1 Stability of equilibrium points & bifurcations

1.1 Simple population model

The population model has in general two solutions (and hence two fixed points) for $\dot{N} = 0$, namely

$$N_1 = 0 \quad \text{and} \quad N_2 = K\frac{\alpha - \beta}{\alpha}.$$

The stability of these fixed points in function of α and β can be summarised as follows:

Parameter region	Fixed points
$\alpha < \beta$	$N_1 = 0$: stable $N_2 < 0$: unstable
$\alpha = \beta$	$N_1 = N_2 = 0$: half-stable (unstable for $N < 0$, stable for $N > 0$)
$\alpha > \beta$	$N_1 = 0$: unstable $N_2 > 0$: stable

The system thus undergoes a transcritical bifurcation at $\alpha = \beta$. Note that the fixed point $N_2 < 0$ is not meaningful in this model, as N represents a non-negative population count.

For the given parameter values, $\alpha > \beta$. Using the above results, we therefore find an unstable fixed point $N_1 = 0$, and a stable fixed point $N_2 = K(\alpha - \beta)/\alpha = 4\,023\,913$. As the population starts at $N > 0$, it will evolve towards N_2. The difference between $N(t)$ and $N(\infty) = N_2$ decays exponentially, as a Taylor approximation of $\dot{N}$ around N_2 can show.

1.2 Gene control model

For $r = 0$, the system equations become decoupled:

$$\dot{x} = \frac{\alpha_1}{2} - x$$
$$\dot{y} = \frac{\alpha_2}{2} - y.$$

We can therefore analyse them separately. It is clear that there is one fixed point, at $x^* = \alpha_1/2$ and $y^* = \alpha_2/2$. It is a globally stable attractor, as $\forall x < x^*$, $\dot{x} > 0$ and $\forall x > x^*$, $\dot{x} < 0$ (and analogously for $\dot{y}$ and y^*). The fixed point is thus an attracting star.
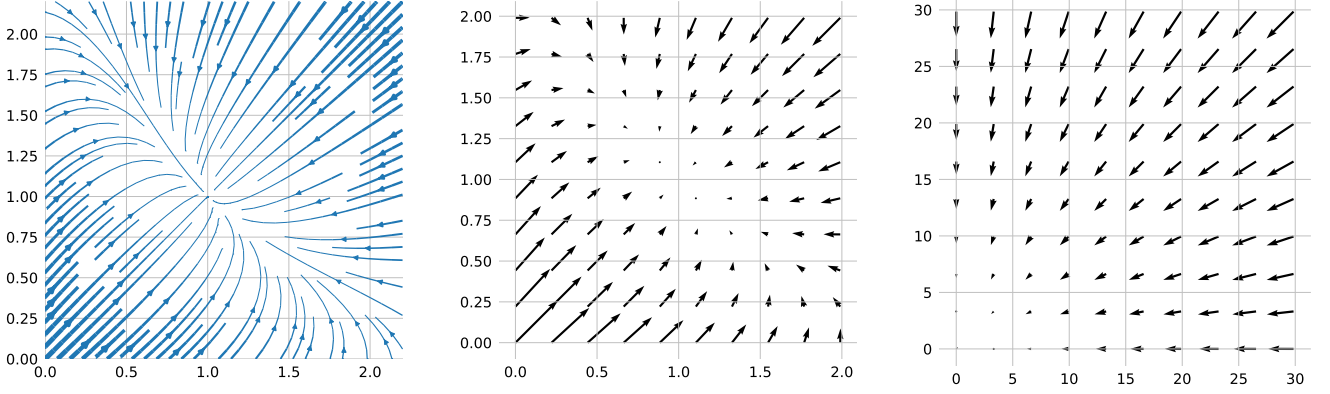
Figure 1: **There is only one fixed point for $0 \leq r \leq 2$.** Phase space plots of the gene control model, for $r = 1$ and $\alpha_1 = \alpha_2 = 2$. *Left*: some (partial) trajectories in phase space. Thicker lines represent a higher local speed. Note the attractor at $(1, 1)$. *Middle*: local velocities, evaluated on a grid. *Right*: same as middle, but for a larger region in phase space.

