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Report on measures of resilience

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Lead authors

**K. Ostasiewicz¹, M.H. Tyc¹, J. Sendzimir² and
P. Magnuszewski¹**

¹ Institute of Physics, Wrocław University of Technology,
Wybrzeże Wyspiańskiego 27, 50-370 Wrocław, Poland

² International Institute for Applied Systems Analysis,
Schlossplatz 1, A-2361 Laxenburg, Austria

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1. Introduction

In recent decades, interest continues to grow in ecological and social systems that exhibit multistability, i.e., having alternative stable states. The early hints, that real ecosystems and socioeconomical systems can exhibit such properties, originated from theoretical models [1, 2]. Although regime shifts are very easy to show and explore in models, considerable time and effort was invested to prove experimentally that such phenomena occur in the real world. Any, even drastic, change in the observed system state may result from change of the entire landscape following the change of some external parameter, and not from bistability. Moreover, there are many difficulties in experimentally identifying factors influencing the behaviour of the system in interest. In spite of methodological and practical difficulties, solid evidence for the existence of alternative stability domains has been found in specific case studies of ecosystems and socio-ecological systems [3, 4, 5]. Moreover, manipulation experiments have also provided direct evidence for alternative stable states [6]. Probably the most famous case of a bistable system is the case of alternative equilibria in shallow lakes [3]. Over certain ranges of nutrient concentration in water column, shallow lakes have two alternative equilibria: a clear state dominated by macrophytic aquatic vegetation, and a turbid state with high algal biomass.

The question of stability of ecosystems' and social systems' states is of great practical importance, for such systems have been observed to fall irreversibly into degraded states. However, more than the mathematical stability itself, the most salient question commonly asked in application is whether the system has the ability to absorb external fluctuations and persist in its current state. Holling [1] has introduced a definition of resilience, as "a measure of the ability of systems to absorb changes of state variables, driving variables, and parameters, and still persist". On the other hand, stability of the system was defined as "ability of the system to return to an equilibrium state after a temporary disturbance. The more rapidly it returns, and with the least fluctuation, the more stable it is". Some case studies suggest that high resilience is not necessarily connected with high stability of states, and visa-versa. For example, the insect populations (spruce budworms [1] and another [7]) in the Northern forests reveal high resilience, yet strong fluctuations both in numbers of insects and surviving trees suggest low stability. However, the fact that extreme fluctuations exhibit a certain predictable periodicity and occur within known bounds such that the system always returns as a boreal forest suggests a resilience over the long term (centuries). On the other hand, other examples show that low variability of the system, connected with rapid recovery from small disturbances, may characterize systems with little resilience. In those cases management to reduce variability eventually led to a less resilient system) [8, 9, 10], and many human activities shrink ecological resilience by attempting to control variability in key ecosystem processes [11].

2. Ecological vs. engineering resilience

The above definition of resilience does not determine how to measure this quantity in a strict mathematical manner. This is a question of great practical importance: how one can examine the resilience properties of a real system, and how can one predict whether the system will persist in the face of external stresses or shocks or survive natural fluctuations? How can we measure resilience in order to forecast its dynamics and manage or prevent the consequences from its breakdown, particularly when it declines to levels where state shift becomes inevitable?

This practical challenge is complicated by terminological confusion in the literature: two different definitions of “resilience”. The first definition concentrates on stability near equilibrium steady state, and regards resilience as a measure of resistance of the system to disturbances and the speed of return to equilibrium [12, 13, 14, 15, 16] (note that this definition corresponds also to another designation, “elasticity” [17]; also, it coincides with the definition of stability, formulated by Holling [1, 18], see above). This definition arises from traditions of engineering, where the motive is to design systems with a single operating objective. On one hand, that makes the mathematics tractable, and on the other, it accommodates an engineer’s goal to develop optimal designs. The second definition concentrates on the conditions far from any equilibrium steady state, where instabilities may flip the system into another regime of behaviour (another stability domain) [1, 8, 11]. This corresponds to the Holling definition cited above.

To avoid this confusion, Holling [18] proposed to distinguish the two as *engineering resilience* and *ecological resilience*. The former would correspond to the first definition recalled above, while the latter to the second definition.

For anyone concerned about regime shift to a new, perhaps less desirable, stability domain, ecological resilience would bear more valuable information about systems. Nevertheless, it could be hard to measure in experiments in the real world. Using a formal model one can follow all possible dynamics of the system. In the real world, however, it would most likely be unethical and impractical to apply shocks to the system in order to measure their value, within which the system will undergo transition to another state. That is, to establish the resilience of the system, a policy that probes the system by, e.g., stimulating it might precipitate causal feedbacks which eventually destroy it. As in the case of ecological and sociological systems one does not have, in general, many copies of identical systems, so replication for experimental rigor and redundancy for safety are impossible. Yet, each system is valuable if not priceless, so probing manipulation is usually too risky for establishing the resilience of such systems. On the other hand, engineering resilience is a quantity that both can be measured in the real systems and would be an estimation (perhaps the most adequate possible) of ecological resilience, but it serves a fundamental assumption that the system has one optimal equilibrium. Flips between different stability domains in a range of ecosystem severely challenge that assumption [19].

Before we proceed to review measures of resilience, let us introduce the useful

concept of potential, which adds mathematical rigor to our use of the cup-and-ball analogy (“stability landscapes”). Such landscapes which graphically illustrates many complex relations normally conveyed through mathematics. For continuous systems, described by a differential equations, $d\vec{X}/dt = \vec{F}(\vec{X})$, the potential is defined as

$$V(\vec{X}) = \int \vec{F}(\vec{X}) d\vec{X}. \quad (1)$$

The conditions for a stationary stable point: $\vec{F}(\vec{X}^*) = 0$, $(d\vec{F}/d\vec{X})_{\vec{X}=\vec{X}^*} < 0$ imply, that for stable stationary point such defined potential has minima. Thus, the system can be considered as a ball rolling in the cup whose walls take a shape defined by that potential, always tending towards the bottom. This illustration will be sometimes used in the general case, to depict universal features of systems, without detailed analysis of particular properties. Let us note, however, that in multi-dimensional systems it is not always possible to define a potential, as the value of the integral in (1) may depend on integration path; a potential exists only if $\partial F_i/\partial X_j = \partial F_j/\partial X_i$ for all (i, j) .

Using these definitions and graphical language we now develop an overview of resilience measures based on known literature. Some of them measure ecological resilience, and may be used in practice only to model systems. Others measure engineering resilience and are of practical use in the real world. However, it is not obvious that they would in each case reflect the ecological resilience with good accuracy. These questions will be examined in each particular case.

3. Measures of ecological resilience

In order to present measures of ecological resilience, let us first introduce the notion of “phase space” for deterministic ecological and social systems. In contrast to physical equations of motion, such models’ equations are differential equations of the first, not second, order. Thus, a “force” in such systems is connected with the first, not second, derivative of state variables. Setting the initial conditions of state variables determines uniquely (together with the “equations of motion”) its whole previous dynamics. That is, the phase space consists only of state variables, not of its derivatives. Motion in this phase space is determined by the shape of the “potential”, as defined in (1). Stationary states of the system are mapped into stationary points of phase space. Each stable stationary point will have its “domain of attraction”: a fraction of the whole phase space, in which starting trajectories will finally end in this stationary point (i.e., a stable stationary point “attracts” nearby trajectories, while an unstable stationary point “repulses” trajectories), see Fig. 1.

According to Holling’s definition of “ecological resilience” of a state [1], there are two measures of this quantity [1, 18]. Firstly, the overall area of the domain of attraction of this state (that in part determines whether shifts in state variables will move to trajectories outside the domain), which in one dimension reduces simply to the width of well. Secondly, the height of the “potential barrier” that separates the basins of attraction of different regimes (that measures how much the forces have to be

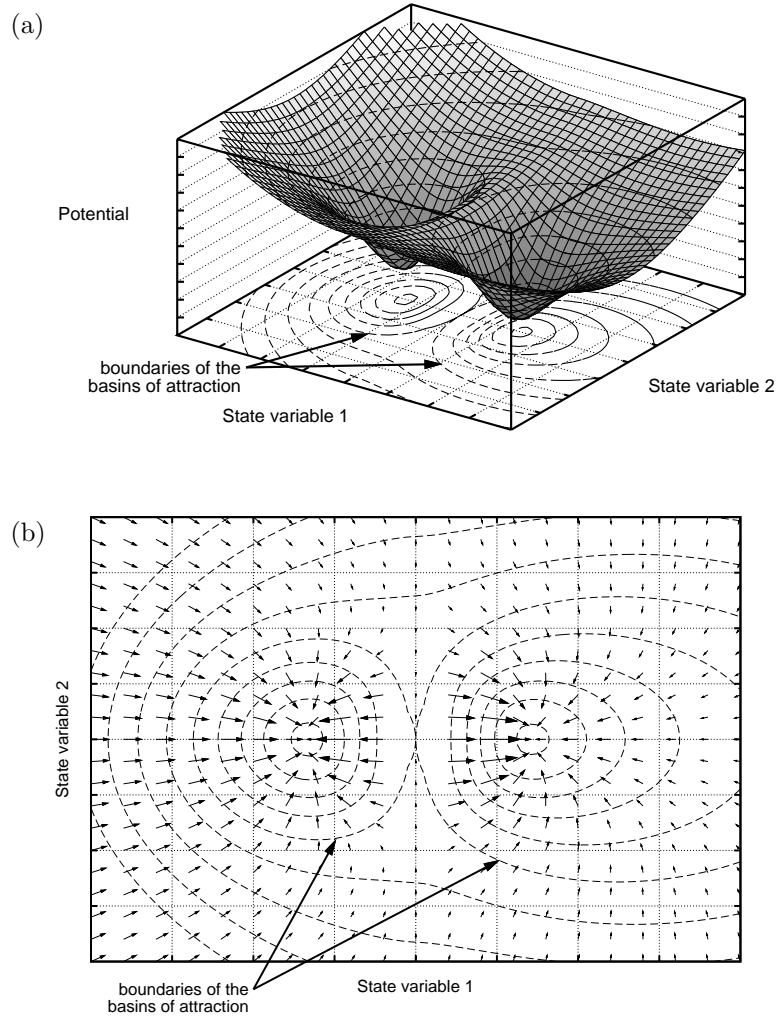


Figure 1. Example potential in a two-dimensional phase space: (a) potential with isolines; (b) isolines with velocity field (direction and strength of attraction marked with vectors)

changed before all trajectories move to another basin of attraction), see Fig. 2. The former corresponds to the maximum perturbation of a state parameter (e.g., an instant mortality event) and the latter to the maximum perturbation of a driving force (e.g., caused by a temperature peak) [20]. Both of these quantities have to be considered jointly to establish a proper value of ecological resilience of a given system. Nevertheless, in many papers only one of them separately is considered as a measure of ecological resilience, mostly the size of attraction basin [21, 22]. Furthermore, since determining the maximum disturbance in the state space for individual-based models and multi-variable models is difficult (and it may be defined in many different ways) [20], some authors propose to use a simpler measure that correlates to the size of the basin of attraction, namely the distance from the control parameter (e.g., a “slow” variable of the system) to its threshold value [20, 23]. However, this simplification would not play

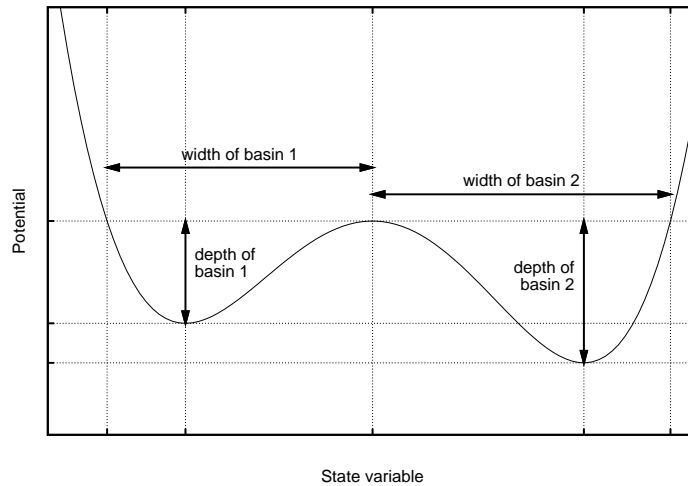


Figure 2. Size of the domain of attraction and height of potential barrier as measures of ecological resilience in one dimension

its role for systems with multiple control parameters. Thus, each case should be given a careful consideration to establish the best possible measure of ecological resilience.

Below, two propositions to facilitate the task of measuring ecological resilience are presented.

In principle, resilience could be measured by fitting a dynamic model to a time series, calculating equilibria, and calculating the size of the basin of attraction. In practice, obtaining adequate fits of such models requires extraordinary data, which are not usually available [24]. Instead of fitting models, one can use insights from models to identify indicators of resilience [25]. For example, many experimental studies have corroborated an old presumption of Darwin (formalized by MacArthur [26]), that increasing the number of species increases the stability of ecosystem function [27, 28]. Thus, the number of species, especially substitute species in an ecosystem that can perform the same functions [29, 30], might be an indicator of degree of resilience of ecosystems.

It should be noted that until they are theoretically validated, such indicators only have the status of empirical generalizations and should be used carefully, as their adequacy is not, in general, undisputed. For example, concerning the relationship between species number and increasing stability of ecological systems, it was argued that the increase of stability gained by adding new species decreases as species richness increases [31], and thus it may be treated as a indicator of degree of resilience only in some range of biodiversity. Moreover, Peterson et al. [21] have recently proposed a more complicated dependence, taking into regard different scales in which different species operate: they argue that ecological resilience is generated by diverse, but overlapping, functions performed by different species within a scale and by apparently redundant species that operate at different (space and temporal) scales, thereby reinforcing function across scales.

