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The Resident Strikes Back: Invader-Induced Switching of Resident Attractor

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The aim of this paper is two-fold: (a) by way of example, we elucidate the phenomenon of invader-induced switches in a resident attractor; (b) we expose in detail how resonance and phase have a strong impact when semelparous organisms (as, *e.g.* Pacific salmon) with different life-cycle lengths compete in a self-induced periodically fluctuating environment.

We analyse a simple model for the competition between annuals and biennials, focusing on the situation that the annual population in isolation converges to a two-cycle. Well-timed biennial mutants sample the periodically varying environment more efficiently than the annual resident. They can invade successfully even when they are inferior to the resident, in the sense that they have lower viability and/or fertility. Successful invasion can lead to resonance-mediated coexistence if the invader is rather inferior to the resident. Remarkably, for mutants that are less inferior to the resident, successful invasion by a mutant strategy will inevitably be followed by extinction of the former invader and concurrent re-establishment of the resident. The expulsion of the invader is brought about by an invasion-induced phase shift or attractor switch. We call this phenomenon "the resident strikes back" and say that the resident strategy is *invasible, yet invincible*. After the resident has struck back, other mutants can successfully invade again. On a longer time-scale, this might lead to an intermittent occurrence of ultimately inferior strategies.

The results show that even in a deterministic setting, successful invasion does not necessarily lead to establishment and that mutual invasibility is not always sufficient for coexistence.

Introduction

Despite the widespread occurrence of non-equilibrium dynamics in natural ecosystems, standard evolutionary theory is largely based on the equilibrium

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paradigm. Some theoretical results, however, point out that competition between traits or strategies may have a different outcome when the environment fluctuates. Relatively well-known examples concern an environment that is not entirely predictable, for example due to a stochastically fluctuating external driver (Tuljapurkar, 1990, 1994). In these cases, strategies that would be inferior in a steady world, can be superior.

However, self-induced (quasi-)periodic or chaotic population dynamics in a deterministic setting also have an impact on competitive (dis)advantages of strategies. In an earlier paper (Diekmann *et al.*, 1999), we described a simple model for the evolution of the age at reproduction of Pacific salmon (*Oncorhynchus* spp.). Pacific salmon is a semelparous species, which means that individuals reproduce only once and then they die. We demonstrated the coexistence of different periodic attractors, with different invasion properties (see also Van Dooren & Metz, 1998). If the resident population density has converged to one of these attractors, then well-timed mutant strategies can invade (whereas ill-timed mutants cannot invade). This can happen despite these mutants being inferior to the resident, in the sense that they reproduce at an age where the contribution to a next generation (as a result of the combined effect of survival and reproductive potential) is lower than at the reproductive age of the resident. In steady-state resident dynamics, such inferior mutants would not have any chance of invading successfully: the strategy which programs individuals to reproduce at a superior age is non-invasible [*i.e.* an evolutionarily stable strategy, or ESS; see Maynard Smith & Price (1973) and Maynard Smith (1982)] as well as an attractor of the adaptive dynamics. Gatto (1993) gives another example of an inferior genotype successfully invading an oscillatory resident [see also Ferrière & Gatto (1995) for a theorem on invasibility and non-equilibrium dynamics and Metz *et al.* (1992) and Rand *et al.* (1994) for more background].

In certain situations (to be described in detail below), successful invasion will inevitably be followed by the extinction of the invader and concurrent regrowth of the resident to its former levels of population density. The expulsion of the invader is achieved by an invasion-induced phase or attractor switch of the resident. In other words, the invader seems to dig its own grave while pestering the resident, by forcing a phase or rhythm shift in its ups and downs. The resident strategy is then “invasible, yet invincible” for these mutants. We call this phenomenon “the resident strikes back”.

Our formulation so far re-iterates the message of Diekmann *et al.* (1999) and Mylius *et al.* (in press) and focuses on adaptive dynamics. The aim of the present paper is to expose in detail how resonance and phase have a strong impact when semelparous organisms with different life cycle lengths compete in a self-induced periodically fluctuating environment. To do so while keeping life simple, we analyse a model of nursery competition between annuals and biennials. We neglect pair formation, sexual reproduction and mode of inheritance and we assume that reproduction is clonal. In Diekmann *et al.* (1999) we addressed both the pure- and the mixed strategy case, but here we will restrict our attention to evolutionary competition between two types, each having a fixed age at reproduction. That is, we focus on a pure-strategy formulation.

We present three main new results. (a) Counterintuitively, better invaders perform worse in the long run due to the reaction they invoke: the resident strikes back at strong competitors while tolerating the coexistence of the weaker ones. (b) We show how the transition from “stable coexistence of the annual with one line of the biennial" to "the resident strikes back "is achieved by a complicated global bifurcation involving two heteroclinic tangencies and a heteroclinic tangle in between. (c) We describe the interaction between the annual and both lines of the biennial in the "resident strikes back" subset of parameter space in terms of an attracting heteroclinic cycle at the boundary, corresponding to an infinitely extended sequence of ever more delayed upswings and downswings of, alternatingly, the even-year and the odd-year subpopulation of the biennial.

The Basic Population Model and its Dynamics

Assume that reproduction only happens at age k. Let the variable $x(t)$ denote the number or density of young–of–the–year (YOY). When intraspecific competition is restricted to the breeding spots and/or the nursery we can postulate that the dynamics of the population is described by the delayed difference equation

$$x(t) = f(c\,x(t-k)) , \tag{1}$$

where the parameter c combines the relevant information about individual survival and reproductive potential at the reproductive age k. For f, we take

$$f(x) = x\,\phi(x) , \tag{2}$$

where ϕ is a decreasing function with $0 < \phi \leq 1$ and $\phi(0) = 1$, which measures the effect of intraspecific competition in the breeding spot or nursery on successful maturation. We assume that the graph of f has a "humped" shape. For the functions ϕ that we consider, population dynamics exhibits convergence to equilibrium for small c. Increase of c will lead to a cascade of period-doubling bifurcations. Well-known examples from the literature include the logistic equation, the Ricker (1954) equation, Hassell's (1975) equation, and others. We choose $\phi(x) = \exp(-x)$, for computational simplicity. Other choices yield qualitatively the same results. Furthermore, we scale the system by $x \to c\,x$, to get

$$x(t) = c\,x(t-k)\,e^{-x(t-k)} . \tag{3}$$

Notice that eqn (3) is equal to Ricker's equation when we look every k-th year, as with a strobe light. This reflects the reproductive isolation of the various year classes.

In Fig. 1 we have depicted the attractors of the scaled system (3), as a function of c. When c increases beyond c_A (which can be shown to be equal to e^2), the equilibrium solution loses stability due to a period-doubling (flip) bifurcation and a stable period-two solution $x_+x_- \cdots$ comes into being. Here, years of x_+ are referred to as *good* and years of x_- are referred to as *bad*. These epithets reflect the viewpoint of an individual organism: in good years the number of reproducing individuals is low [*i.e.* $x(t-k) = x_-$] and, consequently, the *per capita* reproduction is high, whereas in bad years the number of reproducers is high [*i.e.* $x(t-k) = x_+$] and *per capita* reproduction is low. The period-two solution loses stability at $c = c_B$, where a period-four solution originates. In the