For $r \geq 0$ and $\alpha_1 = \alpha_2 = 2$, the equilibrium equations become

$$x(1 + y^r) = 2$$
$$y(1 + x^r) = 2.$$

It is easily verified that $(1, 1)$ is a solution and hence a fixed point. We have already shown that it is the only fixed point for $r = 0$. Plotting the gradient in phase space for different $r \in (0, 2)$ strongly suggests that it is also the only fixed point for nonzero $r < 2$ (at least for $x \geq 0$ and $y \geq 0$). See e.g. fig. 1 for $r = 1$. As a final piece of evidence, different trajectories simulated back in time all either tend towards (∞, ∞) or cross into forbidden $x < 0$, $y < 0$ territory.

To analyse the stability of the $(1, 1)$ fixed point, we approximate $(\dot{x}, \dot{y})$ as a linear system around this point. The Jacobian of $(\dot{x}, \dot{y})$ evaluated in $(1, 1)$ is:

$$\begin{pmatrix} -1 & -\frac{r}{2} \\ -\frac{r}{2} & 1 \end{pmatrix}.$$

It has two distinct eigenvalue-eigenvector pairs:

$$\lambda_1 = -\frac{r}{2} - 1, \quad \mathbf{v}_1 = (1,\ 1)$$
$$\lambda_2 = \frac{r}{2} - 1, \quad \mathbf{v}_2 = (-1,\ 1).$$

For $0 \leq r < 2$, $\lambda_1 \in (-2, -1]$ and $\lambda_2 \in [-1, 0)$. Both eigenvalues are negative, and $(1, 1)$ is therefore a stable node. Because $\lambda_1 < \lambda_2$, $\mathbf{v}_1 = (1, 1)$ is the fast eigendirection and $\mathbf{v}_2 = (-1,\ 1)$ is the slow eigendirection, as can be seen in fig. 1. (For $r = 0$, both eigenvalues are equal; i.e. $(1, 1)$ is then a star node).

Based on phase space plots for different values of r, it seems that a supercritical pitchfork bifurcation occurs at $r = 2$. As the problem is symmetrical for $\alpha_1 = \alpha_2$, this is expected (Strogatz 1994 [1]).
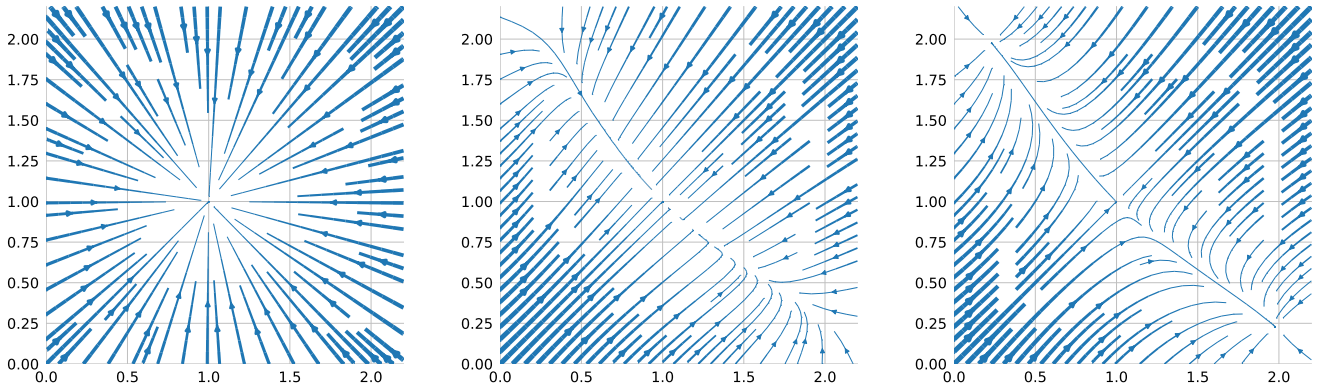
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Figure 2: **Topologies of phase space**. *Left*: $r = 0$. The single fixed point is an attracting star node. (For the intermediate case between $r = 0$ and $r = 2$, see fig. 1).*Middle*: $r = 2$. There is still only one fixed point. Because we are exactly at the bifurcation point, the approach to the fixed point occurs very slowly (i.e. no longer exponentially fast). This is known as critical slowing down. *Right*: $r = 3$. There are three fixed points: a saddle point at $(1, 1)$, and two attracting nodes (mirror symmetric around $y = x$).
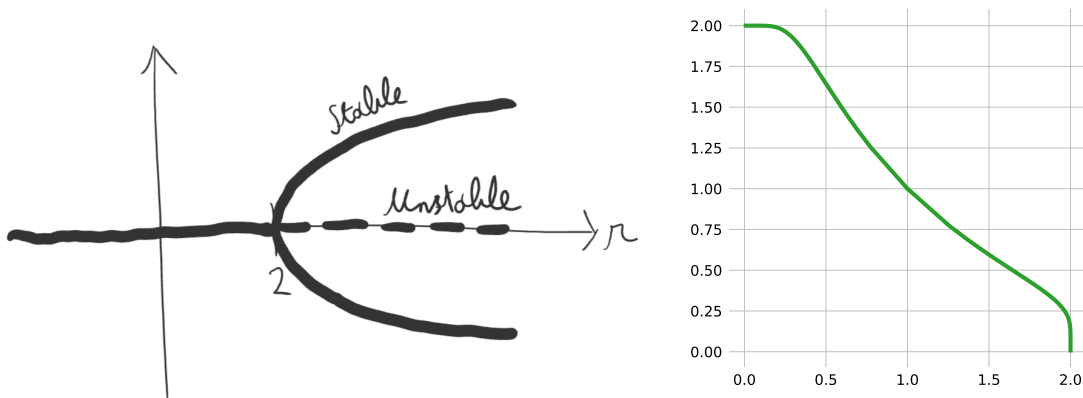

