# Noise Promotes Species Diversity in Nature

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Species diversity in nature is accomplished by coexistence. In a spatial environment, inferior but rapidly moving species can coexist with superior but relatively stationary species. Recent work showed that chaotic dynamics can provide the spatiotemporal variation in the fitness required for coexistence, via the dynamical mechanism of synchronization and intermittency. Utilizing a realistic model that consists of two interacting species in a two-patch environment, we discovered a stochastic-resonance phenomenon where noise can significantly enhance the coexistence and thereby promote species diversity.

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The beneficial role of background noise in physical systems [1] has been appreciated, particularly since the discovery of stochastic resonance [2]. Indeed, a nonlinear system in general cannot respond to a weak, subthreshold signal, but the presence of background noise can enhance the probability of threshold crossing, thereby increasing a system's response. Some proper measure of the response, e.g., signal-to-noise ratio [1] or correlation, can reach a maximum at an optimal noise level or in a range of noise levels [3]. It is in this sense that noise can be regarded as beneficial. Over the past two decades, stochastic resonance has been identified in many natural and man-made systems [1,4]. A related phenomenon is coherence resonance, where noise can induce a dominantly periodic motion [5] and enhance it. If a regular motion is desired, then noise can again be beneficial.

In this Letter, we argue that the benefits of noise may go far beyond the range of phenomena explored by traditional stochastic or coherence resonance: noise can in fact promote species diversity in nature. As diversity is accomplished by coexistence of species, we will focus on how noise affects species coexistence. To address this problem, we shall be interested in how an inferior species may coexist with a superior one in a patchy environment. In order to survive in a 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 [6]. It was shown by Holt and McPeek [7] 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 [8] 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 phases. Thus, the more frequently desynchronization occurs, the more likely and robust that the inferior species is able to survive and coexist with the superior one. We will show 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 realized by an optimal level of noise. This is a stochastic resonance. The goal of this Letter is to establish and quantify this phenomenon in relation to species coexistence.

Some background of the coexistence problem in ecology is as follows. Traditional approaches to species coexistence tended to focus on niche partitioning that includes differentiations in resource use and in response to predators and parasites [9]. The importance of spatial heterogeneity and dispersal in species coexistence was recognized [6]. In an environment consisting of local communities coupled in space, dispersal can facilitate coexistence at the landscape scale because it introduces a trade-off between colonizing and competitions among species [10]. More important is the temporal variation in the evolutionary dynamics of the dispersal because, without such variations, spatial heterogeneity alone does not appear to favor the evolution [11,12]. It was discovered recently in theoretical ecology through patchy-dynamical models that even without spatial heterogeneity, insofar as the nonlinear population dynamics is chaotic, the resulted spatiotemporal variation in fitness may be appropriate for the evolution of dispersal and, consequently, for coexistence to be favored [7,13,14]. These pioneering studies introduced a new, nonlinear-dynamics-based approach to the problem of coexistence.

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Taking this nonlinear-dynamical approach, we study a representative class of population models in which clones compete in patches and disperse among them. For simplicity, we assume that within patches all clones are equivalent, but their rates of movement among patches are generally different. If the population dynamics generates temporally varying states, two or more clones differing significantly in dispersal rates can coexist permanently [7,13–15]. Because of the equivalence of clones in any patch, there is no trade-off between colonizing and competitive abilities, in contrast to the traditional approach [9]. A plausible mechanism for coexistence, which was studied in detail recently [8], is that the system can produce distinct dynamical behaviors and it can shift between these behaviors in concordance with temporal variation in average dispersal rates. In particular, normalized patch populations tend to synchronize with each other, which is interspersed by rapid excursions from the synchronous state. Synchronization occurs as a result of strong coupling among the patch populations, which can be expected when the dispersal rates are high. This favors low dispersal, driving the system towards lower dispersal rates, which in turn reduces the amount of effective coupling among the dynamics of different patches and triggers the occurrence of desynchronization. During desynchronization, a selective advantage of dispersal emerges. The intermittent alternations between synchronization and desynchronization thus makes possible the coexistence of the highly dispersing species with the relatively stationary ones.

