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Interim Report IR-00-074

Bifurcation Analysis of Population Invasion: On-Off Intermittency and Basin Riddling

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IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 51

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Abstract

We investigate the local bifurcations experienced by a time-discrete dynamical system from population biology when there is an attractor in an invariant subspace that loses stability. The system describes competition between two species in a constant environment; invariant subspaces contain single-species attractors; the loss of stability of the attractor in one invariant subspace means that the corresponding species (i.e. the 'resident' species) becomes invadible by its competitor. The global dynamics may be understood by examining the sign structure of Lyapunov exponents transverse to the invariant subspace. When the transverse Lyapunov exponent (computed for the natural measure) changes from negative to positive on varying a parameter, the system experiences a so-called blowout bifurcation. We unfold two generic scenarios associated with blowout bifurcations: (1) a codimension 2 bifurcation involving heteroclinic chaos and on-off intermittency and (2) a sequence of riddling bifurcations that cause asymptotic indeterminacy. An ingredient that both scenarios have in common is the fact that the 'resident' species subspace contains multiple invariant sets with transverse Lyapunov exponents that do not change sign simultaneously. This simple model adds on a short list of archetypical systems that are needed to investigate the structure of blowout bifurcations. From a biological viewpoint, the results imply that mutual invasibility in a constant environment is neither a necessary nor a sufficient condition for coexistence.

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Bifurcation Analysis of Population Invasion: On-Off Intermittency and Basin Riddling

Oscar De Feo and Régis Ferrière

1 Introduction

Invasion is an important concept in population biology. On the ecological timescale, invasibility underlies criteria for the maintenance of diversity of animal or plant communities [Turelli, 1978; Chesson & Ellner, 1989]. On the evolutionary timescale, the long-term dynamics of the process of natural selection are determined by the so-called invasion function of mutant genes [Metz *et al*., 1992; Rand *et al*., 1994; Ferriere & Gatto, 1995; Dieckmann, 1997]. How can one define invasion in the language of nonlinear dynamical systems theory? Competition between two different species or types can be modelled as a dynamical system operating on the phase space of population densities, with two invariant subspaces corresponding to the single-type populations. The restriction of the dynamical system to the invariant subspace of either type contains the attractor of a pure population of that type (which is assumed to be unique). Then we say that type X is *not* invadible by type Y whenever the single-type X attractor A_X is also an attractor in the full phase space [Metz *et al*., 1992; Rand *et al*. 1994; Ferriere & Gatto, 1995]. This depends on the sign of the largest Lyapunov exponent χ computed for the natural measure on A_X with respect to perturbations in the subspace which is transverse to the X invariant manifold. When χ is negative, A_X attracts trajectories transversely in the vicinity of the X invariant manifold ; if χ is positive, trajectories in the neighborhood of the X invariant manifold are repelled away from it, hence A_X is transversely unstable and Y invades. The set of Y trait values for which the transverse Lyapunov exponent is zero is called the invasion boundary of X [Ferriere & Gatto, 1995]. As the system crosses the invasion boundary, it experiences a ‘blowout’ bifurcation — a term coined by Ott & Sommerer [1993] although the phenomenon was earlier recognised by Pikovsky [1984] and Yamada & Fujisaka [1984].

A question of considerable interest in community ecology and evolutionary theory is whether mutual invasibility is a necessary and sufficient condition for long-term coexistence [May, 1973; Chesson & Ellner, 1989; Hofbauer & Sigmund, 1998]. Let us formu-

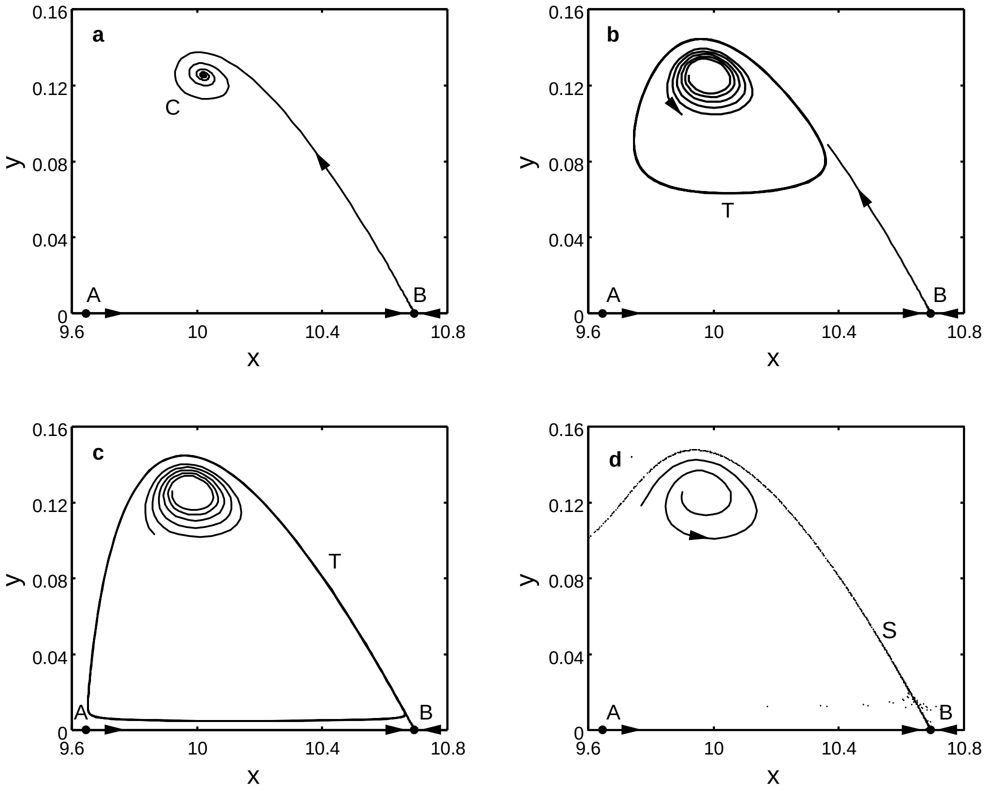

Figure 1 Sequence of bifurcations beyond the onset of invasion. Parameter r_2 varies near to the invasion boundary of X when there is a period-3 saddle (A) and a stable 3-cycle (B) on the x axis. The phase portrait of the third-iterate map is shown. Fixed parameters: r_1 = 33.0, s_1 = 0.004, s_2 = 0.02.

a r_2 = 16.65 ($\chi = 0.0308$). Internal focus born from transcritical bifurcation.

b r_2 = 16.72 ($\chi = 0.0342$). Torus from Neimark-Sacker bifurcation.

c r_2 = 16.722217985 ($\chi = 0.0343$). Close to heteroclinic connection.

d r_2 = 16.75 ($\chi = 0.0354$). Heteroclinic chaos.

late this problem more precisely. Assume that each type X and Y is characterized by a set of demographic parameters (the reproductive rate and survival probability of individuals of a given type) that determine X and Y population dynamics. Assume that type X has fixed demographic parameters. Now let Y parameters vary in such a manner that the transverse Lyapunov exponent of Y always remains positive whereas the transverse Lyapunov exponent χ of X passes from negative to positive values. In other words, we make type Y cross the invasion boundary of X into the parameter domain of mutual invasibility. Then we ask, is this sign change of χ accompanied with a transition from exclusion (of Y) to coexistence of X and Y ?