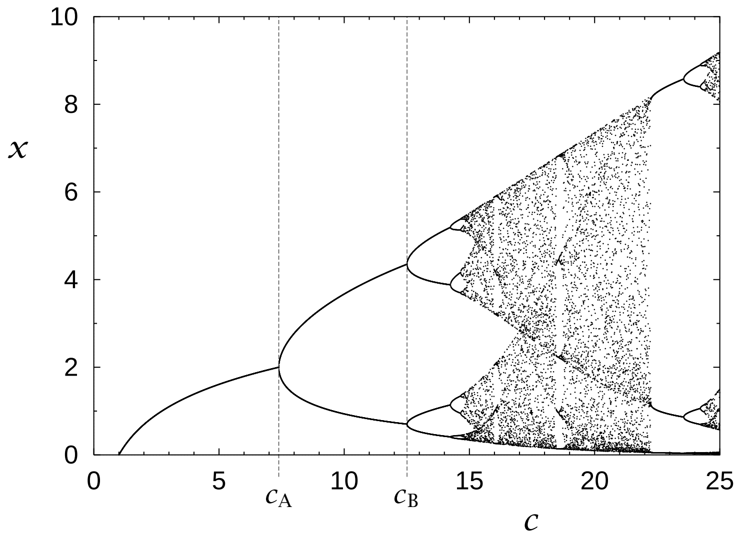

FIG. 1: Attractors of $x(t)$ as a function of c, generated by the delayed difference equation (3), $x(t) = c\,x(t-k)\,\exp(-x(t-k))$, for $k \in \{1, 2, \ldots\}$. Between $c_{\mathrm{A}} = e^2 \approx 7.389$ and $c_{\mathrm{B}} \approx 12.509$, a stable period-two solution exists.

rest of this paper, we will concentrate on the period-two solution, and only look below c_{A} or above c_{B} for reasons of comparison or to check for robustness. By convention, we always start with the good years being the even years and the bad years being the uneven ones.

The bifurcation diagram in Fig. 1 is identical for all positive integer numbers k. When we look at every k years in a delayed version ($k > 1$), x_+ and x_- alternate in the same way as in an "ordinary" ($k = 1$) version when we look every year. In a delayed version, however, each year (modulo k) corresponds to a different subpopulation or "line", independently coexisting in time with the other $k - 1$ subpopulations. Together, these lines show a periodic pattern of period ik, where $i = 2$ if the subpopulations oscillate with period two and $i = 4$ for a period-four attractor, and so on. The resulting true (*i.e.* smallest) period may be a divisor of ik. It turns out that for small k, the k subpopulations together show, modulo translation, only a relatively small number of periodic patterns (see Diekmann *et al.*, 1999; Diekmann & van Gils, 2000). These different attractors correspond to different combinations of phase of the uncoupled subpopulations.

The periodic solutions for each subpopulation are stable when they are stable as solutions of the ordinary difference equation. Then the periodic solutions of the entire population are also stable.

Competition Between Annuals and Biennials

Suppose an annual resident competes with a biennial invader which is inferior in the sense that $c_1 = c$ and $c_2 = sc$, with $0 < s < 1$. What will happen?

Looking Every Year

If we denote by x the density of annual young–of–the–year (YOY) in the present year, by y_1 the YOY of the biennial subpopulation or "line" that emerged in the previous year, and by y_2 the YOY of the biennial subpopulation that emerged in the present year (and also two years before), then we can describe the state in the next year by the following two-parameter family of maps $F : \mathbb{R}^3 \to \mathbb{R}^3$:

$$\begin{pmatrix} x \\ y_1 \\ y_2 \end{pmatrix}' = F \begin{pmatrix} x \\ y_1 \\ y_2 \end{pmatrix} := \begin{pmatrix} c\, x\, \phi(x + y_1) \\ y_2 \\ s\, c\, y_1\, \phi(x + y_1) \end{pmatrix}, \tag{4}$$

where $\phi(x+y_1)$ expresses the effect of the presence of both annual and biennial YOY in the breeding spot. (It should be noted that the interpretation of one of the state variables is different from the others: the second component of the state vector is not a present number of YOY but only serves to store information concerning YOY in the previous year.)

Looking Every Other Year

Following the dynamics of YOY of one of the biennial lines amounts to looking, "stroboscopically", every other time step. That is, we apply the map F twice. For this purpose, we define the map $G : \mathbb{R}^3 \to \mathbb{R}^3$ as

$$G := F \circ F. \tag{5}$$

The reproductive isolation of the biennial subpopulations is reflected mathematically by the invariance of the boundary planes $y_1 \equiv 0$ and $y_2 \equiv 0$ for the map G. Notice also that F is a symmetry for G, meaning that F and G commute.

Invasibility, Coexistence and Stability

We now assume that the annual resident has settled in the period-two attractor on the boundary, and introduce biennials in a good year (*i.e.* even year, by convention).

To answer the invasibility question, we first observe that the biennials as well as their offspring, grandchildren, *etc.*, are all born in a good year, whereas for the annual resident good and bad years alternate. The values of ϕ in good and bad years are, by necessity, such that on (geometric) average, the life-time *per capita* YOY production by one resident YOY is equal to one. Averaging over a period of two years, we can express this as $\sqrt{c^2\phi_+\phi_-} = 1$, where ϕ_+ is the density-dependent effect on survival and reproduction in the good years, and ϕ_- in the bad years. The biennial clone can invade if its average *per capita* YOY production exceeds one. That is, if $s c \phi_+ > 1$. By looking 4 years ahead, we can write this as $s^2c^2\phi_+^2 > 1$, which, by using the above-mentioned $c^2\phi_+\phi_- = 1$, leads to the following criterion for the successful invasion of one line of the biennial:

$$s > \sqrt{\frac{\phi_-}{\phi_+}}. \tag{6}$$

Similar calculations for other ages at reproduction and corresponding periodic attractors, can be found in Diekmann *et al.* (1999). Notice that only particular combinations of age at reproduction on the one hand, and period on the other hand, are worth studying: the greatest common divisor of age–at–reproduction and period should be greater than one. For example, annual invaders can never take advantage of periodicity as they will never be able to systematically avoid bad years.

For the choice $\phi(x) = \exp(-x)$, we have analytical expressions of the period-two resident cycle (see Appendix A). This enables us to derive a parameterization of the boundary of the subset in (c, s) parameter space where the invasion criterion (6) is satisfied (see Appendix B). The resulting curve appears in Fig. 2 as the part between c_A and c_B (to make sure that the resident oscillates with period two) of the solid curve marked TC. At the left-hand side of this curve, the annual population is stable against the invasion of biennials. As the curve is crossed, well-timed though inferior ($s < 1$) biennials can successfully invade the annual population. When s is close to one, the annuals are only slightly superior to the biennials and consequently, for successful invasion to occur, the difference between good and bad years need not be very large. As we can see in Fig. 2, it is large enough, already close to the first resident period-doubling at c_A. The more inferior the biennials are, the higher this difference needs to be, to compensate. This is reflected in the fact that the curve TC is decreasing.

Coexistence

We now focus on the interaction of the annual with one line of the biennial. Recall that only biennials that reproduce in good years can invade successfully. Since a period-two solution of the resident system is equivalent to an equilibrium solution of the same system when we stroboscopically look every other year, it is convenient to consider the map G, restricted to the plane $y_1 \equiv 0$. Writing y for y_2, we can express this two-dimensional system, with time steps of two years, as

$$\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} c^2\, x\, \phi(x)\, \phi(c\, x\, \phi(x) + y) \\ s\, c\, y\, \phi(c\, x\, \phi(x) + y) \end{pmatrix}. \tag{7}$$

[The dynamics in the plane $y_1 \equiv 0$ is equivalent to the dynamics in the plane $y_2 \equiv 0$, in the sense that F maps orbits to orbits. Applying F twice amounts to shifting one position along the orbit. So when reading the following, one might imagine two boundary quarter planes of the positive cone of $\mathbb{R}^3$, and our description of the dynamics pertaining to each of these invariant quarter planes (*cf.* Figs 7 and 8). We conjecture that for $s < 1$, every orbit starting in the interior of the positive cone of $\mathbb{R}^3$ will ultimately get ever closer to the union of the boundary quarter planes.]

