Emergence of Chaotic Itinerancy in Simple Ecological Systems

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(Dated: February 4, 2008)

Chaotic itinerancy is a universal dynamical concept that describes itinerant motion among many different ordered states through chaotic transition in dynamical systems. Unlike the expectation of the prevalence of chaotic itinerancy in high-dimensional systems, we identify chaotic itinerant behavior from a relatively simple ecological system, which consists only of two coupled consumer-resource pairs. The system exhibits chaotic bursting activity, in which the explosion and the shrinkage of the population alternate indefinitely, while the explosion of one pair co-occurs with the shrinkage of the other pair. We analyze successfully the bursting activity in the framework of chaotic itinerancy, and find that large duration times of bursts tend to cluster in time, allowing the effective burst prognosis. We also investigate the control schemes on the bursting activity, and demonstrate that invoking the competitive rise of the consumer in one pair can even elongate the burst of the other pair rather than shorten it.

Since attractors determine the long-term behavior of dynamical systems, the concept of attractors is central to the analysis of many natural and artificial systems [1]. In general, the phase space of a nonlinear dynamical system is partitioned into various basins of attraction from which states evolve towards the respective attractors. These stable attractors can lose their stability with a change of the system condition such that the basin of attraction of each attractor becomes connected to each other through unstable manifolds. Hence, a dynamical state which sequentially traces out all of the destabilized attractor ruins emerges. This is referred to as a chaotic itinerant state [2]. The notion of chaotic itinerancy has received considerable attention in studying the adaptability of complex systems, especially in relation to brain information processing [2, 3].

To embed a chaotic itinerant state, a system is expected to have a high degree of complexity; therefore, models of chaotic itinerancy are mostly built on high-dimensional phase space [4]. Albeit relatively low-dimensional systems, two coupled Morris-Lecar neural oscillators were found to exhibit chaotic itinerancy [5], the result seems to be limited to a rather special case concerns the satiability level of the consumers

$$\frac{dC_{1(2)}}{dt} = aC_{1(2)} \left[ \frac{R_{1(2)}}{\kappa + R_{1(2)}} + DR_{2(1)} \right] - bC_{1(2)} ,$$

$$\frac{dR_{1(2)}}{dt} = R_{1(2)} - R_{1(2)}^2 - \frac{[C_{1(2)} + DC_{2(1)}]R_{1(2)}}{\kappa + R_{1(2)}} , \quad (1)$$

where $C_{1(2)}$ and $R_{1(2)}$ represent the population of consumer 1 (2) and resource 1 (2), respectively. $a$ and $b$ denote the growth and decay rates of the population of consumers. $\kappa$ concerns the satiability level of the consumers taking resources. For simplicity in our analysis, we do not distinguish the parameter sets of the two consumer-resource pairs. In this equation, $R_{1(2)}$ is taken by $C_{1(2)}$ primarily, as well as by $C_{2(1)}$ with a relative small uptake rate $D$, which ranges from 0 to 1.

When $D$ is equal to zero, Eq. (1) splits into two Holling type-II forms of Lotka-Volterra equations [6], and the populations of each consumer-resource pair can exhibit a limit cycle oscillation. If $D$ takes a nonzero value close to 0 or 1, synchronous limit cycle oscillation between the two consumer-resource pairs arises. Complicated dynamics develop at intermediate range of $D$, where we can observe irregular bursting activities as in Figs. 1(a)–1(c). Time trajectories of $C_1$ and $C_2$ in Fig. 1(c) show the bursting behaviors, and those of $R_1$ and $R_2$ show the similar patterns as well. $C_1$ and $C_2$, or $R_1$ and $R_2$, fire bursts in an antiphase-synchronized way, such that the explosion of $C_1$ or $R_1$ co-occurs with the shrinkage of $C_2$ or $R_2$, and vice versa. It is worth noting that other equations with similar systems to Eq. (1) also support the existence of such antiphase-synchronized irregular bursts [8]. For numerical simulations, we use the parameters $a = 2, b = 0.82, \kappa = 0.33,$ and $D = 0.57$ unless specified.

