



Detecting dynamic system regime boundaries with Fisher information: the case of ecosystems

Eva König¹ · Heriberto Cabezas² · Audrey L. Mayer³

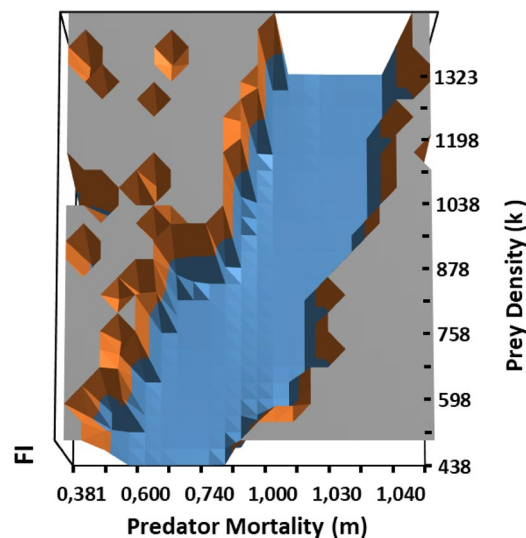
Received: 27 January 2019 / Accepted: 7 June 2019 / Published online: 13 June 2019
© The Author(s) 2019

Abstract

The direct measurement of the resilience (resistance to disturbances) of an ecosystem's current regime (or “alternative stable state”) remains a key concern for managing human impacts on these ecosystems and their risk of collapse. Approaches which utilize statistics or information theory have demonstrated utility in identifying regime boundaries. Here, we use Fisher information to establish the limits of the resilience of a dynamic regime of a predator–prey system. This is important because previous studies using Fisher information focused on detecting whether a regime change has occurred, whereas here we are interested in determining how much an ecological system can vary its properties without a regime change occurring. We illustrate the theory with simple two species systems. We apply it first to a predator–prey model and then to a 60-year wolf–moose population dataset from Isle Royale National Park in Michigan, USA. We assess the resilience boundaries and the operating range of a system's parameters without a regime change from entirely new criteria for Fisher information, oriented toward regime stability. The approach allows us to use system measurements to determine the shape and depth of the “cup” as defined by the broader resilience concept.

Graphic abstract

The direct measurement of the resilience (resistance to disturbances) of an ecosystem's current regime remains a key concern for managing human impacts on these ecosystems and their risk of collapse. Here, we use Fisher information to establish the limits of stability of a dynamic regime of a predator–prey system. The region of stability is represented by the “floor of the canyon” in the adjacent graphic. While the theory is illustrated with an ecosystem example, it is applicable in its present form to dynamic systems in general.



Keywords Fisher information · Ecosystems · Dynamic regime · Resilience · Isle Royale · Wolf · Moose · Regime threshold

Introduction

Ecosystems are dynamic and constantly interact with a range of external and internal drivers including species extinction, climate change, human activity, and other causes (Valiente-Banuet and Verdú 2013; Suding et al. 2015; Seddon et al. 2016). The resilience of an ecosystem, as defined by the system's ability to remain within a particular regime in the presence of disturbances, determines how and to what magnitude ecosystems will change in response to these drivers (Holling 1973; Grimm and Wissel 1997; Carpenter et al. 2001; Dai et al. 2015; Gao et al. 2016). To measure the vulnerability of systems to regime-changing disturbances, it is essential to understand the mechanisms of ecological resilience to natural and anthropogenic disturbances (Veraart et al. 2012; MacDougall et al. 2013; Suding and Hobbs 2014; Suding et al. 2015; Levine et al. 2016). This knowledge then contributes to effective environmental policy, identifying pressure points in the system which can be influenced through policies which reduce stressors (such as pollutants, invasive species or diseases, or land use change) or boost stabilizing factors (such as increasing native species populations).

Regime change, or the movement of a system from one regime (or alternative stable state) to another, can be triggered by exogenous disturbances (such as fire or the introduction of disease), or internal causes (e.g., loss of species, increased mortality, etc.; Spanbauer et al. 2014). The likelihood of regime change is determined by the system's resilience to that disturbance and, in other words, its ability to maintain itself in that regime through internal feedbacks and interactions (Scheffer and Carpenter 2003; Folke et al. 2004). Note that in this paper, we will only be focused on one regime as our measure of resilience, and not multiple regimes or the recovery of a system to a previous regime after disturbance [where recovery time is an alternative measure of resilience; see Grimm and Wissel (1997)]. The identification of the location of regime boundaries, also known as thresholds or tipping points, is of critical importance as early warning systems for the management and sustainability of coupled human–environment systems (Guttall and Jayaprakash 2009; Scheffer et al. 2009; Scheffer 2010; Horan et al. 2011; Spanbauer et al. 2014; Suding and Hobbs 2014).

Holling (1973) adopted a quantitative view of the behavior of ecological systems (Carpenter et al. 2001). Perspectives on ecosystem resilience have been expanded and refined since Holling (1973) to explicitly consider nonlinear dynamics, boundaries, uncertainty and unpredictability, and how such dynamics interact across different time and

spatial scales (Carpenter et al. 2001; Folke 2006; Brand and Jax 2007; Scheffer 2010; Veraart et al. 2012; Scheffer et al. 2015). Generally, resilience may be estimated by computing the eigenvalues of the system at its equilibrium (Lade and Niiranen 2017), but this approach does not provide any information about the behavior of a system right before the patterns decay.

Neubert and Caswell (1997) investigated several measures of a transient response, such as the maximal possible growth rate that directly follows the perturbation, the biggest proportional deviation that can be generated by any perturbations, and the time at which the amplification occurs. Scheffer et al. (2015) presented methods based on the critical slowing-down phenomena, which implies that recovery from small perturbations becomes slower as a system approaches a regime threshold. They also characterized the resilience of alternative regimes in probabilistic terms, measuring critical slowing down by using generic indicators related to the fundamental properties of a dynamic system (Scheffer et al. 2015). Levine et al. (2016) reported contradictory predictions in the sensitivity and ecological resilience of Amazon forests to changes in climate, sometimes resulting in biomass stability, other times in catastrophic biomass loss; transitions between regimes was continuous (no thresholds observed). Other drivers, including fire disturbances, grazing, logging, or other anthropogenic activities, are also capable of amplifying these climate change-driven transitions between forests and savanna globally (Mayer and Henareh Khalyani 2011). The identification of these ecosystem transitions depends upon the availability of long-term data, which is expensive and resource intensive.

Information theory has been applied to assess the sustainability of dynamic systems (Eason and Cabezas 2012), mainly to detect transitions from one dynamic regime to another (Mayer et al. 2006; Karunanithi et al. 2008; Spanbauer et al. 2014; Eason et al. 2016; Sundstrom et al. 2017; Vance et al. 2017). The “ball and cup” mental model has been central to this work (Gunderson 2000). As a common analogy for dynamic regimes, a system (the ball) moves within a cup—a specific regime. The ability of the ball to remain in that same cup (or basin of attraction) is the resilience of the system (Grimm and Wissel 1997). To functionally relate resilience to regimes and regime change, we must determine (1) how large the cup is (regime resilience) and (2) whether the system is in the cup or outside of it (regime shift). In this paper, we apply Fisher information to identify the boundaries of the regime (the size and depth of the cup) relative to the position of the ecological system (the ball) from actual values of system variables. This is important because it moves the state of the science beyond discussing

symbolic cups meant to represent basins of attraction to working with the actual basin of attraction for the system. Unlike in prior studies (e.g., Sundstrom et al. 2017), where boundaries were identified post-regime shift, we identify regime boundaries before the system has a regime change. Knowing the size and shape of the basin of attraction makes it possible to take remedial action, to keep the system away from the regime boundaries before a shift has occurred. (Or, conversely in a restoration attempt, how far a system will need to be pushed in order to flip it into a more desirable regime). We illustrate the concept with a simple modeled system and with a two-species predator–prey system (the wolves and moose of Isle Royale National Park, Michigan, USA). We further show that Fisher information can determine the range of predator–prey abundance over which the ecosystem remains in one regime and hence exhibits resilience.

