon \xi_j(t)$, where ϵ is the noise amplitude and $\xi_j(t)(j=1,2)$ are independent random variables of zero mean and unit variance. The noise terms thus enter the Holt-McPeek model in a sophisticated way in the sense that it is neither additive nor multiplicative but may be a complicated combination of both.

A convenient quantity to characterize the degree of synchronization [7] is $Q(t) \equiv N_{T1}(t)/K_1 - N_{T2}(t)/K_2$, where N_{T1} and N_{T2} are the total population in patches 1 and 2, respectively. It has been demonstrated [8] that noise typically enhances the intermittent behavior in $Q(t)$. The intermittent dynamics can be characterized by the distribution of the time interval τ during which the patchy populations are temporally synchronized. Extensive numerical computations suggest that, for small noise, $\langle \tau \rangle$ remains approximately constant

and it starts to decrease algebraically as ϵ is increased [8],

$$\langle \tau \rangle \sim \begin{cases} \text{const}, & \text{for } \epsilon < \epsilon_c, \\ \epsilon^{-\alpha}, & \text{for } \epsilon > \epsilon_c, \end{cases} \qquad (3)$$

where $\alpha > 0$ and ϵ_c is a constant. The observation that the average synchronization time starts to decrease with ϵ for $\epsilon > \epsilon_c$, where ϵ_c corresponds to the magnitude of random fluctuations of about 1% of the carrying capacities, has a significant consequence. As the desynchronization bursts become more often, the fast-dispersing species experiences more frequent episodic increases, resulting an increase in its population. Indeed, we find [8] that the average frequency $\bar{p}_1(\epsilon) \equiv \lim_{T \to \infty}(1/T)\Sigma_{t=1}^{T}p_1(t)$ starts to increase for $\epsilon > \epsilon_c$, while it remains approximately constant for $\epsilon < \epsilon_c$. Suppose, in the absence of noise, the population of the dispersing species falls below that of the relatively stationary species—i.e., $\bar{p}_1(0) < \bar{p}_2(0)$. As ϵ is increased through ϵ_c, $\bar{p}_1(\epsilon)$ increases but this means a simultaneous reduction in the average frequency of the stationary species [since $\bar{p}_1(\epsilon) + \bar{p}_2(\epsilon) = 1$]. That is, *coexistence is enhanced by noise*. We can imagine that for a higher level of noise, an equilibrium point may be reached where the average frequencies of the two species become equal, signifying an *optimal* state of coexistence. As the noise level is increased further, $\bar{p}_1(\epsilon)$ exceeds $\bar{p}_2(\epsilon)$ so that the trend is reversed: coexistence tends to be weakened for very large noise. All these point to a phenomenon similar to stochastic resonance: *coexistence can be optimized by noise*.

To derive the scaling law (3), we use a simplified version of the Holt-McPeek model [7], a two-dimensional noninvertible map that retains the essential ecological ingredients of the full model. The map can be approximated by a typical on-off intermittent dynamical system. Under noise, the system can be analyzed by using the Fokker-Planck (FP) Eq. [15]. A unique feature not present in previous analyses is that in the canonical model for on-off intermittency derived from the Holt-McPeek model, the equivalant additive noise term contains two contributions: one from random noise and another from deterministic dynamics. This affects the choice of proper boundary conditions when solving the FP equation. In particular, the noise amplitude and the deterministic fluctuations define the location of a reflecting barrier in the domain where the FP equation holds. The common feature between noise and deterministic fluctuations is that they both can induce desynchronization bursts. If the effect of noise is shadowed by that of the deterministic fluctuations, the location of the reflecting boundary condition is determined by the dynamics and is independent of the noise amplitude. Otherwise it is determined by the noise amplitude. Analysis of the first-passage time leads to the scaling law (3).

To construct an analyzable model, we recall that the typical setting to address the coexistence problem in species dispersal, as in the Holt-McPeek model, is that one species is nearly stationary and another is rapidly moving between patches. Coexistence is indicated by a nonzero average population of the dispersing species. The influential dynamical variables are thus the populations of the dispersing species in different patches. As an approximation, we can regard the populations of the nearly stationary species as entirely sta-

tionary and drop these populations from consideration. The physical effects of the stationary populations, however, cannot be neglected. A reasonable assumption is that the stationary species only affects the resources available to the dispersing species but not contributing to dispersal itself. Accordingly, we consider a one-species, two-patch model where the existence of the stationary species (with its time-varying population densities) affects the system by imposing time-dependent resources availability. The influence of the stationary clone is modeled in the system by the choice of $K_j(t)$'s, time-varying carrying capacities. The model becomes

$$N_1(t + 1) = (1 - e)W_1(t)N_1(t) + meW_2(t)N_2(t),$$

$$N_2(t + 1) = (1 - e)W_2(t)N_2(t) + meW_1(t)N_1(t), \quad (4)$$

where the growth dynamics in the two patches are given by $W_1(t) = e^{r[1 - N_1(t)/K_1(t)]}$ and $W_2(t) = e^{r[1 - N_2(t)/K_2(t)]}$.

