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

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Harrison *et al*. [Phys. Rev. E **63**, 051905 (2001)] recently proposed that the temporal synchronization and desynchronization between populations in different habitats leads to species coexistence and occurs through a pattern of on-off intermittency. As noise is unavoidable in ecological systems, we show, using the same example, that "attractor bubbling" appears to be another plausible hypothesis to explain the scenario leading to species coexistence. The interest of attractor bubbling in ecology is confirmed by other examples concerning the evolution of intermittent rare species.

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In ecology, it has recently been suggested that dynamics associated with the transverse stability of an invariant subspace (e.g., riddled basins or on-off intermittency) can have important outcomes and provide working assumptions to explain observed dynamics [1,2]. For example, on-off intermittency may describe the dynamics of natural populations, where variable periods of time at low rarity alternate with sudden outbreaks of high abundance in a seemingly unpredictable way [2,3].

The aim of a recent paper by Harrison *et al*. [4] was to demonstrate that on-off intermittency can explain the erratic alternation of the synchronized-desynchronized behavior of two species abundances in a two-patch ecological system, leading to species coexistence.

It has been demonstrated that complex nonlinear population dynamics can produce the appropriate conditions that favor the coexistence of competing species [5,6]. Studying the coexistence of two different species in a two-patch system, Holt and McPeek [5] showed that coexistence arises because of the alternation in the system dynamics, between two qualitatively distinct dynamical behaviors associated with temporal variation in the mean dispersal rates. The populations in the two patches tend to be synchronized when the frequency of the high-dispersal species is large because there is a strong coupling between the two patches. But in this nearly synchronized state, dispersal becomes disadvantageous, leading to a decrease in high-dispersal species and, hence, over time the patch dynamics becomes progressively uncoupled. As the system evolves towards lower dispersal rates, the dynamics of different patches may become desynchronized, providing the conditions in which dispersal is, once again, advantageous.

Then Harrison *et al*. [4] argued that this scenario explaining the coexistence, synchronization → desynchronization → synchronization → ..., with unpredictable time intervals between each phase is a pattern of on-off intermittency. Nevertheless, as noise is unavoidably present in ecological systems, another plausible and interesting hypothesis to explain this scenario leading to coexistence should be "attractor bubbling" [7–9].

Bubbling of attractors is a form of noise-driven intermittence associated to locally riddling basins [8], which appears with a weakly stable invariant manifold, contrary to on-off intermittency which is associate to weakly unstable invariant manifold. Noise destroys the stability of the invariant manifold which induces a continual sequence of intermittent burst from the invariant manifold. But as this manifold is asymptotically stable it reattracts typical orbits in its neighborhood [7].

Here we illustrate the interest of attractor bubbling in understanding the dynamics of competing species in spatially extended systems and we emphasize, with other examples of intermittent rare species, that these behaviors might be widespread and ecologically more likely than on-off intermittency.

In this study we have used the Holt-McPeek model [5] and its simplified version for two identical patches [4]. The Holt-McPeek model is given by

$$\begin{aligned} x_1(t+1)&=(1-e_x)x_1(t)f_1(t)+me_xx_2(t)f_2(t),\\ y_1(t+1)&=(1-e_y)y_1(t)f_1(t)+me_yy_2(t)f_2(t),\\ x_2(t+1)&=(1-e_x)x_2(t)f_2(t)+me_xx_1(t)f_1(t),\\ y_2(t+1)&=(1-e_y)y_2(t)f_2(t)+me_yy_1(t)f_1(t), \end{aligned} \tag{1}$$

where x_i and y_i are the two species in patch i, $f_i(t)$ is the density dependent growth function of patch i [$f_i(t)=\exp(r_i[1-(x_i(t)+y_i(t))/k_i])$], k_i is the carrying capacity, r_i is the growth rate, $e_{x,y}$ is the species dependent dispersion rate, and $(1-m)$ is the cost of dispersal.