Fisher information theory

The concept now known as Fisher information was first introduced by the statistician Ronald Fisher (1922) in the context of fitting a parameter to data. Starting from the seminal work of Fisher, an expression for computing the Fisher information (Mayer et al. 2007) from time series has been developed with the form of,

$$I = \int \frac{1}{p(s)} \left[\frac{dp(s)}{ds} \right]^2 ds \tag{1}$$

where $p(s)$ is now the simple probability density for observing particular values of s and $dp(s)/ds$ is the slope of $p(s)$.

Fisher information is also closely related to the concept of order in dynamic systems. A very ordered dynamic system is one where repeated observations of the system yield about the same result. In the case of a system with one observable variable s , this means that repeated measurements of s give about the same value. In that case, $p(s)$ is very narrow and sharp around the mean value of s , and the slope $dp(s)/ds$ is a high number. Since the Fisher information is proportional to $dp(s)/ds$ squared, the Fisher information has a correspondingly high value as well. In the extreme example of a system where the measurable variables are constant, the system is said to be perfectly orderly, $dp(s)/ds \rightarrow +\infty$, and the Fisher information is positive infinity. In the case of a very disorderly dynamic system with again one observable variable s , each measurement of s yields a more or less different value. Therefore, $p(s)$ is broad and relatively flat, and the slope $dp(s)/ds$ of $p(s)$ is near zero. Correspondingly, the Fisher information for a very disorderly dynamic system is near zero. In the extreme,

of a system completely lacking order, each measurement of s yields a different value. Then, $p(s)$ is flat, $dp(s)/ds$ is zero, and the Fisher information for this completely disorderly system is exactly zero. In summary, the Fisher information of an ordered system is high and that of a disordered system is low. One should also note that work of Al-Saffar and Kim (2017) explored the mathematical behavior of Fisher information under different perturbations and oscillatory regimes with possible implications for small populations of one species.

For systems that have more than one observable variable, the aforementioned arguments apply, except that s now represents an n -dimensional state of the system which depends on all of the observable variables of the system. Hence, a state of the system s for a dynamic system with n measurable variables x_1, x_2, \dots, x_n is defined by a particular value of each of the n variables. Even two states that differ by the value of only one variable are different states of the system. Note that this can lead to a very large number of states of the system, each one being unique.

To develop a practical and computable expression for Fisher information, consider that for a sequence of observations of s that have been taken over a time period, there is a one-to-one correspondence between observations and the time at which they were taken. Hence, $p(s)ds = p(t)dt$ where t is time, and $p(t)$ is the probability density for sampling at a particular time. Now, $T = \int dt$ is the total time over which the observations were made. For a cyclic system, T should generally be at least equal to one cycle, if it is desired to capture changes in system behavior. Since sampling at any time point is equally probable, $p(t) = 1/T$. Then, $p(s) = (1/T)/(ds/dt)$ where now ds/dt is the transit speed of the system in s space. Inserting these results into Eq. 1 gives the following expression for Fisher information after some manipulations,

$$I = \frac{1}{T} \int_t^{t+T} \frac{[R'']^2}{[R']^4} dt' \tag{2}$$

where $R' \equiv ds/dt$ is the speed and $R'' \equiv d^2s/dt^2$ is the acceleration. For the case where $s(x_1, x_2, \dots, x_n)$ depends on n measurable variables, R' and R'' can be calculated from the Euclidean metric in a linear space where the coordinates are again time and the measurable variables x_1, x_2, \dots, x_n . We call this linear space the system phase space. Then, R' can be calculated from,

$$R' \equiv \frac{ds}{dt} = \sqrt{\sum_{i=1}^n \left[\frac{dx_i}{dt} \right]^2} \tag{3}$$

and R'' can be calculated from,

$$R'' \equiv \frac{d}{dt} \left[\frac{ds}{dt} \right] = \frac{1}{R'} \sum_{i=1}^n \frac{dx_i}{dt} \frac{d^2x_i}{dt^2} \quad (4)$$

where R' and R'' are the speed and acceleration tangential to the path of the system in its phase space.

The expressions in Eqs. 2, 3, and 4 are the practical expressions that will be used to compute Fisher information. If a differential equation model is available as in the case of the prey–predator system used in this work, the derivatives dx_i/dt and d^2x_i/dt^2 can be computed from the model equations directly. In cases where a differential equation model is not available, the derivatives can be approximated with finite difference methods (see Hamming 1973). There are also many cases including this study where computing the integral in Eq. 2 is not possible analytically, and a numerical approximation is necessary. For such cases, the Fisher information can be approximated from

$$I = \frac{1}{T} \sum_i^{t+T} \frac{[R'']^2}{[R']^4} \Delta t. \quad (5)$$

Resilience from Fisher Information

The resilience of an ecological system has been defined by Holling (1973) as the ability of the system to continue functioning within the same dynamic regime despite externally inflicted perturbations. Within the same regime, the system can be very resilient to some kinds of disturbances over a long period of time, and not at all resilient to others. The resilience of an ecological system in a regime can change over time, such as with the loss of species or gradually changing external conditions, at the same time that stability can appear constant. (The system does not change regimes.) Regime shift occurs when one or more thresholds have been reached (e.g., a catastrophic disturbance, or the loss of too many species). In previous research, Fisher information has been used retroactively, to identify regime thresholds after regime shifts have occurred (Mayer et al. 2006; Sundstrom et al. 2017; Vance et al. 2017). Identifying regime thresholds without first observing a regime shift is a different problem.

Consider that it is possible to compute Fisher information for an ecosystem as a function of any of its characteristic parameters (species mortality, growth rate, etc.). A perturbation or perturbations can be represented as changes in the characteristic parameters—note that the characteristic parameters of an ecosystem can change for other reasons as well. However, the Fisher information would be relatively low within the range of parameter values consistent with the existence of a functioning ecosystem since the system is dynamic, and the Fisher information would have a relatively high value for the range of parameter values leading to a

non-functional or static and dead system. A Fisher information calculation, however, is an observational process. It provides information about the system dynamic regimes and the changes in those regimes. It can provide hints at what changes in the system parameters may be driving the changes, but its primary purpose is not to determine cause and effect. That requires either an explicit mathematical model of the system such as the prey–predator model, or an implicit model such as the observations for the moose–wolf population data for Isle Royale, both of which are discussed later.