Probably the most universal and most frequently used indicator of ecological resilience is engineering resilience [20, 32]. Engineering resilience and various ways of its measuring will be a subject of the next section. Also, its validity as an indicator of ecological resilience will be briefly discussed.

Besides resilience indicators, statistical distributions of systems' variables offer another possibility for estimating ecological resilience. For ecological populations, as ecological resilience of populations is strictly related to probability of their extinction, knowing the distribution of surviving population sizes within any given control parameter allows calculation of the probability of a population size equal to zero, i.e., of the extinction, and thus to estimate the ecological resilience [1]. For example, it was shown that the distribution of surviving population sizes for *Brevicoryne brassicae* (cabbage aphid) at any given moment of the season (different values of control parameters in different moments) does not differ seriously from the negative binomial [33]. Fitting the parameters of this distribution, one is able to estimate the probability of extinction and degree of system resilience. For each kind of system, it will be important to explore first the theoretical models so that the appropriate distributions and their behaviour can be identified. It will then be quite feasible, in the field, to sample populations in defined areas, apply the appropriate distribution, and use the parameter values as measures of the degree of resilience [1]. For multi-variable systems, e.g., multi-species ecosystems, Batabyal has proposed a similar probabilistic approach to estimate ecological resilience: considering an ecosystem which consists of N species, in which at least m species must survive so that the system be stable, the measure of ecological resilience has been proposed as $\lim_{t \rightarrow \infty} P[A(t) = m]$, where $A(m)$ denotes the number of species that are alive at time t , and it can be computed with the distributions of the probabilities that a certain species is alive/dead.

Concluding these short considerations about ecological resilience, it is clear that this quantity is not easy to measure. Straightforward measures resulting from the very definition of ecological resilience (disturbance of a state variable or of a control parameter resulting in force disturbance) are not easy to quantify for multi-dimensional models. Moreover, it is not clear how the comparison of the degree of resilience for different systems with different variables (possibly of different scales) would be possible. Indicators of resilience are more tractable, although — on the other hand — much less validated. As it was mentioned above, the best examined indicator of ecological resilience is engineering resilience. This last quantity itself may be measured in a few different ways. Now we will proceed to a short review of measures of engineering resilience.

4. Measures of engineering resilience

4.1. Return time (recovering rate)

Return time was introduced as a measure of resilience since the very first attempts to examine the concept of resilience in ecological and social sciences. Using the distinction

introduced by Holling (see above), return time is a measure of engineering resilience — an often useful, but not perfect, indicator of the status of the system under examination. Let us first recall the theoretical foundations of this measure, separately for discrete [34] and for continuous [35] systems. Then we will briefly discuss its validity.

In both discrete and continuous case, we will deal with a system described by a set of N equations, for N quantities characterizing the state of the system:

$$\vec{x}_{t+1} = \vec{F}(\vec{x}_t) \quad (2)$$

in the discrete case, and

$$\frac{d\vec{x}}{dt} = \vec{F}(\vec{x}) \quad (3)$$

in the continuous case. The stable states of the systems, \vec{x}^* , are determined by the conditions:

$$\begin{aligned} \vec{x}_t^* &= \vec{F}(\vec{x}_t^*) \\ \frac{d\vec{x}^*}{dt} &= \vec{F}(\vec{x}^*) = 0 \end{aligned}$$

for discrete and continuous systems, respectively.

In both cases, one may consider a small perturbation from a stationary state, $\vec{x} = \vec{x}^* + \delta\vec{x}$, and examine its time evolution.

4.1.1. Discrete systems Let us linearize the set of equations in the vicinity of stationary state:

$$\vec{x}^* + \delta\vec{x}_{t+1} = \vec{F}(\vec{x}^*) + \nabla\vec{F}(\vec{x}^*) \cdot \delta\vec{x}_t.$$

As

$$\vec{x}^* = \vec{F}(\vec{x}^*),$$

one gets a matrix equation for the time evolution of $\delta\vec{x}$:

$$\delta\vec{x}_{t+1} = \mathbf{M}\delta\vec{x}_t,$$

with

$$M_{ij} \equiv \left. \frac{\partial F_i}{\partial x_j} \right|_{\vec{x}^*}.$$

As the elements of matrix \mathbf{M} are constant, the perturbation at any moment may be expressed in terms of the initial perturbation:

$$\delta\vec{x}_t = \mathbf{M}^t \delta\vec{x}_0. \quad (4)$$

The solution of 4 may be found as

$$\delta\vec{x}_t = \sum_i^N \lambda_i^t \vec{v}_i,$$

where λ_i are the eigenvalues of matrix \mathbf{M} :

$$\mathbf{M}^t \vec{w}_i = \lambda_i^t \vec{w}_i,$$

and \vec{v}_i 's are projections of the initial vector $\delta\vec{x}_0$ onto the directions of eigenvectors \vec{w}_i :

$$\delta\vec{x}_0 = \sum_i^N \alpha_i \vec{w}_i \equiv \sum_i^N \vec{v}_i.$$

Let us denote by λ_{\max} the eigenvalue of the largest absolute value, and rewrite the solution as:

$$\delta\vec{x}_t = \lambda_{\max}^t \sum_i^N \left(\frac{\lambda_i}{\lambda_{\max}} \right)^t \vec{v}_i.$$

The perturbation from a stationary state will die away in time on the condition that

$$|\lambda_{\max}| < 1.$$

The rate in which it will die away is determined by the value of $|\lambda_{\max}|$. Thus, one may define the return time as

$$T_R \equiv \frac{1}{1 - |\lambda_{\max}|}.$$

The shortest possible return time equals to 1, and the longest is infinite. For $|\lambda_{\max}| > 1$, this time becomes negative, what means that for unstable equilibria the concept of return time has no meaning.

4.1.2. Continuous systems Following Wissel [35], let us examine the general properties of systems described by continuous differential equations (3).

1D case One may linearize the differential equation, describing the system:

$$\frac{dx}{dt} = F(x, b), \tag{5}$$

where dependence on control parameter b was explicitly expressed; in the vicinity of a stationary state,

$$\frac{d(x^* + \delta x)}{dt} = F(x^*, b) + \frac{\partial F}{\partial x}(x^*, b)\delta x.$$

As

$$F(x^*, b) = 0,$$

the solution for δx is:

$$\delta x = (\delta x)_0 e^{\lambda t} \equiv (\delta x)_0 e^{-t/T_R}, \tag{6}$$

with $-1/T_R = \lambda = \frac{\partial F}{\partial x}(x^*, b)$, where such defined T_R is the characteristic return time. It is clear, that this quantity has sense only for $\lambda < 0$, as for $\lambda > 0$ the stationary point becomes unstable. Thus, a deviation of x from the (stable) equilibrium x^* will return exponentially in the course of time with the characteristic return time T_R .

Let us examine, how this characteristic return time changes when the control parameter b approaches the threshold b_T (at which one of the equilibria vanishes). One can see that at the threshold $\frac{\partial F}{\partial x}(x^*, b_T) = 0$. Therefore, the increase of a characteristic

return time with approaching b_T may be expected. Indeed, let us introduce a small deviation:

$$y = x - x^*(b_T).$$

Expanding F in terms of y and $\delta b = |b - b_T|$:

$$\begin{aligned} F(x, b) &= F(x^*(b_T), b_T) + \frac{\partial F}{\partial x}(x^*(b_T), b_T)y \\ &\quad + \frac{1}{2} \frac{\partial^2 F}{\partial x^2}(x^*(b_T), b_T)y^2 + \frac{\partial F}{\partial b}(x^*(b_T), b_T)\delta b. \end{aligned} \quad (7)$$

As the two first terms on the right hand side of the above equal zero, we have:

$$\begin{aligned} F(x, b) &= \alpha y^2 + \beta \delta b \quad (8) \\ \alpha &\equiv \frac{1}{2} \frac{\partial^2 F}{\partial x^2}(x^*(b_T), b_T), \\ \beta &\equiv \frac{\partial F}{\partial b}(x^*(b_T), b_T). \end{aligned}$$

From this, one can write for y^* :

$$\alpha(y^*)^2 + \beta \delta b = F(x^*, b) = 0,$$

and

$$y^* = \pm \left(-\frac{\beta}{\alpha} \delta b \right)^{1/2}.$$

As

$$\lambda = \frac{\partial F}{\partial x}(x^*, b) = \frac{\partial F}{\partial y}(y^*(\delta b), \delta b)$$

and (differentiating (8))

$$\frac{\partial F}{\partial y} = 2\alpha y,$$

then, for λ in the vicinity of threshold, one obtains:

$$\lambda = 2\alpha y^*(\delta b) = \pm 2(\alpha\beta\delta b)^{1/2}. \quad (9)$$

Thus, the general law for the characteristic return time in 1D system reads:

$$T_R \propto |b - b_T|^{-1/2}. \quad (10)$$

This result means that as it approaches a threshold a disturbed system needs more time to reach an equilibrium.

N-dimensional case To generalize results (6) and (10) to N -dimensional case (N different species, age classes, etc.):

$$\frac{d\vec{x}}{dt} = \vec{F}(\vec{x}, b) \quad (11)$$

some matrix algebra is needed. Let us only recall here the final conclusions (for details, see Wissel [35]). There are two possible kinds of behaviour after a perturbation from

stable equilibrium: exponential return to the equilibrium *or* exponentially damped oscillations around the equilibrium:

$$x_i(t) - x_i^* = \begin{cases} \delta x_i^0 e^{-t/T_R} \\ \delta x_i^0 e^{-t/T_R} \cos(t + \varphi_i), \end{cases} \quad (12)$$

with corresponding characteristic return time

$$T_R \propto \begin{cases} |b - b_T|^{-1/2} \\ |b - b_T|^{-1}. \end{cases} \quad (13)$$

As it seems that equation (11) is quite general for ecological models, the behaviour of the characteristic return time near the threshold point (13) should be a universal law. This makes it possible to predict the value of the threshold b_T in empirical studies of ecosystems. To this end one has to disturb the equilibrium state to obtain a few values of the control parameter b (safely below the threshold point) and measure the return time to a stable state. Then, if the observed behaviour was exponential, one should plot T_R^{-2} versus b , or, if the behaviour was exponentially damped oscillations, T_R^{-1} versus b . According to (13), these points should be fitted to a straight line which would cross the axis b at a threshold value b_T . Thus, empirical data obtained far from the threshold can serve to determine the value of threshold.

At least one experiment preliminarily corroborates Wissel's theory. Harvesting experiments with *Brachionus rubens* (a species of rotifers) have shown [36] exponentially damped oscillations[‡], in agreement with (12). The measured characteristic return times for two different values of harvesting (control parameter) are in agreement with the theoretical result (13). To fully verify (13), further experimental data are needed.

We should note some apparent discrepancy in the stability conditions. Having a discrete model (2), one may write down its continuous version in the form of (3):

$$x_{t+1} - x_t = F(x_t) - x_t \rightarrow \frac{dx}{dt} = F(x) - x.$$

Linearizing a discrete equation and its continuous counterpart, one gets:

$$\begin{aligned} \delta x_{t+1} &= \lambda^N x_0 && \text{in the discrete case} \\ \delta x(t) &= (\delta x)_0 \exp[(\lambda - 1)t] && \text{in the continuous case.} \end{aligned}$$

Thus, in the discrete case the stability condition is $|\lambda| < 1$, while in the corresponding continuous case $\lambda < 1$ the question is: what is the status of this non-overlapping region, $\lambda < -1$? Let us note, that for $\lambda < -1$, the sign of x in the discrete model changes from one time step to another, in addition $x_{t+1} - x_t$ grows in time, and the differential equation is not a good approximation of such a discrete model.

4.1.3. Stochastic model The two above models, discrete and continuous, are deterministic ones, within which existence and attainability of a stationary state are assumed. Although there exist biological systems in which variables of interest are

[‡] after special correlation analysis, used to eliminate the random influences.

sufficiently constant and perturbations sufficiently large and infrequent to estimate return times to equilibrium (e.g., [37, 38]), they are probably exceptions. Most real systems are continuously buffeted by environmental fluctuations and description in terms of stochastic models would be more appropriate. An analog of the equilibrium in a stochastic model is a joint stationary distribution of the model's variables. Thus, the analog of the characteristic return time will be the rate at which the transition distribution approaches the stationary distribution. Here a rapid approach corresponds to a more resilient system.