When the patches are identical and the influence of the stationary clone is also identical, we have $K_1(t) = K_2(t) = K(t)$ and $r_1 = r_2 = r$. It is convenient to normalize the populations in terms of the carrying capacities and make the following change of variables:

$$u(t) = \frac{1}{2}\left[\frac{N_1(t)}{K_1(t)} + \frac{N_2(t)}{K_2(t)}\right], \qquad v(t) = \frac{1}{2}\left[\frac{N_1(t)}{K_1(t)} - \frac{N_2(t)}{K_2(t)}\right].$$

In the new variables, we have

$$u(t + 1) = [AW_1(t) + AW_2(t)]u(t) + [AW_1(t) - AW_2(t)]v(t),$$

$$v(t + 1) = [BW_1(t) - BW_2(t)]u(t) + [BW_1(t) + BW_2(t)]v(t),$$
$$\quad (5)$$

where $A = 1 - e + me$ and $B = 1 - e - me$. In the vicinity of the synchronization state, we have $v \approx 0$. Using the Taylor expansion to the first order, $e^{\pm rv(t)} \approx 1 \pm rv(t)$, we obtain the time-dependent growth factors $W_{1,2}(t)$,

$$W_1(t) = e^{r[1 - u(t) - v(t)]} \approx e^{r(1 - u(t))}[1 - rv(t)],$$

$$W_2(t) = e^{r[1 - u(t) + v(t)]} \approx e^{r(1 - u(t))}[1 + rv(t)]. \quad (6)$$

Near the synchronization state, $v(t) \approx 0$. Thus, to first order in v, we obtain

$$u(t + 1) = Ae^{\{r[1 - u(t)]\}}u(t),$$

$$v(t + 1) = Be^{\{r[1 - u(t)]\}}[1 - ru(t)]v(t). \quad (7)$$

The remarkable observation is that Eq. (7) is similar to the model equation for synchronization and on-off intermittency in nonlinearly coupled, identical maps [16]. This allows us to understand these dynamical phenomena in a more explicit way. For instance, we see that the synchronization state $v = 0$ is invariant under Eq. (7) and, hence, if it is transversely stable, perfect synchronization $v = 0$ can be realized.

When $K_1(t) \neq K_2(t)$, we obtain from Eq. (4), in the (u, v) coordinates, the following [again by Taylor expansion to the first order in $v(t)$]:

$$u(t + 1) = e^{r(1 - u(t))}[A_+ u(t) + A_-(A_- - 1 + e)rv(t)u(t)$$
$$\qquad - (A_- - 1 + e)v(t)],$$

$$v(t + 1) = e^{r(1 - u(t))}[-B_+ rv(t)u(t) + B_+ v(t) - (B_- - 1 + e)u(t)],$$
$$\quad (8)$$

where the quantities A_+, A_-, B_+, and B_- are given by $A_+ = 1 - e + me[K_1^2(t) + K_2^2(t)]/[2K_1(t)K_2(t)]$, $A_- = 1 - e + me[K_1^2(t) - K_2^2(t)]/[2K_1(t)K_2(t)]$, $B_+ = 1 - e - me[K_1^2(t) + K_2^2(t)]/[2K_1(t)K_2(t)]$, and $B_- = 1 - e - me[K_1^2(t) - K_2^2(t)]/[2K_1(t)K_2(t)]$. Since the patches are nonidentical, the synchronization state is now defined by $N_1/K_1 = N_2/K_2$. In addition, the variable v also appears in the equation for u. If the patches are nearly identical—i.e., $K_1(t) \approx K_2(t)$—Eq. (8) can be further reduced, as follows. Let $K_1(t) \equiv K(t)$ and $K_2(t) = K(t) + \delta(t)$, where $\delta(t)$ is small compared to $K(t)$. In this case after neglecting terms of order δ^2 or higher, we obtain $A_+ \approx 1 - e + me$, $A_- \approx 1 - e - me\delta(t)/[K(t) + \delta(t)]$, $B_+ \approx 1 - e - me$, and $B_- \approx 1 - e + me\delta(t)/[K(t) + \delta(t)]$. We thus have

$$u(t + 1) = e^{r[1 - u(t)]}\left[Au(t) + \frac{me\delta(t)rv(t)u(t)}{K(t) + \delta(t)} + \frac{me\delta(t)v(t)}{K(t) + \delta(t)}\right],$$

$$v(t + 1) = Be^{r[1 - u(t)]}[1 - ru(t)]v(t)$$
$$\qquad + e^{r[1 - u(t)]}me\delta(t)u(t)/[K(t) + \delta(t)]. \quad (9)$$