For concreteness, we consider a population model consisting of two species and two patches: the Holt-McPeek model [7]. 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 $W_{ij}(t) = \exp\{r_{ij}[1 - N_{Tj}(t)/K_j]\}$, 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 [7]. 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 $e_i$ migrates at each generation from their natal 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 $(1 - m)$. To have a model feasible for computation and analysis, the following ecologically realistic assumptions were also made [7]: (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. The resulted model can be written as a four-dimensional, discrete-time, noninvertible map [7]: $N_{i1}(t + 1) = (1 - e_i)W_1[N_{t1}(t)]N_{i1}(t) + me_iW_2[N_{t2}(t)]N_{i2}(t)$ and $N_{i2}(t + 1) = (1 - e_i)W_2[N_{t2}(t)]N_{i2}(t) + me_iW_1[N_{t1}(t)] \times N_{i1}(t)$, for $i = 1, 2$.

The effect of small, *additive* noise on a reduced, two-dimensional Holt-McPeek model [8] has been considered in [16]. 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 nominal values: $K_j(t) = \bar{K}_j + \epsilon\xi_j(t)$, where $\epsilon$ is the noise amplitude and $\xi_j(t)$ $(j = 1, 2)$ are independent random variables of zero mean and unit variance. The noise term thus enters 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.

Consider the situation where two species, one relatively stationary and another fast-moving, compete for a common resource. We can conveniently classify the fast-moving species as *inferior* because it would in general be displaced by the stationary species and becomes extinct if the population dynamics exhibits a stable fixed point [7]. Computationally, the two species can be distinguished by setting very different values for their dispersal rates, say $e_2 \ll e_1$ so that clone 1 is the inferior species. For concreteness, we choose $e_1 = 0.5$ and $e_2 = 0.01$, and other parameters to be $\bar{K}_1 = 100$, $\bar{K}_2 = 50$, $m = 1$, and $r_1 = r_2 = r$, where $r$ is a bifurcation parameter. If $r$ is small (say around the value of 1.0), the system's asymptotic dynamics is a stable fixed point, leading to the extinction of the inferior clone [7]. For higher values of $r$ (say about 3.0), chaotic attractors are common. In this case, the high-dispersal clone can persist and experience episodic increases in population [7]. A convenient quantity to measure the ability of the high-dispersal clone to coexist with the stationary clone is the frequency: $p_1(t) = [N_{11}(t) + N_{12}(t)]/[N_{11}(t) + N_{12}(t) + N_{21}(t) + N_{22}(t)]$. Figure 1(a) shows, for $r = 3.0$ and in the absence of noise ($\epsilon = 0$), a time trace of $p_1(t)$. The average value of $p_1(t)$ is about 0.34, indicating that under chaotic dynamics the inferior species can coexist with the superior one, although the frequency of the former is relatively smaller. The dynamical origin of the episodic increases in Fig. 1(a) can be understood by observing that, in the phase space, trajectories on the chaotic attractor tend to spend most time in the vicinity of the line defined by $N_{T1}/K_1 = N_{T2}/K_2$, with occasional deviations away from it [8]. Dynamics on the line can be regarded as a state of synchronization between the populations in the two patches, normalized by their respective carrying capacities. The quantity $Q(t) = N_{T1}(t)/K_1 - N_{T2}(t)/K_2$ can thus be used to characterize the degree of synchronization, as shown in Fig. 1(b) for

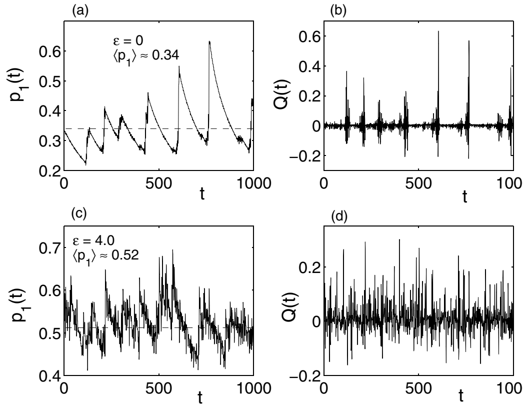

FIG. 1. For $r = 3.0$, (a) time evolution of the frequency $p_1(t)$ of the inferior species in the absence of noise ($\epsilon = 0$), and (b) on-off intermittency in $Q(t)$. (c), (d) $p_1(t)$ and $Q(t)$, respectively, for $\epsilon = 4.0$.