Following [16, 39], let us consider here a nonlinear first-order stochastic process:

$$\vec{X}_t = \vec{f}(\vec{X}_{t-1}, \vec{R}_t), \quad (14)$$

where \vec{R}_t is a random variable (with mean $\vec{0}$) representing fluctuations of the system's variables caused by environmental variables. If (14) has a stationary distribution \vec{X}_∞ , it may be approximated using a Taylor expansion around $\vec{X} = \vec{X}_\infty$ and $\vec{R}_t = 0$:

$$\vec{X}_t \approx \vec{A} + \mathbf{B}\vec{X}_{t-1} + \vec{E}_t, \quad (15)$$

$$\vec{A} = \vec{f}(\vec{X}_\infty, \vec{0}) - \mathbf{B}\vec{X}_\infty \quad (16)$$

$$\mathbf{B} = \left. \frac{\partial \vec{f}}{\partial \vec{X}} \right|_{(\vec{X}_\infty, \vec{0})} \quad (17)$$

$$\vec{E}_t = \left. \frac{\partial \vec{f}}{\partial \vec{R}} \right|_{(\vec{X}_\infty, \vec{0})} \vec{R}_t \quad (18)$$

A linearized process (15) has a stationary distribution provided that all eigenvalues of the matrix \mathbf{B} lie within the unit circle. If this condition is fulfilled, a transition distribution of \vec{X}_t conditional on the initial value of $\vec{X} = \vec{x}_0$ depends on the particular form of \vec{R}_t . For example, for a normal random variable \vec{R}_t , \vec{X}_t is also a random variable with mean vector $\vec{\mu}_t$ and covariance matrix \mathbf{V}_t :

$$\vec{\mu}_t = \vec{\mu}_\infty + \mathbf{B}^t(\vec{x}_0 - \vec{x}_\infty) \quad (19)$$

$$\mathbf{V}_t = \mathbf{\Sigma} + \mathbf{B}\mathbf{\Sigma}\mathbf{B}^T + (\mathbf{B}^2)\mathbf{\Sigma}(\mathbf{B}^2)^T + \dots + (\mathbf{B}^{t-1})\mathbf{\Sigma}(\mathbf{B}^{t-1})^T, \quad (20)$$

where $\mathbf{\Sigma}$ denotes the covariance matrix of random variable \vec{E}_t . In the simplest 1D case,

$$X_t = a + bX_{t-1} + E_t, \quad (21)$$

transition distribution has the following parameters:

$$\mu_t = \mu_\infty + b^t(x_0 - \mu_\infty) \quad (22)$$

$$v_t = v_\infty[1 - (b^2)^t]. \quad (23)$$

The lower the value of $|b|$ (provided that $|b| < 1$), the more rapidly μ_t converges towards μ_∞ and the system is more resilient.

Let us stress two important differences between return time in deterministic and stochastic systems. First, convergence rates of different moments of stochastic processes can, in general, be different (e.g., in the model (21) mean value converges as b^t while variation converges as $(b^2)^t$). Only the convergence rate of the mean value has its

counterpart in deterministic systems. Second, a short return time in a deterministic system makes the system in some sense more predictable — i.e., irrespective of initial perturbation from stationary state, the system will soon be near the stationary state. On the other hand, in stochastic systems the variance of distribution grows in time, finally obtaining a stationary value. Thus, the more rapid the convergence to the stationary distribution, the more quickly we lose the information about the system’s state.

4.1.4. Discussion The idea connected with return time as a measure of resilience is, that the more quickly the system returns to the stable state, the more resilient it is (if the perturbation grows with time, the system is not resilient at all). It is expected that approaching the critical point, where the system is driven to another basin of attraction, the return time grows to infinity — this is an analogue of a phenomenon known in physics as “critical slowing down”. However, the intuition connecting recovery rate with global properties of the system may be misleading — namely, return time is not necessarily a proper estimation of ecological resilience. As it was mentioned above, Holling [1] pointed out, that return time corresponds more to stability than to the resilience of the system. Let us give here three simple examples of the inadequacy of this measure:

- a) **Stable oscillations.** Populations of spruce budworms in boreal forests are examples of systems that reveal stable oscillations around some average state. Such perturbations are chronic, appearing with a periodicity of 30 to 50 years [40], and as they do not vanish in time, the return time is infinite. Nonetheless, in the ecological sense, such systems are highly resilient.
- b) **Plateau of potential.** The second example (Fig. 3a) shows another case of very long or even infinite return time of a system, which may be highly resilient. Although the system does not return to the primary state (or returns extremely slowly), the parameters of the state in which it stays after a little perturbation are very close to the initial parameters. Thus no catastrophic regime shift takes place, and the system is resilient.
- c) **Non-specificity of return time.** The third example (Fig. 3b) shows that two systems, having the same return time, may have very different levels of resilience — thus, sometimes this measure gives no good comparison of different systems, or different states of the same system.
- d) **Variability.** As it was mentioned in Section 1, there exist in the literature examples of systems, for which reduced variability, resulting in rapid return to the equilibrium after small disturbance, does not enhance but reduces ecological resilience [8, 9, 10].

In conclusion, the return time is not a perfect indicator of ecological resilience. It is only a measure of engineering resilience. However, in many situations it gives a simple and useful estimation of the real system state.

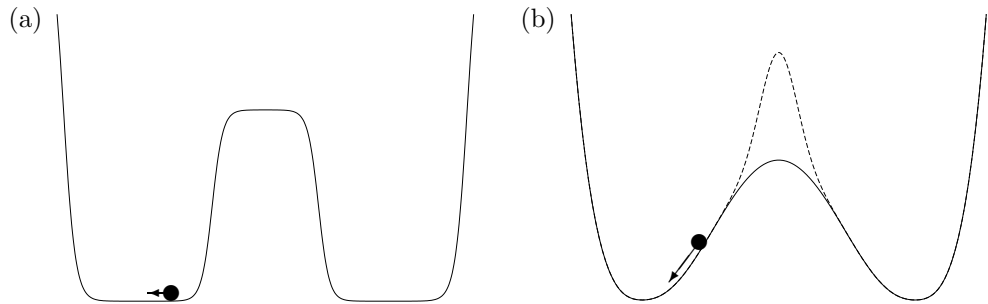


Figure 3. Inadequacy of return time as a measure of ecological resilience in specific cases: (a) very long or even infinite return time resulting from a plateau of potential at the bottom of the attraction basin; (b) equal return times for systems with different depths of their attraction basins

4.2. Time of return and reactivity

The characteristic time of return is an asymptotic property, characterizing the system within $t \rightarrow \infty$. This measure ignores short-term transient behaviour. Numerous authors have proposed using the whole time required for return to pre-disturbance levels of state variables as a measure of resilience in laboratory or field experiments [37, 41, 42]). A mathematical formula taking into account the duration of perturbation was proposed by Patten and Witkamp [43] as§:

$$R = \frac{X_0 \delta t}{\Delta X \Delta t}, \quad (24)$$

where X_0 is an equilibrium value of the system variable, ΔX denotes the perturbation from equilibrium, δt — duration time of perturbation, and Δt — the time needed to return to original equilibrium.

This formula (24) was further improved by Jordan et al. [45] to take into account the strength of perturbation:

$$R = \frac{r(\text{pert}) X_0 \delta t}{r \Delta X \Delta t}, \quad (25)$$

where $r(\text{pert})$ denotes the value of the disturbing parameter during perturbation, r denotes the value of the same parameter when the system remains in its steady state, and the other symbols are the same as in (24).

In model systems various authors have used as a measure of resilience the integral of perturbation over the time of the whole simulation (put here as ∞ , assuming that simulations run long enough), either in unscaled form [46, 47]:

$$T = \int_0^\infty \|\delta \vec{X}(t)\|^2 dt, \quad (26)$$

§ In fact, the authors didn't call the quantity for which the formula was proposed "resilience", but "relative stability" — their paper was prior to introducing the notion "resilience" by Holling — but description of their "relative stability" is now regarded, at least by some authors, as coinciding with definition of "engineering resilience", see [44]

where $\delta\vec{X}(t)$ denotes perturbation changing in time after an initial perturbing pulse, and $\|\cdot\|$ is an Euclidean measure of the vector of state variables \vec{X} ; or in the scaled form [48, 49]:

$$T = \frac{1}{\|\delta\vec{X}_0\|^2} \int_0^\infty \|\delta\vec{X}(t)\|^2 dt, \quad (27)$$

$\delta\vec{X}_0$ denotes the initial displacement from a stable state, and the rest of the notation is as in (26). For cases in which the initial perturbation is not the maximum value of perturbation after a perturbing pulse, another form of scaled formula has been proposed [50, 38]:

$$T = \frac{1}{\|\delta\vec{X}_{\max}\|^2} \int_0^\infty \|\delta\vec{X}(t)\|^2 dt, \quad (28)$$

with $\delta\vec{X}_{\max}$ denoting the maximum value of displacement from equilibrium.

Neubert and Caswell have noticed [44], that one can use the return time, not only to describe a particular behaviour succeeding a given particular perturbing pulse, but to characterize a general property of the system. In order to do this one must use some property of the distribution of the return times generated by a collection of different perturbations, such as the maximum or the mean. They proposed a measure that takes into account all possible initial perturbations, but yields as a result one value that will characterize the system. This measure is called ‘‘reactivity’’ and describes transient behaviour of the system, as a complement to the characteristic return time, describing asymptotic behaviour.

4.2.1. Reactivity

Continuous-time deterministic model Reactivity is defined as the maximum amplification rate, over all initial perturbations, immediately following the perturbing pulse [44]:

$$reactivity \equiv \max_{\|\delta\vec{X}_0\| \neq 0} \left[\frac{1}{\|\delta\vec{X}\|} \frac{d\|\delta\vec{X}\|}{dt} \Bigg|_{t=0} \right], \quad (29)$$

and an associated measure, *maximum amplification*, as [44]:

$$\rho_{\max} \equiv \max_{t \geq 0} \max_{\|\delta\vec{X}_0\| \neq 0} \frac{\|e^{\mathbf{A}t} \delta\vec{X}_0\|}{\|\delta\vec{X}\|} \quad (30)$$

The growth rate of perturbation at any time can be expressed as

$$\frac{d\|\delta\vec{X}\|}{dt} = \frac{d\sqrt{\delta\vec{X}^T \delta\vec{X}}}{dt} = \frac{\delta\vec{X}^T (d\delta\vec{X}/dt) + (d\delta\vec{X}/dt)^T \delta\vec{X}}{2\|\delta\vec{X}\|}. \quad (31)$$

Linearizing the model (3) around equilibrium, one gets for the time evolution of perturbation:

$$\frac{d\delta\vec{X}(t)}{dt} = \mathbf{A}\delta\vec{X}(t), \quad (32)$$

with $\mathbf{A} \equiv (\partial \vec{F} / \partial \vec{X})_{\vec{X}=\vec{X}^*}$ (\vec{X}^* denoting the vector of system variables in stationary state). Substituting (32) into (react1), one gets:

$$\frac{d\|\delta\vec{X}\|}{dt} = \frac{\delta\vec{X}^T(\mathbf{A} + \mathbf{A}^T)\delta\vec{X}}{2\|\delta\vec{X}\|}. \quad (33)$$

The matrix $\frac{1}{2}(\mathbf{A} + \mathbf{A}^T)$ is called the *symmetric part* or *Hermitian part* of \mathbf{A} and is designated by $H(\mathbf{A})$. Using this result (33) to (29) one obtains:

$$\left. \frac{1}{\|\delta\vec{X}\|} \frac{d\|\delta\vec{X}\|}{dt} \right|_{t=0} = \frac{\delta\vec{X}_0^T H(\mathbf{A}) \delta\vec{X}_0}{\delta\vec{X}_0^T \delta\vec{X}_0}. \quad (34)$$

As $\delta\vec{X}$ is real and matrix $H(\mathbf{A})$ is real and symmetric, the right hand side of (34) is a Rayleigh quotient of \mathbf{A} and $\delta\vec{X}$: $R(\mathbf{A}, \delta\vec{X})$. It is known that for any \mathbf{M} and \vec{V} , their Rayleigh quotient has the following properties:

$$\lambda_{\min} \leq R(\mathbf{M}, \vec{V}) \leq \lambda_{\max}, \quad (35)$$

$$R(\mathbf{M}, \vec{m}_i) = \lambda_i, \quad (36)$$

where $\lambda_{\min, \max, i}$ are minimum, maximum and arbitrary eigenvalues of matrix \mathbf{M} , respectively, and $\vec{m}_{\min, \max, i}$ are corresponding eigenvectors. Thus, in order to evaluate (29) there is no need to sample all possible initial conditions, and:

$$reactivity = \lambda_{\max}(H(\mathbf{A})). \quad (37)$$

Stationary states, for which $\lambda_{\max}(H(\mathbf{A})) > 0$, will be called *reactive*, what means, that some perturbations, no matter how small, will initially grow in magnitude. Let us also note that in 1D case ($\mathbf{A} = A$) we have $H(A) = A = \lambda$, and negative reactivity coincides with the inverse characteristic return time: $reactivity = -1/T_R$ for $reactivity < 0$.

Following [44], let us examine a simple example comparing two systems with the same characteristic return time and different reactivity. Let:

$$\mathbf{A}_1 = \begin{bmatrix} -1 & 0.5 \\ 0 & -2 \end{bmatrix} \quad (38)$$

and

$$\mathbf{A}_2 = \begin{bmatrix} -1 & 10 \\ 0 & -2 \end{bmatrix}. \quad (39)$$

Both \mathbf{A}_1 and \mathbf{A}_2 have the same eigenvalues: $\{-2, -1\}$. Thus, their characteristic return times are equal. Nevertheless, the dynamics of systems with \mathbf{A}_1 and \mathbf{A}_2 differs qualitatively (see Fig. 4). Only in the second of them the perturbation grows initially. Let us calculate reactivity of both systems. For the first one:

$$H(\mathbf{A}_1) = \begin{bmatrix} -1 & 0.25 \\ 0.25 & -2 \end{bmatrix}. \quad (40)$$

and largest eigenvalue $\lambda_{\max}^1 = (\sqrt{5} - 6)/4 \approx -0.94 < 0$, and for the second one:

$$H(\mathbf{A}_2) = \begin{bmatrix} -1 & 5 \\ 5 & -2 \end{bmatrix}. \quad (41)$$

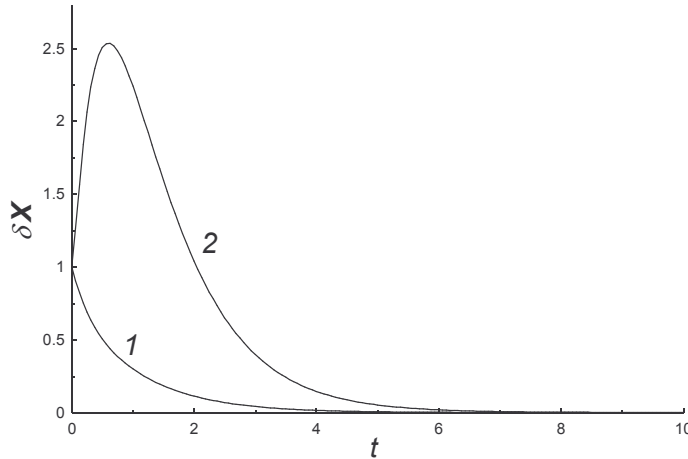


Figure 4. Dynamics of the example systems described by \mathbf{A}_1 and \mathbf{A}_2 (curves labelled 1 and 2, respectively)

and largest eigenvalue $\lambda_{\max}^1 = (\sqrt{101} - 3)/2 \approx 3.52 > 0$. This simple example of two systems reveals qualitatively different behaviours, which may strongly influence the probability of persistence of the system in the initial regime. This difference in behaviour is not reflected in characteristic return times. Reactivity does reflect different kinds of behaviour of these systems taking place during the short time after perturbation. Thus, reactivity seems to be a powerful tool for examining properties of dynamic systems, and, in conjunction with characteristic return time, of measuring resilience of the systems, as their ability to persist perturbation.