Figure 3: **The gene control model undergoes a supercritical pitchfork bifurcation**. *Left*: sketch of the bifurcation diagram. The vertical axis denotes distance in the bifurcation subspace from the $(1, 1)$ point. *Right*: the one-dimensional bifurcation subspace embedded in two-dimensional phase space.

Figure 2 shows the different types of phase portrait that occur as $r \geq 0$ is varied. Figure 3 sketches the bifurcation diagram.
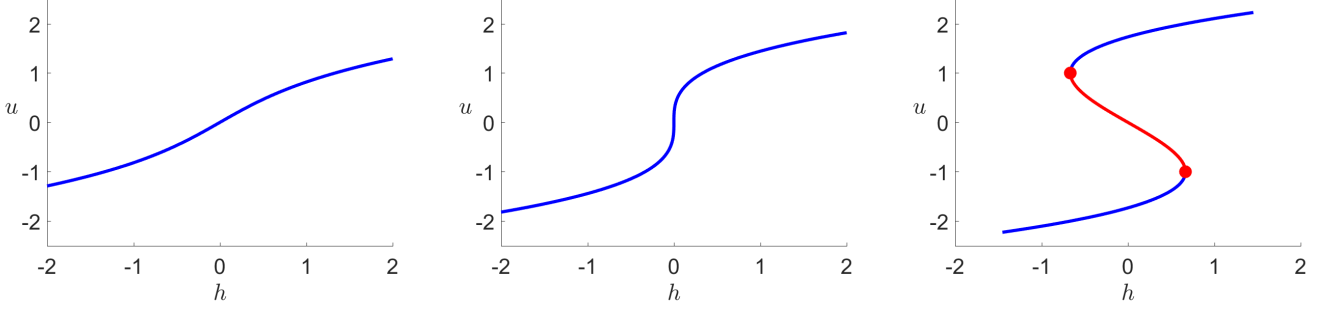
Figure 4: (h, u)-**bifurcation diagrams**. Blue lines denote stable equilibria, red lines denote unstable equilibria, and red circles indicate saddle-node bifurcations. Left: $r = -1$. (Phase space topologies for other $r < 0$ are equivalent). Center: $r = 0$. Right: $r = 1$. (Phase space topologies for other $r > 0$ are equivalent).
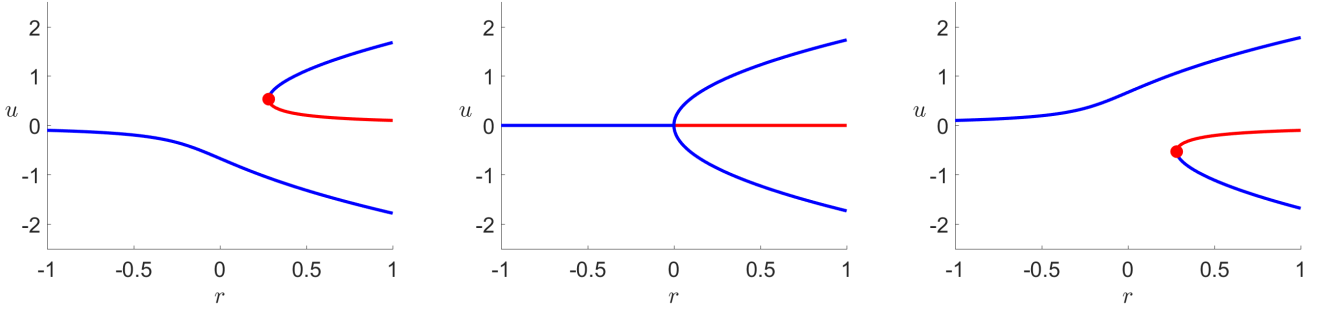