In the specific case of one system parameter being perturbed, a two-dimensional plot of Fisher information versus the parameter values would appear as a “cup” with steep walls. The systems with parameter values at the bottom of the “cup” are dynamic and functioning, and those on the steep wall have very low resilience as they can “flip” into a different regime. If two parameters are being simultaneously perturbed, a three-dimensional plot of Fisher information versus the two parameters would generally appear as a “canyon” with steep walls, and again the systems with parameter values at the bottom of the “canyon” are dynamic and functioning systems and those on the steep walls have low resilience. In the transition where the system is not functioning well and has lost resilience, the observable variables of the system would fluctuate beyond the values normally seen in a healthy functioning ecosystem. This means that the measurable values of the system variables would fluctuate more widely about their mean leading to a broadening and flattening of $p(t)$, and a Fisher information lower than that of a resilient and orderly system and much lower than that of a system with very low resilience. Hence, if we were to continuously compute the Fisher information as a system transitions from resilient to less so, we would see a nonzero value for the Fisher information of the resilient system, a much lower value for the system in transition, and a high value after the ecosystem has shifted out of the regime and into a new one. This is important, because we can “see” the system moving toward a new regime before it has done so. Such a detailed calculation requires either a model capable of representing the transition or finely grained data capturing the transition. However, consistent with the *Sustainable Regimes Hypothesis* of Fath et al. (2003), we can state the following criteria:

$$\langle I \rangle|_h > 0 \quad \text{and} \quad \left. \frac{d\langle I \rangle}{dt} \right|_h \cong 0 \quad (6a)$$

$$\langle I \rangle|_t \ll I|_h \quad \text{and} \quad \left. \frac{d\langle I \rangle}{dt} \right|_f \neq 0 \quad (6b)$$

$$\langle I \rangle|_d \gg I|_h \quad \text{and} \quad \left. \frac{d\langle I \rangle}{dt} \right|_d = 0 \quad (6c)$$

where the average Fisher information $\langle I \rangle$ over some time interval t is defined by $\langle I \rangle \equiv \frac{1}{T} \int_0^T I(t) dt$, and the subscripts h, f , and d refer to ecosystems that are healthy, in flux or transition, and totally dysfunctional, respectively. It is important to note that the prey–predator model system that is described later is unable to represent the transition since it is too simple of a model, and because the Heaviside step function applied to the model system eliminates the stage where the system goes from living to dead.

The aforementioned conjectures can be summarized mathematically by proposing the hypothesis that the averaged Fisher information of a stable system does not significantly change with changes in the value of the system parameters under a perturbation. For the specific case of a system with one parameter (α), for example, the mortality rate of a species, a perturbation can be expressed by:

$$\frac{d\langle I \rangle}{d\alpha} \cong 0 \tag{7}$$

For the case of two system parameters (α and β) perturbed, for example, the mortality rate and the growth rate, the expression can be generalized to:

$$\left. \frac{\partial \langle I \rangle}{\partial \alpha} \right|_{\beta} \cong 0 \tag{8a}$$

$$\left. \frac{\partial \langle I \rangle}{\partial \beta} \right|_{\alpha} \cong 0 \tag{8b}$$

Finally, for the general case of an arbitrary number (n) of ecosystem parameters (α_i) under perturbation, the corresponding expression is:

$$\left. \frac{\partial \langle I \rangle}{\partial \alpha_i} \right|_{\alpha_{j \neq i}} \cong 0 \quad i = 1, 2, \dots, n \tag{9}$$

where I is now the average Fisher information defined for the one perturbed parameter case of Eq. 7 by $\langle I \rangle \equiv \int [I(\alpha) d\alpha] / \int d\alpha$, for the two parameter case of Eqs. 8 by $\langle I \rangle \equiv [\int \int I(\alpha, \beta) d\alpha d\beta] / \int \int d\alpha d\beta$, and for the general case of Eq. 9 by $\langle I \rangle \equiv [\int \int \dots \int I(\alpha_1 \alpha_2 \dots \alpha_n) d\alpha_1 d\alpha_2 \dots d\alpha_n] / \int \int \dots \int d\alpha_1 d\alpha_2 \dots d\alpha_n$.

The image for the behavior of Fisher information as a function of three or more model parameters would lie in a four- or higher-dimensional space. This is unfortunately outside the range of human perception. But the mathematical approach is still valid. The algorithm that one would pursue in investigating such a system would be similar to the one used here for one and two parameter systems. Hence, we could start by varying parameter α_1 over the range of interest while holding all parameters $\alpha_{i \neq 1}$ constant at some predetermined value. One would then proceed to

varying α_2 while holding all parameters $\alpha_{i \neq 2}$ constant. At the end, we would have a set of Fisher information values that depend on the aforementioned n parameters, i.e., $I(\alpha_1, \alpha_2, \dots, \alpha_n)$. The process for identifying the parameter range over which the system is resilient would involve looking for regions where the Fisher information is flat in this n parameter space. These are ranges of parameter values where the Fisher information does not significantly vary as given in Eqs. 7, 8, and 9.

The result of these conjectures emanating from Fisher information considerations is that of providing the mathematical machinery that is necessary to estimate how much the system parameters can vary, without inducing a change in the dynamic regime of the system. One would then argue that the wider the range of parameter variation that can be tolerated without a regime change, the more resilient the system.

Predator–prey model system

Our simple ecological system model is a predator–prey model adopted from the work of Fath et al. (2003). The initial parameter values are also those used by Fath et al. (2003). The population is naturally fluctuating in time, and the populations are depending on one another as well as on other parameters, like the mortality rate or reproduction rate of the predator and the growth or density rate of the prey. The system is defined by a Lotka–Volterra-type mathematical model. The model variables and parameters are as follows:

- y_1 Population mass of the prey [mass]
- y_2 Population mass of the predator [mass]
- g_1 Growth rate of prey [1/time]
- l_{12} Loss rate to prey due to predator feeding [1/time]
- g_{21} Feeding rate of predator [1/time]
- m_2 Mortality rate of predator [1/time]
- k Density dependence of prey [mass]
- β Reproduction rate of predator [mass/mass]

Definition of the population fluctuation:

$$\frac{dy_1}{dt} = g_1 \left(1 - \frac{y_1}{k} \right) y_1 - \frac{l_{12} y_1 y_2}{1 + \beta y_1} \tag{10a}$$

$$\frac{dy_2}{dt} = \frac{g_{21} y_1 y_2}{1 + \beta y_1} - m_2 y_2 \tag{10b}$$

Since this pure mathematical model is able to increase the population even from an infinitesimally small population number, which is biologically impossible, it is necessary to force the model to set the population exactly to zero after it reaches a lower limit where the system is biologically not sustainable. Hence, we set the values of y_1 and y_2 to zero

when they became 1 or less. This is reflected in Eq. 11 where a Heaviside step function is applied to both y_1 and y_2 .

$$y_1 = \begin{cases} 0 & \text{if } (y_1 - 1) < 0 \\ y_1 & \text{if } (y_1 - 1) \geq 0 \end{cases} \quad (11a)$$

$$y_2 = \begin{cases} 0 & \text{if } (y_2 - 1) < 0 \\ y_2 & \text{if } (y_2 - 1) \geq 0 \end{cases} \quad (11b)$$

By solving Eq. 10 with the logic statement from Eq. 11, we get the values for y_1 and y_2 in each time step. Replacing the values of the population into the Eq. (10), we get the values for dy_1/dt and dy_2/dt also in each time step. In order to be able to calculate the Fisher information, we also need the values of d^2y_1/dt^2 and d^2y_2/dt^2 . Therefore, we need to express the second time derivative of Eq. (10).

$$\frac{d^2y_1}{dt^2} = g_1 \frac{dy_1}{dt} - 2 \frac{g_1}{k} y_1 \frac{dy_1}{dt} - \left(\frac{1}{1 + \beta H(y_1 - 1) y_1} \right) \left[l_{12} y_2 \frac{dy_1}{dt} - l_{12} y_1 \frac{dy_2}{dt} \right] + l_{12} y_1 y_2 \left(\frac{1}{1 + \beta y_1} \right)^2 \beta \frac{dy_1}{dt} \quad (12a)$$

$$\frac{d^2y_2}{dt^2} = g_{21} y_2 \frac{dy_1}{dt} \left(\frac{1}{1 + \beta y_1} \right) + g_{21} y_1 \frac{dy_2}{dt} \left(\frac{1}{1 + \beta y_1} \right) - g_{21} y_1 y_2 \left(\frac{1}{1 + \beta y_1} \right)^2 \beta \frac{dy_1}{dt} - m_2 \frac{dy_2}{dt} \quad (12b)$$

In summary, for purposes of this study of a model prey–predator system, we compute the Fisher information from Eq. 5 setting $\Delta t = 1$ and using y_1 and y_2 computed as a function of time from Eqs. 10 and 12.