The even-year system (7) has a unique positive stationary solution $(\hat{x}, \hat{y})$. That is, an equilibrium in which annuals coexist with one line of biennials. For the choice $\phi(x) = \exp(-x)$, we even have an analytical expression for this equilibrium (see Appendix C). In Appendix D, we show that $(\hat{x}, \hat{y})$ is stable in $\mathbb{R}^3$: low densities of the other biennial line decrease as long as one is near the stationary solution. By linearizing eqn (7) around $(\hat{x}, \hat{y})$, we can calculate

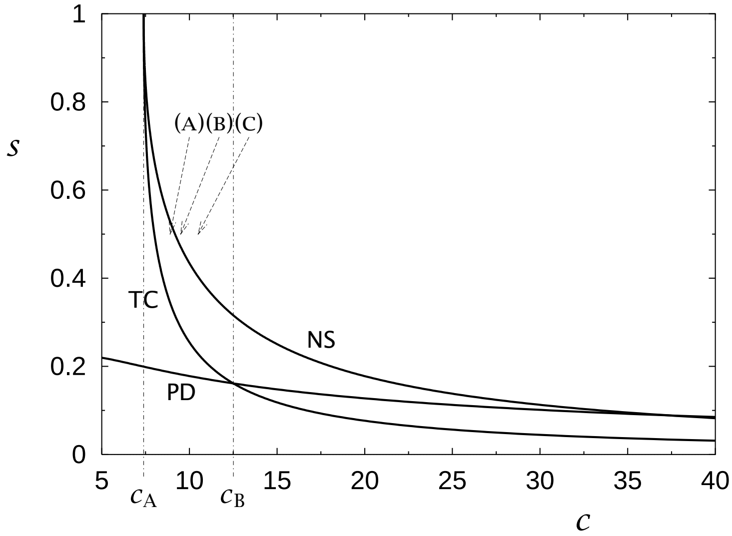

FIG. 2: Stability boundaries of the dimorphic equilibrium $(\hat{x}, \hat{y})$ of the even-year system (7), with $\phi(x) = \exp(-x)$. Bifurcation curves are solid (TC: transcritical, NS: Neimark–Sacker, PD: period-doubling bifurcation). The stable region of the equilibrium is bounded by these three curves. Between c_A and c_B the annual resident is in time–modulo–2 (stroboscopic) equilibrium (*cf.* Fig. 1). Labels (A), (B) and (C) refer to the numerical experiments in Fig. 3.

the region in (c, s)-space where the equilibrium exists and is stable within the invariant plane $y_1 \equiv 0$ (see, *e.g.* Edelstein-Keshet, 1988 and Appendix E).

Figure 2 depicts the region of stability of the annual–biennial equilibrium. In the sickle-shaped region, bounded by the three curves TC, NS and PD, the equilibrium exists and is stable. If we increase c, starting at $c = c_A$, the equilibrium branches off from the invariant line $y \equiv 0$ into the interior when the curve marked TC is crossed. This is a transcritical bifurcation (see, *e.g.* Kuznetsov, 1995). Note that this event coincides with neutrality (*i.e.* equality, rather than inequality) of the invasion criterion (6). At the left-hand side of the curve TC the annual two-cycle is not invasible and there is no dimorphic stroboscopic equilibrium, whereas at the right-hand side invasion in the good years has success and leads to stable coexistence.

In Fig. 3(A), we plotted the results of numerical experiments which show invasion of biennials in the good-year stroboscopic equilibrium $(x_+, 0)$ of the resident, leading the system to the dimorphic equilibrium $(\hat{x}, \hat{y})$. In fact, we performed a series of different, small perturbations of $(x_+, 0)$ and plotted all orbits from these experiments, to visualize the unstable manifold and the attractor. For these perturbations and for the calculations of the isoclines and unstable manifolds in the figure we used GRIND (de Boer, 1983). The dimorphic equilibrium loses stability at higher values of c and/or s, by a Neimark–Sacker bifurcation (curve NS in Fig. 2; see Kuznetsov, 1995). Just beyond this bifurcation, a closed invariant attracting curve ("limit cycle") is surrounding the unstable stationary equilibrium point $(\hat{x}, \hat{y})$, and successful invasion leads to coexistence on this interior attractor [Fig. 3(B)].

For extreme biennial inferiority (*i.e.* small s-values, below curve TC in Fig. 2),

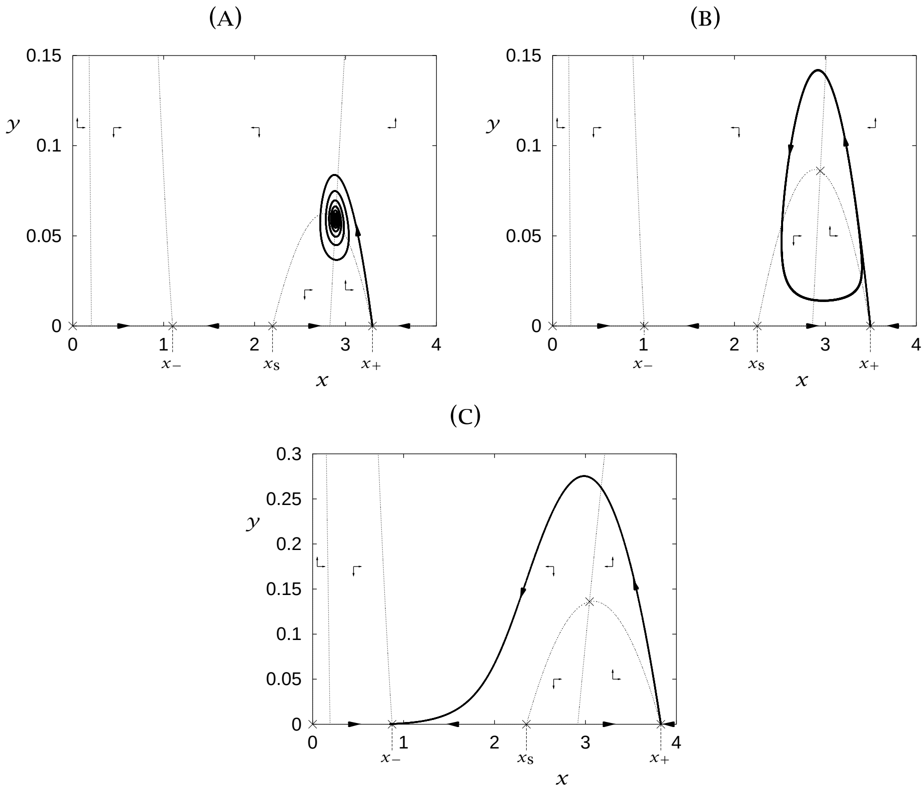

FIG. 3: Numerical experiments with system (7), showing invasion of biennials in the good years of the annual period-two point, $(x_+, 0)$. Panel (A) stable dimorphic equilibrium ($c = 9.0$); panel (B) stable invariant circle ($c = 9.5$); panel (C) the resident strikes back ($c = 10.5$). For all experiments, $s = 0.5$. Densities were plotted every other time step. Dotted curves indicate where the movement changes sign in either the x- or the y-direction, ▸ and → symbols indicate the direction, and × symbols mark stationary points.