Since $\delta(t)$ is small, the last term in the $v(t + 1)$ equation can be considered a small amplitude, additive random noise. In addition, the leading term in the $u(t + 1)$ equation is $Ae^{r(1 - u(t))}u(t)$, which typically generates chaotic dynamics. The effect of $v(t)$ on $u(t)$ is coupled with the small parameter $\delta(t)$ and, hence, the $u(t)$ dynamics can be regarded as being approximately independent of $v(t)$. The v equation can thus be written concisely as

$$v(t + 1) = \alpha(t)v(t) + \eta(t), \quad (10)$$

where

$$\alpha(t) \equiv Be^{r[1 - u(t)]}[1 - ru(t)],$$
$$\quad (11)$$
$$\eta(t) \equiv e^{r[1 - u(t)]}me\delta(t)u(t)/[K(t) + \delta(t)]$$

are effectively random processes. Equation (10) is the canonical model for on-off intermittency [15,17].

For small $v(t)$, its evolution is determined mainly by the effective additive noise term $\eta(t)$. For on-off intermittency the behavior of large $v(t)$ is important, where the effect of $\eta(t)$ can be neglected. Letting $y(t) = \ln|v(t)|$, for $|v(t)| \gg |\eta(t)|$ we can write Eq. (10) as

$$y(t + 1) \approx y(t) + \nu + \beta(t), \quad (12)$$

where the constant ν is the average value of $\ln|\alpha(t)|$ and $\beta(t)$ is the deviation of $\ln|\alpha(t)|$ from ν [$\beta(t)$ has zero mean: $\langle\beta(t)\rangle = 0$]. Equation (10) models a random walk. The on-off intermittent dynamics can be analyzed by setting a threshold y_{th}, and the average dwelling time of the walker in the "off" state is the mean first-passage time through the threshold. In the continuous-time approximation, the first-passage time problem can be solved by using the following Fokker-Planck equation:

$$\partial P(y,t)/\partial t = -\nu \partial P(y,t)/\partial y + (D/2)[\partial^2 P(y,t)/\partial y^2], \qquad (13)$$

where $P(y,t)$ is the probability density function of y and $D \equiv \langle [y(t+1)-y(t)]^2 \rangle = \langle [\beta(t)]^2 \rangle$ is the diffusion coefficient. To solve Eq. (13), it is necessary to choose initial and boundary conditions. The choice of the initial condition is standard [15]; i.e., the walkers start somewhere below the threshold, $P(t=0,y) = \delta(y-y_0)$, where $y_0 < y_{th}$. A walker reaching the threshold is considered lost (corresponding to the "on" state) and, hence, there is an absorbing boundary condition at $y = y_{th}$: $P(t, y=y_{th}) = 0$.

A key feature in our random-walk model, Eq. (12), which differs from the previous treatment of noise-induced on-off intermittency in the literature [15], is the selection of the second boundary condition for the Fokker-Planck equation. In particular, if the additive noise is independent of the system dynamics, its effect can be taken into account conveniently by setting a reflecting boundary condition in the y space at a location determined by the noise amplitude. In our model, however, the additive noise term $\eta(t)$ is not completely independent of the dynamical variables $u(t)$ and $v(t)$ [Eq. (11)]. In fact, $\eta(t)$ is a result of both deterministic dynamics and noise. Heuristically, one can imagine two scales in the y space, one determined by the dynamics and another by noise. If the noisy scale is smaller than the dynamical scale, the reflecting boundary is at the dynamical scale, which is independent of the noise amplitude. In the opposite case, the boundary is determined by the noisy scale. We thus have the following reflecting boundary condition: $-\nu P(y = y_b, t) + (D/2)\partial P(y,t)/\partial y|_{y=y_b} = 0$, where

$$y_b = \begin{cases} \text{const,} & \text{for } \epsilon < \epsilon_c, \\ \ln \epsilon, & \text{for } \epsilon > \epsilon_c. \end{cases} \qquad (14)$$