Figure 5: (r, u)-**bifurcation diagrams**. Colors as in fig. 4. Left: $h = -0.1$. Center: $h = 0$. Right: $h = 0.1$.

2 Imperfect bifurcations

When h is varied, we observe saddle-node bifurcations for $r > 0$ (see fig. 4). For $r = 0$, these two points coalesce into a single degenerate bifurcation point at $h = 0$, where u experiences critical slowing down as it approaches the origin. This is a codimension-2 bifurcation.

When r is varied, only one saddle-node bifurcation can be observed for each fixed h (fig. 5). The saddle-node appears at positive u for negative h, and vice versa. For $h = 0$, the system undergoes a supercritical pitchfork bifurcation (at $r = 0, u = 0$). h is an 'imperfection' parameter: without it, the system is symmetric (i.e. identical for $u = -u$).

Figure 6 shows the continuation curve of the saddle-node bifurcations. We note that there are indeed no saddle-node bifurcations for $r < 0$, and that there are two possible saddle-node bifurcations for $r > 0$, as already seen in figs. 4 and 5. The symmetries observed in those figures are also apparent here. The codimension-2 bifurcation is visible
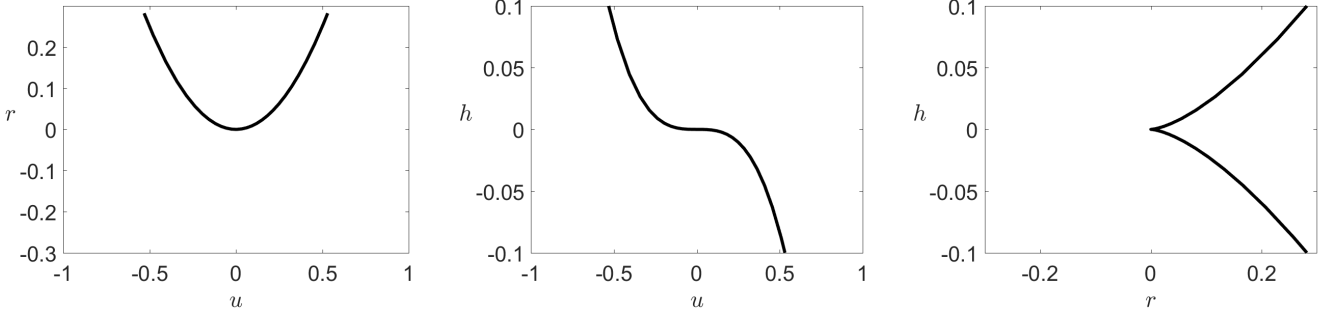
Figure 6: **Fold curve**. Continuation of the saddle-node bifurcations (the red circles in figs. 4 and 5), projected on the (u, r), (u, h), and (r, h) planes.

in the (r, h) plane as the cusp point at $(0, 0)$ (where the two branches meet tangentially). In (u, r, h)-space, the continuation curve has a spiral-like shape. It starts out in the $(+, +, -)$-octant, climbing towards the $(0, 0, 0)$ cusp point, where it is locally flat along the h-axis. It then continues its climb in the $(-, -, +)$-octant.

We now discuss some parameters of the numeric continuation algorithm used [2]. `cont.ItMX` is the maximum number of continuation steps taken along a branch. Reducing this parameter (in conjunction with shorter step sizes) results in shorter found branch segments.

For each continuation step, a solution (i.e. a fixed point) is searched for some parameter step size Δh. The maximum number of iterations of this root-finding phase can be specified with `corr.ItMX`. If no root is found within this number of iterations, the parameter step size Δh is reduced, and the root-finding phase repeats. The maximum and minimum step sizes Δh can be set using `h_max` and `h_min`, respectively.