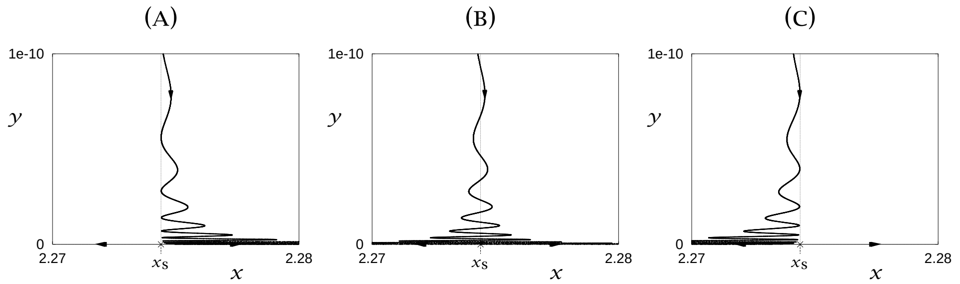

FIG. 4: Numerical experiments with system (7), showing the formation of the heteroclinic tangle, in an extreme blow-up around the saddle point $(x_S, 0)$. Panel (A) just before the tangency ($c = 9.7220740807$); panel (B) the heteroclinic tangle ($c = 9.7220740809$); panel (C) just beyond the tangency ($c = 9.7220740811$). For all experiments, $s = 0.5$. Notation as in Fig. 3.

there is no dimorphic equilibrium. As a side remark we report that in the region between the curves PD and TC, beyond the second period-doubling of the resident ($c > c_B$), the dimorphic equilibrium is a saddle point, with its unstable manifold connected to the (period-four or higher) boundary attractors of the resident population. When c increases, this interval of s-values grows somewhat, at the cost of the interval between the curves PD and NS, where the dimorphic equilibrium is stable.

THE RESIDENT STRIKES BACK

When the biennials are only slightly inferior to the annuals (*i.e.* at intermediate or large s-values), coexistence with annuals, in a dimorphic equilibrium, a limit cycle or another interior attractor, is harder to achieve for the biennials than when they survive less or reproduce less (*i.e.*, have a lower s-value). This counterintuitive result is due to the resident striking back.

Numerical experiments show that, when c and/or s is increased further beyond the Neimark–Sacker curve NS, the interior attractor disappears by the formation of a heteroclinic tangle. This is a trajectory structure, connecting the high equilibrium $(x_+, 0)$, through the interior, with the saddle point $(x_S, 0)$ on the boundary. The trajectory is coiled infinitely many times extremely close to the boundary $y \equiv 0$ (see, *e.g.* Kuznetsov, 1995). For small c-values this happens when the invariant circle collides with the stable manifold of the saddle point $(x_S, 0)$.

In Fig. 4, we show an extreme blow-up of the region around the boundary saddle point $(x_S, 0)$, in three series of numerical experiments. Panel (A) depicts the situation just before the unstable manifold of $(x_+, 0)$ is tangent to the stable manifold of $(x_S, 0)$. Panel (B) shows the tangle (*i.e.* infinitely many intersections, by necessity, of unstable and stable manifold), and in panel (C) we see that the intersection has just dissolved. In the latter situation, the resident strikes back and the unstable manifold of $(x_+, 0)$ coils downward to lower and lower y-values while approaching $(x_-, 0)$.

The parameter region in which the tangle exists is extremely narrow for small c-values, but grows somewhat larger when c increases. After the tangle has dissolved, a direct connection between the high equilibrium $(x_+, 0)$ and the

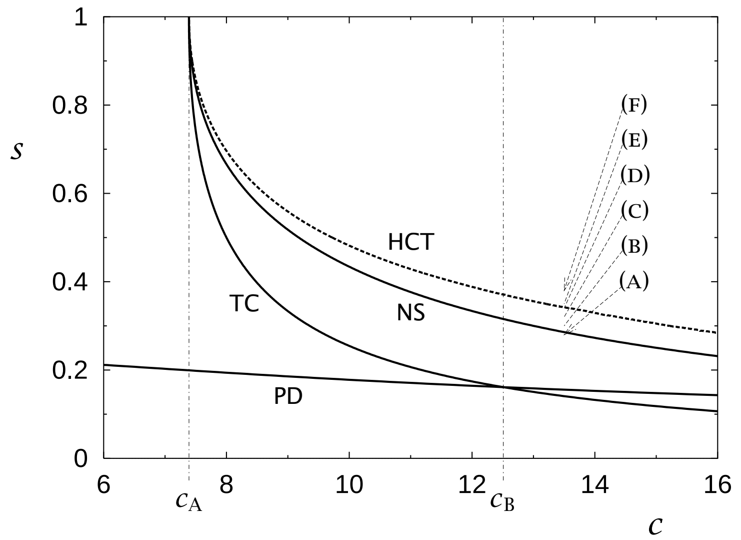

FIG. 5: Bifurcation curves of the even-year system (7). Local bifurcation curves of the dimorphic equilibrium are solid, and labelled as in Fig. 2. The heteroclinic tangle is located at the dashed curve (HCT). Labels (A) to (F) refer to the numerical experiments in Fig. 6.

low equilibrium $(x_-, 0)$ remains [Fig. 3(C)]. Successful invasion in the high equilibrium is followed by extinction, and the resident is left in the low equilibrium. This corresponds to a phase shift, resulting in the interchange of good and bad years in the original system, when we look every year.

The manifold from $(x_+, 0)$ to $(x_-, 0)$ is called a heteroclinic connection in the plane $y_2 \equiv 0$. In $\mathbb{R}^3$ there are, by symmetry, two such connections, one in the boundary plane $y_1 \equiv 0$ and one in the boundary plane $y_2 \equiv 0$. The set consisting of the period-two points $(x_+, 0)$ and $(x_-, 0)$ and the two connecting orbits in the boundary planes is a heteroclinic cycle. Calculations (see Appendix F) as well as numerical simulations show that the heteroclinic cycle is attracting for all parameter combinations for which it exists.

We have continued the heteroclinic tangencies numerically by a bisection method in (c, s)-space. In Fig. 5 we show an overview of our results. Suppose we choose an s-value above the period-doubling curve PD and a c-value below c_A, and then let c increase while performing experiments of introducing some biennial invaders in the annual resident population (*cf.* Fig. 3). We then successively see as attractors in any of the two invariant boundary planes: a non-invasible annual resident in steady state; after the line $c = c_A$ has been crossed, a non-invasible annual in a period-two attractor; after the curve TC has been crossed, a stable annual–biennial period-two attractor; beyond the curve NS, a dimorphic invariant circle and/or a menagerie of more complicated interior attractors; and, finally after the two almost overlapping curves of heteroclinic tangency, denoted together by HCT have been crossed, an “invasible yet invincible” annual period-two attractor (*i.e.* an equilibrium of G).

To show, for completeness, that the coexistence of annuals and biennials in several types of interior attractors, and also the heteroclinic tangle and the resident–strikes–back phenomenon extend to other regions of parameter space than between c_A and c_B, we have included Fig. 6. In the experiments shown in this figure, the annual resident has settled on a period-four attractor before biennials are introduced. Notice that we plotted the values of x and y every fourth time step. With increasing s, we see that invasion is possible from both "high' periodic points of the resident [shown in panels (A), (B) and (F)], and that the interior attractor is subject to period-doubling bifurcations [panel (B)] and has become a strange attractor [panels (C), (D)] before the heteroclinic tangency is formed [panel (E)]. The parameter region for the heteroclinic tangle is less narrow now, and after the tangle has dissolved, the resident strikes back by mapping both high boundary points onto the low points [panel (F)].

Finally, it should not pass unnoticed that an *increase* in s (*i.e.* higher survival and/or reproduction) may make a biennial *less* successful in the competition. The initial performance of the invader is positively correlated with s, both in terms of invasion success (see Fig. 5) and in terms of the maximum density reached after successful invasion (see Figs 3 and 6). Triggered by this high invasion success, however, the resident strikes back by changing its pace.

