



Regime changes in ecological systems: an information theory approach

Brian D. Fath^a, Heriberto Cabezas^{b,*}, Christopher W. Pawlowski^{b,†}

^a *Biology Department, Towson University, Towson, MD 21252, USA*

^b *Sustainable Environments Branch, Sustainable Technology Division, National Risk Management Research Laboratory, US Environmental Protection Agency, 26 West Martin Luther King Drive, Cincinnati, OH 45268-0001, USA*

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Abstract

We present our efforts at developing an ecological system index using information theory. Specifically, we derive an expression for Fisher Information based on sampling of the system trajectory as it evolves in the space defined by the state variables of the system, i.e. its state space. The Fisher Information index, as we have derived it, is a measure of system order, and captures the characteristic variation in speed and acceleration along the system's periodic steady-state trajectories. When calculated repeatedly over the system period, this index tracks steady states and transient behavior. We believe that such an index could be useful in detecting system 'flips' associated with a regime change, i.e. determining when systems are in a transient between one steady state and another. We illustrate the concepts using model ecosystems.

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1. Introduction

Ecosystems are subject to periodic fluctuations from abiotic forcing (e.g. diurnal, lunar, seasonal, solar, etc.) to biotic interactions (e.g. predator–prey, synergistic, coevolutionary). Despite such forcing, ecosystems generally maintain a single regime of behavior for a certain length of time. A regime can be identified by a characteristic set of values for one or more state variables that describe the system, and a given dynamic behavior over this set. Periodic forcing will move the state variables within the characteristic bounds of the regime through a variety of mechanisms, but the system's dynamic response generally does not undergo a significant change. However, a system can, as a result of the differential and complementary contribution of intrinsic and extrinsic pressures, be pushed out of one regime of behavior into another. This involves a period

of transient behavior followed by the establishment of a new regime.

In consideration of the above, there has been much interest in identifying regimes and regime changes, and the mechanisms that cause a system to change regime. Ecosystem resilience as defined by [Holling \(1973\)](#) is one approach to quantifying the effect of disturbances on system dynamics (see for example [Walker et al., 1999](#); [Peterson et al., 1998](#); [Gunderson, 2000](#); [Carpenter et al., 2001](#)). Ecosystem resilience is a measure of the ability of an ecosystem to maintain function in the presence of disturbance and change. It is based on the dynamic systems concept of multiple equilibria or steady states, and is typically visualized as the 'size' of the associated basins of attraction, i.e. the size of the region in state space over which the system returns to its previous steady state. Another concept related to resilience is buffer capacity, which is the ecosystem's ability to reduce the direct influence of external perturbations ([Jørgensen, 1992](#)). When resilience is breached or buffer capacity is exceeded, behavior can significantly, abruptly, and in some cases catastrophically change as the system moves through the boundary from one basin of attraction to another. The potential impact of this

*Corresponding author. Tel.: +1-513-569-7350; fax: +1-513-569-7111.

E-mail address: cabezas.heriberto@epa.gov (H. Cabezas).

† Postdoctoral Research Fellow, Oak Ridge Institute for Science and Education.

concept is becoming more apparent as an increasing number of real systems have been found to have the potential to ‘flip’ between multiple stable dynamic regimes (Scheffer et al., 2001).

While most work has focused on understanding the factors or characteristics of ecosystems that contribute to resilience or buffer capacity, we are interested in developing means to detect directly when a system moves from one regime to another. Specifically, we are interested in developing an index that is sensitive to transient behavior in ecosystems in the hope of being able to distinguish ‘typical’ fluctuations from those that portend a fundamental change in dynamic regime. For this we use concepts from information theory and dynamic systems (Cabezas and Faith, 2002).

2. Information theory in ecology

Information theories have played a key role in our understanding biological systems, and it is not new to look at ecosystems themselves as information systems (Nielsen, 2000; Straškraba, 1995). For example, Brooks and Wiley (1986) and Wicken (1987) pointed out the importance of entropy, thermodynamics, and information in evolutionary processes. Although a debate among them ensues over the approach, they both view evolution as an information-based process. Ecosystem-level information has also been incorporated into thermodynamically oriented metrics such as exergy. As ecosystems develop, they move further from equilibrium. One hypothesis is that this results in organisms with greater genetic information capacity (Jørgensen and Nielsen, 1998). Therefore, this use of information combines the internal make-up of individual organisms with the overall ecosystem’s structural organization. Our interest here is to apply information theory to measure ecosystem order, particularly as a way to detect regime changes through changes in system state variables.