Discrete-time stochastic model An analogue of (29) for discrete-time stochastic systems (14), (15) was proposed by Ives et al. [39]:

$$\text{reactivity} \equiv \max \left[\frac{\mathbb{E} \left[\left\| \mathbb{E}[\vec{X}_t | \vec{X}_{t-1}] - \vec{\mu}_\infty \right\|^2 \right] - \mathbb{E} \left[\left\| \vec{X}_{t-1} - \vec{\mu}_\infty \right\|^2 \right]}{\mathbb{E} \left[\left\| \vec{X}_{t-1} - \vec{\mu}_\infty \right\|^2 \right]} \right], \quad (42)$$

where $\mathbb{E}[\cdot]$ denotes the expected value (in particular, $\mathbb{E}[\vec{X}_t | \vec{X}_{t-1}]$ denotes the expected value of \vec{X}_t On the condition that in the previous time-step the vector \vec{X} was equal \vec{X}_{t-1}), $\|\vec{Y}\|^2 \equiv \vec{Y}^T \vec{Y}$, and $\vec{\mu}_\infty$ denotes the mean of stationary distribution. Matrix $\mathbf{B}^T \mathbf{B}$ is a positive-definite symmetric matrix (and therefore it has orthogonal eigenvectors). Thus it may be decomposed as $\mathbf{B}^T \mathbf{B} = \mathbf{K} \mathbf{\Theta} \mathbf{K}^T$, where $\mathbf{\Theta}$ is a diagonal matrix containing eigenvalues of $\mathbf{B}^T \mathbf{B}$, and \mathbf{K} is a matrix containing in its columns the corresponding eigenvectors, $\mathbf{K} \mathbf{K}^T = \mathbf{I}$. Introducing notation $\vec{Z} = \mathbf{K}^T \vec{X}$, and $\vec{\nu} = \mathbf{K}^T \vec{\mu}$ ($\vec{\mu}$ — mean of \vec{X} , and $\vec{\nu}$ — mean of \vec{Z}), expected values from (42) may be calculated as:

$$\begin{aligned} \mathbb{E} \left[\left\| \mathbb{E}[\vec{X}_t | \vec{X}_{t-1}] - \vec{\mu}_\infty \right\|^2 \right] &= \\ &= \mathbb{E} \left[\left\| \mathbf{A} + \mathbf{B} \vec{X}_{t-1} - \vec{\mu}_\infty \right\|^2 \right] = \mathbb{E} \left[\left\| \mathbf{B} (\vec{X}_{t-1} - \vec{\mu}_\infty) \right\|^2 \right] \\ &= \mathbb{E} \left[(\vec{X}_{t-1} - \vec{\mu}_{t-1} + \vec{\mu}_{t-1} - \vec{\mu}_\infty)^T \mathbf{B}^T \mathbf{B} (\vec{X}_{t-1} - \vec{\mu}_{t-1} + \vec{\mu}_{t-1} - \vec{\mu}_\infty) \right] \end{aligned}$$

$$\begin{aligned}
&= \mathbb{E} \left[(\vec{X}_{t-1} - \vec{\mu}_{t-1})^T \mathbf{B}^T \mathbf{B} (\vec{X}_{t-1} - \vec{\mu}_{t-1}) \right] \\
&\quad + \left[(\vec{\mu}_{t-1} - \vec{\mu}_\infty)^T \mathbf{B}^T \mathbf{B} (\vec{\mu}_{t-1} - \vec{\mu}_\infty) \right]
\end{aligned} \tag{43}$$

where the first equality results from (21), and the second from (19). To obtain the reactivity of the system averaged over a long time period, we can let the distribution of \vec{X}_{t-1} be a stationary distribution, $\vec{X}_{t-1} = \vec{X}_\infty$. In this case, the second term in (43) becomes zero,

$$\begin{aligned}
\mathbb{E} \left[\|\mathbb{E}[\vec{X}_t | \vec{X}_{t-1}] - \vec{\mu}_\infty\|^2 \right] &= \\
&= \mathbb{E} \left[(\vec{X}_{t-1} - \vec{\mu}_{t-1})^T \mathbf{B}^T \mathbf{B} (\vec{X}_{t-1} - \vec{\mu}_{t-1}) \right] \\
&= \mathbb{E} \left[(\vec{Z}_{t-1} - \vec{v}_{t-1})^T \mathbf{K}^T \mathbf{B}^T \mathbf{B} \mathbf{K} (\vec{Z}_{t-1} - \vec{v}_{t-1}) \right] \\
&= \mathbb{E} \left[(\vec{Z}_{t-1} - \vec{v}_{t-1})^T \mathbf{\Theta} (\vec{Z}_{t-1} - \vec{v}_{t-1}) \right] = \sum_i \varphi_i \gamma_{ii},
\end{aligned} \tag{44}$$

where φ_i are eigenvalues of $\mathbf{\Theta}$ (and $\mathbf{B}^T \mathbf{B}$) and γ_{ii} are diagonal elements of the covariance matrix of \vec{Z}_{t-1} . Similarly,

$$\mathbb{E} \left[\|\vec{X}_{t-1} - \vec{\mu}_\infty\|^2 \right] = \sum \gamma_{ii}. \tag{45}$$

The worst case scenario is when all φ_i 's but the one corresponding to the largest eigenvalue of $\mathbf{B}^T \mathbf{B}$ equal zero. Thus,

$$\text{reactivity} = \max \left[\frac{\sum_i \varphi_i \gamma_{ii} - \sum_i \gamma_{ii}}{\sum_i \gamma_{ii}} \right] = \max \lambda_{\mathbf{B}^T \mathbf{B}}. \tag{46}$$

This is an analogue of the formula (37) for discrete-time stochastic systems. Proper formulae for continuous-time stochastic systems and discrete-time deterministic systems may be obtained in a parallel way.

4.3. Variance

There exist numerous experimental evidences that an impending regime shift is signalled by a rise of spatial and/or time variance (e.g., [51, 52]). Although the variance component is difficult to distinguish from environmental noise, there are methods that allow for it and do not require detailed knowledge about mechanisms underlying the regime shift [32]. It is clear, that time variance in the system variables arises as a reaction to environmental time-fluctuations. Spatial variance of the system's variables can be interpreted as caused by spatial variation in the environment — but also, as it can be shown [53], by temporal environmental fluctuations, in the absence of any fixed spatial environmental variation. It is also intuitively clear that the value of a system's variables variation is tightly connected with the above discussed measures of resilience: characteristic return time and/or reactivity. Using the illustrative cup-and-ball analogy, one may expect that following any perturbation, the ball in the cup with a short return time rolls instantly towards the bottom of the basin, in contrast to the ball in the cup with long return time. In the latter case, the ball in the cup spends more time away from the basin bottom, what means greater variance of the state [39]. The reasons for rising

variance near the threshold seem general, and should apply to a wide range of plausible models of regime shifts. Increasing variance in the vicinity of threshold corresponds to fluctuations in physical models, that grow infinitely near phase transition. Therefore, increased variance may be an important clue of regime shifts even in cases where the appropriate model is unknown. Furthermore, increased variance may provide a leading indicator of regime shifts that can be used in ecosystem management [32].

Mathematical foundation for the treatment of system variance may be found in [54, 55]. For a 1D system, it is easy to obtain a proper dependence for the variability of the system on the strength of environmental fluctuations and details of the system's potential. Let us deal here with the continuous counterpart of the 1D case of (14):

$$dX_t = F(X_t, b)dt + \sigma dW_t. \quad (47)$$

where W_t denotes a standard Wiener process, σ measures the noise intensity, and b denotes the control parameter. The stationary probability density function for such system is [54, 55] (see also the next subsection for more details):

$$p_0(X, b) = \frac{1}{N} e^{-2V(X, b)/\sigma^2}, \quad (48)$$

with N as a normalizing constant, and $V(X, b)$ denoting the potential defined in (1). Let us expand $V(X, b)$ in a Taylor series around $X^*(b)$, denoting the stationary point of the deterministic counterpart of (47), $F(X^*(b)) = 0$:

$$\begin{aligned} V(X, b) = V(X^*(b), b) + \left. \frac{\partial V(X, b)}{\partial X} \right|_{X=X^*(b)} (X - X^*(b)) \\ + \frac{1}{2} \left. \frac{\partial^2 V(X, b)}{\partial X^2} \right|_{X=X^*(b)} (X - X^*(b))^2. \end{aligned} \quad (49)$$

Substituting (49) and observing that from the definition of the stationary state it follows that $(\partial V(X, b)/\partial X)_{X=X^*(b)} = 0$, and one obtains the stationary probability density function in the form:

$$p_0(X, b) = \frac{1}{N} \exp \left[- \left. \frac{\partial^2 V(X, b)}{\partial X^2} \right|_{X=X^*(b)} \frac{(X - X^*(b))^2}{\sigma^2} \right], \quad (50)$$

where N is different than in (48), but still denotes a normalization constant. Expression (50) has the form of a normal distribution with mean value $\mu = X^*(b)$ (which coincides with the solution of the deterministic version of (47) and variance

$$S^2 = \frac{\sigma^2}{2} \left(\left. \frac{\partial^2 V(X, b)}{\partial X^2} \right|_{X=X^*(b)} \right)^{-1}. \quad (51)$$

Approaching a critical value of the control parameter b , variance (51) tends to infinity (as $(\partial^2 V(X, b)/\partial X^2)_{X=X^*(b)}$ tends to zero). Thus, system variance compared to variance from environmental fluctuations may be a measure of resilience that increases infinitely in the vicinity of a critical value of the control parameter. Let us also note that in continuous 1D case $F = -\partial V/\partial X$, and the value of $2S^2/\sigma^2$ coincides with the return time T_R .

The problem of connecting variability with resilience in multivariate systems is much more complicated. Since resilience is a property of the entire system rather than of separate variables, the question is how to combine the variabilities of different system variables to obtain a single community-level measure of resilience [39]. Let us consider the simplest multidimensional case, i.e., a linear equation:

$$\frac{d\vec{X}}{dt} = \vec{A} + \mathbf{B}\vec{X} + \vec{E}, \quad (52)$$

with \mathbf{E} denoting the vector for noise, normally distributed with mean $\vec{0}$ and covariance matrix Σ . A stationary distribution of the random variable \vec{X} has a Gaussian form with mean value: $\vec{\mu} = -\mathbf{B}^{-1}\vec{A}$ (again coinciding with deterministic stationary solution) and a variance satisfying the relationship:

$$\mathbf{S}^2 = (\mathbf{B} + \mathbf{1})\mathbf{S}^2(\mathbf{B} + \mathbf{1})^T + \Sigma. \quad (53)$$

Having found a covariance matrix of the stationary distribution (from (53) for linear system), there are two ways of comparing variances for multi-dimensional systems, proposed by Ives et al. (see [16, 39]). The first involves measuring the variance in the stationary distribution along axes given by the eigenvectors of \mathbf{B} . The second method for comparing the variance of probability distributions uses determinants to measure the “volume” of covariance matrices. Since the covariance matrices \mathbf{S}^2 and Σ give the variances of the stationary distribution and process errors, respectively, the volume of the difference $\mathbf{S}^2 - \Sigma$ measures the degree to which species interactions increase the variance of the stationary distribution relative to the variance of the process error [39]. To avoid dependence on the dimensionality of the system, the proper measure of resilience would be defined as:

$$\left[\frac{\det(\mathbf{S}^2 - \Sigma)}{\det(\mathbf{S}^2)} \right]^{1/N} = \det(\mathbf{B} + \mathbf{1})^{2/N} = (\lambda_1 \lambda_2 \cdots \lambda_N)^{2/N}, \quad (54)$$

which is simply a square of the geometric mean of all eigenvalues. Thus, the second method takes into account all eigenvalues of the matrix \mathbf{B} , while the first takes into account only the largest.

As it was mentioned above, the variance of the system is tightly connected with the return time. Thus, as a measure of resilience these same problems with variance arise as with the return time. Namely, the variability of the system does not necessarily reflect its ecological resilience (e.g., stable oscillations, special shape of potential — see examples (a)–(c) in the previous subsection). That is, variance may be a measure of engineering resilience, not the ecological resilience itself. However, the empirical evidence suggests, that rising variance may be in most of the situations an useful indicator of impending threshold. Note, that more important are the changes in variance, not its value itself (e.g., in an oscillating system as long as variance — however large — does not change, the system may be expected to remain in its current regime).