Chesson & Ellner [1989] have addressed this issue for monotonic competition in a random environment. Using a two-dimensional system of stochastic difference equations on $R_+ \times R_+$ to describe competition, they define a type as ‘persisting’ if the sto-

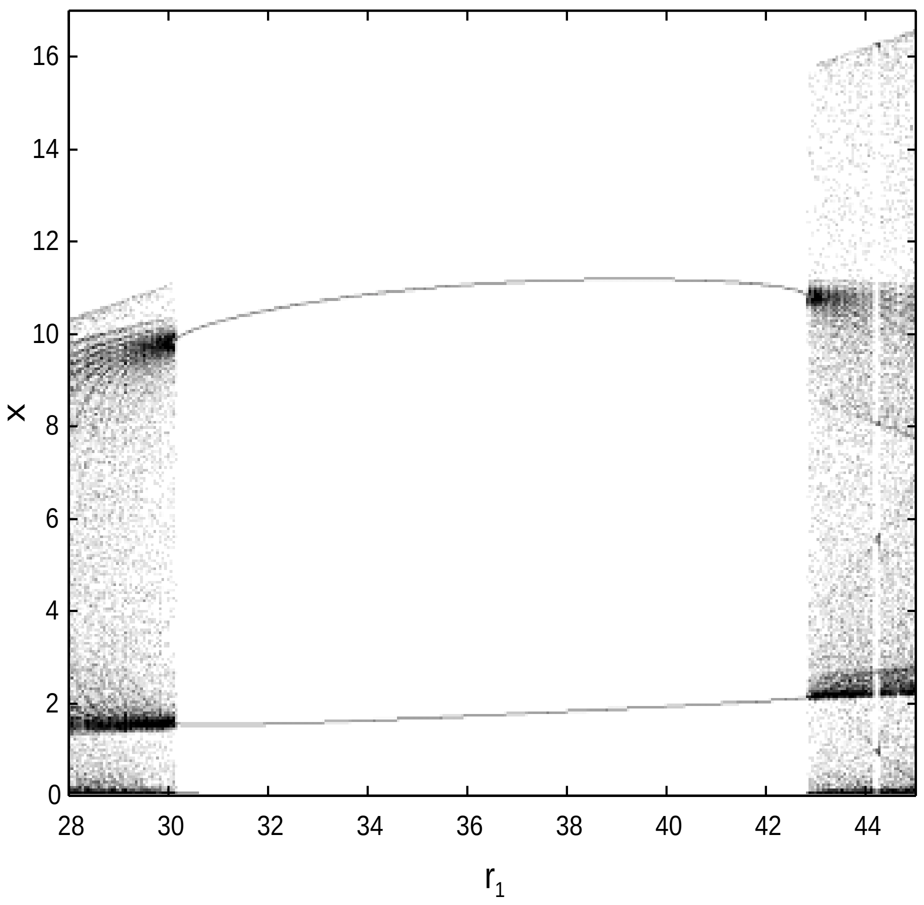

Figure 2 Feigenbaum diagram of resident attractor with respect to r_1, for s_1 = 0.004.

chastic boundedness criterion applies, that is the distribution of population size isbounded below by that of a positive random variable [Chesson, 1982]. They show that mutual invasibility implies coexistence in the sense that each type is stochastically boundedly persistent, and conversely that a negative long-term invasion exponent implies extinction almost surely. The important biological assumption here is monotonicity of the competitive effects, which entails that intraspecific competition is never so severe that a higher density now results in a lower density after one unit of time. Monotonicity implies that each single-type model in its deterministic version has very simple dynamical properties: a unique attractor (a stable, monotonically convergent equilibrium) which is also the unique invariant set of the system in R_+^*.

The existence of multiple invariant sets, however, may be the rule, rather than the exception, in population models. In particular, the existence of a chaotic attractor does entail that there is also an infinite number of unstable periodic orbits. A simple model in a constant environment that violates the monotonicity assumption is the Ricker-Gatto