Several methodologies have been developed to calculate system information from a probability density function (PDF), e.g. Shannon Information, Gini-Simpson Information and Fisher Information. The most common application of information measures in ecology has been the use of Shannon Information as a diversity index. Shannon and Weaver (1949) developed the following measure concerning signals from a signal to a receiver:

$$H = - \sum_i p(y_i) \ln p(y_i), \quad (1)$$

where H is the Shannon Information, $p(y)$ is the PDF, and the sum is taken over all possible values of the variable y . In this formulation, H measures the degrees of freedom of the system. Communication systems with

few degrees of freedom have a clear signal transmission and high information content. In contrast with communication systems, ecological systems with many degrees of freedom (i.e. biodiversity) are deemed favorable for their apparent stability (see McCain (2000) on the diversity–stability debate). Therefore, the application in ecology has been to use the Shannon Information as an index of biodiversity. Ulanowicz (1986, 1997) used a similar form of the Shannon Information along with total system throughflow to develop a macroscopic metric of ecosystem organization called ascendancy. Gini-Simpson Information has not found its way into the ecological literature, but it has been used extensively by mathematicians (Colubi, 1996). The index, which is scaled between zero and one, is given by

$$G = 1 - \sum_i p(y_i)^2, \quad (2)$$

where all the symbols have the previously assigned interpretation. One way that biological diversity can be classified is using species evenness, which is a measure of the relative abundance of each species. Both indices, Shannon and Gini-Simpson, can be used to assess species evenness, in which case p_i is the normalized probability (probability density) of finding species i when sampling an ecosystem. In this manner, the PDF is a distribution of the abundance of species at a given time. For example, a system that has ten different species with $p_i = [0.1 \ 0.1 \ 0.1 \ 0.1 \ 0.1 \ 0.1 \ 0.1 \ 0.1 \ 0.1 \ 0.1]$ yields a Shannon index equal to 2.30 and a Gini-Simpson index of 0.90. A second system, also with ten species and a distribution, $p_i = [0.91 \ 0.01 \ 0.01 \ 0.01 \ 0.01 \ 0.01 \ 0.01 \ 0.01 \ 0.01 \ 0.01]$, gives $H = 0.50$ and $G = 0.17$. Although both systems have the same number of species the indices have dropped substantially because of the uneven distribution in the second case. One feature of these indices is that they are global properties of the system in that a different ordering of the same species probabilities would yield the same level of information. For an indicator of biodiversity this property is useful since there is no natural species ordering (there is no ‘central’ species around which others are distributed, for example). However, in some situations there is a notion of ordering, and in such cases the probability density takes on a characteristic local ‘shape’. A primary example of such a situation is data linked to temporal dynamics, since time is a naturally ordering variable. Fisher Information is sensitive to changes in probability distribution shape since it involves a derivative term, and is in these terms a local measure. In what follows, we apply the concept of Fisher Information to time-series data generated by a dynamic model system. We calculate Fisher Information over the system’s state trajectory and show that changes in Fisher Information track changes in the dynamic regime of the system.

3. Fisher Information in ecology

Ronald Fisher (1922) developed a statistical measure of indeterminacy now called Fisher Information. Fisher Information can be 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 (Frieden, 1998). Fisher Information, I , for a single measurable variable is calculated as follows:

$$I = \int \frac{1}{p(\epsilon)} \left(\frac{dp(\epsilon)}{d\epsilon} \right)^2 d\epsilon, \quad (3)$$

which can be extended to an n -dimensional system. Here $p(\epsilon)$ is the probability density as a function of the deviation, ϵ , from the true value of the variable. The integration is carried over all possible values of ϵ from zero to infinity. In the application to follow, epsilon will be the deviation from a reference state, which is treated as the ‘true’ state of the system. The information integral that results will be written in terms of system time, and it will be a measure of the lack of variability or the order in the system’s steady-state dynamics.

Frieden (1998) proposes Fisher Information as the basis for a unifying theory for physics and has used it to derive many fundamental equations of physics. These include those describing relativistic quantum physics, classical electrodynamics, general relativity, and classical statistical physics to name but a few. (Frieden et al., 2001) have applied Fisher Information to problems of population genetics and growth of cancer cells (Gatenby and Frieden, 2002).