Choosing step sizes `h_max` that are too large can result in missed branches (fig. 7). The continuation algorithm assumes a relatively smooth branch shape. When h becomes very small however, the derivative along the branch at $(0, 0)$ becomes very steep, and this assumption is violated. Only with small step sizes can the branch still be followed. Choosing *minimum* step sizes `h_min` that are too large can also miss branches, or even report non-existent saddle-node bifurcations (fig. 8).
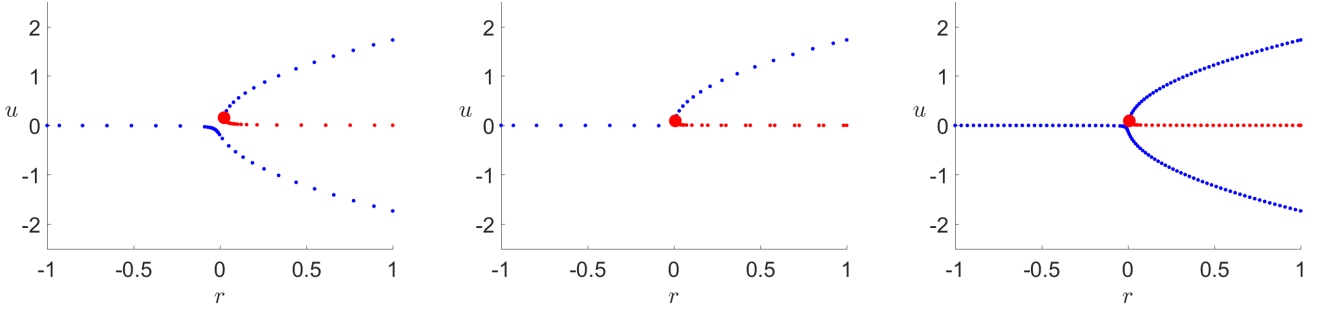
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Figure 7: **Continuation is a discrete process**. Bifurcation diagrams for $h = -0.0025$ (left) and $h = -0.0005$ (center and right). Each dot is the solution of one continuation step. Colors as in fig. 4. The (maximum) step size `h_max = 0.2` is identical in the left and center figures; yet in the center figure, the lower stable branch is not found. When the step size is decreased to `h_max = 0.05` however, the lower branch is found (right). (Other parameters were left to their default COCO settings: `cont.ItMX = 100`, `corr.ItMX = 10`, `h_max = 0.01`, etc).
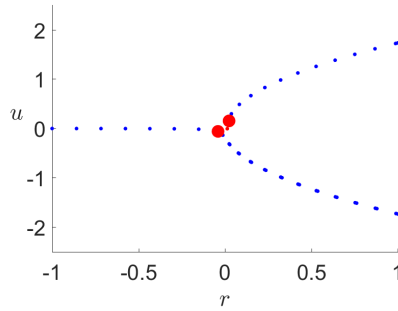

Figure 8: **Incorrect second saddle-node bifurcation**. Bifurcation diagram for $h = -0.0025$ and `h_min = h_max = 0.2`. (Other parameter settings as in fig. 7). Note the missed unstable branch, and the two saddle-node bifurcations (where there should only be one).

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3 Study of a predator-prey model

We study the system

$$\dot{x} = x(x - a)(1 - x) - bxy$$
$$\dot{y} = xy - cy - d,$$

with $a = 0.1$ and $b = 1.5$. The following could be an ecological interpretation of this system as a predator-prey model:

The $-d$ term represents a constant decline of species y; This would correspond to a linear decrease in y over time, with slope d, if this was the only term present. Maybe an environmental agency eliminates a fixed number d of y-type animals every time period, to keep the ecosystem balanced.

The $-cy$ term represents a proportional pressure on y, corresponding to an exponential decline of y over time with time constant $1/c$ (i.e. faster decline for larger c). There might be a fixed amount of resources available for the y species. Then, a larger number of y animals will result in a proportionally smaller amount of resources per animal.

The xy term represents a growth of y that is both proportional to the other species and to itself. For constant x, this would correspond to exponential growth of y with time constant $1/x$ (i.e. faster growth for more x). y could be a multiplying parasite, and x could be its host.

The $-bxy$ term represents a decline of the x species proportional to both itself and to the other species y. For constant y, this would correspond to an exponential decline of x with time constant $1/(by)$. The y parasite might be pathological for x. Both more parasites y and more hosts x yield a higher probability of transmitting the parasite between hosts.