Results for a model prey–predator system

Based on the research of Fath et al. (2003), the default position of our calculation was a parameter set where the system has a stable limit cycle behavior for the populations of the prey and predator species (Fig. 1): $g_1 = 1$, $l_{12} = 0.01$, $g_{21} = 0.01$, $m_2 = 1$, $k = 625$ and $\beta = 0.005$. Equations 11a and 11b are implemented in MATLAB solved by the ODE15 solver for 300 time steps, with initial values 5 and 15 for y_1 and y_2 , respectively. Note that the initialization is not important, since the system populations become independent from the initial values as the system migrates to its steady-state regime. The resulting values of y_1 and y_2 were imported into the Excel spreadsheet software, and all further calculations, namely the values of the first and second derivatives as well as the numerical assumption of the Fisher information, were executed in Excel. The value of the Fisher information for this specific parameter set and model system in its steady-state regime is around 0.00,015. However, it is the relative values of Fisher information and the relative changes

in Fisher information values that are critical here, not the value itself.

The system depicted in Fig. 1 represents a typical ecological system which is alive and functioning with both species present and a finite and steady value of its Fisher information. If the value of the parameter k were changed enough—increased and decreased—the fluctuation of the populations eventually ceases because one of the species becomes extinct. If the parameter k reaches a lower border value of around 395, the predator (y_2) immediately dies out and the prey population grows to its upper limit (Fig. 2). If the parameter k is increased until it reaches its upper border of about $k \approx 1325$, the same phenomena are perceptible but delayed; that is, after a period of fluctuation, the predator dies out and the prey population grows to its upper limit

(Fig. 3). At both of the edges, the value of the Fisher information grows to a relatively high value (Fig. 4). The reason why Fisher information reaches a high value is that with $m_2 = 1$, the system becomes a static ecosystem (Fig. 2) when the value of k is above the upper limit ($k > 1325$) or below the lower limit ($k < 395$). As Fisher information is a measure of order, a static system has very high order and high Fisher information.

When the stable range of the parameter k had been defined, we started to vary the m_2 parameter (the mortality of the predator) in the middle of the stable k range when $k = 860$. It was found that the system is much more sensitive to variation in mortality; it has a stability range. The parameter m_2 can be varied between 0.38 and 1.045. If m_2 reaches its lower end and k is in the middle, the prey dies out earlier; therefore, the predator also dies out soon afterward (Fig. 5). These kinds of collapses occur where one of the species dies out on the edges, immediately or after one or two periods. Our study showed that order of the Fisher information is around 10^{-3} if the system has stable dynamics, and it grows suddenly when the system collapses as species populations start going to zero. Out of the stability range, the value of the Fisher information is over the order of 10^{15} (Figs. 6; 7). It is important to note that these system collapses define a different system (Mayer et al. 2006), one lacking at least one of the two species.

Fig. 1 The fluctuation of the model populations of prey (y_1) and predator (y_2) in time with default parameter values of $k = 625, m_2 = 1$

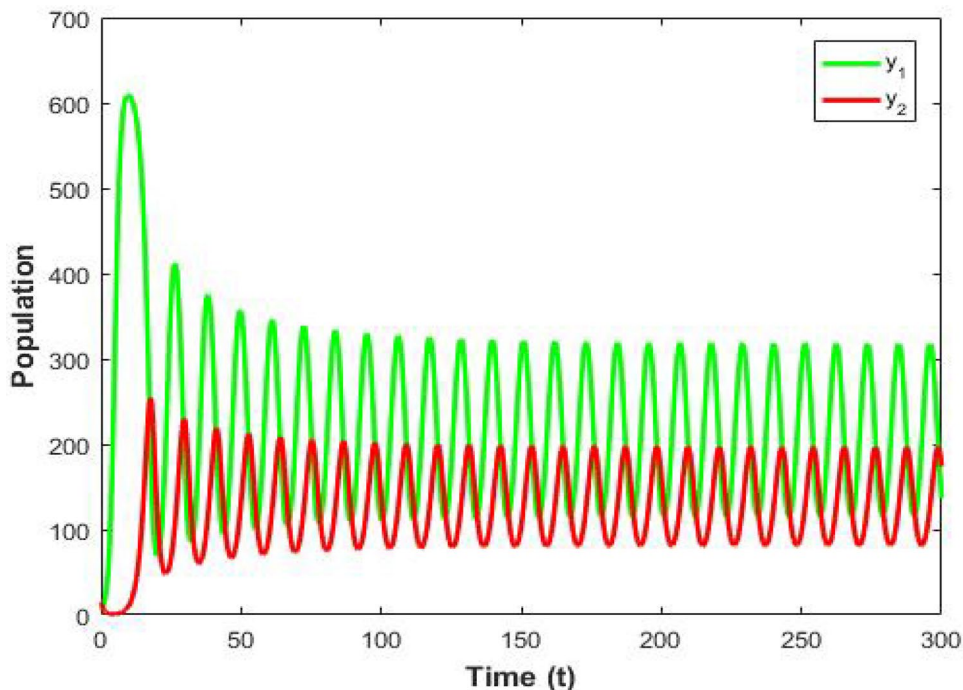
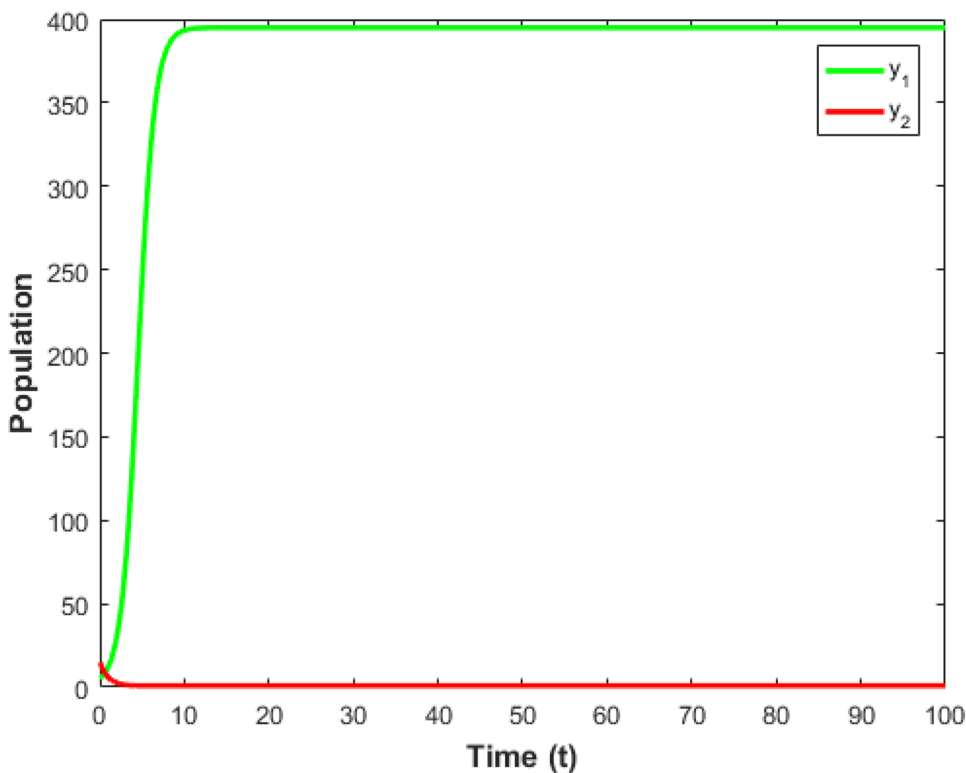