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To check whether the apparent irregularity of the bursts implies their initial condition sensitiveness, we
we drop the subscript of \( M_{1(2)}(t) \) due to the statistical equivalence of \( C_1(t) \) and \( C_2(t) \). One can employ \( M(t) \) for determining the necessary time for the discrepancy to be significant between the bursting times of \( C_{1(2)}(t) \) and of \( C'_{1(2)}(t) \). It is observed that \( M(t) \) evolves rapidly from 1 to 0 in the irregular bursting regime; thus, the half-life time \( \tau_h \) of \( M(t) \) can serve as the characteristic time scale of the discrepancy growth. Figure 1(d) shows that \( \tau_h \) scales logarithmically to \( \varepsilon \), and using \( R_{1(2)}(t) \) and \( R'_{1(2)}(t) \) instead of \( C_{1(2)}(t) \) and \( C'_{1(2)}(t) \) in Eq. 2 does not alter the current result. This logarithmic scaling reveals that the bursting is sensitive to the initial conditions, i.e., behaves chaotically 9.

To address such antiphase-synchronized chaotic bursts in detail, we divide a period of bursts into four stages - S1, S1′, S2, and S2′, as in Fig. 1(e). In stage S1, \( C_1 \) and \( R_1 \) dominate \( C_2 \) and \( R_2 \), while \( C_1 \), which is supported primarily by \( R_1 \), depresses severely the growth of \( R_2 \), and thereby of \( C_2 \). Nonetheless, \( R_2 \) increases gradually in the negligible presence of \( C_2 \), and \( R_1 \) comes to decline with overpopulated \( C_1 \) which takes both \( R_1 \) and \( R_2 \). In stage S1′, the resultant shrinkage of \( R_1 \) ensures that \( C_1 \) depends mostly on \( R_2 \) for survival. Meanwhile, \( R_2 \) can boost the increase of \( C_2 \), which then suppresses both \( R_2 \) and \( R_1 \), thereby leading to the drastic decay of \( C_1 \) in stage S2 10. The dominance of \( C_2 \) and \( R_2 \) in stage S2 is totally symmetric to that of \( C_1 \) and \( R_1 \) in stage S1. Accordingly, stage S2′ analogous to stage S1′ follows, and leads to stage S1 for the next period.

Each stage occupies finite time-span, forming a quasi-stable dynamical state. The alternating dominance of each species along the stages may be equivalent to the switching events among the sets of attractor ruins. In order to elucidate the underlying attractor ruin for a given stage, we consider an invariant subspace of \( (C_1, R_1, C_2, R_2) \) which contains only the species governing the stage [see Fig. 1(e)]: at stage S1, \( (C_1, R_1, 0, 0) \); at stage S1′, \( (C_1, 0, 0, R_2) \); at stage S2, \( (0, 0, C_2, R_2) \); at stage S2′, \( (0, R_1, C_2, 0) \). The populations confined within each invariant subspace approach their own asymptotic solution. For instance, the limit cycle oscillation of \( C_1 \) and \( R_1 \) characterizes the asymptotic solution in the invariant subspace of stage S1 and thus underlies the bursting activity at this stage. Figure 2(a) shows an actual time trajectory of the populations in phase space, which also embeds the asymptotic solutions in the invariant subspaces. Near an invariant asymptotic solution, the trajectory remains there for a long time, but finally escapes towards another invariant solution at the next stage.

This escaping event is due to an existence of unstable manifolds outward from an invariant subspace. Along the transverse direction of the invariant subspace, we then perform a linear stability analysis to find the unstable
and $R$ with $S_1$ and $S_1'$ reveals which species causes the instability of a given stage; the instability of stages $S_1$ and $S_1'$ is invoked by the increase of $R_2$ and $C_2$, as described above in the ecological argument. From Eq. (3), we recognize that increase of $D$ tends to reduce the coefficients in the right-hand sides, i.e., to decrease the escape rates along the unstable manifolds. The resultant relaxation of the switching events among attractor ruins is identified by comparing Figs. 2(a) and 2(b), where consistently the trajectory between the invariant solutions looks less intermingled with increased $D$. The most evident effect of elongated residence in attractor ruins appears in Fig. 2(c): the distribution of burst duration $T$ shifts to large value as $D$ increases. Moreover, the larger $D$ is, the higher the right peak of the bimodal duration distribution is, relatively to the left peak. We conclude that in the chaotic bursting regime, the enhanced coupling strength induces either of the consumer-resource pairs to dominate the other for a long time by an elongated bursting activity.