Considering one of the two species (y_i) with dispersal rate near zero and with stationary behavior, the dynamics of the high-dispersing species (x_i) can be described in the case of two identical patches by the simplified version of the Holt-McPeek model established in [4]

$$\begin{aligned} u(t+1)&=A\exp\{r[1-u(t)]\}u(t),\\ v(t+1)&=B\exp\{r[1-u(t)]\}[1-ru(t)]v(t), \end{aligned} \tag{2}$$

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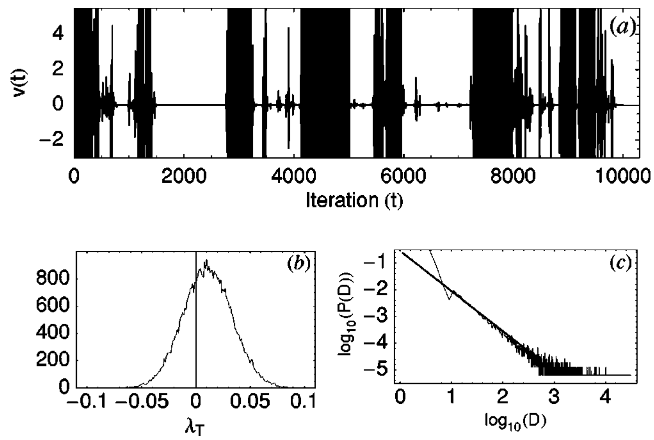

FIG. 1. On-off intermittency in the simplified Holt-McPeek model (2). (a) Intermittent dynamics of $v(t)$, the difference between the high-dispersing species (x_i) of the two patches. (b) Distribution of the finite time fluctuations of $\lambda_\perp$ ($\lambda_T \equiv \lambda_\perp$) characterizing the stability of the synchronization manifold, $v=0$. (c) Distribution of the "off" phases (defined by perfect synchronous dynamics $v=0$) of duration D. In (c) the straight line corresponds to the theoretical distribution with slope $\beta=-3/2$. The parameter values are $r=4.5$, $e=0.45$, and $m=0.336$.

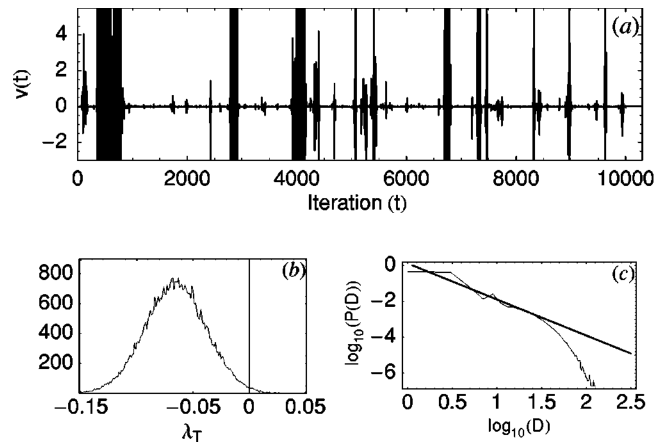

FIG. 2. Bubbling in the simplified Holt-McPeek model (2). (a) Intermittent dynamics of $v(t)$, the difference between the high-dispersing species (x_i) of the two patches. (b) Distribution of the finite time fluctuations of $\lambda_\perp$ ($\lambda_T \equiv \lambda_\perp$) characterizing the stability of the synchronization manifold, $v=0$. (c) Distribution of the "off" phases (defined by perfect synchronous dynamics $v=0$) of duration D. In (c) the straight line corresponds to an estimated slope $\hat{\beta} \approx -2$. The parameter values are $r=4.5$, $e=0.45$, $m=0.350$, and $\sigma=10^{-8}$.

where $A=1-e+me$, $B=1-e-me$, $u(t)=[x_1(t)+x_2(t)]/2k(t)$, $v(t)=[x_1(t)-x_2(t)]/2k(t)$, and $k(t)$ is the time dependent carrying capacities of the two identical patches $[k(t)=k_1(t)=k_2(t)]$.

Figure 1 summarizes some of the results presented by Harrison *et al.* [4]. Figure 1(a) shows the intermittent evolution of $v(t)$. The line $v=0$ defined the synchronization manifold of which the stability is characterized by the transverse Lyapunov exponent ($\lambda_\perp$). The "off" state is defined by the synchronization of the high-dispersal species, $v=0$. During the "on" state the populations of the two patches are repelled from $v=0$ and become desynchronized. After some period of time the trajectories in the "on" state will be reattracted toward the "off" state [see, Fig. 1(a)]. Figure 1(b) displays the distribution of the finite time fluctuations of $\lambda_\perp(t)$ and underlines that in this particular case the synchronization manifold is slightly unstable ($\lambda_\perp \gtrsim 0$). Then on-off intermittency can develop. Figure 1(c) confirms the occurrence of on-off intermittency in the behavior of $v(t)$ showing that the probability distribution of the "off" phases $P(D)$ depends on their duration D as $P(D) \propto D^\beta$, with $\beta=-3/2$ the universal scaling coefficient characterizing on-off intermittency [10].