Interaction of the biennial lines

In the subset of parameter space bounded by TC, PD and NS we have bistability: the annual can coexist in a stable period-two orbit with either the even or the odd biennial subpopulation (see Appendix E). Numerical experiments suggest that: (a) also beyond NS up to HCT we have bistability, but now of more complicated attractors in the two boundary planes; (b) the bistability is global: wherever we start in the interior of $\mathbb{R}^3_+$, the orbit converges to one of the two coexistence boundary planes. That is, only one biennial line can coexist with the annual population. In support of the second point we note that solving $F(\mathbf{x}) = \mathbf{x}$ and $F^2(\mathbf{x}) = \mathbf{x}$ [where $\mathbf{x} = (x, y_1, y_2)^{\mathrm{T}}$; see system (4)] yields neither an equilibrium nor a period-two solution, in which both odd- and even-year biennial subpopulations coexist with the annual population. So between the curves TC and HCT we have bistability: it will depend on the initial conditions (in particular the phase of the period-two resident attractor) as to which line will stay present when both are introduced. Beyond the HCT curve, however, it is possible that repeated upswings and downswings lead to a form of coexistence over time.

In Fig. 7, we show a numerical experiment of competition between both lines of the biennial, introduced at low densities in an annual resident population that has converged to the period-two attractor. Parameter values are in the resident–strikes–back region [using system (4), with $c = 10$ and $s = 0.6$] and initial conditions are such that the good years are the even years. After the immediate rise and subsequent fall of the even-year subpopulation, the odd-year line starts building up, triggered by the phase shift caused by the even-line invasion. The rise of the odd-year line brings the annual back to the original phase, causing the fall of the odd-year line and creating new possibilities for the even-year line, *etc.* This leads to ever longer periods of ever lower densities in between short but substantial biennial peaks.

A similar experiment is shown in Fig. 8, where we introduced "life-history noise", by assuming that 5 % of each biennial line "mistake", by already reproducing after one year. In this situation, the bad-year line is protected against extinction by individuals leaking out of the current good-year line. This leads to an

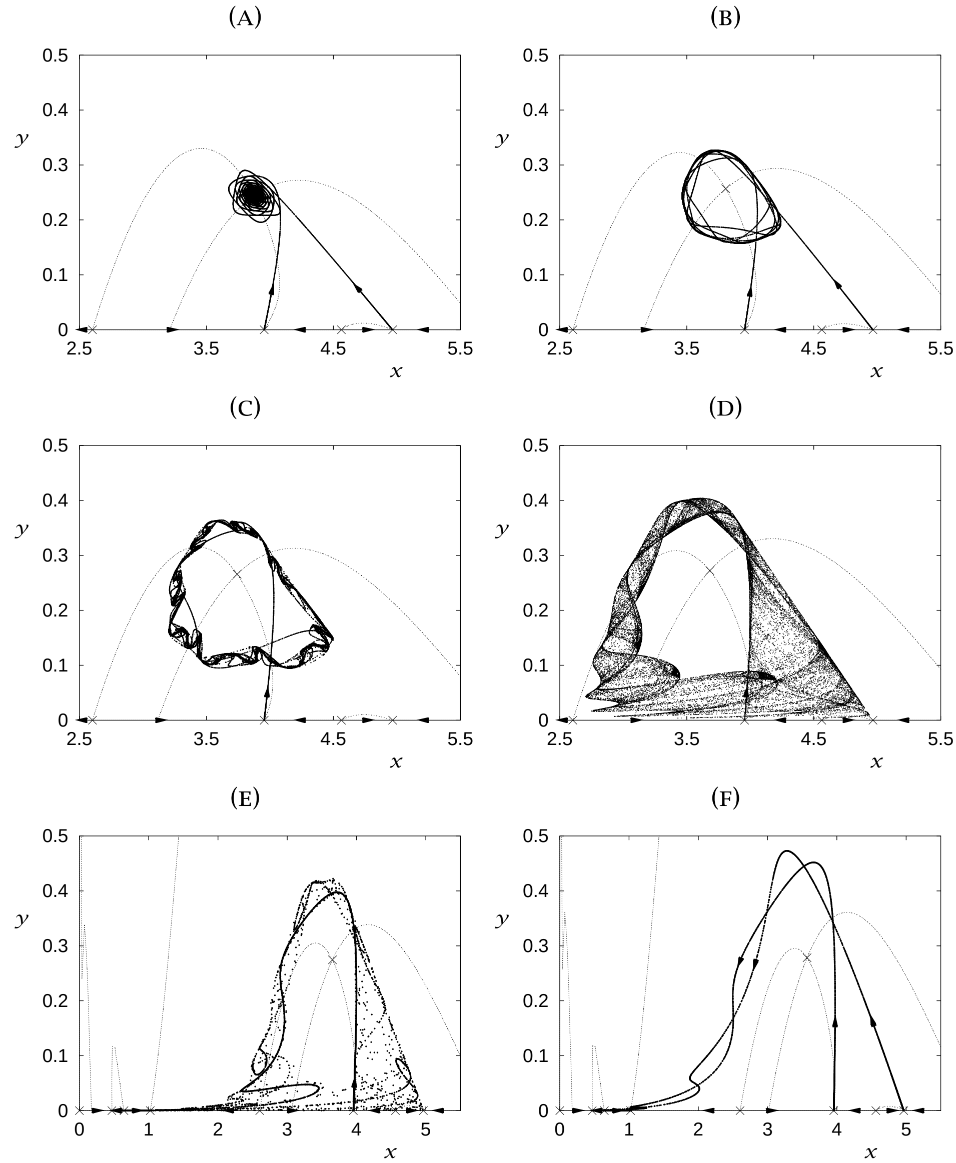

FIG. 6: Numerical experiments with system (7), showing invasion of biennials in both high periodic points of an annual resident in a period-four attractor ($c = 13.5$). Panel (A) $s = 0.28$; (B) $s = 0.30$; (C) $s = 0.32$; (D) $s = 0.34$; (E) $s = 0.35$; (F) $s = 0.38$. In panels (A), (B) and (F) biennials were introduced in both high period-four points, in panels (C), (D) and (E) only in the lower one. Densities were plotted every fourth year. Notation as in Fig. 3.

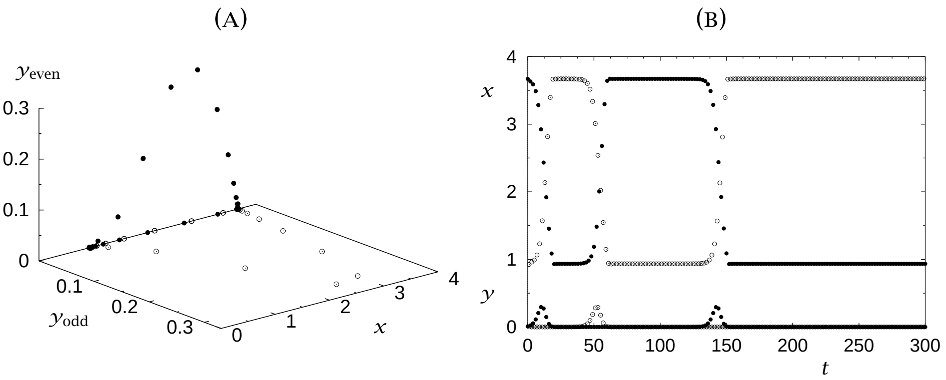

FIG. 7: A numerical experiment with system (4), in which both lines of the biennial are introduced at low densities in an annual resident population in a period-two attractor. Panel (A) phase plot; (B) time plot. Parameters: $(c, s) = (10, 0.6)$. Initial condition: $(x(0), y_1(0), y_2(0)) = (3.67, 0.01, 0.01)$. Population densities in even and in odd years are plotted with $\bullet$ and $\circ$ symbols, respectively.