Fig. 2 The fluctuation of the populations ceases, the predator (y_2) immediately dies out, and the prey (y_1) stops growing when k it reaches its lower limit ($k = 395, m_2 = 1$)



Strange inverse peaks appear outside of the stability range that can be seen on the right side of Fig. 6 or on the left side of Fig. 7. (And another one appears on the other side of the canyon.) These peaks come from numerical problems with the calculation method. Since we have discrete time

steps and values of y_1 and y_2 in each time step, technically Eq. (3) becomes a sum instead of an integral. This is shown in Eq. (6), note that we set $\Delta t = 1$. The state of the system where these peaks appear is dysfunctional, namely the prey population dies out after a period. Therefore, the predator

Fig. 3 The fluctuation of the model populations of prey (y_1) and predator (y_2) in time with default parameter values at its upper limit of $k = 1325$, $m_2 = 1$

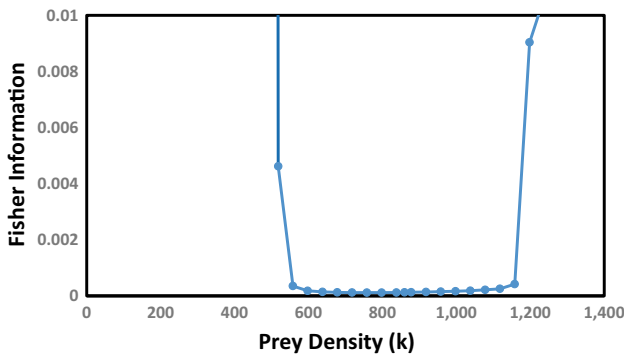
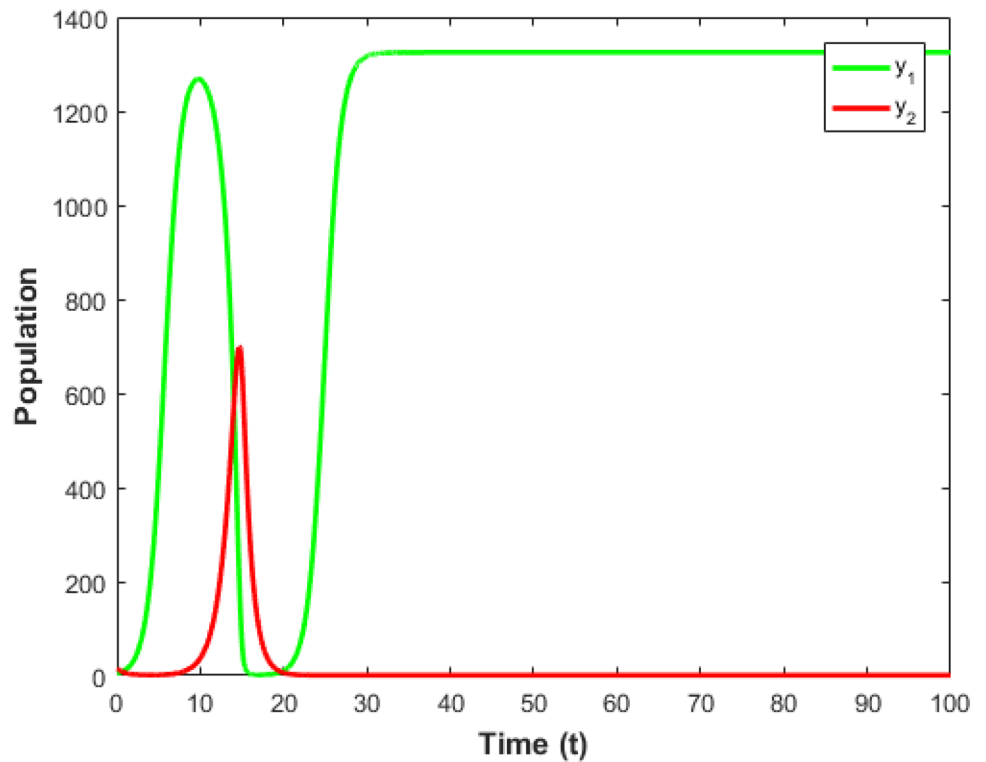


Fig. 4 Fisher information for a prey–predator model system where the prey density parameter (k) is varied, while the predator mortality (m) is held constant at $m=0.9996$. Note that the systems where $518 \leq k \leq 1158$ are functioning systems with two species and systems where $k < 518$ and $k > 1158$ are dysfunctional systems where at least one species has gone extinct. Note that the vertical scale has been truncated so that the more important details around $500 \leq k \leq 1300$ become easier to visualize

population dies out as well after this first period (see Fig. 8). Practically, in these cases R' becomes exactly zero, but in mathematics division by zero has no meaning. Therefore, while calculating the Fisher information, we can only consider those time steps where the division is valid, i.e., while the value of R' is over zero. In the specific case shown in Fig. 8, the division is valid until $t \approx 26$, and the system is functional between $t = 0$ and $t = 26$.

Results for a real prey–predator ecosystem

To study the application of the methodology, we include in our analysis the case of a real predator–prey system represented by the wolf–moose (*Canis lupis*, *Alces alces*) system from Isle Royale National Park in the USA. The data originate from a 60-year research project (1957 to present) of the dynamics of wolf and moose populations (and their impacts on the vegetation) on Isle Royale, a remote 540 km² island in Lake Superior (Vucetich and Peterson 2012; Mlot 2017). The population sizes of wolves and moose are surveyed each winter; the dataset includes the precise number of wolves and estimated number of moose. The system has been in the news in the past several years after the wolf population began an unsustainable decline in abundance; as of 2017, only one inbred pair of wolves lived on the island, and the moose population was increasing rapidly in the absence of sufficient predation (Mlot 2017).

We calculated the Fisher information using the one-tenth of the length of the 60 years (1957–2017) we have data for, i.e., a 6-year-long moving time window for this dataset that is plotted in Fig. 9. The wolf and moose population values (normalized so that both fit on the second y-axis) are also plotted in Fig. 9. All population values are dimensionless in Fig. 9; values are divided by the first value (in 1959) for each species to improve the readability of the graph.