Finally, the $x(1 - x)$ factor of the first term describes logistic growth (i.e. exponential growth from the origin, which switches halfway to exponential decay up to a carrying capacity – which is 1 in this case). This is a common model for constrained species growth. The $(x - a)$ multiplier has the effect that the growth does not start until x reaches a: for $x < a$, the species will decline instead of grow. This could model the fact that more than a few individuals are necessary for succesful long-term reproduction.

3.1 A qualitative study for $d = 0$

Simulating the system for $y = 0$ confirms the predictions made above for the standalone behaviour of $x(t)$ (fig. 9): logistic growth above the threshold a, and decay to zero below this threshold.

The system has four fixed points for $d = 0$. Three of these lie on the x-axis. They are listed in table 1, together with the eigenvalues and corresponding eigenvectors of the
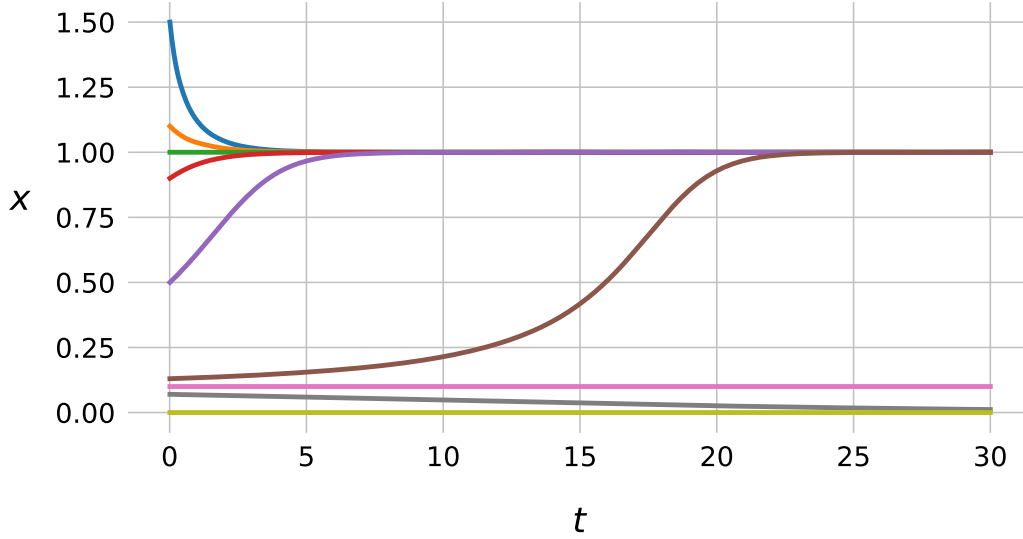
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Figure 9: **Behaviour of x without y.** Simulated trajectories $x(t)$ for $y = 0$ and different initial values x_0 (from top to bottom: 1.5, 1.1, 1.0, 0.9, 0.5, 0.13, 0.1, 0.07 and 0). Note the stable fixed points at 0 and at the carrying capacity 1, and the unstable fixed point at $a = 0.1$.

Fixed point	Eigenvalues	Eigenvectors
$(0,\ 0)$	$-a$	$(1,\ 0)$
	$-c$	$(0,\ 1)$
$(a,\ 0)$	$a - a^2$	$(1,\ 0)$
	$a - c$	$(ab/(c - a^2),\ 1)$
$(1,\ 0)$	$a - 1$	$(1,\ 0)$
	$1 - c$	$(-b/(2 - c - a),\ 1)$

Table 1: **Fixed points on the x-axis.** (x, y)-coordinates of the fixed points, and eigenvalue-eigenvector pairs of the Jacobian.

Jacobian in these points. The fourth fixed points has coordinates $(c,\ (c - a)(1 - c)/b)$, and the eigenstructure of its Jacobian is rather more.. complex. Its trace τ and determinant Δ have simpler analytical expressions however: $\tau = c(1 + a - 2c)$ and $\Delta = c(c - a)(1 - c)$. The following paragraphs describe the topological structure near these four fixed points.

$(0,\ 0)$ is an attractor node. In the common case that $c > a = 0.1$, the x-axis is the slow eigendirection. When $c < a$, the y-axis is the slow eigendirection.