4.4. “Reddering” of the spectrum

In addition to changes in values of variance, it was also observed that in the vicinity of a threshold, the power spectrum of the overturning becomes “redder”, i.e., more energy is contained in the low frequencies [56, 57]. In the simple heuristic picture of cup-and-ball analogy this is a result of flattening of the bottom of the cup. Let us analyse the 1D case, described by Eq. (47). Linearizing it around a stationary state X^* , one gets:

$$dX_t = AX_t dt + \sigma dW_t, \quad (55)$$

with

$$A \equiv \left. \frac{\partial F(X_t, b)}{\partial X_t} \right|_{(X^*(b), b)}.$$

It is known [58] that the spectrum of a process described by (55) (Ornstein–Uhlenbeck process) is:

$$S(\omega) = \frac{1}{2\pi} \frac{\sigma^2}{A^2 + \omega^2}. \quad (56)$$

To examine the properties of the spectrum (56) in the vicinity of a threshold, we will use the results from Section 4.1. From (9), it follows that:

$$\begin{aligned} \left. \frac{\partial F(X_t, b)}{\partial X_t} \right|_{(X^*(b), b)} &= \pm 2(\alpha\beta\delta b)^{1/2}, \\ \alpha &\equiv \frac{1}{2} \left. \frac{\partial^2 F}{\partial x^2} \right|_{(x^*(b_T), b_T)}, \\ \beta &\equiv \left. \frac{\partial F}{\partial b} \right|_{(x^*(b_T), b_T)}, \\ \delta b &\equiv |b - b_T|, \end{aligned} \quad (57)$$

where b_T denotes the threshold value of the control parameter. Substituting (57) into (56), one gets:

$$S(\omega) = \frac{1}{2\pi} \frac{\sigma^2}{4\alpha\beta\delta b + \omega^2}. \quad (58)$$

One can see (cf. Fig. 5) that indeed, approaching the threshold value of the control parameter, the magnitude of the power spectral density in the limit of zero frequency increases inversely proportionally to the distance to the bifurcation point, while the cutoff frequency (the frequency where the spectrum changes from a horizontal to a decreasing shape) decreases proportionally to the square root.

4.5. Mean first-exit time

As it was mentioned above, most of the real ecological and sociological systems should be regarded as a stochastic ones. If such a system reveals multistability, in the presence of noise neither regime is strictly speaking stable — i.e., there is positive probability that random fluctuations will convert the system to another state. Here we will briefly

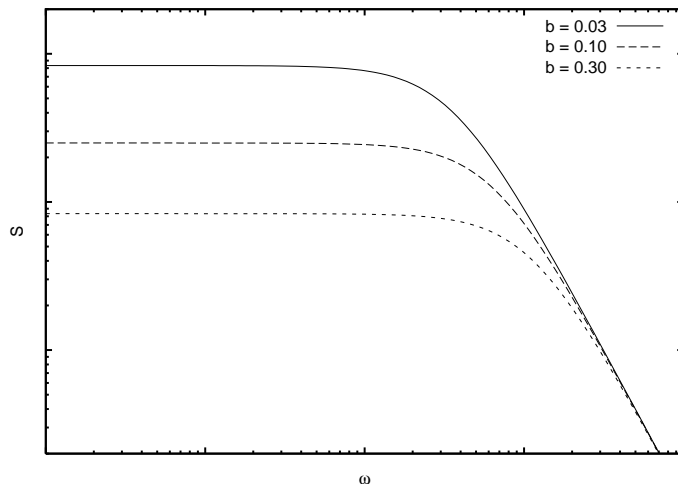


Figure 5. “Reddering” of the spectrum. The spectra $S(\omega)$ for three values of the control parameter b in a log-log plot (arbitrary units)

discuss connections with this concept of *mean first-exit time* [54, 55, 56, 59]. As in the previous subsection, we will deal here with the continuous counterpart of (14), namely:

$$d\vec{X}_t = \vec{F}(\vec{X}_t)dt + \Sigma d\vec{W}_t, \quad (59)$$

where \vec{W}_t denotes a standard vector-valued Wiener process, with $d\vec{W} d\vec{W}^T = \mathbf{1} dt$ ($\mathbf{1}$ — identity matrix) and Σ measures the noise intensity. For simplicity, let us consider a 1D case of (59):

$$dX_t = F(X_t)dt + \sigma dW_t. \quad (60)$$

One of methods to characterize the dynamics of the equation (60) is to determine the probability density function $p(X, t)$ of X_t (hereafter abbreviated as PDF), which gives all the information on the instantaneous state of the system. The density is given by the normalized solution of the Fokker–Planck equation [54]:

$$\frac{\partial}{\partial t}p(X, t) = \frac{\partial}{\partial X} \left[\frac{\partial}{\partial X}V(X)p(X, t) \right] + \frac{\sigma^2}{2} \frac{\partial^2}{\partial X^2}p(X, t) \equiv \hat{L}p(X, t), \quad (61)$$

with

$$-\frac{d}{dX}V(X) \equiv F(X). \quad (62)$$

The stationary solution of (61) is

$$p_0(X) = \frac{1}{N}e^{-2V(x)/\sigma^2}, \quad (63)$$

with N as a normalizing constant. As $dp_0/dX = (-2/\sigma^2)(dV(x)/dX)e^{-2V(x)/\sigma^2}$, p_0 will have the same number of extrema as $V(x)$. Thus, for multi-well potentials, i.e., for multi-stable systems, the stationary PDF will never be concentrated solely in one of the basins of attraction. Even starting from initial conditions with the PDF as a spike of probability near one (“desired”) minimum of the potential, from the above

considerations it is known, that given sufficient time the PDF will “leak” to other stable states, obtaining eventually a stationary multimodal form of (63). In other words, even if the deterministic bifurcation point has not been reached, there still is a finite probability that the stochastic system will leave the potential well. Thus the question of great practical importance arises: how long does it take for the PDF to obtain a significant non-zero value out of the region of initial concentration? The life time of the quasi-stationary state of the system can be described by the mean first exit time from the potential well.

The time needed to obtain a stationary distribution may be determined based on spectral theory [55]. Stationary density (63) is an eigenfunction of the operator \hat{L} in (61) with eigenvalue 0. Let us order eigenvalues of \hat{L} : $\dots \lambda_k < \dots \lambda_2 < \lambda_1 < 0$. Decomposing $p(X, t)$ on a basis of eigenfunctions of \hat{L} , we see that p approaches the stationary solution in a characteristic time of order:

$$\tau = \frac{1}{|\lambda_1|}. \quad (64)$$

In the small-noise limit, the first-exit time from an initial subset of phase space D (containing a stable equilibrium point) is asymptotically exponential with the expectation value (Kramers’ formula) [54]:

$$\tau_{\text{Kramers}} = e^{2(V_1 - V_0)/\sigma^2}, \quad (65)$$

with $V_1 - V_0$ as a height of a barrier separating two (meta)stable states. As this height decreases, the first-exit time drops exponentially. Within time $t \approx \tau_{\text{Kramers}}$ the initial spike of the PDF approaches the bimodal stationary form. Then, if the relative stabilities of two states are close, a significant probability of flipping to the another state arises.

It is obvious that in case of substantial asymmetry between states, in spite of bimodality of the PDF, the stationary behaviour of the system will be more like that of a system with a unimodal distribution than that with a bimodal. Monahan [60] has introduced the term *stabilization* to denote the preferred state, reflected in the stationary PDF, of one regime relative to the other. Although in the presence of noise neither regime is strictly speaking “stable,” but only metastable, a distinct preference of the system for one regime over the other justifies using this term.

Nevertheless, in each case of multistability there is a finite probability of leaving a certain state. Assuming the system is in the stationary state, the mean time needed for this “escape” can be estimated from:

$$\tau = \frac{p}{S} = \frac{2}{\sigma^2} \int_{y_1}^{y_2} \exp\left[-\frac{2}{\sigma^2}V(X)\right] dX \int_{y_{\min}}^A \exp\left[\frac{2}{\sigma^2}V(X)\right] dX, \quad (66)$$

where the first integral is the probability that the system is within the potential well limited by y_1 and y_2 ; the second integral is the estimation of the inverse probability current from the potential minimum, y_{\min} , to a point A outside this potential well.

Thus the mean first-exit time is a measure of resilience for stochastic systems: the larger value of this quantity, the less probable is the flip of the system into distinct subset of phase space.

4.6. Fisher Information

One example of current work showing promise in finding new measures of resilience is that which links *Fisher Information* to the concept of resilience [61, 62]. By now it has been shown, that Fisher Information is an indicator of regime flips, both for models [61] and for field studies [62]. Moreover, Fath et al. claim that Fisher Information may be a useful measure to identify the degree to which a system is at risk of “flipping” into a different dynamic regime and hypothesize that it may be possible to infer the system resilience by the change in Fisher Information [61, 62].

Let us recall briefly the mathematical foundations of Fisher Information [61, 62]. Fisher Information can be variously interpreted as a measure of the ability to estimate a parameter, as the amount of information that can be extracted from a set of measurements, and also as a measure of the state of order of a system or phenomenon [62], and is defined as follows:

$$I = \int \frac{1}{p(\epsilon)} \left(\frac{dp(\epsilon)}{d\epsilon} \right)^2 d\epsilon, \quad (67)$$

where $p(\epsilon)$ is the probability density as a function of the deviation, ϵ , from the true value of the variable. In the application to measure resilience of the system, ϵ will measure a deviation from some reference state, as will be shown below.

Ecological Fisher Information will apply to the systems which may be described as continuous dynamics systems, and have stable periodic states (including equilibria). Dividing the steady-state closed loop trajectory in the state space into k sub-segments of length Δs , one has to choose an arbitrary *reference state* among these k possible. Then ϵ will measure a distance of an arbitrary state from this chosen one. The probability of observing the system at a particular position is proportional to the amount of time the system spends in the sub-segment Δs corresponding to that position. This time equals to

$$\Delta t = \frac{\Delta s}{\bar{v}(s)},$$

where $\bar{v}(s)$ denotes the average speed of the system in that segment, or, in the limit $\Delta s \rightarrow \infty$,

$$dt = \frac{ds}{R'(s)},$$

where $R'(s)$ denotes the value of velocity at s . Thus, probability that the system is in state s equals

$$P(s) = A dt = A \frac{ds}{R'(s)},$$

with some constant A . Noting, that $\int P(s) ds$ over whole loop should equal 1, one has for constant A : $A = \left(\int_0^S (1/R'(s)) ds \right)^{-1} \equiv 1/T$, where T is the period of the system's

motion in its state space. As probability density relates to probability by $p(s)ds = P(s)$, thus for probability density one has:

$$p(s) = \frac{1}{T} \frac{1}{R'(s)},$$

or, for $p(t)$:

$$p(t) = \frac{1}{T} \frac{1}{R'(t)}, \quad (68)$$

(here $T \equiv \int_0^T dt$). Fisher Information (67) may be rewritten as:

$$I = \int_0^T \frac{1}{p(t)} \left(\frac{dp(t)}{dt} \right)^2 \frac{dt}{R'(t)},$$

or, using (68):

$$I = \frac{1}{T} \int_0^T \frac{(R''(t))^2}{(R'(t))^4} dt. \quad (69)$$

The speed ($R'(t)$) and the acceleration ($R''(t)$) of the n -dimensional system are obtained from differential equations by:

$$R'(t) = \sqrt{\sum_{i=1}^n \left(\frac{dx_i}{dt} \right)^2}$$

$$R''(t) = \frac{1}{R'(t)} \left[\sum_{i=1}^n \frac{dx_i}{dt} \frac{d^2x_i}{dt^2} \right].$$

It is clear from (69) that for a system spending an equal amount of time in any state Fisher Information will be zero; for the equilibrium point Fisher Information will be infinite. As it was mentioned above, it has been shown, that changes in Fisher Information are an adequate indicator of regime shifts, both for field studies and model systems. Whether it may serve also as a measure to compare resilience of two steady states is still an open question.

4.7. Summary of measures of engineering resilience

Although very different in details, most of the above reviewed measures of engineering resilience seem to have much in common. Very simple heuristic analysis within cup-and-ball analogy may predict that a system with a short return time will also have little variance, low reactivity [39] and a long time to first exit. Let us summarize by comparing the behaviour of a ball in cups of two different shapes, which will be called for simplicity “steep” and “shallow”.

- a) **Characteristic return time.** In the shallow basin, the ball will move to the bottom more slowly than in the steep basin, after being moved to the basin rim by disturbance.

- b) **Variance.** If the balls in both the steep and shallow basins are subjected to continuous perturbations that occur randomly in either direction, after perturbation the ball in the steep basin rolls rapidly towards the bottom of the basin, while the ball in the shallow basin rolls to the bottom slowly. As a result, the ball in the shallow basin spends more time away from the basin bottom, leading to a stationary distribution with greater variance than the ball in the steep basin.
- c) **Spectrum.** For a steep basin, the ball will return rapidly after disturbance, thus the frequencies of its oscillatory movement will be larger than in the shallow basin, for which a ball will move slowly, with low frequencies.
- d) **Reactivity.** For a steep basin, disturbances may push a ball away from the bottom of the basin, yet on average the ball is pulled strongly towards the bottom of the basin between each successive time steps. In contrast, in the shallow basin the same disturbances on a ball starting at the same distance from the bottom of the basin may leave the ball farther from the bottom, because the ball is not brought strongly back towards the bottom between successive disturbances. This represents a more reactive system than that of the steep basin;
- e) **Time of first-exit.** As in the shallow basin the probability of large displacement is larger than in the steep basin (greater variance), the time needed to occur for a disturbance large enough to throw the ball out the cup is less for the shallow basin than for the steep one.