A brief delay is perceptible in the Fisher information trend compared to the population trends, but as expected,

Fig. 5 The prey dies out after a half of a period; therefore, the predator also dies out afterward ($k = 860, m_2 = 0.38$)

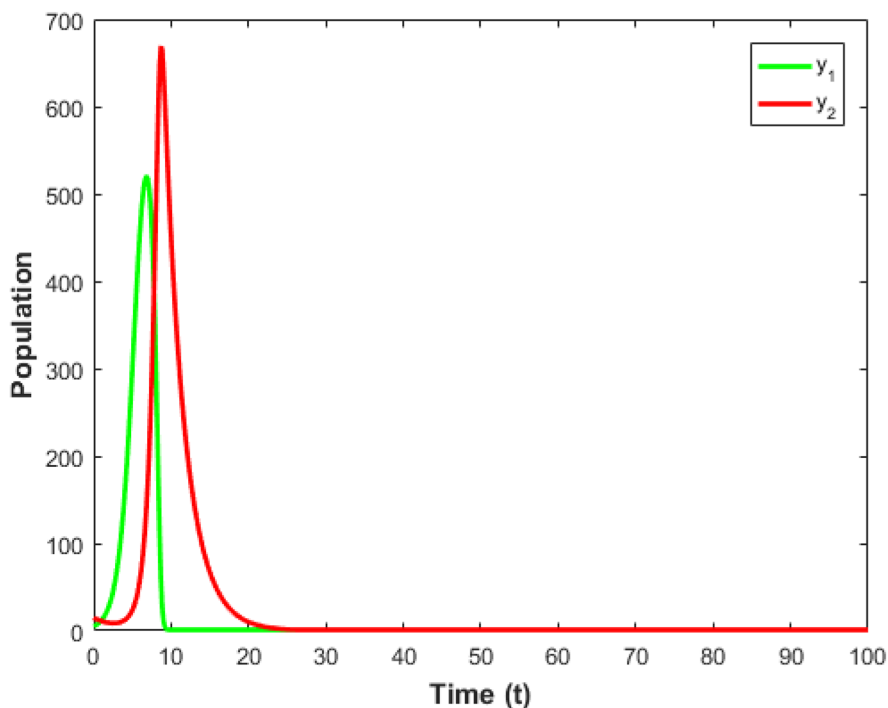
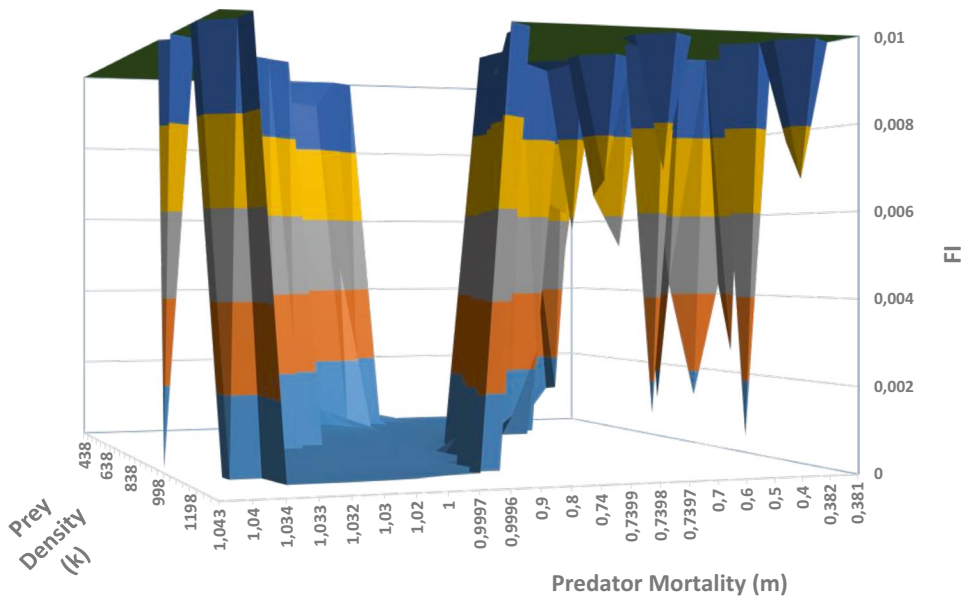


Fig. 6 The value of the Fisher information as a function of prey density (k) and predator mortality rate (m_2) from a side view. Note that a functioning ecosystem with two species present exists only for combined values of k and m_2 within the confines of the bottom of the “canyon.”



Fisher information is high when population fluctuations are low and drops when the fluctuations intensify. The Fisher information calculated here indicates that there is, perhaps, a functional state with relatively high dynamic order that persisted in the 1970s, where wolf populations were around 40 individuals and moose around 1000. However, this region may not be entirely resilient, as since that time this system has spent the bulk of its time in a low Fisher information region of less than 20 wolves and well over 1000 moose. The sharp decline of wolves in 1981 (echoed in a decline in

Fisher information) was due to the accidental introduction of canine parvovirus to the island (Wilmers et al. 2006). It is notable that Fisher information indicated (via a slight increase) a brief period between 2000 and 2007 when the wolf and moose populations appeared to be more stable (but were not, according to Fisher Information). In this period, the populations roughly echoed the numbers seen in the stable era of the 1970s.

However, this resilience degraded as the wolf population entered a sharp decline after 2009. Fisher information’s

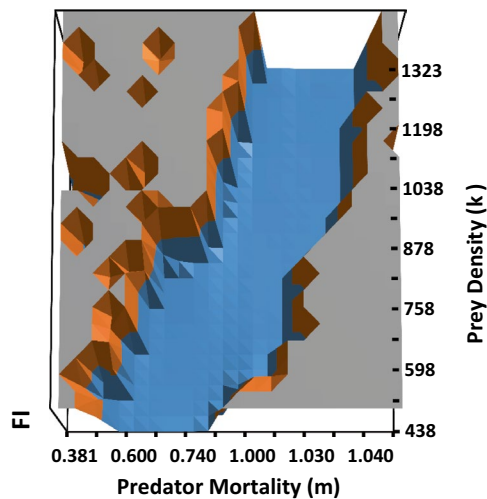
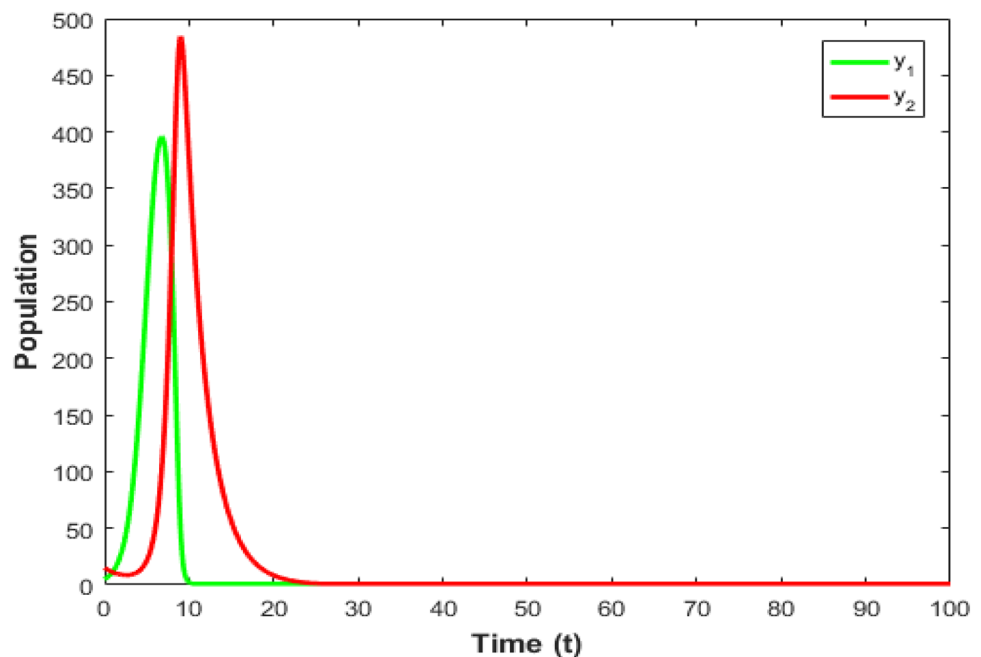