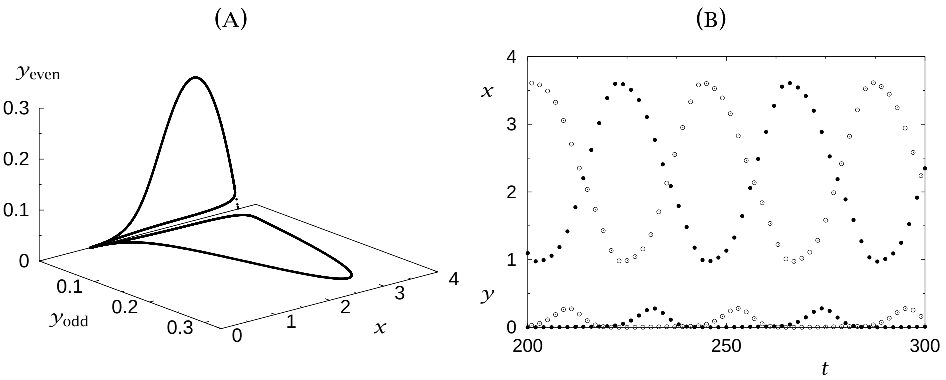

FIG. 8: A numerical experiment with a variant of system (4), in which 5 % of the biennials reproduce annually. Parameters: $(c, s) = (10, 0.6)$. Initial condition: $(x(0), y_1(0), y_2(0)) = (3.67, 0.0, 0.01)$. Notation as in Fig. 7.

infinitely ongoing alternation of favourable and unfavourable conditions, with each line having repeatedly short periods of high abundance. Other perturbations of system (4), like demographic stochasticity or environmental noise, will disturb the regularity of this pattern. However, the phenomenon of repeated upswings followed by downswings due to the resident changing its pace, is robust.

Conclusions and discussion

The resonance of life span relative to population-dynamic fluctuations, with the invader taking advantage of its better synchronization with the good years, can have a profound effect on the competitive success of an invading life history. We analysed the mechanism by which successful invasion in one attractor, with the invader population growing to an appreciable size, can be followed by extinction of the former invader, ultimately leading the resident to a phase-shifted attractor (or, as another possibility, a different attractor: see Diekmann *et al.*, 1999). For the mathematically interested reader, we have shown that this is achieved by a heteroclinic connection between the “good” and the “bad” periodic points of the resident population dynamics. The transition from resonance-mediated coexistence to “the resident strikes back” (*i.e.* the heteroclinic connection) is characterized by an attractor collapse due to colliding invariant manifolds.

Surprisingly enough, in low-periodic attractors, “inferior” invaders do a better job than invaders that survive and/or breed almost as well as the resident. Depending on the exact difference between good and bad years, certain well-timed inferior clones can invade and coexist, whereas well-timed better ones get ousted out inevitably. In this region of parameter space, the complete system of annual and both biennial populations shows bistability: one of the biennial lines is doomed to go extinct. If evolution or environmental changes will lead to less inferior biennials in a coexisting annual–biennial population, we expect instability of the dimorphic attractor due to the heteroclinic tangle. The repeated occurrence of low population densities will then result in extinction of the biennial type.

If an invading biennial goes extinct, for example due to demographic stochasticity, without the resident settling into the phase-shifted attractor, new even-year biennial mutants or immigrants can successfully invade again. If, after a successful invasion, the resident does shift phase, odd-year biennials stand a good chance of invading successfully. This leads (also with noise added) to a form of intermittent existence, with odd- and even-year biennial uprises and almost monomorphic periods in between. The attracting heteroclinic cycle in $\mathbb{R}^3$ serves as a template for such dynamics.

We emphasize that the resident–strikes–back phenomenon is possible only when invasion exponents are multi-valued, as a result of coexisting attractors (or a chaotic attractor with invasion exponents of a different sign: see Hofbauer *et al.*, 1998). This can in particular be expected whenever the population consists of subpopulations that interact only weakly or not at all before a mutant appears. That condition was clearly fulfilled here as well as in Doebeli (1998), and in Van Dooren & Metz (1998), who show another case of multi-valued invasion functions in the context of temporally structured populations.

From a biological viewpoint, the interior attractor that is formed close to the heteroclinic tangency, and the heteroclinic tangle itself, are hardly relevant, firstly, because they occur in a relatively small region of parameter space. Secondly, they will cause the extinction of the invader because it repeatedly passes through periods with very low population densities. But between successful invasion and extinction it will have reached higher numbers, so we could also say that in this case the resident strikes back by driving the invader to low population numbers.

Will noise restore the straightforward situation that we observed in population-dynamical steady state? One might argue that with enough noise there will be no multiplicity of local attractors and, consequently, no attractor shifts. In our view, however, the cyclic dynamics and long periods of low mutant densities in the examples with noise are just another manifestation of the mechanism that promotes exclusion of the invader.

A related reservation is that we have not taken the mode of inheritance into account. Hammerstein & Selten (1994; Hammerstein, 1996) have postulated that genetic constraints may be negligible in long-term evolution, in favour of game-theoretical approaches (see also Matessi & Di Pasquale, 1996). Weissing (1996) extrapolated the scope of their results to nonlinear fitness functions, but at the same time stressed their limitations: giving a game-theoretical characterization of evolutionary stability seems to be a formidable task when, among others, population composition is polymorphic and when population dynamics does not show long-term stable equilibria. This is easily the case in our salmon example. Kaitala & Getz (1995) already noted that spatial heterogeneity may easily lead to assortative mating and, additionally, semelparity and the resonance phenomenon have assortative mating as a side effect. Consequently, when a trait relates to spatio-temporal inhomogeneity while population dynamics creates fluctuations, the need to consider genetics may be bigger.

A locally non-invasible strategy restricts invaders to playing only slightly different strategies. This concept is especially important if one assumes that mutant phenotypes originate with only slight deviations from the resident wild-type. If mutations are limited to small steps, the phenomenon of sudden invasion-driven attractor shifts will be replaced by a resident phenotype-driven continuation of the attractor (Geritz *et al.*, in press). However, we see no reason for mutational steps to be necessarily small in traits like timing of reproduction and probability of dispersing. In our opinion, this is a strong motivation to work with traits that allow for a mechanistic, rather than phenomenological, interpretation. For instance, it seems reasonable to assume that salmon base the irreversible transition to prepare for the return to fresh water on some indicator of their physi(ologi)cal condition, like size. In combination with a stochastic food supply, or a probabilistic description of growth, this then may easily lead to some returning at different ages than others.

How realistic and how general is the resident–strikes–back phenomenon? For real-world salmon (*e.g. Oncorhynchus gorbuscha*), period-two population dynamics have been observed in a time series of several decades. However, this has been attributed to a rigid two-year life cycle of the species and the absence, for long periods, of one of the two lines in certain areas (Neave, 1953; Ricker, 1954; Peterman, 1977). The mechanism behind this periodicity, and why the levels of abundance of the lines occasionally are reverted is, to our knowledge, still unclear.

The dispersal example (Doebeli, 1998), from a totally different context, and the widespread occurrence of non-equilibrium dynamics in natural ecosystems, suggest some generality. The total set of prerequisites present in our model (strict semelparity, intercohort competition confined to the nursery, the deterministic nature of the model at the individual level, *etc.*) makes it rather caricatural and degenerate. But the coexistence of attractors with different invasion properties is a robust phenomenon. That is, it survives perturbations of the model like the addition of a small amount of noise. Successful invasion of one boundary attractor leading in the end to another attractor in the same boundary is a robust phenomenon as well.