$(a,\ 0)$ is a saddle when $c > a$. Its stable manifold is then the x-axis, and its unstable manifold is locally spanned by $(ab/(c - a^2),\ 1)$, which is an upwards pointing vector, rotated slightly right. When $c < a$, both dimensions are unstable, and $(a,\ 0)$ is then a repellor node. For $c > a^2$, the slow eigendirection is $(ab/(c - a^2),\ 1)$. For $c < a^2$, the
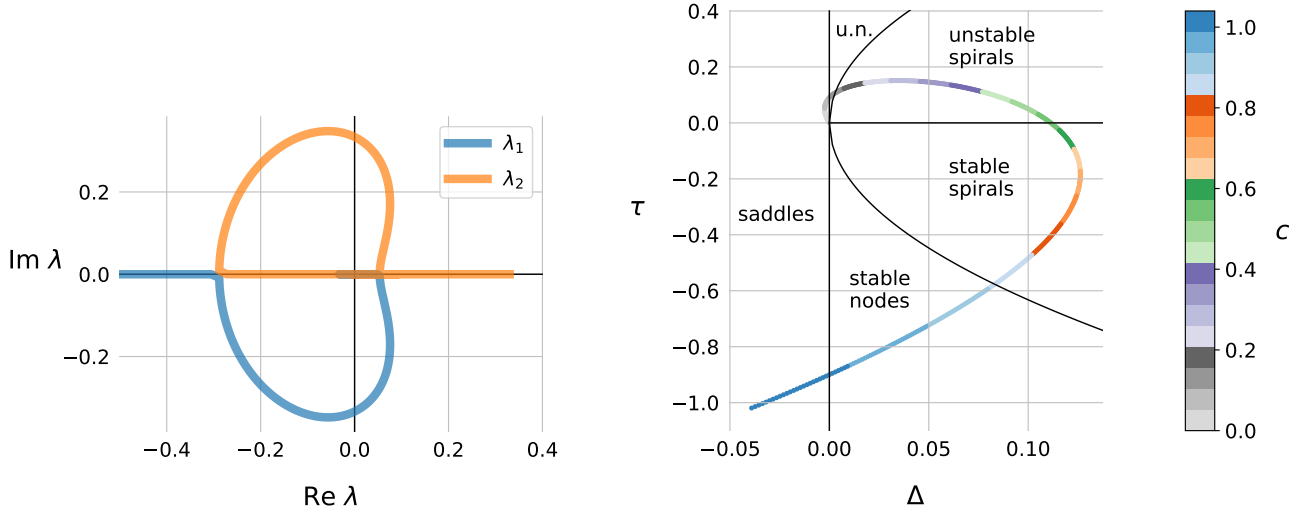
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Figure 10: **Linear system analysis of the fixed point** $(c,\ (a-c)(c-1)/b)$. *Left*: eigenvalues of the Jacobian at the fixed point, for $a = 0.1$ and $c \in [0, 1.5]$ ($c = 1.5$ at the far right, and at the far left outside the figure). *Right*: trace τ and determinant Δ of the Jacobian at the fixed point, for $a = 0.1$ and $c \in [0, 1.04]$ (for larger c, the (τ, Δ) curve simply extends further down in the 3rd quadrant). u.n.: unstable nodes.

x-axis is the slow eigendirection.

$(1,\ 0)$ is a saddle when $c < 1$. With $a = 0.1$, the stable manifold is the x-axis, and the unstable manifold is locally spanned by $(-b/(2-c-a),\ 1)$, which is an upwards pointing vector, rotated slightly *left*. When $c > 1$, both dimensions become stable, and $(1,\ 0)$ is then an attracting node. Because $c < 1.5$ in this exercise, the slow eigendirection is $(-b/(2-c-a),\ 1)$.

The final fixed point, $(c,\ (c-a)(1-c)/b)$, has a wider range of behaviours (fig. 10). It is a saddle for $c > 1$, and for $0 < c < a$. It is an unstable node for $a < c < c_u$, an unstable spiral for $c_u < c < (a+1)/2$, a stable spiral for $(a+1)/2 < c < c_s$, and a stable node for $c_s < c < 1$. c_u and c_s are the solutions to

For $a = 0.1$, c_u and c_s are numerically determined to be $c_u = 0.1259..$ and $c_s = 0.8783...$