Fig. 7 The value of the Fisher information as a function of prey density (k) and predator mortality rate (m_2) from a top down view. Again note that a functioning ecosystem with two species present exists only for combined values of k and m_2 within the confines of the bottom of the “canyon”

behavior for this real-world system is consistent with the behavior observed for the model system, although the impact of the noise in a real-world system on the clarity of Fisher information behavior is easy to see. This is to be expected with real data from real systems. However, broadly speaking, Fisher information indicates that some event (internal or external) occurred in the early 1980s, despite the appearance of some stability in population numbers in the early 2000s,

Fig. 8 The prey dies out after a half of a period; therefore, the predator also dies out afterward ($k = 598, m_2 = 0.381$)



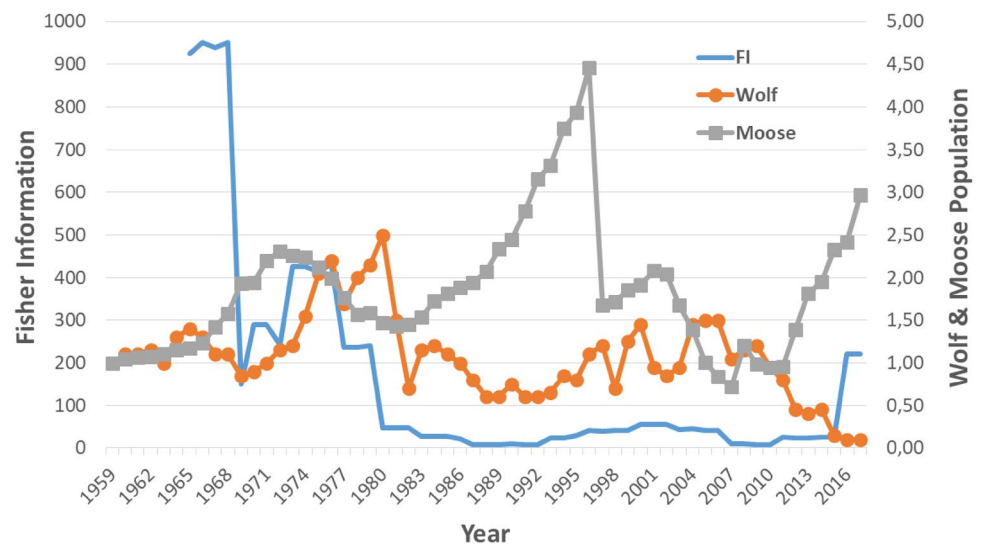
which set this system on a less resilient pathway from which it has not yet recovered.

Discussion

The previous work related to system regimes and Fisher information focused mostly on regime changes when a system shifts from one regime into another. The goal of this research was to develop a method to calculate where a resilient system has its borders and to identify the ranges of the interacting parameters where the system persists in one regime independently of the perturbations. By the criterion formulated as Eq. 7, it is possible to decide whether a dynamic system is in a healthy, dynamically changing state, in a dysfunctional and therefore static state, or in transition from a healthy state into a dysfunctional one. The criterion, defined by Eqs. 8, 9, and 10, tells where a system is resilient when there is only one, two, or more varying system parameters, respectively.

Fisher information theory is well known and applied in several scientific fields, but it has not been utilized for measuring system resilience directly. The method described in this paper provides a technique to measure the resilience of a dynamic system by checking the criteria defined in Eqs. 7, 8, 9, and 10. As with previous iterations of Fisher information, it remains highly sensitive to the quality of the data (Mayer et al. 2006); accordingly, users must assure that the variables selected are relevant to characterizing changes in the system's condition; otherwise, the Fisher information results are uninformative. In the wolf–moose example, other variables

Fig. 9 The trend of Fisher information in a 6-year-long moving time window together with the normalized population of wolf and moose in Isle Royale National Park



such as winter ice cover of Lake Superior and seasonal temperature and precipitation may be important to include in future iterations of calculating the Fisher information of the system. However, even with only the two species data, Fisher information may provide valuable information to the management of the resilience of the wolf–moose system on Isle Royale National Park. For example, in 2016–2017 the National Park Service debated which of several management options it should pursue to stabilize the wolf and moose populations, such as doing nothing (waiting to see if wolves return via an ice bridge over Lake Superior), or reintroducing several wolf packs from Canada over a period of 3 years (81 Federal Register 91192 2016; Mech et al. 2017). In 2018, the National Park Service decided to go ahead with a slow introduction of very small numbers of wolves each year, releasing the first four in October 2018 (Mlot 2018). With better refinement, Fisher information could help park managers and wildlife biologists determine whether this management option is having the desired effect (increasing the resilience of the wolf and moose populations). For example, Fisher information suggests that the island system with parvo present may not allow for a resilient wolf–moose regime, and a policy prescription of parvo vaccinations for all wolves may be warranted.

While the theory has been illustrated via the prey–predator model system and the wolf–moose population data, it can be applied in its present form to larger, more complicated systems. It should also be noted that the theory in its present form is applicable to any dynamic system as long as model differential equations or time-series data are available for the system variables. The system can be biological, social, economic, or technological. This means that it is possible to generally assess the resilience of a system by assessing the impact of changes in system parameters on the value of Fisher information. It is easy to represent the

line or the surface of Fisher information as a function of two varying parameters (as shown in Fig. 4 or Figs. 6, 7). By three or more varying parameters, the plot becomes four or higher dimensional, which is more difficult to visualize but the method is still valid. Further work will need to develop methods to interpret Fisher information accurately in these higher dimensions, particularly when recommending specific policy interventions.

Conclusions

The Fisher information of any system is a fundamental and computable property that is a measure of order. When applied to ecological systems, we find that living functioning systems have relatively low but steady Fisher information, while dysfunctional ecosystems can have either very high or very low Fisher information, depending upon the variability in the system parameters. Fisher information is very sensitive to the dynamic behavior of complex systems which makes it a good indicator of regime shift. Here, we use it to measure the range of system parameter values over which a system remains within the same regime; larger range indicates higher resilience. Resilience defined and measured in this manner can be accomplished irrespective of the specific perturbation affecting the ecosystem; we measure change without having information on the perturbation causing it. While it would be optimal to know which disturbance is responsible for observed resilience loss, this information is not always available. This form of resilience is, therefore, a measure of robustness or ruggedness in the face of often unpredictable perturbations. While much work remains to understand its strengths and limitations, the index shows promise as a way to characterize an important aspect of

resilience in ecological systems and other dynamic systems generally.