Although misleading in some special cases (cf. an example in subsection 4.2), in most of cases this simple analysis proves correct. In principle, one cannot assume that one of these measures gives the information of all the others and sufficiently characterizes the system. Although using only one of the measures is mostly justified, one should keep in mind a possible inconsistency. Measuring (or calculating) more than one of the above measures may give a more comprehensive description of the system's properties.

5. Examples

In this section we will examine three models known from literature: shallow lakes model [3], Brock–Durlauf model [63, 64] and predator–prey model [34].

It will not be our goal here to explore whole ranges of variabilities of models: it would be (and was) a subject of much more extensive papers. Here we intend only to calculate *examples* of measures of resilience, keeping values of most of parameters fixed, varying the value of only one of them. We will be especially interested in *comparing* different measures, possibly by correlating them. Of course, finding positive correlation of various measures for such chosen values of parameters cannot imply that the measures correlate in the whole wide range of possible parameter values. However, it would be a step in this direction. On the other hand, the lack of strong positive correlation would be a hint that (some of, or all) measures of resilience should be treated with high caution.

In the 1D models, we will calculate characteristic return time as a measure of

engineering resilience (reactivity and variance coincide, up to a constant, with this measure), and width of potential well and barrier height as a measure of ecological resilience. In the 2D model, we will calculate characteristic return time, reactivity and variance as measures of engineering resilience, and size of the basin of attraction as a measure of ecological resilience. Van Nes and Scheffer reported [20], that they found “almost linear dependence” of recovery rate (inverse of characteristic return time) and ecological resilience, which they took as a distance from threshold. However, according to Wissel theory, linear dependence should hold not for recovery rate but rather for its square, in the vicinity of threshold. Moreover, as it will be shown, the distance from threshold is not a simple function of well width or barrier height (standard measures of ecological resilience).

Therefore, it would be rather arbitrary to select only return time or recovery rate, or its square, for comparison with other resilience measures; we will investigate correlations of all three mentioned measures with other ones.

5.1. The shallow lakes model

The minimal model of ecosystem showing multistability (and hysteresis) was proposed by Scheffer et al. [3] and consists of a single differential equation describing dynamics of an “unwanted” ecosystem property x :

$$\frac{dx}{dt} = a - bx + rf(x). \quad (70)$$

The factor a promotes the x in the system, b is its decay rate and r — its recovery rate. With $r \neq 0$ and appropriate choice of the function $f(x)$, the system may exhibit multiple equilibria in some range of parameters. The Hill function,

$$f_H(x) = \frac{x^p}{x^p + h^p}, \quad (71)$$

was proposed by Scheffer et al.; it has the following properties (cf. Fig. 6):

- (i) $f_H(0) = 0$, $\lim_{x \rightarrow \infty} f_H(x) = 1$;
- (ii) $f_H(h) = 1/2$;
- (iii) it increases steeply at the threshold h (the greater the value of p , the more steeply).

Let us analyse the existence, number and character of stationary points of the model (70). Stationary points are determined from the condition

$$\frac{dx}{dt} = 0 \iff r \frac{x^p}{x^p + h^p} = bx - a. \quad (72)$$

From the shape of function $f_H(x)$ it follows, that there may exist one or three solutions of condition (72). The necessary condition for the existence of three solutions is the existence of at least one point in which $rf'_H(x) > b$. For any set of parameters (r, p, h, b) fulfilling $rf'_H(x)|_{\max} > b$, the actual existence of three solutions depends on the value of a (an example is shown in the upper plots in Fig. 7).

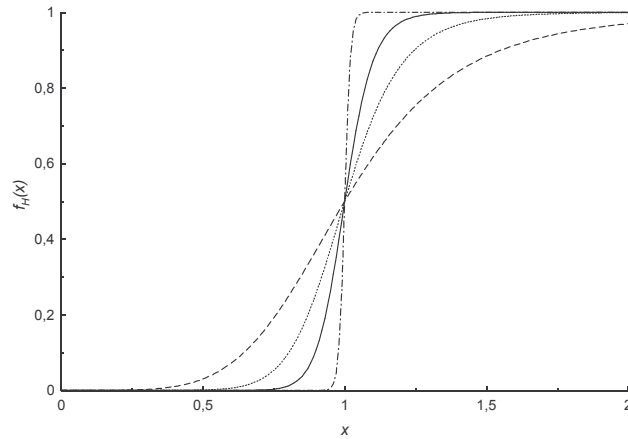


Figure 6. The plot of Hill function for $h = 1$ and $p = 5$ (----), $p = 10$ (.....), $p = 20$ (—), $p = 100$ (-·-·-).

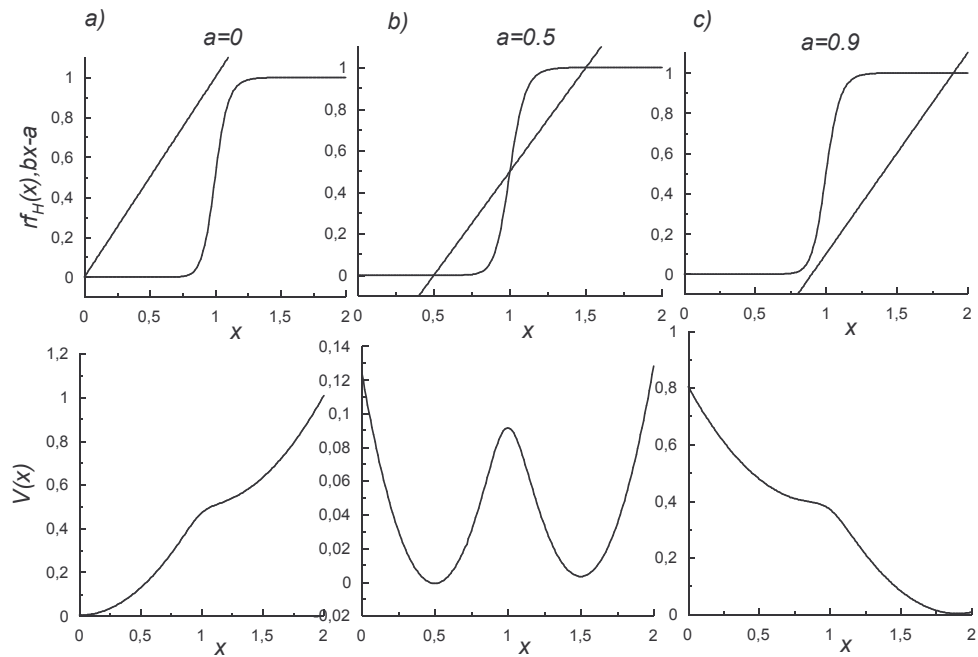


Figure 7. At the top: solutions of Eq. (72) for $h = 1$, $p = 20$, $b = 1$ and $a = 0$ (a); $a = 0.5$ (b); $a = 0.9$ (c). At the bottom: corresponding potentials (73) for the same values of parameters

From now on, we will deal with systems satisfying this condition. It would be illustrative to use the concept of “ecological potential” defined by

$$\frac{dx}{dt} = -\frac{dV(x)}{dx}. \quad (73)$$

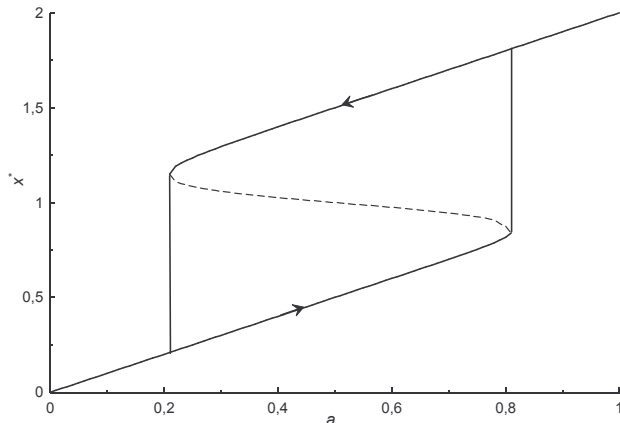


Figure 8. Hysteresis in shallow lake model. While a (the supply of x) is gradually increased, the system remains in the state with lower value of x , following the lower solid curve, until it disappears at $a_2 \approx 0.81$. After the system got “trapped” in the state with higher value of x , it follows the upper solid curve when a is decreased, until this state disappears at $a_1 \approx 0.21$. The dashed curve depicts the unstable state corresponding to the potential maximum

For each solution of (72), i.e., for each stationary point, there exist an extremum in the potential. It is clearly seen which of these stationary points are stable (potential’s minima), and which are unstable (potential’s maxima), cf. the lower plots in Fig. 7.

Let us assume that the supplies of x into the system gradually increases (changes of a are very slow compared to dynamics of x), beginning from $a = 0$; and that for this initial value of a , also $x = 0$. This is possible, as for $a = 0$ there always exists stationary (and stable or metastable) point at $x = 0$ (the existence of the two other equilibria depends on the interplay of parameters (b, r, h, p)). With increasing value of a , there appears the second stable stationary state (or, if it already existed, the relative stability of these two stationary states changes). Within some critical value of a_2 , the stationary state with lower value of x vanishes, and the system undergoes a rapid transition to the second stationary state. When trying to re-convert the system into the state with lower value of x , it is not sufficient to decrease a below a_2 , as the system got “trapped” in the unfavourable state with higher value of x . In order to return to the state with lower value of x , it is necessary to decrease the supply of x below the value a_1 , $a_1 < a_2$. Therefore, hysteresis emerges, as shown in Fig. 8.

When the system is in the “desirable” state (lower value of x), the characteristic return time T_R grows when the parameter a approaches the threshold value a_2 ; this growth is hardly noticeable far from a_2 and extremely rapid in the vicinity of the threshold, cf. Fig. 9a. The square of the recovery rate (T_R^{-2}) steeply drops to zero when approaching a_2 , as shown in Fig. 9b. The linear dependence $T_R^{-2} \propto |a - a_2|$ described by Wissel’s theory can be observed only in very close to the threshold. At the same time, both ecological resilience measures — the well width and the barrier height — decrease to zero (Fig. 10).

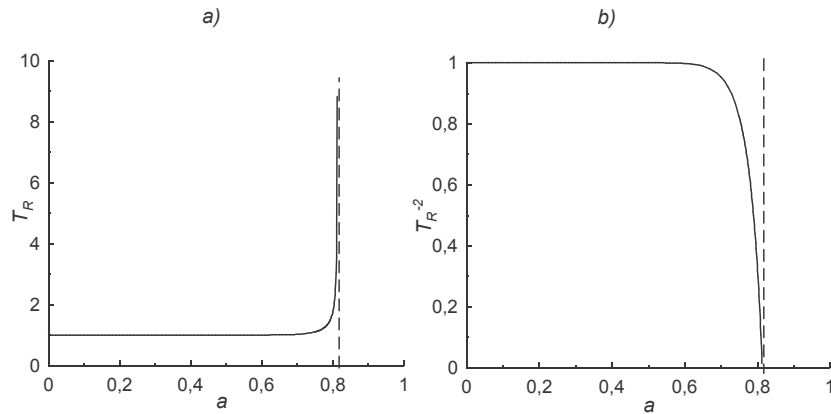


Figure 9. Characteristic return time T_R (a) and square of the recovery rate T_R^{-2} (b) as functions of the parameter a in the lower stable branch of the shallow lake model; the threshold at $a_2 \approx 0.81$ is marked with the vertical dashed line

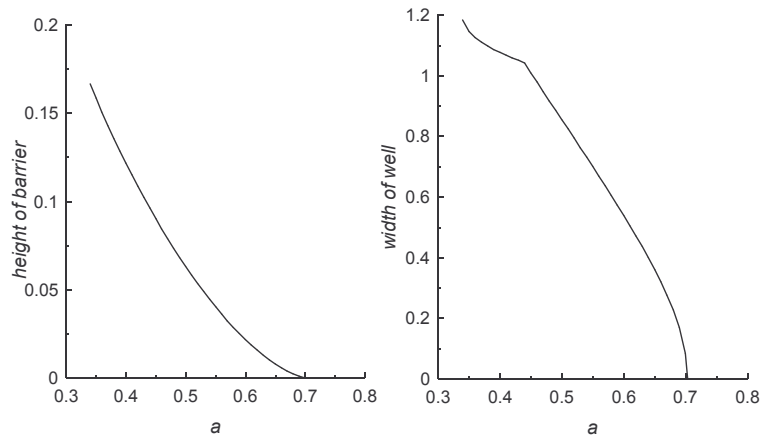


Figure 10. Width of the left potential well (at the left) and height of the barrier (at the right) as functions of the parameter a in the lower stable branch of the shallow lake model

The relations of the measures of engineering resilience (T_R , T_R^{-1} and T_R^{-2}) to the measures of ecological resilience (the well width and the barrier height) are shown in Fig. 11. It can be seen that the dependences between ecological and engineering resilience measures have monotonic character.