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APPENDIX A Monomorphic Annual Period-two Solution

A period-two solution of the annual resident system (1) is an equilibrium solution of the same system when we look at every other time step. That is, we are interested in the solution of $\bar{x} = f(f(\bar{x}))$ or, for $\phi(x) = e^{-x}$,

$$\bar{x} \;=\; c^2\,\bar{x}\,e^{-\bar{x}}\,e^{-c\,\bar{x}\,e^{-\bar{x}}}. \tag{A.1}$$

We neglect the trivial solution $\bar{x} = 0$. It is convenient to express the "high" (good-year) period-two point x_+ as a perturbation, with magnitude ξ, of the equilibrium point x_s, which is equal to $\ln c$. Then we can write x_+ as $\ln c + \xi$, and eqn (A.1) as

$$\begin{aligned} 1 \;=\; c^2\,e^{-(\ln c+\xi)}\,e^{-c\,(\ln c+\xi)\,e^{-(\ln c+\xi)}} \quad &\Leftrightarrow \quad 1 \;=\; c\,e^{-\xi}\,e^{-(\ln c+\xi)\,e^{-\xi}} \quad \Leftrightarrow \\ \ln c \;=\; \xi + (\ln c + \xi)\,e^{-\xi} \quad &\Leftrightarrow \quad \ln c\,(1-e^{-\xi}) \;=\; \xi\,(1+e^{-\xi}) \quad \Rightarrow \end{aligned}$$

$$\ln c \;=\; \xi\,\frac{1+e^{-\xi}}{1-e^{-\xi}}\,. \tag{A.2}$$

If we substitute eqn (A.2) in $x_+ = \ln c + \xi$ we find that

$$x_+ \;=\; \frac{\xi\,(1+e^{-\xi}) + \xi\,(1-e^{-\xi})}{1-e^{-\xi}} \;=\; \frac{2\,\xi}{1-e^{-\xi}}\,. \tag{A.3}$$

The other ("low") period-two point, x_-, which alternates with x_+, is equal to $f(x_+)$:

$$x_- \;=\; c\,x_+\,e^{-x_+} \;=\; c\,x_+\,e^{-(\ln c+\xi)} \;=\; x_+\,e^{-\xi} \;=\; \frac{2\,\xi\,e^{-\xi}}{1-e^{-\xi}}\,. \tag{A.4}$$

APPENDIX B Biennial Invasion in Period-two Annual Resident

Using eqns (A.3) and (A.4), we can write the ratio between good and bad years as

$$\frac{\phi_-}{\phi_+} \;=\; \frac{e^{-x_+}}{e^{-x_-}} \;=\; \exp\left(\frac{2\,\xi\,e^{-\xi}}{1-e^{-\xi}} - \frac{2\,\xi}{1-e^{-\xi}}\right) \;=\; e^{-2\,\xi}\,. \tag{B.1}$$

So we can write the biennial invasion criterion (6) as

$$s \;>\; e^{-\xi} \tag{B.2}$$

and use eqn (A.2) to parameterize a curve in (c,s)-space which bounds the region where the criterion for successful invasion is satisfied:

$$(c(\xi), s(\xi)) \;=\; \left(\exp\left[\xi\,\frac{1+e^{-\xi}}{1-e^{-\xi}}\right], \exp\left[-\xi\right]\right)\,. \tag{B.3}$$

Appendix C Dimorphic Annual/Biennial Solution

To find the dimorphic equilibrium $(\hat{x}, \hat{y})$ of the even-year system we substitute $\hat{x}$ for x' and x, and $\hat{y}$ for y' and y in eqn (7), and divide the equations by $\hat{x}$ and $\hat{y}$, respectively, to obtain the system of equations

$$\left\{ \begin{array}{lcl} 1 & = & c^2\,\phi(\hat{x})\,\phi(c\,\hat{x}\,\phi(\hat{x}) + \hat{y}) \\ 1 & = & c\,s\,\phi(c\,\hat{x}\,\phi(\hat{x}) + \hat{y})\,. \end{array} \right. \tag{C.1}$$

Dividing eqn (C.1b) by cs we can express the common factor $\phi(c\hat{x}\phi(\hat{x}) + \hat{y})$ in these equations as $1/(cs)$. Substituting this in eqn (C.1a) we find $\phi(\hat{x}) = s/c$, or $\hat{x} = \phi^{-1}(s/c)$. Substituting $\phi(\hat{x}) = s/c$ in eqn (C.1b) we obtain $\phi(s\hat{x} + \hat{y}) = 1/(cs)$, or $s\hat{x} + \hat{y} = \phi^{-1}(1/(cs))$. Using $\hat{x} = \phi^{-1}(s/c)$ to solve this equation for $\hat{y}$ we end up with

$$\left\{ \begin{array}{lcl} \hat{x} & = & \phi^{-1}\left(\dfrac{s}{c}\right) \\ \hat{y} & = & \phi^{-1}\left(\dfrac{1}{cs}\right) - s\,\phi^{-1}\left(\dfrac{s}{c}\right)\,. \end{array} \right. \tag{C.2}$$

For the choice $\phi(x) = \exp(-x)$, *i.e.* $\phi^{-1}(x) = -\ln x$, this reads as

$$\left\{ \begin{array}{lcl} \hat{x} & = & \ln c - \ln s \\ \hat{y} & = & \ln c + \ln s - s\,(\ln c - \ln s)\,. \end{array} \right. \tag{C.3}$$

Appendix D Stability of the Dimorphic Annual/Biennial Solution in $\mathbb{R}^3$

In Appendix E we discuss the stability of $(\hat{x}, \hat{y})$ as an equilibrium of eqn (7). That is, in $\mathbb{R}^2$, *within* the invariant plane $y_1 \equiv 0$. Here we shall verify the *transversal stability* of $(\hat{x}, \hat{y})$ in $\mathbb{R}^3$, by which we mean that small perturbations out of the plane $y_1 \equiv 0$ necessarily decay as long as the system state is near the fixed point

$$\begin{pmatrix} x \\ y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} \hat{x} \\ 0 \\ \hat{y} \end{pmatrix} \tag{D.1}$$

of the map G.

From eqn (4) we deduce that G is given by

$$G\begin{pmatrix} x \\ y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} c^2\,x\,\phi(x + y_1)\,\phi(c\,x\,\phi(x + y_1) + y_2) \\ s\,c\,y_1\,\phi(x + y_1) \\ s\,c\,y_2\,\phi(c\,x\,\phi(x + y_1) + y_2) \end{pmatrix}. \tag{D.2}$$

From this expression one can read right away that the third eigenvalue of the linearization of G at the fixed point, *i.e.* the one with an eigenvector that has a non-trivial second component, equals $sc\phi(\hat{x})$. (Indeed, the y_1 component is multiplied by $sc\phi(x + y_1)$, a number which equals $sc\phi(\hat{x})$ at the fixed point.) Now recall from Appendix C that $\phi(\hat{x}) = s/c$. Hence, $sc\phi(\hat{x}) = s^2 < 1$.

Appendix E Stability of the Dimorphic Solution in $\mathbb{R}^2$

First we write the even-year system (7) as

$$\begin{aligned} x' &= f_1(x,y)\,, \\ y' &= f_2(x,y)\,. \end{aligned} \tag{E.1}$$