$\epsilon = 0$. We see that $Q(t)$ exhibits an on-off intermittent behavior. Under noise, we expect more desynchronous bursts to occur. Since the existence of the high-dispersal clone is favored by such desynchronzation events between the populations in the two patches, heuristically we expect noise to enhance the survivability of this inferior clone and hence to promote species coexistence. Figure 1(c) shows, for $\epsilon = 4.0$, the time evolution of $p_1(t)$, where we see that its average value is now increased to about 0.52, indicating that at this noise level (which corresponds to random fluctuations of magnitude of a few percent of the carrying capacities), the inferior and superior species appear almost equally often during the time evolution. The more frequent occurrence of the desynchronzation bursts in $Q(t)$ is shown in Fig. 1(d).

To demonstrate a more dramatic case of the positive role of noise in promoting coexistence, we set $r = 2.6$ for which $p_1(t)$ asymptotically approaches zero (i.e., the inferior species becomes extinct) in the absence of noise, as shown in Fig. 2(a). However, the presence of noise can help restore and sustain the population, as shown in Fig. 2(b), where $\epsilon = 4.0$. We see that, on average, the inferior species appears almost frequently as the superior species. Examination of the synchronization dynamics indicates that, when noise is present, frequent and irregular desynchronization bursts dominate the evolution of $Q(t)$, similar to Fig. 1(d).

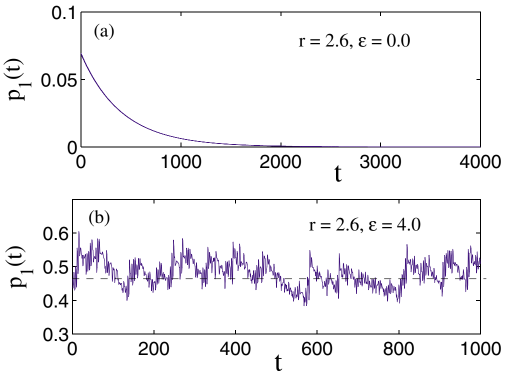

FIG. 2 (color online). For $r = 2.6$, (a) for $\epsilon = 0$ the frequency of the inferior species $p_1(t)$ asymptotically approaches zero, and (b) restoration of the population by noise for $\epsilon = 4.0$. In both cases, an initial transient of 1000 iterations is disregarded.

The intermittent dynamics can be conveniently characterized by the distribution of the time interval $\tau$ during which the patchy populations are temporally synchronized. The distribution can be numerically obtained by setting an arbitrary (small) threshold $Q_{\text{th}}$ and constructing histograms of the time intervals during which $Q(t) < Q_{\text{th}}$. Figure 3(a) shows, for $r = 3.0$, on a semilogarithmic scale, histograms of $\tau$ for four values of the noise amplitude. For relatively small noise (say $\epsilon = 1.0$), the distribution exhibits an apparent exponential tail in the large $\tau$ range. For larger noise, the distributions are dominantly exponential. For a given noise amplitude, an average synchronization time $\langle\tau\rangle$ can thus be meaningfully defined. Figure 3(b) shows $\langle\tau\rangle$ versus $\epsilon$ on a logarithmic scale. We observe that for small noise, $\langle\tau\rangle$ remains approximately constant and starts to decrease algebraically as $\epsilon$ is increased:

$$\langle\tau\rangle \sim \begin{cases} \text{constant}, & \text{for } \epsilon < \epsilon_c \\ \epsilon^{-\alpha} & \text{for } \epsilon > \epsilon_c, \end{cases} \tag{1}$$

where $\alpha > 0$ and $\epsilon_c \approx 1.0$.

The observation that the average synchronization time starts to decrease with $\epsilon$ for $\epsilon > \epsilon_c$, where $\epsilon_c$ 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 in an increase in its population. Indeed, we find that the average frequency $\bar{p}_1(\epsilon) \equiv \lim_{T\to\infty}(1/T)\sum_{t=1}^{T} p_1(t)$ starts to increase for $\epsilon > \epsilon_c$, while it remains approximately constant for $\epsilon < \epsilon_c$.