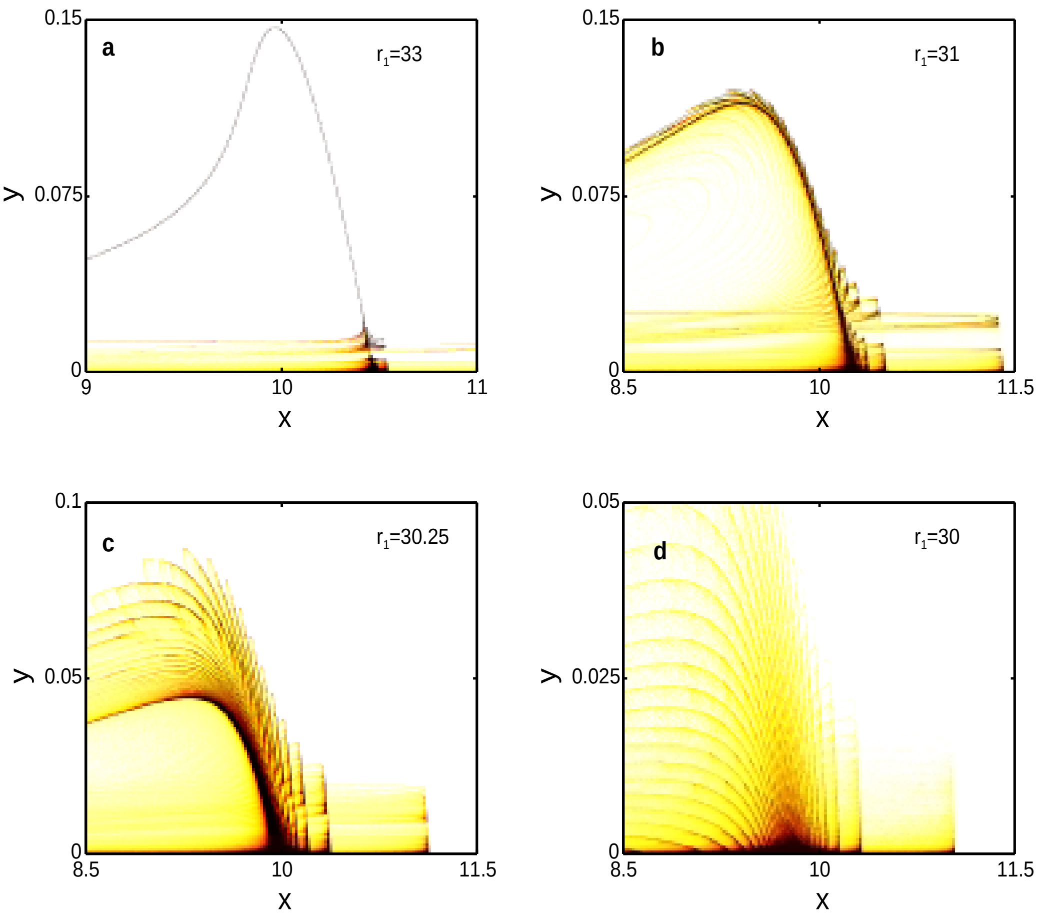

Figure 3 Phase portrait for the third iterate map: heteroclinic chaos (a-c) and on-off intermittency (d). Fixed parameters: $s_1 = 0.004$, $r_2 = 16.75$, $s_2 = 0.02$. The resident attractor on the x axis is a transversely unstable cycle, except in the bottom-right panel where it is a transversely unstable chaotic attractor. Upper-left panel: $r_1 = 33.0$, upper-right: 31.0, bottom-left: 30.25, bottom-right: 30.0. Colors indicate how frequently each pixel of the phase portrait image is visited by an orbit. Yellow: low visit rate, red: intermediate, black: high.

(RG) model, which involves variable reproductive success according to the Ricker formula [Ricker, 1954]. The two-type population dynamics in the RG model are expressed as

$$x(t+1) = r_1 x(t)\exp[-x(t) - y(t)] + s_1 x(t)$$

$$y(t+1) = r_2 y(t)\exp[-y(t) - x(t)] + s_2 y(t)$$

(assuming equal competitive coefficients in the density-dependent term). The first term on the right-hand side represents density-dependent reproductive success and the second term represents the survival of adults. Thus, each type is characterized by two demographic parameters: the intrinsic reproductive success r_i and adult survival probability

s_i. For suitable values of reproductive success and survival, the single-type population

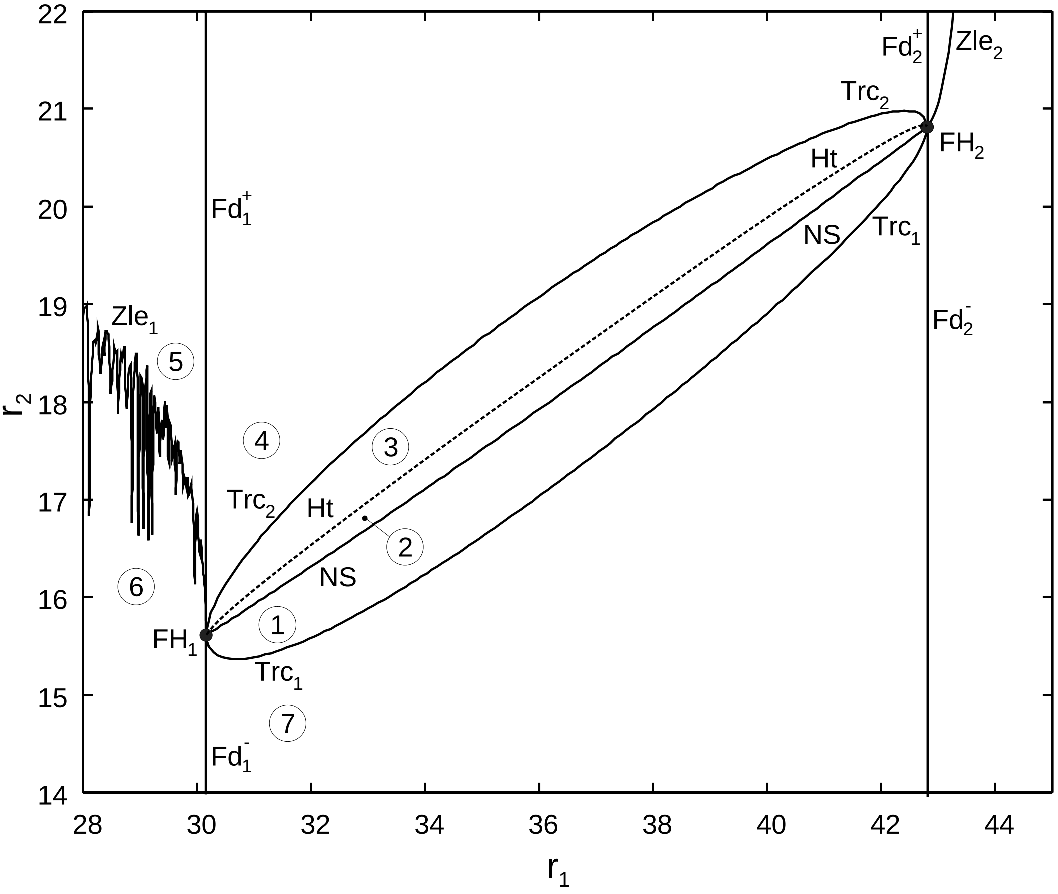

Figure 4 Fold-Hopf organizing centers in (r_1, r_2) parameter space. Fixed parameters: s_1 = 0.004, s_2 = 0.02. Notice that the r_1 parameter range (horizontal axis) is the same as in Fig. 2. See text for explanations.

dynamics may involve coexisting stable and unstable cycles or chaotic attractors [Gatto, 1993] (also see May & Oster [1976] for the analysis of the semelparous case $s = 0$). Invasibility properties of RG models have been explored by Gatto [1993] and Ferriere & Gatto [1995]. If both types are semelparous, that is, all individuals die after one single reproductive event ($s_1 = s_2 = 0$), the transverse Lyapunov exponent of the type with largest r is positive, whereas that of the other type is negative. Then the study of permanence by Hofbauer et al. [1987] shows that the exclusion principle holds true. If at least one type is iteroparous (that is, an individual may reproduce several times during its lifetime, hence s_1 or $s_2 \neq 0$), mutual invasibility may occur, in which case Gatto [1993] has provided numerical evidence that the two types can coexist.