5.2. Brock–Durlauf model

In the general framework of utility function binary-choice models, there exists a widely discussed Brock–Durlauf model [63, 64]. The model describes a set of individuals, each of them faced to a repeating choice. In each times an individual has to choose (+1) or (−1), depending on relative gains and losses upon each possible choice. Gains and losses are evaluated using so-called *utility function*, containing external influences, mutual

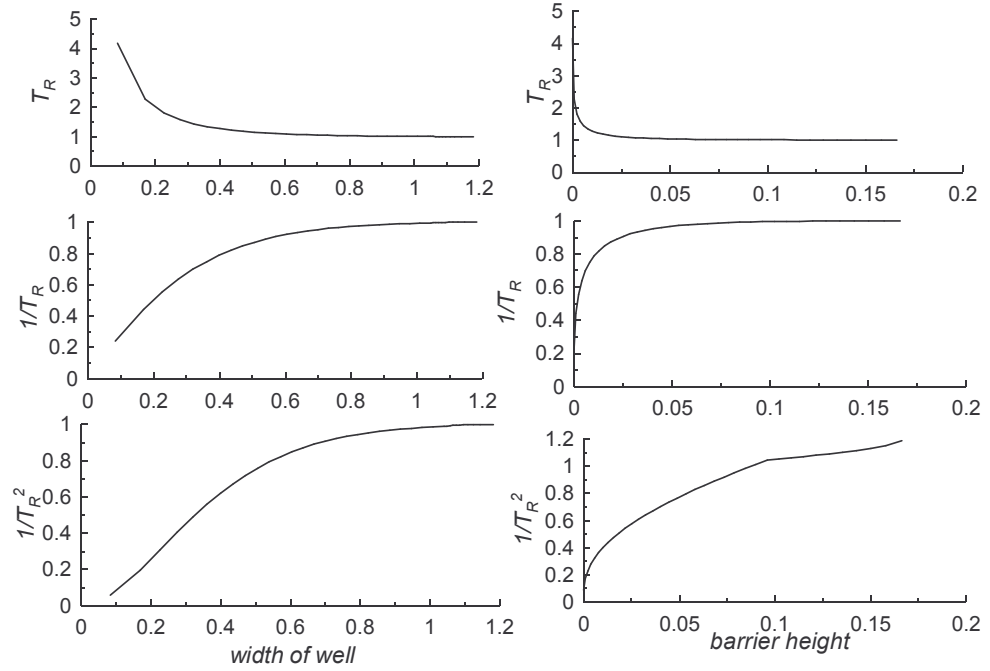


Figure 11. Dependences between ecological and engineering resilience measures (T_R , T_R^{-1} and T_R^{-2} versus well width and barrier height) in the lower stable branch of the shallow lake model

interactions among individuals, and a random term:

$$\sigma_i = \operatorname{argmax}_{\sigma_i \in \{-1, +1\}} \left[h_i \sigma_i + \sigma_i \sum_{j \neq i} \frac{J_{ij}}{2} \sigma_j + \epsilon_i(\sigma_i) \right], \quad (74)$$

and

$$U(\sigma_i) = h_i \sigma_i + \sigma_i \sum_{j \neq i} \frac{J_{ij}}{2} \sigma_j + \epsilon_i(\sigma_i), \quad (75)$$

where h_i denotes external field, J_{ij} — strength of interaction between individuals i and j , and $\epsilon_i(\sigma_i)$ is a random term. Note that, as the choice is undertaken upon the *difference* $U_i(-1) - U_i(+1)$, only the difference $\epsilon_i(-1) - \epsilon_i(+1)$ plays the role in decision making. The random variable ξ_i being the difference $\epsilon_i(-1) - \epsilon_i(+1)$ is taken to be logistic one:

$$\xi_i \equiv \epsilon_i(-1) - \epsilon_i(+1) \quad (76)$$

$$P(\xi_i < z) = \frac{1}{1 + \exp(-\beta z)}, \quad (77)$$

where β is a constant playing the role of inverse temperature []. The mean-field approximation to the model assumes that each individual interacts with all the others, and that the values of parameters are uniform across the system. Thus, the mean-field continuous-time version of the model is described by a differential equation:

$$\frac{dm}{dt} = \tanh \beta(h + Jm) - m, \quad (78)$$

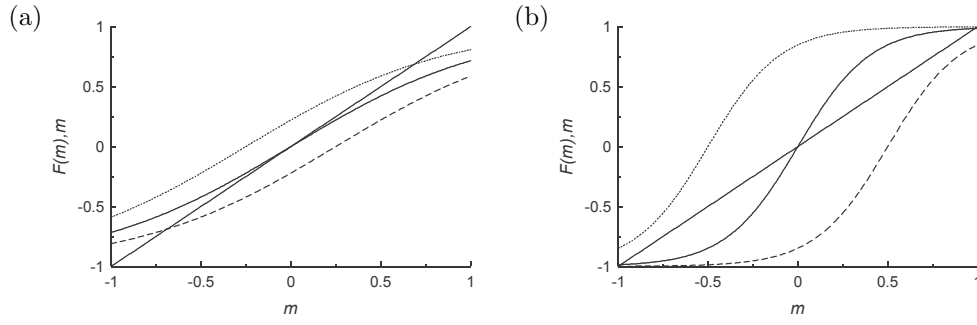


Figure 12. The number of solutions (intersections of the curve $F(m)$ and the straight line m) in Brock–Durlauf model: (a) $\beta J < 1$ — always one solution, $F(m)$ plotted for $h = 0$ (—), $h = +0.2$ (⋯⋯⋯) and $h = -0.2$ (----); (b) $\beta J > 1$ — three solutions for $|h|$ sufficiently small, $F(m)$ plotted for $h = 0$ (—), $h = +0.5$ (⋯⋯⋯) and $h = -0.5$ (----)

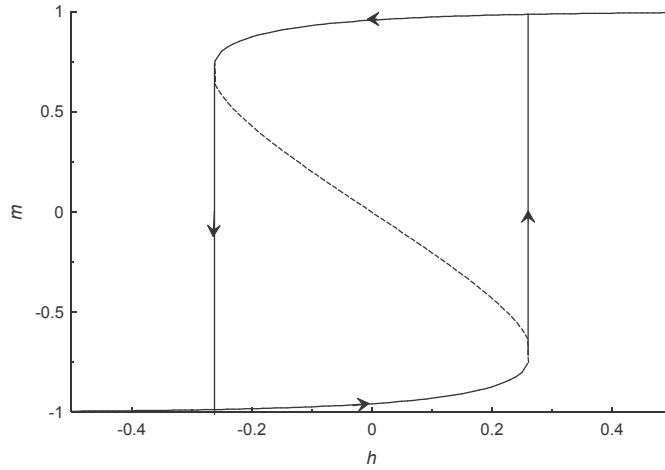


Figure 13. Hysteresis in Brock–Durlauf model

where m denotes the mean choice of all individuals:

$$m = \frac{1}{N} \sum_j \sigma_j.$$

The potential for (78) reads:

$$V(m) = \frac{m^2}{2} - \frac{1}{\beta J} \ln \cosh \beta(h + Jm). \quad (79)$$

Under the condition $\beta J > 1$, there exists some range of h values within which the model (78) has three solutions (and the potential (79) has two minima — two stable stationary points), as shown in Fig. 12. Let us fix the values of β and J : $\beta = 2$, $J = 1$. A stationary state with $m < 0$ exists for $h \in (-\infty, +0.2664)$, while two stable stationary states exist for $h \in (-0.2664, +0.2664)$, and a stationary state with $m > 0$ exists for $h \in (-0.2664, +\infty)$. This produces a hysteresis of width $2 \times 0.2664 = 0.5328$, cf. Fig. 13.

Now we will proceed to examine the degree of resilience of a stationary state with negative mean choice while changing value of h . With increasing h , the left potential

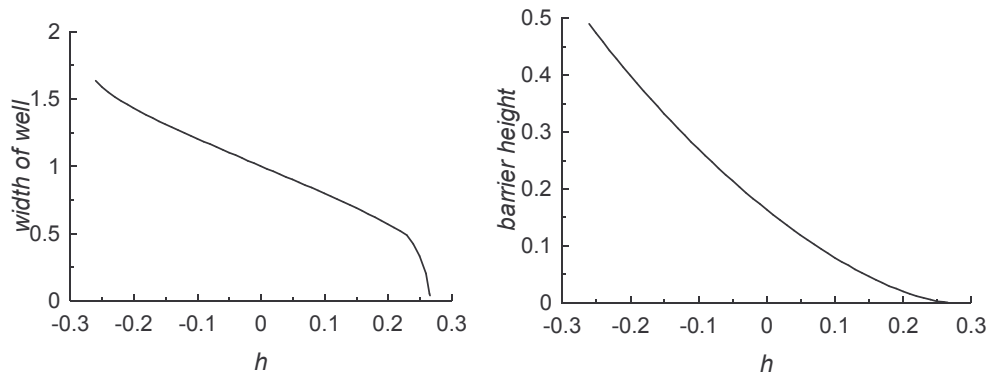


Figure 14. Width of the left potential well (at the left) and height of the barrier (at the right) in Brock–Durlauf model with alternative stable states ($\beta = 2$, $J = 1$)

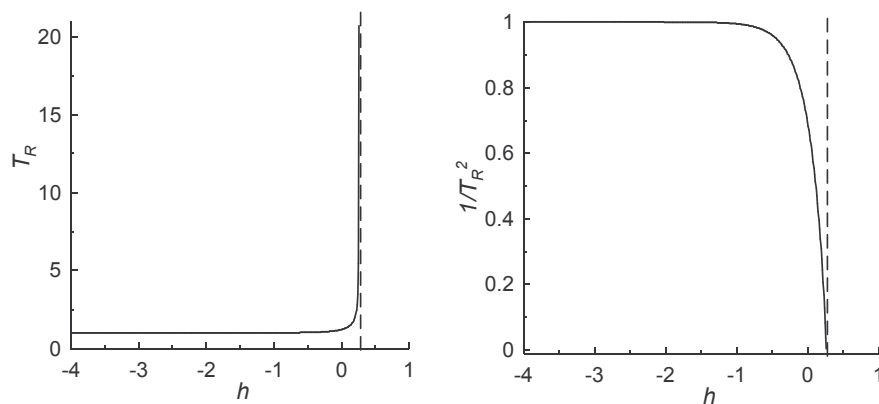


Figure 15. Characteristic return time T_R (a) and square of the recovery rate T_R^{-2} (b) as functions of the external fields h in the $m < 0$ state of Brock–Durlauf model ($\beta = 2$, $J = 1$); the threshold at $h = +0.2664$ is marked with the vertical dashed line

well becomes more and more narrow and shallow, and finally disappears at $h = +0.2664$, as shown in Fig. 14.

As depicted in Fig. 15, the characteristic return time T_R increases with h approaching the threshold value $h_T = +0.2664$, very slowly far from the threshold and rapidly in its vicinity. The square of the recovery rate T_R^{-2} falls to zero at the threshold, but its linear dependence on $|h - h_T|$ predicted by Wissel’s theory can be observed only very close to h_T .

The results of our attempts to correlate the measures of engineering resilience (T_R , T_R^{-1} and T_R^{-2}) with the measures of ecological resilience (the well width and the barrier height) are shown in Fig. 16. Monotonic dependences between ecological and engineering resilience measures can be observed.

5.3. Predator–prey model

Let us analyse a discrete-time two dimensional model that is used to describe the interactions between predators and preys populations. The simplest form of predator–

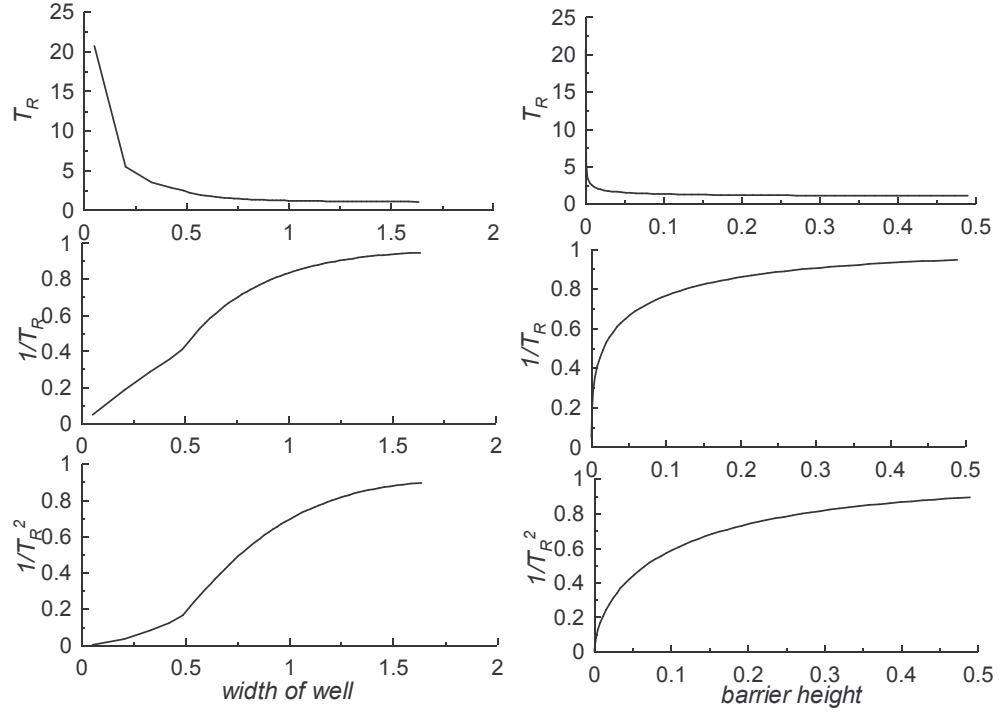


Figure 16. Dependences between ecological and engineering resilience measures (T_R , T_R^{-1} and T_R^{-2} versus well width and barrier height) in Brock–Durlauf model with alternative stable states ($\beta = 2$, $J = 1$)

prey model reads [34]:

$$\begin{cases} N_{t+1} = N_t e^{r(1-N_t/K) - aP_t} \\ P_{t+1} = P_t \alpha \max \left\{ 0, \frac{N_t}{P_t} (1 - e^{-aP_t}) - \beta \right\}, \end{cases} \quad (80)$$

where N_t denotes prey population, P_t — predators population, r is the unrestricted rate of increase of the prey, K is the carrying capacity, a is the “attack rate” of the predators and α is the “efficiency” with which preys are converted into new adult predators. Biologically feasible parameter values are such that $\varphi = \alpha\beta \in (0, 4)$, $\theta = a\alpha K > 1 + \varphi$. The model (80) has three equilibrium points (defined by $N_{t+1} = N_t = N^*$ and $P_{t+1} = P_t = P^*$):

$$\begin{aligned} P^* &= 0, & N^* &= 0, \\ P^* &= 0, & N^* &= K, \\ P^* &= \frac{r}{a} \left(1 - \frac{N^*}{K} \right), & N^* &\neq K : r \left(1 - \frac{N^*}{K} \right) (1 + \alpha\beta) = a\alpha N^* [1 - e^{-r(1-N^*/K)}]. \end{aligned} \quad (81)$$