To investigate the bimodality appearing in Fig. 2(c), we plot a return time map for burst initiations of consumers by considering the terms between the initiation of stage $S_1$ and that of stage $S_2$, and between the initiation of stage $S_2$ and that of stage $S_1$, and so on. Figures 3(a) and 3(b) display nearly one-dimensional curves of such return time maps, where stepwise jumps between the upper and lower extremes are responsible for the bimodality in Fig. 2(c). The relative expansion of upper extremes in Fig. 3(b) induces the right side of the duration distribution in Fig. 2(c) to be highly peaked.

Referring to the return time maps, we find that mapping trajectories are frequently trapped in boxed area B in Figs. 3(a) and 3(b). The distribution of residual times $N$ (total number of iteration) within boxed area B is indeed more right-skewed than those of any other areas (e.g., B') with the same size [Figs. 3(c) and 3(d)]. The distribution within area B follows exponential fit
burst duration. Since a rise of prognosis efficiently.

The past duration could be beneficial to improve the burst
Fig. 1(c). In this regard, the known information about
of bursts tend to cluster in time, as partially observed in
relatively long durations of bursts, large duration times
vivability follows a poissonian process, but with considerable sur-
time. This indicates the residual dynamics within area B
\[ D = 0 \]

\[ \text{terms in Eq. (1).} \]

of \( R \) for surrogated data (\( \text{resource competition between} \)
so essential to elongating the burst duration, despite the
noticed that the effect of delayed rise of \( C \) prevents the overpopulation of
\( \text{perturbation during the arrowed time interval by reducing} \)
(c)–(f): initially the same as (a) and (b), but subjected to
(c), (d) or doubling \( aC_2 \) [(e), (f)], given the
two

\[ = 0 \]

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\[ \text{Figures 4(e) and 4(f) indeed illustrate the possibility that} \]
a sufficiently large perturbation to increase \( C_2 \) withdraws
transiently \( R_1 \) and \( C_1 \), but also delays the growth of \( R_2 \)
thereby elongating the bursting activity [11].

In summary, we investigated a simple dynamical sys-
tem, which consists only of two consumer-resource pairs
but exhibits chaotic itinerancy naturally. The mathem-
atical simplicity of the system gives rise to a clear view
of the organization of a chaotic itinerant state, where
each consumer-resource relationship underlies its corre-
sponding attractor ruin as a dynamical ‘building block’.
Such concept of building blocks could be generically uti-
ized when one designs other systems exhibiting chaotic
itinerancy. In addition, analysis on a chaotic itinerant
state was found to be applicable to the prognosis and
control of the dynamical system, in the rather counterin-
tuitive way. Beyond the suggested ecological system, any
dynamical system which shows antiphase-synchronized
chaotic bursts might be analyzable in the framework of
chaotic itinerancy via our methodology. We expect that
host-parasitoid systems with whiteflies and their para-
sitic wasps could be employed for experimental valida-

tion of our results, since parasitic wasps (consumers) are
known to have overlapped hosts (resources) in a manner
similar to the present model [12].

The authors thank D. E. Postnov, Dong-Uk Hwang,
Hwang-Yong Kim for useful discussion. This work
was supported by the Korean Systems Biology Re-
search Project (M10309020000-03B5002-00000) (P.-J.K.
and H.J.), the Creative Research Initiatives of the Ko-


eran Ministry of Science and Technology (T.-W.K. and
K.J.L.), the SBD-NCRC program (R15-2004-033-07001-
0), and the BK21 program at Chungbuk University (S.K.H.).

\[ P(N) \propto p^N \] with \( p = 0.64 \) for \( D = 0.5 \) and \( p = 0.68 \)
for \( D = 0.57 \), and shows significantly larger \( p \) than the
surrogated data (\( p = 0.33 \) for \( D = 0.5 \), \( p = 0.28 \) for
\( D = 0.57 \)) with the same distribution of burst duration
time. This indicates the residual dynamics within area B
follows a poissonian process, but with considerable sur-
vivability \( p \) per iteration. Since area B corresponds to
relatively long durations of bursts, large duration times
of bursts tend to cluster in time, as partially observed in
Fig. (1c). In this regard, the known information about
the past duration could be beneficial to improve the burst
prognosis efficiently.