Here we make use of local bifurcation analysis (e.g., Kuznetsov [1998]) to investigate the structure of blowout bifurcations that underlie the process of invasion in the RG model. Calculations are based on continuation methods (see Kuznetsov [1998] for a comprehensive survey) as implemented in the specialized software LOCBIF [Khibnik et al., 1993]. After recalling some basic results on the RG system (Sec. 2), we describe two scenarios for blowout bifurcations associated with invasion. First we unfold a codimension 2 scenario akin to a fold-Hopf bifurcation (Sec. 3). In particular, as the transverse Lyapunov exponent of the resident attractor is slightly positive, a heteroclinic connection arises between the resident attractor and another invariant set in the resident subspace. If the resident attractor is chaotic, the invader experiences on-off intermittency, an extreme kind of population bursting [Heagy et al., 1994; Venkataramani et al., 1995, 1996; Ashwin et al., 1998]. The alternative scenario (Sec. 4) is a sequence of riddling bifurcations [Ashwin et al. 1996, Nagai & Lai 1997] which develops as the resident transverse Lyapunov exponent approaches zero from the negative side. This bifurcation route involves a chaotic resident attractor and is mediated by the loss of transverse stability of unstable periodic orbits embedded in that chaotic attractor [Nagai & Lai, 1997]. Riddling entails that the resident attractor is no longer a topological attractor in the full phase space: its basin of attraction is a fractal set riddled with holes that belong to the basin of another internal attractor. That is, for every initial density condition that drives the alternative type to extinction, there are initial densities arbitrarily nearby that leads to a coexistence attractor. Riddled basins in ecological models had previously been detected in a few instances [Alexander et al., 1992; Hastings, 1993; Kaitala & Heino, 1996].

This bifurcation analysis shows that mutual invasibility in constant environment is neither a necessary nor a sufficient condition for coexistence. When on-off intermittency occurs, the intermittent type, although invading, faces a high probability of extinction due to demographic stochasticity. On the other hand, basin riddling implies that a noninvading strategy has yet a positive probability, for arbitrarily small initial density, of reaching a coexistence attractor. The distribution of finite-time transverse Lyapunov exponents can be used to evaluate the extinction probability of an on-off intermittent type and to quantify the effect of small random noise on riddled basins [Ferriere & Cazelles, 1999, Ferriere & De Feo, unpublished results].

2 Elementary Properties of the Ricker-Gatto Model

For biologically meaningful values of parameters r and s ($r > 0$, $0 < s < 1$), each single-type population governed by the RG equation possesses two fixed points: 0 and $\ln(r/1-s)$. The equilibrium 0 is stable if $r + s < 1$. The nontrivial equilibrium is stable if $1 < r/(1-s) < \exp(2/1-s)$. For fixed s and increasing r there is a transcritical bifurcation when $r + s = 1$; then the nontrivial equilibrium passes through the origin and becomes positive and stable, whereas the equilibrium 0 becomes unstable. As r is increased fur-

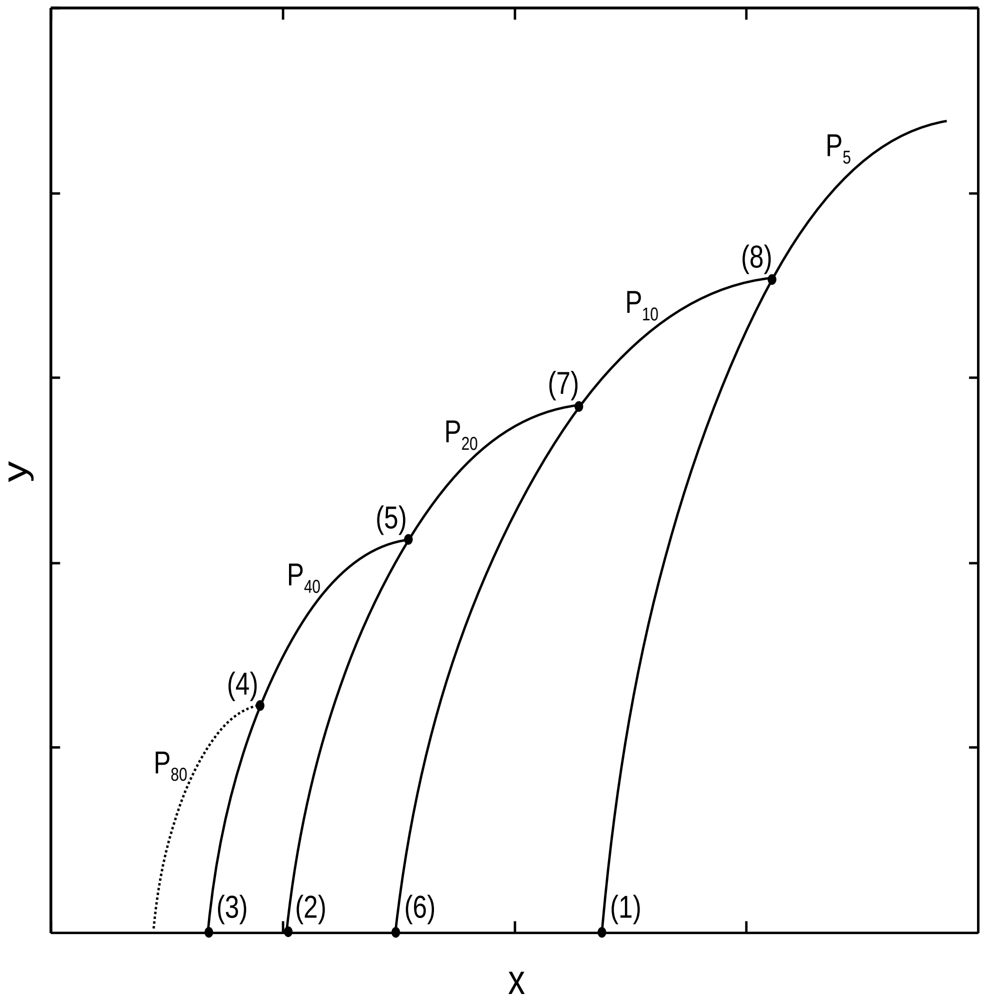

Figure 5 Riddling bifurcations. Schematic diagram of the cascade of periodic saddles losing transverse stability (transcritical bifurcations on the x axis) and reverse-flip bifurcations of internal cycles as r_2 is increased. Actual numerical analysis performed with r_1 = 22.0, s_1 = 0.007815, s_2 = 0.5. Bifurcation points: (1) r_2=2.791586 (transcritical) — (2) r_2=2.861159 (transcritical) — (3) r_2=2.873062 (transcritical) — (4) r_2=2.887210 (flip) — (5) r_2=2.887899 (flip) — (6) r_2=2.888366 (transcritical) — (7) r_2=2.893935 (flip) — (8) r_2=2.897663 (flip).

ther, the stable nonzero equilibrium looses its stability through a supercritical flip bifurcation at $r < (1-s)\exp(2/1-s)$ that yields a stable period-2 cycle [Ferriere & Gatto, 1993].