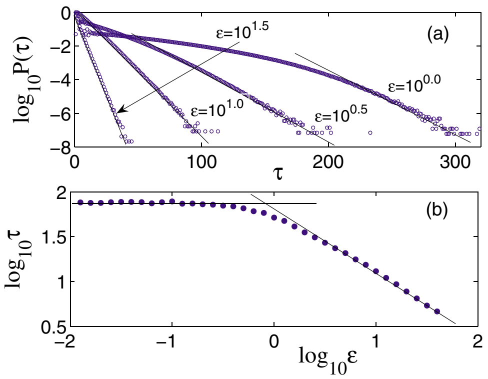

FIG. 3 (color online). For $r = 3.0$, (a) distributions $P(\tau)$ for four noise levels and (b) average synchronization time $\langle\tau\rangle$ vs the noise amplitude $\epsilon$.

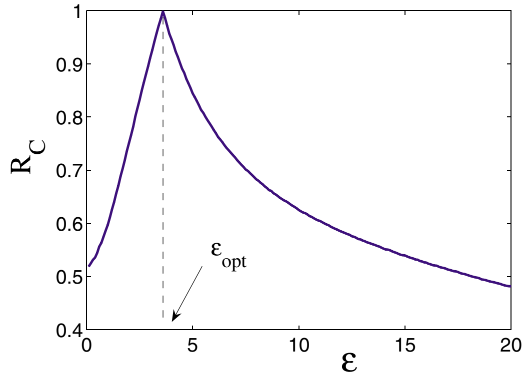

FIG. 4 (color online). For the Holt-McPeek model for $r = 3.0$, stochastic resonance in coexistence as characterized by $R_C(\epsilon)$, the degree of coexistence as a function of noise amplitude.

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 $\epsilon$ is increased through $\epsilon_c$, $\bar{p}_1(\epsilon)$ increases, but this means a simultaneous reduction in the average frequency of the stationary species $[\bar{p}_1(\epsilon) + \bar{p}_2(\epsilon) = 1]$. 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 [1–4]: *coexistence can be optimized by noise*. To enable a quantitative characterization, we introduce the following quantity $R_C$ to measure the *degree of coexistence*: $R_C(\epsilon) \equiv \bar{p}_{\min}(\epsilon)/\bar{p}_{\max}(\epsilon)$, where $\bar{p}_{\min}$ ($\bar{p}_{\max}$) is the smaller (larger) of $\bar{p}_1$ and $\bar{p}_2$. There can be no coexistence if $R_C = 0$, but a maximally possible degree of coexistence occurs if $R_C = 1$. Figure 4 shows, for the Holt-McPeek model for $r = 3.0$, such a stochastic resonance. We see that there indeed exists an optimal noise level for which the degree of coexistence becomes maximal in the sense that both species appear equally frequently in the course of dynamical evolution.

Theoretically, the scaling law (1), which is key to the observed stochastically resonant behavior in coexistence, can be derived based on a canonical model for on-off intermittency, under both symmetry breaking and noise. In fact, a simplified version of the Holt-McPeek model, which is a two-dimensional noninvertible map and amenable to analysis to some extent, can be obtained [8]. This map can be written in a form that models a typical on-off intermittent dynamical system with symmetry breaking [17]. Under noise, the system can be analyzed by using the Fokker-Planck (FP) equation [18]. A unique feature that is not present in previous analyses is the choice of proper boundary conditions when solving the FP equation. In particular, the noise amplitude or a symmetry-breaking parameter determines the location of a reflecting barrier in the domain where the FP approximation holds. The common feature between noise and asymmetry is that they both can induce desynchronization bursts. If the effect of noise is shadowed by that of asymmetry, the reflecting boundary condition is determined by the degree of asymmetry, otherwise it is determined by the noise amplitude. Analysis of the first-passage time leads to the scaling law (1), from which the stochastic-resonance behavior in Fig. 4 can be understood.

In summary, our computations and analysis suggest that noise can be beneficial for the coexistence of species with distinct compatibilities in a spatiotemporal, patchy environment. At a quantitative level, we discovered a stochastic-resonance phenomenon displaying the power of random noise to optimize coexistence. The conclusion that noise can promote and significantly enhance coexistence could be insightful for answering the fundamental questions concerning species diversity in nature through the nonlinear-dynamical-system approach.

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