The separatrices between basins of attraction are the stable manifolds of saddles. The stable manifold of a saddle at $(x^*,\ y^*)$ can be found numerically by simulating a trajectory back in time. The initial point of this trajectory is $(x^* + \Delta x,\ y^* + \Delta y)$, where Δx and Δy are small perturbations along the eigenvector of the Jacobian corresponding to this manifold (i.e. the eigenvector with a positive eigenvalue).
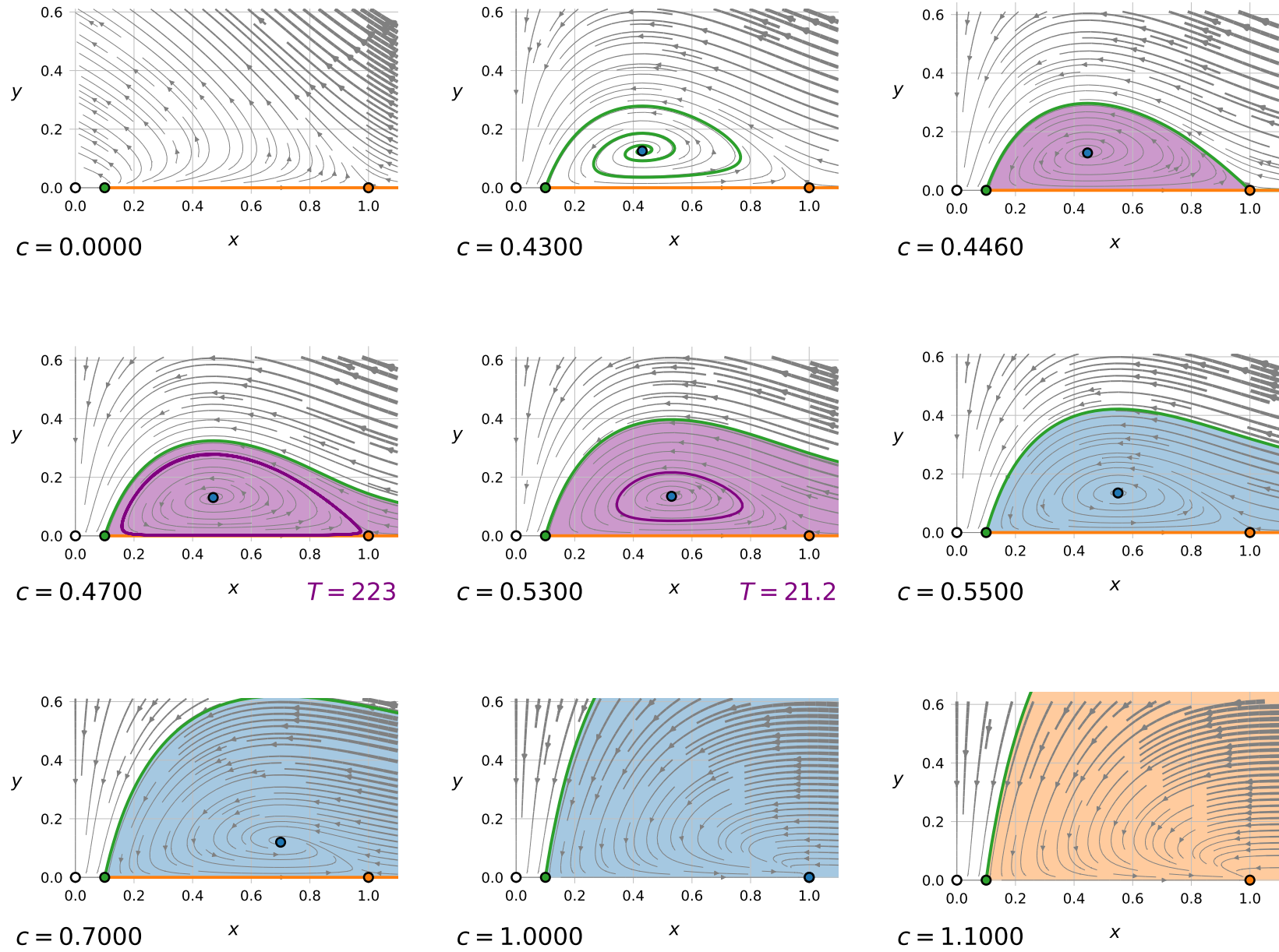
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Figure 11: **Phase space diagrams for different predator-decay rates** c. Fixed points are indicated with colored dots. Their manifolds of attraction are given the same color. The limit cycle for $0.446... = c_h < c < 0.55$, and its basin of attraction, are indicated in purple.

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[1] Steven H. Strogatz. *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering*. Perseus Books, 1994.

[2] Frank Schilder and Harry Dankowicz. *COCO: Continuation Core and Toolboxes*. 2018. URL: https://sourceforge.net/projects/cocotools/.