Considering the full RG competition system, in addition to the trivial equilibrium at the origin, the phase space contains a ‘degeneracy line’ of equilibria $(\hat{x},\hat{y})$ whenever $r_1/1-s_1 = r_2/1-s_2\,(=R)$. That degeneracy line is then given by $\hat{x}+\hat{y}=\ln R$. In this paper, our goal is to analyse the bifurcations associated with invasion and global behavior in competition systems characterized by two invariant subspaces (the single-type population subspaces). Therefore we shall ignore the case where there exists a degeneracy line of equilibria, which is anyhow restricted to a very special range of parameters s_i and r_i. Also, for parameters very close to the degeneracy line, infinitely many bifurcations may occur and a singular bifurcation analysis is required to obtain insights into their structure. This work lies beyond the scope of the present paper and will be reported elsewhere.

3 First Scenario: Fold-Hopf Bifurcation and On-Off Intermittency

The first bifurcation scenario occurs near the invasion boundary of X where the transverse Lyapunov exponent is slightly positive. It may develop for any kind of resident attractor: stable equilibrium, stable cycle or chaotic attractor, provided that the $x > 0$ axis contains other invariant sets.

To describe this route we consider an example where there are a period-3 saddle, A, and a stable period-3 (P_3) cycle, B, on the x axis, both being transversely stable. Another period-3 saddle, C, exists in the fourth quadrant. Let r_2 increase. The saddle C first collides on B and exchanges transverse stability through a transcritical bifurcation. At this point, the invasion exponent changes sign, from negative to positive. Now C is an attractor in the positive first quadrant and B has become a saddle (transversely unstable) See Fig. 1a. Next C undergoes a Neimark-Sacker bifurcation: C becomes an unstable focus while a torus (T) is born around it (Fig. 1b). The torus T further approaches the two saddles A and B on the axis and eventually forms a heteroclinic connection between them (Fig. 1c). As the connection is established, T breaks down and is replaced by a strange attractor S (Fig. 1d).

A similar scenario is likely to apply when the resident attractor is chaotic and contains infinitely many unstable periodic orbits. This can be best illustrated by starting from the chaotic attractor due to the heteroclinic connection between the resident saddle A and stable cycle B (Fig. 1d), fixing r_2 and decreasing r_1. The A and B cycles appear to belong to a window of periodicity in the Feigenbaum diagram of species X with respect to r_1 (Fig. 2). Moving r_1 towards the chaotic region on the left-hand side of the window causes A and B to collide and disappear through a fold bifurcation. As long as A and B exist, the heteroclinic connection drives the system dynamics (Fig. 3a-c). As the resident attractor becomes chaotic, the internal attractor S still presents a striking heteroclinic structure (Fig. 3d). Trajectories concentrate around a point on the x axis which is close to the former B saddle and where chaotic orbits in the resident attractoralso tend to accumulate (Fig. 2). There they are repelled upward along vertical direc-

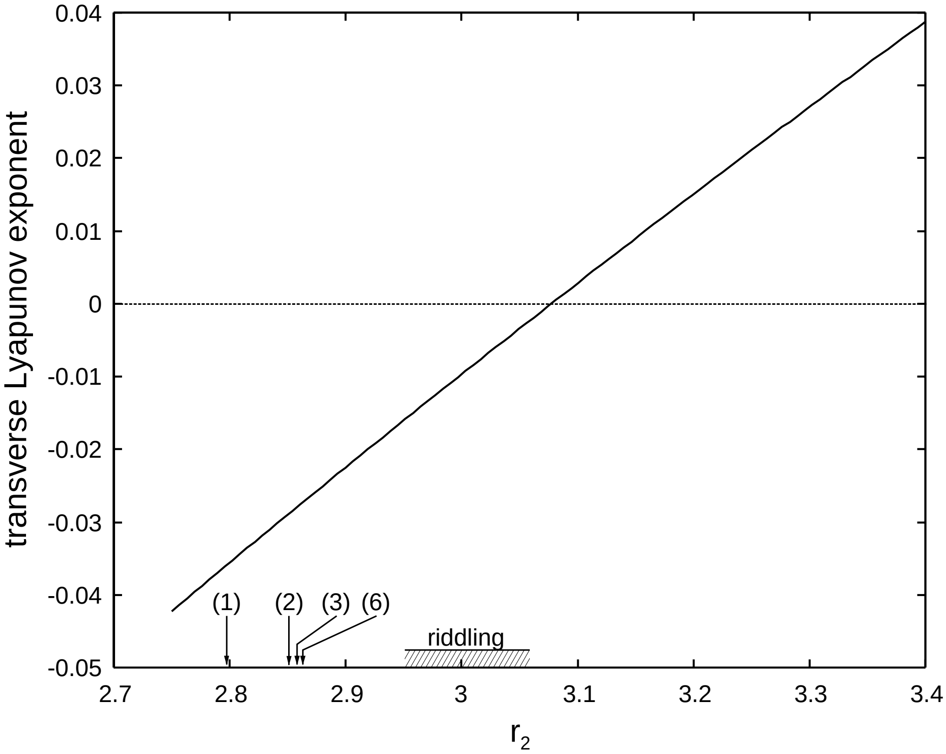

Figure 6 Transverse Lyapunov exponent of natural measure on chaotic attractor S on the x-axis, as a function of r_2. Values of r_1, s_1 and s_2 values as in Fig. 5. Transcritical bifurcations of saddles in S are indicated (see Fig. 5 for corresponding numbering). Basin riddling occurs as saddles lose transverse stability.

tions that parallel (locally at least) the previous unstable manifold of B. This is the phenomenon known as on-off intermittency in physics, one which has received much attention over the past few years (see Sec. 5).

We now show that this scenario unfolds around a codimension 2 fold-Hopf organizing center [Kuznetsov, 1998]. Notice that the fold-Hopf organizing center is defined usually for three-dimensional continuous time systems. However, because of a cylindric symmetry, the truncated normal form of this bifurcation is a continuous time system in two dimensions only, with an invariant axis corresponding to the axis of the cylindric symmetry. In our case, the symmetry axis is the x axis, which is actually invariant. (The reason why a fold-Hopf bifurcation does not admit a real normal form is explained in Guckenheimer & Holmes [1983], Wiggins [1990] or Kuznetsov [1998].)