Another interesting behavior that can also explain the scenario leading to the coexistence of dispersing species is attractor bubbling. To study bubbling we have added some uniform noise to the equation of $v(t)$ with intensity σ. Figure 2 summarizes our results. Figure 2(a) displays the intermittent dynamics of $v(t)$, Fig. 2(b) the distribution of the transverse Lyapunov exponent, and Fig. 2(c) the power law of the frequency of laminar phases of duration D. The pattern of the intermittences shown on Fig. 2 is different from the previous case (Fig. 1) and is typical of attractor bubbling, i.e. noise-driven intermittences despite that the synchronization manifold $v=0$ is asymptotically stable. As the synchronization manifold is weakly stable [$\lambda_\perp \lesssim 0$, see Fig. 2(b)], it is locally repelling thus small perturbation will result in a brief excursion from the synchronization manifold. These desynchronization events recur because the chaotic evolution brings it into the neighborhood of the repelling trajectories an infinite number of times. In this case the power law is deviating from the universal power law governing on-off intermittency ($\beta=-3/2$), and we observe $\hat{\beta} \approx -2$.

To corroborate our results about the importance of attractor bubbling in population dynamics, we provide another example concerning the evolution of intermittent rare species.

Competition between different species can be modeled as a dynamical system with an invariant subspace corresponding to the extinction of one (or more) species [1–3], for instance $x_i=0$ in the Holt-McPeek model (1). The loss of stability of the attractor in the invariant subspace means that the corresponding species (x_i) can invade and coexist with other species (y_i) [2].

Figure 3 displays an example of dynamics associated to attractor bubbling in this particular context with the Holt-McPeek model (1). Figure 3(a) displays the intermittent dynamics of $x_1(t)$ [similar erratic dynamics is observed for $x_2(t)$]. Figure 3(b) shows the distribution of the transverse Lyapunov exponent and Fig. 3(c) shows the probability distribution of the frequency of the phase of rarity $[x_i(t)=0]$ of duration D. As in Fig. 2, the pattern of the intermittences shown on Fig. 3 is typical of attractor bubbling, i.e., noise-driven intermittences with asymptotically stable invariant manifold $x_i=0$. As the invariant manifold is weakly stable [$\lambda_\perp \lesssim 0$, see Fig. 3(b)], it is locally repelling thus a small perturbation will result in a brief excursion from the invariant manifold, i.e., in a brief intermittent invasion of the rare species x_i. In this case the probability distribution of the

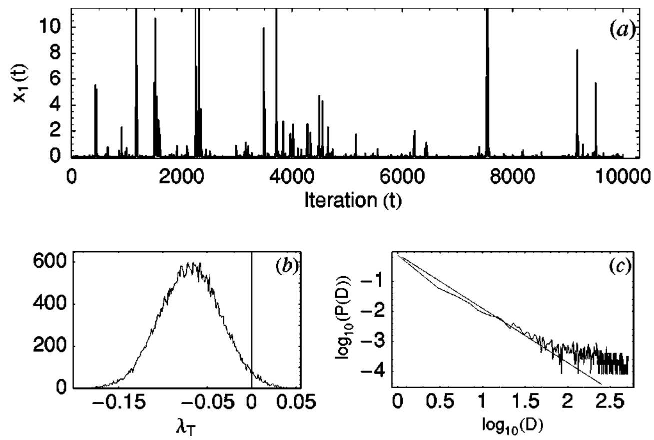

FIG. 3. Bubbling in the Holt-McPeek model (1) when the invariant manifold is defined by the extinction of the x_i species. (a) Intermittent dynamics of $x_1(t)$. (b) Distribution of the finite time fluctuations of $\lambda_\perp$ ($\lambda_T \equiv \lambda_\perp$) characterizing the stability of the invariant manifold, $x_i=0$. (c) Distribution of the "off" phases (defined by the extinction of the x_i species) of duration D. In (c) the straight line corresponds to an estimated slope $\hat{\beta} \approx -1.8$. The parameter values are $e_1=0.5$, $r_1=3$, $k_1=100$, $e_2=0.01$, $r_2=3$, $k_2=50$, $m=0.19$, and $\sigma=10^{-4}$.