Acknowledgements Open access funding provided by Pázmány Péter Catholic University (PPKE). The authors would like to thank John Vucetich for the Isle Royale wolf/moose population data and three anonymous reviewers for the constructive comments.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

- Al-Saffar A, Kim E-J (2017) Sustainable theory of a logistic model - Fisher information approach. *Math Biosci* 285:81–91
- Brand FS, Jax K (2007) Focusing the meaning(s) of resilience: resilience as a descriptive concept and a boundary object. *Ecol Soc* 12(1): 23. <http://www.ecologyandsociety.org/vol12/iss1/art23/>
- Carpenter S, Walker B, Anderies JM, Abel N (2001) From metaphor to measurement: resilience of what to what? *Ecosystems* 4(8):765–781
- Dai L, Korolev KS, Gore J (2015) Relation between stability and resilience determines the performance of early warning signals under different environmental drivers. *Proc Natl Acad Sci USA* 112(32):10056–10061
- Eason T, Cabezas H (2012) Evaluating the sustainability of a regional system using Fisher information in the San Luis Basin, Colorado. *J Environ Manag* 94(1):41–49
- Eason T, Garmestani AS, Stow CA, Rojo C, Alvarez-Cobelas M, Cabezas H (2016) Managing for resilience: an information theory-based approach to assessing ecosystems. *J Appl Ecol* 53(3):656–665
- Fath BD, Cabezas H, Pawlowski CW (2003) Regime changes in ecological systems: an information theory approach. *J Theor Biol* 222(4):517–530
- Fisher RA (1922) On the mathematical foundations of theoretical statistics. In: *Philosophical transactions of the Royal Society of London. Series A, containing papers of a mathematical or physical character*, vol 222, pp 309–368. www.jstor.org/stable/91208. Accessed 21 Mar 2017
- Folke C (2006) Resilience: the emergence of a perspective for social-ecological systems analyses. *Glob Environ Change* 16(3):253–267
- Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Evol Syst* 35:557–581
- Gao J, Barzel B, Barabási A-L (2016) Universal resilience patterns in complex networks. *Nature* 530:307–312
- Grimm V, Wissel C (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323–334
- Gunderson LH (2000) Ecological resilience: in theory and application. *Annu Rev Ecol Syst* 31:425–439
- Guttal V, Jayaprakash J (2009) Spatial variance and spatial skewness: leading indicators of regime shifts in spatial ecological systems. *Theor Ecol* 2:3–12
- Hamming RW (1973) *Numerical methods for scientists and engineers*. Dover, New York
- Holling CS (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4(1):1–23
- Horan RD, Fenichel EP, Drury KLS, Lodge DM (2011) Managing ecological thresholds in coupled environmental-human systems. *Proc Natl Acad Sci USA* 108(18):7333–7338
- Karunanithi A, Cabezas H, Frieden BR, Pawlowski C (2008) Detection and assessment of ecosystem regime shifts from Fisher information. *Ecol Soc* 13(1): 22. <http://www.ecologyandsociety.org/vol13/iss1/art22/>
- Lade SJ, Niiranen S (2017) Generalized modeling of empirical socio-ecological systems. *Nat Resour Model* 30(3):e12129. <https://doi.org/10.1111/nrm.12129>
- Levine NM, Zhang K, Longo M, Baccini A, Phillips OL, Lewis SL, Feldpausch TR (2016) Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proc Natl Acad Sci* 113(3):793–797
- MacDougall AS, McCann KS, Gellner G, Turkington R (2013) Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* 494:86–90
- Mayer AL, Henareh Khalyani A (2011) Grass trumps trees with fire. *Science* 334(6053):188–189
- Mayer AL, Pawlowski CW, Cabezas H (2006) Fisher information and dynamic regime changes in ecological systems. *Ecol Model* 195(1):72–82
- Mayer AL, Pawlowski CW, Fath BD, Cabezas H (2007) Applications of fisher information to the management of sustainable environmental systems. In: Frieden BR, Gatenby RA (eds) *Exploratory data analysis using fisher information*. Springer, London
- Mech LD, Barber-Meyer S, Blanco JC, Boitani L, Carbyn L, Delguidice G, Fritts SH, Huber D, Liberg O, Patterson B, Thiel RR (2017) An unparalleled opportunity for an important ecological study. *Bioscience* 67(10):875–876
- Mlot C (2017) Two wolves survive in world’s longest running predator-prey study. *Science*. <https://doi.org/10.1126/science.aal1061>, 18th April 2017
- Mlot C (2018) Classic wolf-moose study to be restarted on Isle Royale. *Science* 361(6409):1298–1299
- Neubert MG, Caswell H (1997) Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology* 78(3):653–665
- Scheffer M (2010) Foreseeing tipping points. *Nature* 467:411–412
- Scheffer M, Carpenter S (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol* 18(12):648–656
- Scheffer M, Bascompte M, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. *Nature* 461:53–59
- Scheffer M, Carpenter SR, Dakos V, van Nes EH (2015) Generic indicators of ecological resilience: inferring the chance of a critical transition. *Annu Rev Ecol Syst* 46:145–167
- Seddon AWR, Macais-Fauria M, Long PR, Benz D, Willis KJ (2016) Sensitivity of global terrestrial ecosystems to climate variability. *Nature* 531:229–232
- Spanbauer TL, Allen CR, Angeler DG, Easton T, Fritz SC, Garmestani AS, Nash KL, Stone JR (2014) Prolonged instability prior to a regime shift. *PLoS One* 9(10):e108936
- Suding K, Hobbs RJ (2014) Threshold models in restoration and conservation: a developing framework. *Trends Ecol Evol* 24(5):271–279
- Suding K, Higgs E, Palmer M, Callicott JB, Anderson CB, Baker M, Gutrich JJ, Hondula KL, LaFevor MC, Larson BMH, Randall A, Ruhl JB, Schwartz KZS (2015) Committing to ecological restoration. *Science* 348(6235):638–640
- Sundstrom SM, Eason R, Nelson RJ, Angeler DG, Barichievy C, Garmestani AS, Graham NA, Granholm D, Gunderson L, Knutson

- M, Nash KL (2017) Detecting spatial regimes in ecosystems. *Ecol Lett* 20(1):19–32
- Valiente-Banuet A, Verdú M (2013) Human impacts on multiple ecological networks act synergistically to drive ecosystem collapse. *Front Ecol Environ* 11(8):408–413
- Vance L, Eason T, Cabezas H, Gorman ME (2017) Toward a leading indicator of catastrophic shifts in complex systems: assessing changing conditions in nation states. *Heliyon* 3(12):e00465
- Veraart AJ, Faassen EJ, Dakos V, van Nes EH, Lürling M, Scheffer M (2012) Recovery rates reflect distance to a tipping point in a living system. *Nature* 481:357–359
- Vucetich JA, Peterson RO (2012) The population biology of Isle Royale wolves and moose: an overview. <http://www.isleroyalewolf.org/data/data/home.html>. Accessed 12 June 2019
- Wilmers CC, Post E, Peterson RO, Vucetich JA (2006) Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecol Lett* 9(4):383–389

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Affiliations

Eva König¹ · Heriberto Cabezas²  · Audrey L. Mayer³

✉ Audrey L. Mayer
almayer@mtu.edu

Eva König
konig@dcs.uni-pannon.hu

Heriberto Cabezas
cabezas.heriberto@ppke.hu

¹ Department of Computer Science and Systems Technology, University of Pannonia, Veszprem, Hungary

² Institute for Process Systems Engineering and Sustainability, Pazmany Peter Catholic University, Budapest, Hungary

³ School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI, USA