For the choice $\phi(x) = \exp(-x)$ we can express the partial derivatives of the right-hand side in the dimorphic equilibrium $(\hat{x}, \hat{y})$ as

$$\begin{aligned} \frac{\partial f_1(\hat{x},\hat{y})}{\partial x} &= c^2\,[\,\phi(\hat{x}) + \phi(c\,\hat{x}\,\phi(\hat{x}) + \hat{y}) + \hat{x}\,(\,\phi'(\hat{x})\,\phi(c\,\hat{x}\,\phi(\hat{x}) + \hat{y}) \\ &\qquad + \phi(\hat{x})\,\phi'(c\,\hat{x}\,\phi(\hat{x}) + \hat{y})\,c\,(\phi(\hat{x}) + \hat{x}\,\phi'(\hat{x}))\,)\,] \\ &= c^2 \left[\frac{s}{c}\,\frac{1}{cs} + \hat{x}\left(\frac{-s}{c}\,\frac{1}{cs} + \frac{s}{c}\,\frac{-1}{cs}\,c\left(\frac{s}{c} + \hat{x}\,\frac{-s}{c}\right)\right)\right] \\ &= 1 - \hat{x}\,(1 + s\,(1-\hat{x})) \;=\; (1-\hat{x})\,(1 - s\,\hat{x})\,, \end{aligned} \tag{E.2}$$

$$\begin{aligned} \frac{\partial f_1(\hat{x},\hat{y})}{\partial y} &= c^2\,\hat{x}\,\phi(\hat{x})\,\phi'(c\,\hat{x}\,\phi(\hat{x}) + \hat{y}) \\ &= c^2\,\hat{x}\,\frac{s}{c}\,\frac{-1}{cs} \;=\; -\hat{x}\,, \end{aligned} \tag{E.3}$$

$$\begin{aligned} \frac{\partial f_2(\hat{x},\hat{y})}{\partial x} &= c\,s\,\hat{y}\,\phi'(c\,\hat{x}\,\phi(\hat{x}) + \hat{y})\,c\,(\,\phi(\hat{x}) + \hat{x}\,\phi'(\hat{x})\,) \\ &= c\,s\,\hat{y}\,\frac{-1}{cs}\,c\left(\frac{s}{c} + \hat{x}\,\frac{-s}{c}\right) \;=\; -s\,\hat{y}\,(1-\hat{x})\,, \end{aligned} \tag{E.4}$$

$$\begin{aligned} \frac{\partial f_2(\hat{x},\hat{y})}{\partial y} &= c\,s\,[\,\phi(c\,\hat{x}\,\phi(\hat{x}) + \hat{y}) + \hat{y}\,\phi'(c\,\hat{x}\,\phi(\hat{x}) + \hat{y})\,] \\ &= c\,s\left[\frac{1}{cs} + \hat{y}\,\frac{-1}{cs}\right] \;=\; 1 - \hat{y} \end{aligned} \tag{E.5}$$

[where we use, in each second step, that $\phi'(x) = -\phi(x)$ and $\phi(c\hat{x}\phi(\hat{x})+\hat{y}) = 1/(cs)$ and $\phi(\hat{x}) = s/c$].

This results in the following Jacobian matrix of the even-year system in $(\hat{x}, \hat{y})$:

$$\begin{pmatrix} (1-\hat{x})\,(1-s\,\hat{x}) & -\hat{x} \\ -s\,\hat{y}\,(1-\hat{x}) & 1-\hat{y} \end{pmatrix}. \tag{E.6}$$

Its determinant ($\mathcal{D}$) and trace ($\mathcal{T}$) are given by

$$\mathcal{D} = (1-\hat{x})\,(1 - s\,\hat{x} - \hat{y})\,, \tag{E.7}$$

$$\mathcal{T} = s\,\hat{x}^2 - (1+s)\,\hat{x} - \hat{y} + 2\,, \tag{E.8}$$

which yields

$$\mathcal{D} = (\ln c - 1)^2 - (\ln s)^2 \tag{E.9}$$

$$\mathcal{T} = s\,(\ln c - \ln s)^2 - 2\,(\ln c - 1) \tag{E.10}$$

if we substitute the equilibrium values for $\hat{x}$ and $\hat{y}$ from eqn (C.3).

The dimorphic equilibrium $(\hat{x}, \hat{y})$ loses stability by a Neimark–Sacker bifurcation (see Kuznetsov, 1995) when a complex pair of eigenvalues leaves the unit circle. This happens when the determinant $\mathcal{D}$ is equal to 1. From eqn (E.9) we see that this is the case when $(\ln c - 1)^2 = 1 + (\ln s)^2$, or $\ln c = 1 \pm \sqrt{1 + (\ln s)^2}$. Restriction to the case in which $c > 1$ gives us a parameterization of the Neimark–Sacker curve

$$\text{(NS)}: \qquad \ln c \;=\; 1 + \sqrt{1 + (\ln s)^2}\,. \tag{E.11}$$

The dimorphic equilibrium branches off into the interior when a real eigenvalue becomes equal to 1. This happens when $\mathcal{D} = \mathcal{T} - 1$. From eqns (E.9) and (E.10) we see that this is the case when

$$\begin{aligned}
(\ln c - 1)^2 - (\ln s)^2 &= s\,(\ln c - \ln s)^2 \\
&\quad - 2\,(\ln c - 1) - 1 && \Leftrightarrow \\
(\ln c - 1)^2 + 2\,(\ln c - 1) + 1 - (\ln s)^2 &= s\,(\ln c - \ln s)^2 && \Leftrightarrow \\
(\ln c)^2 - (\ln s)^2 &= s\,(\ln c - \ln s)^2 && \Leftrightarrow \\
\ln c + \ln s &= s\,(\ln c - \ln s) && \Leftrightarrow \\
\ln c\,(1 - s) &= -\ln s\,(1 + s)\,,
\end{aligned} \tag{E.12}$$

where we use that $\ln c \neq \ln s$ to proceed from the third to the fourth equation. For $s < 1$ this gives us a parameterization of the transcritical curve

$$\text{(TC)}: \qquad \ln c \;=\; -(\ln s)\,\frac{1 + s}{1 - s}\,. \tag{E.13}$$

The dimorphic equilibrium loses stability due to a period-doubling bifurcation when a real eigenvalue becomes equal to -1. This happens when $\mathcal{D} = -\mathcal{T} - 1$. From eqns (E.9) and (E.10) we see that this is the case when

$$\begin{aligned}
(\ln c - 1)^2 - (\ln s)^2 &= 2\,(\ln c - 1) - s\,(\ln c - \ln s)^2 - 1 \quad \Leftrightarrow \\
(\ln c)^2\,[1 + s] - (\ln c)\,[2\,(2 + s\,\ln s)] + [4 + (s - 1)\,(\ln s)^2] &= 0\,.
\end{aligned} \tag{E.14}$$

The solution of this quadratic equation in $\ln c$ gives us a parameterization of the period-doubling curve

$$\text{(PD)}: \qquad \ln c \;=\; \frac{2 + s\,\ln s \;\pm\; \sqrt{(\ln s)^2 - 4\,s\,(1 - \ln s)}}{1 + s}\,. \tag{E.15}$$

We have corroborated this analysis using CONTENT (Kuznetsov *et al.*, 1996), a software package for numerical bifurcation analysis.

APPENDIX F Stability of the Heteroclinic Cycle

It can be shown [see, *e.g.* Hofbauer and Sigmund (1998), and the references therein] that a heteroclinic cycle like the one between x_+ and x_- is attracting if (a) the product of the multipliers corresponding to the stable manifolds (*i.e.* the incoming directions to the saddle points in the cycle, along the planes $y_1 \equiv 0$ and $y_2 \equiv 0$, respectively) and the multipliers corresponding to the unstable manifolds (*i.e.* the outgoing directions) is less than one (note that the symmetry implies that this product is the same at x_+ and x_-), and (b) x_+ and x_- are both attracting in the transversal direction (*i.e.* along the x-axis).

Along the stable manifold of both period-two points x_+ and x_-, a biennial line has multiplier

$$s\, c\, \phi_- \;<\; 1 \tag{F.1}$$

and along the unstable manifolds a biennial line has multiplier

$$s\, c\, \phi_+ \;>\; 1\,. \tag{F.2}$$

The product equals

$$s^2\, c^2\, \phi_+\, \phi_- \;=\; s^2 \;<\; 1\,. \tag{F.3}$$

(Recall that $c^2 \phi_+ \phi_- = 1$ since the average *per capita* YOY production is assumed to be one.) This shows that in the region $c_{\mathrm{A}} < c < c_{\mathrm{B}}$, where the period-two cycle $x_+ x_-$ is attracting along the x-axis, the heteroclinic cycle between x_+ and x_- is locally attracting.