When compared to one of the four possible unfolding of the fold-Hopf bifurcation, the scenario that we previously described only misses the fold bifurcation on the x axis. In the local parameter region we have considered so far, the only fold bifurcation for the period-3 cycle on the x axis occurs in correpondence with the opening and closure of the period-3 window as r_1 is varied (Fig. 2). In order to identify the fold-Hopf organizing center, we numerically continued the former, opening fold with respect to r_1 and r_2 (shown as $\mathrm{Fd}_1^- \cup \mathrm{Fd}_1^+$ in Fig. 4) and looked for its degeneracy that must occur at the organizing point (denoted by FH_1). Obviously that fold taking place on the axis is not affected by r_2, hence $\mathrm{Fd}_1^- \cup \mathrm{Fd}_1^+$ is a straight, vertical line in Fig. 4. Next we unfolded the structure locally around FH_1 to determine the bifurcation curves organized by this point. The line Trc_1, that separates regions (7) and (1), corresponds to the transcritical bifurcation between the period-3 solution B and the period-3 solution C in the scenario described previously. In region (7) C is a saddle in the fourth quadrant and B is attracting, while region (1) corresponds to the case illustrated by Fig. 1a. Across the NS line (Neimark-Sacker), C looses its stability while a stable torus T appears around it; therefore, region (2) corresponds to the case depicted by Fig. 1b. As we cross the line Ht, the heteroclinic connection between A and B is established and, as the system enters region (3), a strange attractor S (visible in Fig. 1c) originates from the torus T. As one crosses the line Trc_2 , C and A undergo a transcritical bifurcation whereby C moves into the fourth quadrant and A changes its transversal stability. Finally, on the line $\mathrm{Fd}_1^- \cup \mathrm{Fd}_1^+$, A and B collide and disappear. In the region of parameter space where no attractor should exist in continuous time (region $(5)\cup(6)$), however, our discrete-time model gives rise to a chaotic attractor, either an internal one (in region (5) where the transverse Lyapunov exponent is positive), or on the x axis (in region (6) where the transverse Lyapunov exponent is negative). The line Zle_1 that separates region (5) and (6) , along which the transverse Lyapunov exponent vanishes, seems to converge to the organizing point FH_1, thereby adding a new bifurcation to the scenario known for continuous time.

We conducted a similar analysis for the other Fold bifurcation corresponding to the closure of the window of periodicity. The same bifurcation structure was found, organized around a point now denoted by FH_2. Moreover, continuing the lines Trc_1, NS and Trc_2 issued from the two organizing centers FH_1 and FH_2 shows the unexpected result that these lines exactly coincide without leading to any other codimension 2 point. The narrowness of region (5) comprised between Fd_2^+ and Zle_2 may be understood intuitively from the Feigenbaum diagram (Fig. 2) by comparing the shape of the chaotic attractors on the left and on the right of the periodic window. On the right-hand side, the chaotic attractor on the x axis is much wider. The fraction of the attractor that attracts internal trajectories to the axis becomes larger as one moves towards Zle_2 by increasing r_1, and soon dominates the transverse stability of the axis, yielding quickly to a negative transverse Lyapunov exponent.

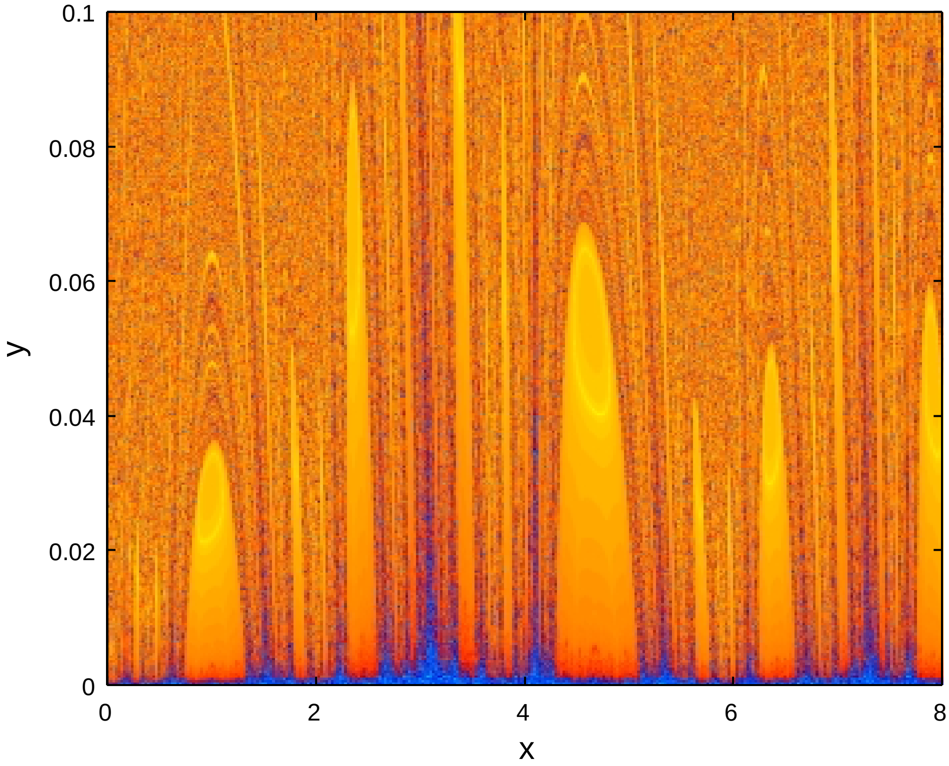

Figure 7 Riddled basin. The chaotic attractor on the axis is transversely stable ($\chi = -0.0161$), yet its basin of attraction is riddled by the basin of the internal period-5 cycle. r_1 = 22.0, s_1 = 0.007815, r_2 = 2.95, s_2 = 0.5. Points attracted to the chaotic set on the axis are colored blue and points attracted to the internal P_5 attractor are colored orange. The color is shaded according to the speed of convergence. Light orange or light blue: fast convergence. Dark orange or dark blue: slow convergence.

4 Second Scenario: Riddling Bifurcations

We now describe a bifurcation scenario which takes place near to the invasion boundary when the resident transverse Lyapunov exponent is slightly negative. We start with a chaotic attractor S on the x axis. We assume that the transverse Lyapunov exponent of S is initially negative, i.e. the chaotic attractor attracts all points in some neighborhood. There are infinitely many periodic orbits embedded in the chaotic attractor which all are saddles or repellors. The loss of transverse stability of the attractor occurs when some properly weighted transverse eigenvalues of these two groups are balanced [Nagai & Lai, 1997].