Under these initial and boundary conditions, the first-passage time is [18]

$$\tau = -\int_0^\infty t\, dt \int_{y_0}^{y_{th}} dy\, \frac{\partial P(y,t)}{\partial t},$$

which can be analytically evaluated to yield [15,18]

$$\tau = (y_{th} - y_0)/\nu + (D/2\nu^2)e^{-2\nu(y_{th}-y_b)/D}[1 - e^{2\nu(y_{th}-y_0)/D}]. \qquad (15)$$

Two time scales are important. One is the diffusion time $\tau_d = (y_{th}-y_b)^2/D$, which is the time for the walker starting at the noise level to reach the threshold due to diffusion. Another is the ballistic time $\tau_b = (y_{th}-y_b)/|\nu|$, which is the time required for the walker to travel from the location determined by the noise level to the threshold via simple drift. In our ecological problem, typically the system remains in an approximate synchronization state for a long time, with occasional and rapid excursion from it. Translating into the walker's space, the diffusion time is much longer than the ballistic time: $\tau_d \gg \tau_b$. Using this condition and also noting that when random diffusion is dominant we have $|\nu(y_{th}-y_0)|/D \gg 1$, we can apply Taylor expansion to Eq. (15) to obtain

$$\tau \approx (D/2\nu^2)e^{2|\nu|(y_{th}-y_b)/D} \sim e^{-2|\nu|y_b/D}. \qquad (16)$$

Substitution of the reflecting boundary condition (14) into Eq. (16) yields the scaling law (3).

In conclusion, we have provided a physical theory to explain the scaling law reported in Ref. [8] that suggests the power of random noise to optimize the degree of species coexistence in a spatiotemporal environment.

[1] G. E. Hutchinson, *An Introduction to Population Ecology* (Yale University Press, New Haven, 1987).

[2] J. Roughgarden and J. Diamond, in *Community Ecology*, edited by J. Diamond and T. J. Case (Harper and Row, New York, 1986).

[3] M. Tokeshi, *Species Coexistence: Ecological and Evolutionary Perspectives* (Oxford University Press, Oxford, 1999).

[4] I. Hanski, *Metapopulation Ecology* (Oxford University Press, Oxford, 1999).

[5] R. D. Holt and M. A. McPeek, Am. Nat. **148**, 709 (1996).

[6] R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, 1973).

[7] M. A. Harrison *et al.*, Phys. Rev. E **63**, 051905 (2001); J. Theor. Biol. **213**, 53 (2001).

[8] Y.-C. Lai and Y. R. Liu, Phys. Rev. Lett. **94**, 038102 (2005).

[9] R. Benzi *et al.*, J. Phys. A **14**, L453 (1981).

[10] F. Moss and K. Wiesenfeld, Sci. Am. (Int. Ed.) **273**, 50 (1995); K. Wiesenfeld and F. Moss, Nature (London) **373**, 33 (1995); J. J. Collins *et al.*, *ibid.* **376**, 236 (1995).

[11] Stochastic resonance is such an extensive field that even a partial list of the literature is prohibitive here. For a comprehensive review, see, for example, L. Gammaitoni *et al.* Rev. Mod. Phys. **70**, 223 (1998), references therein.

[12] J. M. G. Vilar and R. V. Solé, Phys. Rev. Lett. **80**, 4099 (1998).

[13] F. Rollin and B. Cazelles, Phys. Rev. E **66**, 013901 (2002).

[14] P. Ashwin *et al.*, Phys. Lett. A **193**, 126 (1994).

[15] See, for example, A. Čenys and H. Lustfeld, J. Phys. A **29**, 11 (1996).

[16] See, for example, J. F. Heagy *et al.*, Phys. Rev. E **50**, 1874 (1994).

[17] See, for example, E. A. Spiegel, Ann. N.Y. Acad. Sci. **617**, 305 (1981); H. Fujisaka and T. Yamada, Prog. Theor. Phys. **74**, 919 (1985); **75**, 1087 (1986); A. S. Pikovsky and P. Grassberger, J. Phys. A **24**, 4587 (1991); N. Platt, E. A. Spiegel, and C. Tresser, Phys. Rev. Lett. **70**, 279 (1993); Y.-C. Lai, Phys. Rev. E **53**, R4267 (1996), **54**, 321 (1996); T. Yalcinkaya and Y.-C. Lai, Phys. Rev. Lett. **77**, 5039 (1997); D. Marthaler, D. Armbruster, Y.-C. Lai, and E. J. Kostelich, Phys. Rev. E **64**, 016220 (2001).

[18] C. W. Gardiner, *Handbook of Stochastic Methods* (Springer, Berlin, 1983).