Linearizing the set of equations (80) around the stationary point $(N^*, P^* \neq 0)$, one gets:

$$\begin{bmatrix} \delta N_{t+1} \\ \delta P_{t+1} \end{bmatrix} = \begin{bmatrix} e^{r(1-N^*/K) - aP^*} \left(1 - r \frac{N^*}{K} \right) & -a N^* e^{r(1-N^*/K) - aP^*} \\ \alpha (1 - e^{-aP^*}) & -\alpha\beta + a\alpha N^* e^{-aP^*} \end{bmatrix} \begin{bmatrix} \delta N_t \\ \delta P_t \end{bmatrix}. \quad (82)$$

The characteristic equation of the matrix in (82) reads:

$$\lambda^2 + b\lambda + c = 0, \quad (83)$$

where

$$b = \alpha \left(\beta - aN^* e^{-aP^*} \right) - e^{r(1-N^*/K)-aP^*} \left(1 - r \frac{N^*}{K} \right),$$

$$c = -\alpha e^{r(1-N^*/K)-aP^*} \left[\beta \left(1 - r \frac{N^*}{K} \right) + aN^* \left(r \frac{N^*}{K} e^{-aP^*} - 1 \right) \right].$$

The stationary state will be stable under the condition that $|\lambda_{1,2}| < 1$, which leads to

$$|b| < 1 + c < 2. \quad (84)$$

When (84) is satisfied, the system will return to the stationary state after perturbation. Depending on the sign of $b^2 - 4c$, this return will have exponential ($b^2 - 4c > 0$) or oscillatory ($b^2 - 4c < 0$) character. Here we will be interested in resilience of the non-trivial stationary state ($P^* \neq 0$). Using (81), we rewrite the coefficients of the characteristic equation as

$$b = r - 1 + \alpha\beta \left[1 + r \left(1 - \frac{N^*}{K} \right) \right] - a\alpha N^*, \quad (85)$$

$$c = \left(1 - \frac{rN^*}{K} \right) (a\alpha N^* - \alpha\beta) + r^2 \frac{N^*}{K} \left(1 - \frac{N^*}{K} \right) (1 + \alpha\beta). \quad (86)$$

Having such a variety of parameters of the model (80), let us focus on some values of most of the parameters, varying only one of them. Let, for example, $r = 1$, $\alpha = 1$, $\beta = 2$, $K = 1$ (this means that the abundance of prey will be measured as a fraction of the carrying capacity). For such a choice of parameters, the second ($K \neq 0$) solution of (81) will exist for $a \in (3.0, 4.7)$. Let us examine basic measures of resilience within this range of the parameter a . Note that for this model potential does not exist. Thus, as the measure of ecological resilience we will take only the size of the basin of attraction, not the barrier height, as it is impossible to define such quantity here.

The area of the basin of attraction grows with increasing a and reaches its maximum at $a \approx 4.7$ (see Fig. 17a), when the single attraction point turns into a stable cycle. At the other end of the stability range, when approaching $a = 3.0$, the basin of attraction does not vanish either; instead, the nontrivial stable solution moves closer and closer to the trivial stable point ($N = 1, P = 0$), cf. Fig. 17b, until they finally coincide.

The characteristic return time grows rapidly near both threshold values (both ends of the stability range), as shown in Fig. 18. The attraction point attracts slower and slower when it approaches the trivial stable point with predators extinct (near $a = 3.0$), and also when it turns into a stable orbit (near $a = 4.7$).

We have also calculated two other engineering resilience measures, namely reactivity (Fig. 19) and variance (Fig. 20). The value of reactivity does not change much in the whole stability range, though it grows monotonically with a . The behaviour of variance depends on the method used to calculate it; we applied both methods described in Subsection 4.3 — with the maximum eigenvalue (the left graph) and with both eigenvalues (the right graph); $S^2(\lambda_{\max})$ increases when approaching both ends of the

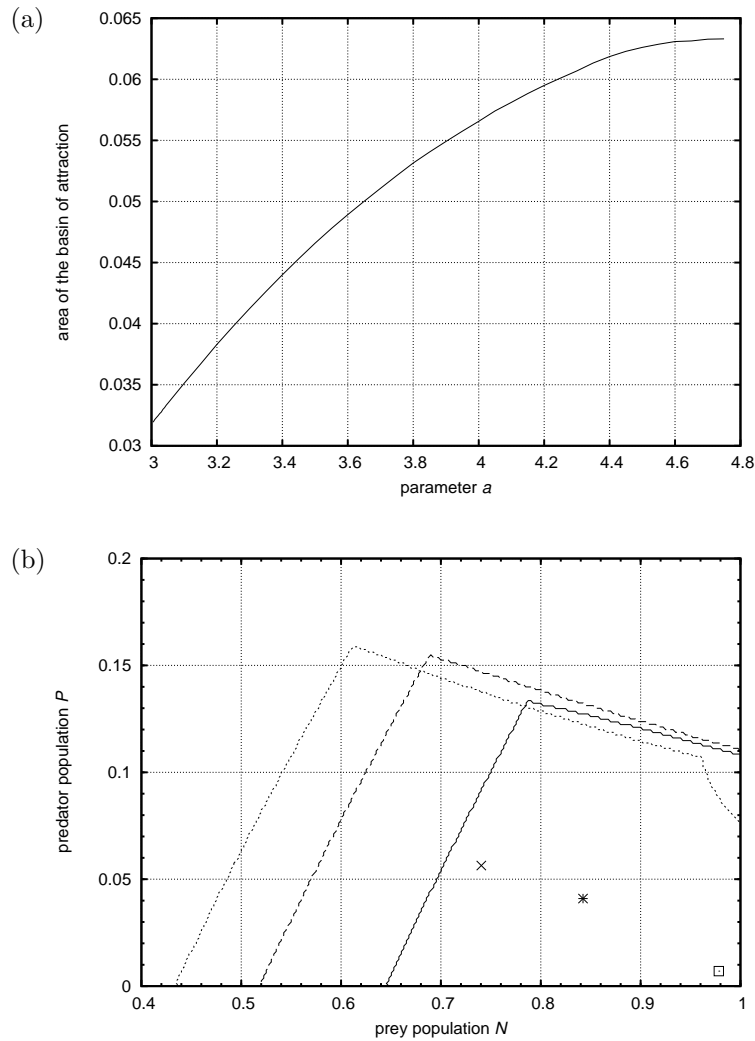


Figure 17. Basin of attraction in predator-prey model: (a) area of the basin of attraction in the (N, P) space as a function of the control parameter a , other parameters as in the main text; (b) shapes of the basin of attraction and the corresponding attraction points for $a = 3.10$ (— and \square), $a = 3.85$ (---- and $*$) and $a = 4.60$ (..... and \times)

stability range, while $S^2(\lambda_1\lambda_2)$ increases near the transition to cyclic behaviour ($a \approx 4.7$) and drops to zero near the predator extinction ($a = 3.0$).

Fig. 21 shows the dependence between the ecological resilience measure (the area of the basin of attraction) and an engineering resilience measure (the characteristic return time). No correlation can be observed in case of this model; it can be related to the fact that the the basin of attraction does not vanish at the ends of the stability range, but changes its character instead.

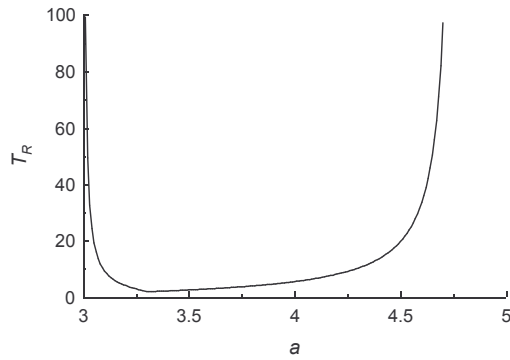


Figure 18. Characteristic return time T_R as a function of the parameter a in the predator–prey model

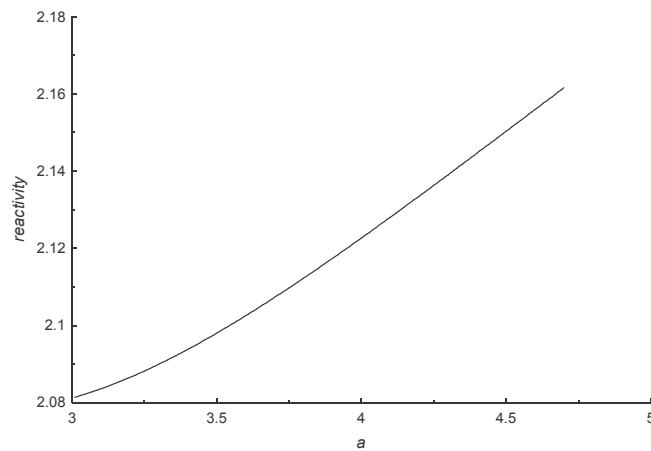


Figure 19. Reactivity as a function of the parameter a in the predator–prey model

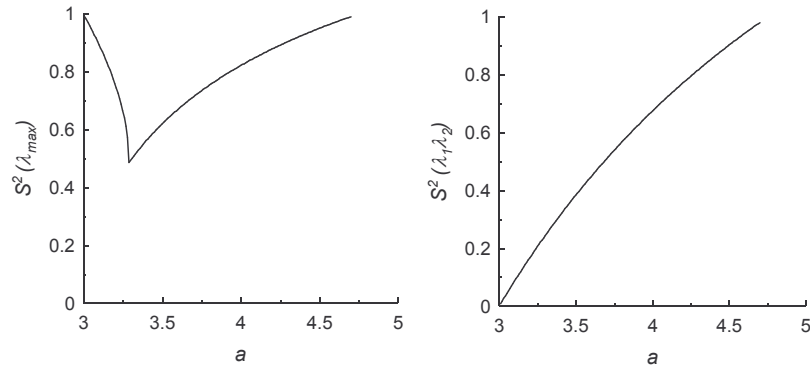


Figure 20. Variance as a function of the parameter a in the predator–prey model, calculated using the maximum eigenvalue (at the left) and both eigenvalues (at the right)

6. Summary

Growing interest in quantifying stability properties and persistence abilities of ecological and sociological systems gave rise to many attempts to measure these properties in both models and real systems. Recently, a concept of “resilience”, introduced by

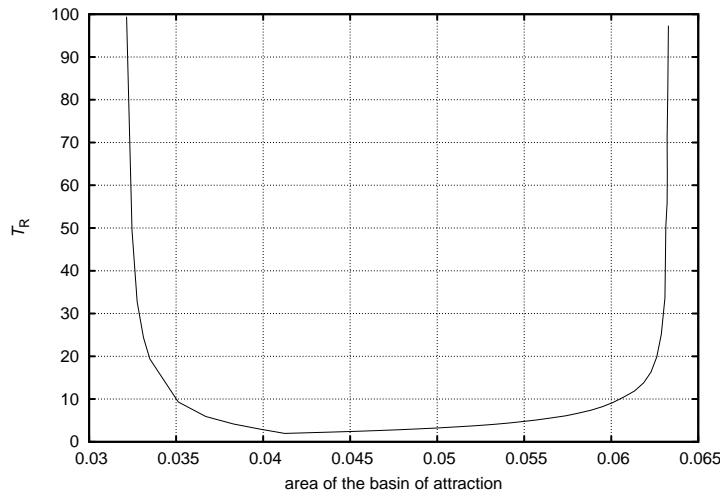


Figure 21. Characteristic return time T_R versus area of the basin of attraction in the predator–prey model

Holling [1], has been increasingly applied in various areas of research to describe numerous kinds of systems: ecological [65, 66, 67], sociological [68], economical [69], socio-ecological [70, 71, 72, 73], socio-economic [74], ecological-economic [75, 76, 77]; and even in urban sciences (planning) to describe properties of cities [78]. Since it has been used in so many contexts and defined in so many ways that the very meaning of “resilience” gets increasingly vague and unspecified [79], (according to Anderies et al. [80], resilience is better described as a collection of ideas about how to interpret complex systems. As a result attempts to add rigor have tried to define specific measures of this quantity: either in a strict mathematical way (for models and, at least in principle, for real systems) or as certain kinds of quantitative indicators (for real systems). We have reviewed a few of the most commonly used measures of resilience: measures in phase space and indicators for “ecological resilience”; return rate, time of return, reactivity, variance and mean time for first escape for “engineering resilience”. Applicability of all these measures depends on the kind of the system: none of them is universal in convenience and its capacity to inform. Our short review does not claim to exhaust all existing propositions of measuring resilience. The literature on this subject is too extensive to be summarized in a short study. Also, the work on this field is still in progress (see, for example, Section 4.6).

Here we have examined only some measures, applicability of which is well established, which are widely used and are relatively universal with reference to different models and systems.

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