As we increase r_2, periodic repellers contained in the fourth quadrant start colliding with saddles in S and undergo a transcritical bifurcation as they pass through the x axis. As they do so, they exchange stability with the corresponding saddles in S: the latter ones become transversely unstable. Figure 5 displays a sequence of saddles arising successively through such a mechanism and bifurcating (reverse flip) into attractors. First, a period-5 (P_5) saddle enters the first quadrant. As r_2 increases, this saddle moves upward whilst a P_{20} saddle, followed by a P_{40} saddle, enter the first quadrant. Then the P_{40} becomes stable through a reverse flip with a stable P_{80} (that likewise had entered the quadrant as a saddle — not shown). As r_2 is increased further, the P_{40} shrinks around the P_{20} saddle and disappears to leaving a stable P_{20}. Keeping on increasing r_2, a P_{10} saddle enters the first quadrant and collides with the P_{20} in another reverse flip. Finally, the stable P_{10} flips with the P_5, and the latter becomes stable. During this process, the system possesses two attractors in the closed positive cone: the strange attractor on the axis, and a $P_{5 \cdot 2^n}$ internal cycle. As saddles enter the positive cone, the transverse stability of the strange attractor S on the x axis is weakened (Fig. 6) and eventually lost, i. e. the transverse Lyapunov exponent of the natural measure on S becomes positive, and P_5 remains as the only attractor. As saddles in S lose transverse stability, basin riddling occurs (Figs. 6 and 7): the basin of attraction of S in the full phase space is riddled with holes that belong to the basin of attraction of the internal $P_{5 \cdot 2^n}$ cycle. The set S is no longer a topological attractor; it is a Milnor attractor, i. e. it attracts a set of initial conditions with positive Lebesgue measure.

The transition to basin riddling can be understood geometrically as follows (Fig. 8). Initially, all trajectories are captured by attracting ‘tongues’ that originate around the saddle cycles embedded in the chaotic attractor (Fig. 8a). When a saddle on the axis undergoes a transcritical bifurcation, it becomes a repellor and the corresponding tongue becomes repelling. A trajectory with initial conditions in the repelling tongue initially takes off but it is likely to be recalled to the axis for the tongue intercepts other nearby attracting tongues (Fig. 8b). Once enough tongues have become repelling as more saddles have entered the positive cone, any trajectory originated near the chaotic attractor has a positive probability of escaping and asymptoting to the internal attractor (Fig. 8c). In our example, this happens as the P_5 is the internal attractor of the system (Fig. 7).

5 Concluding Remarks

Recently, examples of important problems in the physical sciences have motivated the intensive study of nonlinear dynamical systems that possess chaotic dynamics in a smooth invariant manifold of lower dimension than that of the full phase space. These physical systems are typically endowed with symmetries, and any initial state that has the same symmetry as the entire system evolves to other states that also respect the symmetry of the system. The set of such symmetric initial states then forms a manifold that is invariant under the system dynamics. These invariant manifolds can also have the property that the dynamics restricted to the manifold is chaotic, i.e., symmetric initial

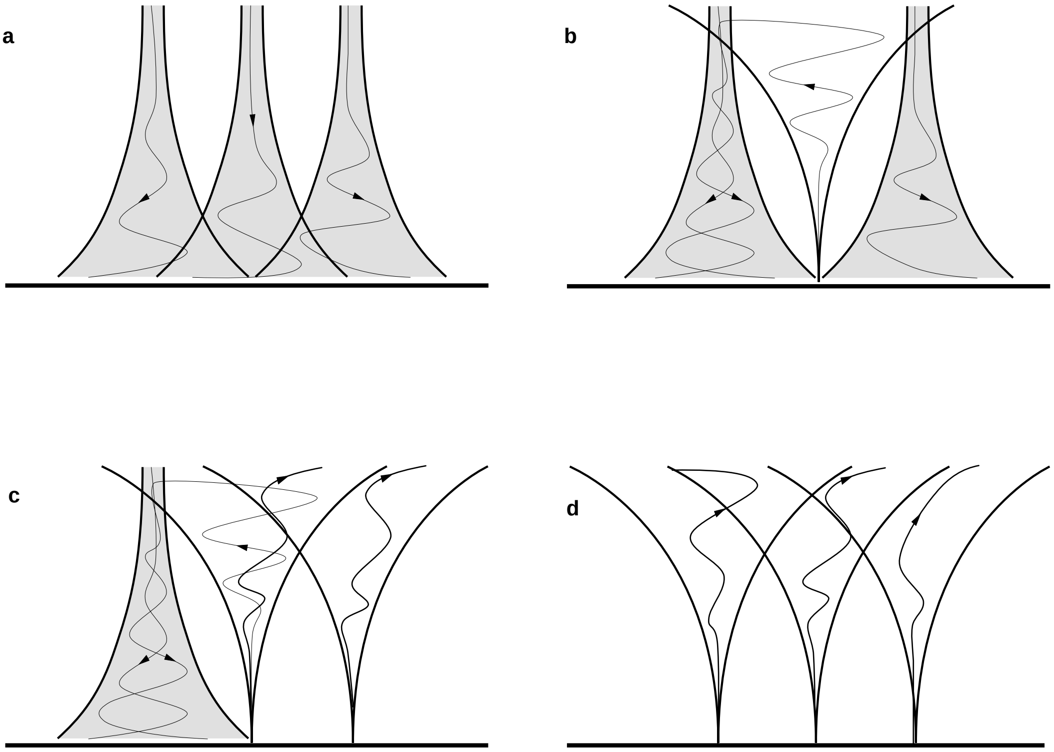

Figure 8 Mechanism of basin riddling. Closer to the invasion boundary, more attracting (shaded) tongues that originate around saddles in the chaotic set on the axis become repelling (white). Trajectories picked at random acquire a positive probability of escaping to the internal attractor, hence basin riddling. See text for further explanations.

states can be attracted to a chaotic set in the manifold. As one varies a ‘normal parameter’ [Ashwin et al., 1996] that only affects the dynamics transverse to the invariant manifold, blowout bifurcations may occur [Ott & Sommerer, 1993].

Blowout bifurcations are local symmetry-breaking bifurcations accompanied either ith bubbling transitions [Ashwin et al., 1994; Venkataramani et al., 1996] and riddled basins [Ashwin et al., 1996; Lai et al., 1996; Astakhov et al., 1997], or with on-off intermittency [Lai, 1996]. Although considerable insights have been gained into the statistics of on-off intermittent dynamics [Heagy et al., 1994; Venkataramani et al., 1995, 1996], their geometrical underpinning had not yet been elucidated (but see Melbourne [1993]). This analysis provides the complete unfolding of a codimension 2 bifurcation scenario that explains on-off intermittency.