An important outcome of the stability analysis on at-
tractor ruins is the application to a control scheme on
burst duration. Since a rise of \( R_{2(1)} \) destabilizes the dom-
nance of \( C_{1(2)} \) and \( R_{1(2)} \), manually repressing the growth
of \( R_{2(1)} \) might elongate the bursts of \( C_{1(2)} \) and \( R_{1(2)} \). As
shown in Figs. (1c) and (1d), the repressed growth of \( R_2 \)
prevents the overpopulation of \( C_1 \) for a while and thus
delays the shrinkage of \( R_1 \) as well as of \( C_1 \). It should be
noticed that the effect of delayed rise of \( C_2 \) herein is not
so essential to elongating the burst duration, despite the
resource competition between \( C_2 \) and \( C_1 \). Counterintu-
itively, even promoting the growth of \( C_2 \) could be helpful
to the burst duration, if resulting in the depression of \( R_2 \).
Figures (1c) and (1f) indeed illustrate the possibility that
a sufficiently large perturbation to increase \( C_2 \) withdraws

\[ aC_{1(2)} \]

\[ \frac{dR_{1(2)}}{dt} = \sigma R_{1(2)} - \gamma R_{1(2)} + \frac{DB_{1(2)}}{\kappa + \mu R_{1(2)}} \]

\[ \text{where} \ C_{1(2)} \text{and} R_{1(2)} \text{represent the population of con-} \]
sumer 1 (2) and resource 1 (2), respectively. The parameters include $a$, $\kappa$, $\mu$, $D$, $b$, $\sigma$, $\gamma$, $\lambda$, of which $\mu$, $\sigma$, $\gamma$, $\lambda$ can be safely removed to give Eq. (1) without loss of generality.

[7] C. S. Holling, Canadian Entomol. 91, 385 (1959).
[8] J. Vandermeer, Am. Nat. 141, 687 (1993).
[9] Because the conventional Lyapunov exponent does not resolve the time scales involved in the present dynamics, we can hardly capture whether the chaotic behavior emerges at slow bursting scales or at fast oscillating scales. To clarify the chaotic activity in slow time scales, we instead utilize Eq. (2), which gives eventually the divergence rate of nearby initial conditions at bursting time scales. From Fig. 1(d), one can obtain constant $\varepsilon e^{q\tau}$ where $q$ is expected to be the rough estimation of the maximum Lyapunov exponent $\lambda_{\text{max}}$, as proven by $q = 0.016$ and $\lambda_{\text{max}} = 0.023$.

[10] If $D$ is small enough that $R_2$ alone cannot maintain $C_1$ as nonzero, $C_1$ becomes already decayed at stage S1’. Otherwise, with sufficiently large $D$ at stage S1’, $C_1$ can show either of stationary or oscillatory behavior depending on the parameters.

[11] For Figs. 4(c)–4(f), let $t_p$ denote the initial time of perturbation, $\Delta t_p$ the duration time of perturbation, and $f_p$ the relative decrease of $R_2 - R_2^2$ [Figs. 4(c) and 4(d)] or increase of $aC_2$ [Figs. 4(e) and 4(f)] with Eq. (1). We change each of $t_p$, $\Delta t_p$, and $f_p$ while the others remain fixed as in Figs. 4(c)–4(f), and observe the burst being elongated for Figs. 4(c) and 4(f) under the limitations $t_p \leq 5573$, $4.5 \leq \Delta t_p$, $0.8 \leq f_p$. Either decreasing $t_p$, increasing $\Delta t_p$, or increasing $f_p$ tends to elongate the burst durations throughout Figs. 4(c)–4(f).

[12] S. M. Greenberg, W. A. Jones, and T. -X. Liu, Environ. Entomol. 31, 397 (2002).