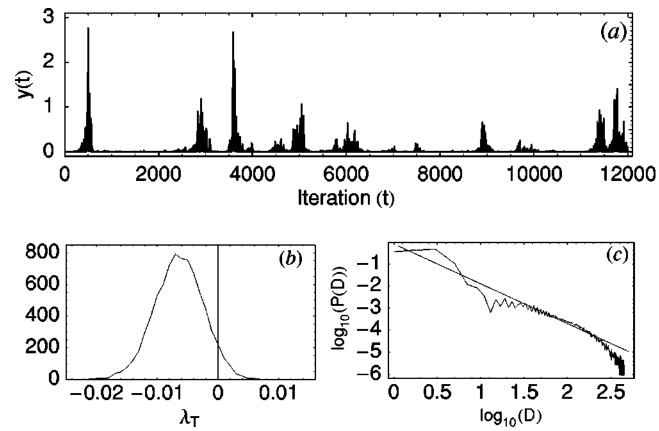

FIG. 4. Bubbling in a host-parasitoids community model (3) with a specialist (y) and a generalist parasitoid (z) when the invariant manifold is defined by the extinction of the specialist parasitoid (y). (a) Intermittent dynamics of $y(t)$. (b) Distribution of the finite time fluctuations of $\lambda_\perp$ ($\lambda_T \equiv \lambda_\perp$) characterizing the stability of the invariant manifold, $y=0$. (c) Distribution of the "off" phases (defined by the extinction of the specialist parasitoid y) of duration D. In (c) the straight line corresponds to an estimated slope $\hat{\beta} \approx -1.8$. The parameter values are $r_1=2.8$, $k_1=5$, $a_2=2.165$, $k_2=0.3$, $a_3=0.5$, $c_3=2$, and $\sigma=10^{-7}$.

frequency of the phase of rarity $[x_i(t)=0]$ shows a well-defined power law with an estimated scaling coefficient $\hat{\beta} \approx -1.8$.

This type of intermittent behavior associated to a weakly stable submanifold is present in all the models of competition between species employed in Refs. [1–3]. One can also observe attractor bubbling in population model with predation or host-parasitoid interactions. To illustrate this last point, we took into account the destabilizing effect of a generalist parasitoid modeled by a Nicholson-Bailey model [11] that invades a dynamically stable "host-specialist parasitoid community" described by a May host-parasitoid model [12]. The model reads

$$x(t+1)=x(t)\exp\left\{r_1\left(1-\frac{x(t)}{k_1}\right)\right\}\left[1+\frac{a_2y(t)}{k_2}\right]^{k_2}\times\exp\{-a_3z(t)\},$$

$$y(t+1)=x(t)\left(1-\left[1+\frac{a_2y(t)}{k_2}\right]^{k_2}\right)\exp\{-a_3z(t)\}, \quad (3)$$

$$z(t+1)=c_3[x(t)+y(t)][1-\exp\{-a_3z(t)\}],$$

where x, y, and z are the host, the specialist parasitoid and the generalist parasitoid, respectively. r_1 is the growth rate of the host, k_1 is the carrying capacity of the environment of the host, a_j are the attack rates of the parasitoid j, k_2 is the parameter of the density dependence of the attack function of the specialist parasitoid, and c_3 is the number of generalist parasitoid produced by infested host.

Figure 4 displays an example of the intermittent dynamics associated to the model (3). Figure 4(a) shows the intermittent behavior of the specialist parasitoid y, Fig. 4(b) shows the distribution of the transverse Lyapunov exponent and Fig. 4(c) shows the power law of the frequency of laminar phases of duration D. The pattern of the intermittences shown on Fig. 4 appears similar to that of previous figures (Figs. 2 and 3) and is typical of attractor bubbling.

Here we have explored noise-induced attractor bubbling but another scenario generating attractor bubbling is linked to parameter mismatches [7,8]. Small changes in some of the parameters can destroy the invariant manifold (defined by synchronous dynamics or species extinction). Nevertheless if the mismatches are small the attractor that exists in the invariant manifold is replaced by an attractor that is restricted in its neighborhood. Then every orbit that approaches the initial manifold can spent some period of time in its vicinity before bursting away. This sort of dynamics can arise in the simplified model described by Harrison *et al.* [4] when the carrying capacities in the two patches are different $[k_1(t) \neq k_2(t)]$. These parameter mismatches break down the stability and the invariance of the synchronization manifold and cause the system to burst away from the invariant manifold intermittently even if on average it is attracting.

These results suggest that on-off intermittency is not the only phenomena that can explain the intermittences leading to the coexistence of competing species in spatially extended ecological systems. As noise and parameter fluctuations are unavoidable and ubiquitous in ecological systems, intermittent dynamics associated to attractor bubbling appears to be another interesting mechanism to explain the erratic alternation of the synchronized-desynchronized behavior of two species in a two-patch system, as well as for the dynamics of intermittent rare species.

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