Blowout bifurcations were known to occur as the perfect symmetry of a dynamical system (a set of coupled identical equations) is broken by making the coupling asymmetric. Blowout bifurcations in competition models of the kind described in this Letter also involve symmetry breaking, but here the system symmetry is broken by making the parameters of sub-systems (single-type populations) slightly different without altering the coupling (competition) terms. In spite of this important qualitative difference, the bifurcation route to basin riddling in biological models involves the same ingredients as in physical systems, namely the change in the transverse stability of periodic saddles embedded in the chaotic set [Lai et al., 1996; Astakhov et al., 1997; Nagai & Lai, 1997] (also see Mira et al. [1994] for a different approach). Thus our results indicate that this bifurcation scenario is even more general than previously thought.

References

Alexander, J. C., Yorke, J. A., You, Z. & Kan, I. [1992] Riddled basins, International Journal of Bifurcation and Chaos 2, 795-813.

Ashwin, P., Aston, P. J. & Nicol, M. [1998] On the unfolding of a blowout bifurcation, Physica D 111, 81-95.

Ashwin, P., Buescu, J. & Stewart, I. N. [1994] Bubbling of attractors and synchronization of chaotic oscillators, Physics Letters A 193, 126-139.

Ashwin, P., Buescu, J. & Stewart, I. N. [1996] From attractor to chaotic saddle: a tale of transverse instability, Nonlinearity 9, 703-737.

Astakhov, V., Shabonin, A., Kapitaniak, T. & Anishchenko, V. [1997] Loss of chaos synchronization through the sequence of bifurcations of saddle periodic orbits, Physical Review of Letters 79, 1014-1017.

Chesson, P. L. [1982] The stabilizing effect of a random environment, Journal of Mathematical Biology 15, 1-36.

Chesson, P. L. & Ellner, S. [1989] Invasibility and stochastic boundedness in monotonic competition models, Journal of Mathematical Biology 27, 117-138.

Dieckmann, U. [1997] Can adaptive dynamics invade? Trends in Ecology and Evolution 12, 128-131.

Ferriere, R. & Cazelles, B. [1999] Universal power laws govern intermittent rarity in communities of interacting species, Ecology (in press).

Ferriere, R. & Gatto, M. [1993] Chaotic population dynamics can result from natural selection, Proceedings of the Royal Society of London B 251, 33-38.

Ferriere, R.& Gatto, M. [1995] Lyapunov exponents and the mathematics of invasion in oscillatory or chaotic populations, Theoretical Population Biology 48, 126-171.

Gatto, M. [1993] The evolutionary optimality of oscillatory and chaotic dynamics in simple populations models, Theoretical Population Biology 43, 310-336.

Guckenheimer, J. & Holmes, P. [1983] Nonlinear oscillations, dynamical systems and bifurcations of vector fields. (Springer-Verlag, New York).

Hastings, A. [1993] Complex interactions between dispersal and dynamics: lessons from coupled logistic equations, Ecology 74, 1362-1372.

Heagy, J. F., Platt, N. & Hammel, S. M. [1994] Characterization of on-off intermittency, Physical Review, Series E 49, 1140-1150.

Hofbauer, J., Hutson, V. & Jansen, W. [1987] Coexistence for systems governed by difference equations of Lotka-Volterra type, Journal of Mathematical Biology 25, 553-570.

Hofbauer, J. & Sigmund, K. [1998] Evolutionary games and population dynamics. (Oxford University Press, Oxford).

Kaitala, V. & Heino, M. [1996] Complex non-unique dynamics in simple ecological interactions, Proceedings of the Royal Society of London B 263, 1011-1015.

Khibnik, A. I., Kuznetsov, Yu. A., Levitin, V. V. & Nikolaev, E. V. [1993] Continuation techniques and interactive software for bifurcation analysis of ODEs and iterated maps, Physica D 62, 360-370.

Kuznetsov, Yu. A. [1998] Elements of Applied Bifurcation Theory. 2nd edition. (Springer-Verlag, New York).

Lai, Y.-C. [1996] Symmetry-breaking bifurcation with on-off intermittency in chaotic dynamical systems, Physical Review, Series E 53, R4267-R4270.

Lai, Y.-C., Grebogi, C., Yorke, J. A. & Venkataramani, S. C. [1996] Riddling bifurcation in chaotic dynamical systems, Physical Review of Letters 77, 55-58.

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

May, R. M. & Oster, G. F. [1976] Bifurcations and dynamics complexity in simple ecological models, The American Naturalist 110, 573-599.

Melbourne, I. [1989] Intermittency as a codimension-three phenomenon, Journal of Dynamics and Differential Equations 1, 347-367.

Metz, J. A. J., Nisbet, R. M. & Geritz, S. A. H. [1992] How should we definess ‘fitness’ for general ecological scenarios? Trends in Ecolology and Evolution 7, 198-202.

Mira, C., Fournier-Prunaret, D., Gardini, L., Kawakami, H. & Cathala, J. C.[1994] Basin bifurcations of two-dimensional noninvertible maps: fractalization of basins, International Journal of Bifurcation and Chaos 4, 343-381.

Nagai, Y. & Lai, Y.-C. [1997] Characterization of blowout bifurcation by unstable periodic orbits, Physical Review, Series E 55, R1251-R1254.

Ott, E. & Sommerer, J. C. [1994] Blowout bifurcations: the occurrence of riddled basins and on-off intermittency, Physics Letters, Series A 188, 39-47.

Pikovsky, A. S. [1984] On the interaction of strange attractors, Zeitschrift für Physik B 55, 149-154.

Rand, D. A., Wilson, H. B. & McGlade, J. M. [1994] Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics, Philosophical Transactions of the Royal Society of London B 343, 261-283.

Ricker, W. [1954] Stock and recruitment, Journal - Fisheries Research Board Canada 11, 559-663.

Turelli, M. [1978] Does environmental variability limit niche overlap? Proceedings of the Naionatl Academy of Sciences of the USA 75, 5085-5089.

Venkataramani, S. C., Antonsen Jr., T. M., Ott, E. & Sommerer, J.C. [1995] Characterization of on-off intermittent time series, Physics Letters A 207, 173-179.

Venkataramani, S. C., Antonsen Jr., T. M., Ott, E. & Sommerer, J. C. [1996] On-off intermittency: Power spectrum and fractal properties of time series, Physica D 96, 66-99.

Venkataramani, S. C., Hunt, B. R. & Ott, E. [1996] Bubbling transition, Physical Review, Series E 54, 1346-1360.

Wiggins, S. [1990] Introduction to applied non-linear dynamical systems and chaos. (Springer-Verlag, New York).

Yamada, T. & Fujisaka, H. [1984] Stability theory of synchronised motion in coupled-oscillator systems, Progress of Theoretical Physics 70, 1240-1248.