Consider a system variable that has a uniform or unbiased PDF, which is flat (Fig. 1a). By this we mean

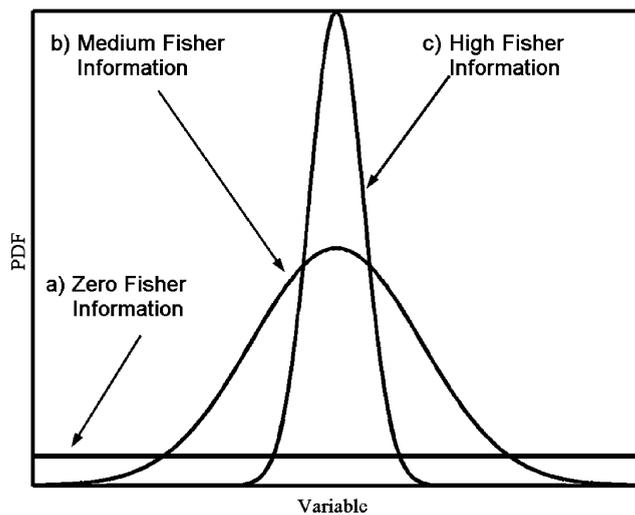


Fig. 1. Comparison of PDFs: A more uniform distribution, (b) will have a lower Fisher Information than the steeper PDF (c), whereas a flat distribution will have zero information (a).

that the probability of the variable taking any particular value is no greater than for any other value. This lack of predictability or order results in a system with zero Fisher Information. A more structured system with low disorder shows bias to a particular set of states and the PDF is more steeply sloped about these values (Figs. 1b and c), in which case Fisher Information increases with the sharpness of the PDF. For isolated (closed to mass and energy) physical (non-living) systems, entropy follows the second law of thermodynamics, increasing monotonically with time. Conversely, Fisher Information decreases with time as entropy (system disorder) increases. However, Fisher Information is not the reciprocal of entropy. Further discussion on the topic is given in Frieden (1998).

3.1. PDF

In order to calculate Fisher Information, it is necessary to determine a PDF for the system in question. We assume that (1) the system behavior can be captured in a continuous dynamic system description and (2) the system dynamic regime is periodic (this includes equilibria). We identify a single PDF for each system that is based on the probability of finding the system in a given state, i.e. sampling the system’s state variables from within a particular set of possible values. The general idea is the following: the more time a system spends in a specific state, the more likely one is to find it in that state when sampling. When normalized over the entire space of possibilities, a PDF over the states of the system results.

To make the concept concrete, consider a dynamic system of n state variables whose steady-state trajectory forms a closed loop in state space with period T . Fig. 2 shows the steady-state trajectory of a prey–predator system, $n = 2$. We divide the trajectory into a finite

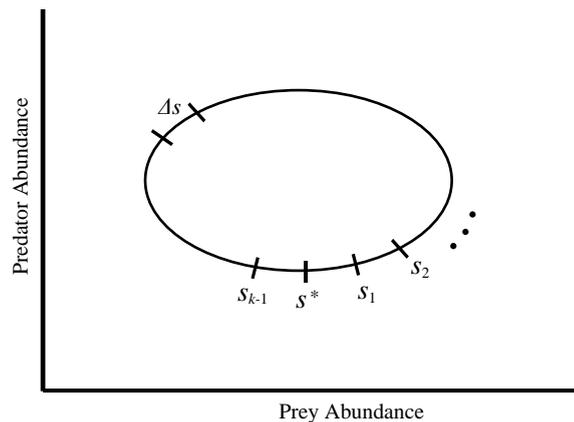


Fig. 2. Two-dimensional phase space plot of a predator–prey system, with k sub-segment states. The time spent in a state depends on sub-segment length, Δs , and the speed of the system over this length.

number, k , of sub-segments of length Δs . Let the variable s denote the position of each sub-segment along the path relative to a fixed initial position, s^* . Because the variable s is indexed relative to s^* , if we treat s^* as the ‘true’ or zero position of the system, s is exactly the deviation from that true position ($\varepsilon = s - 0 = s$). The periodicity of the system and our indexing scheme make our choice of s^* arbitrary.

An observed position, s , maps to particular values of the state variables and has a speed along the system path associated with it, reflecting the rates of change of the system variables. These rates of change are captured by the differential equations according to which a model system evolves, or derived from time-series data in the case of real systems. The probability of observing the system at a particular position is thus related to the amount of time the system state spends in the sub-segment Δs corresponding to that position. We write this probability as $P(s)$. For a sub-segment s of finite length Δs , the average time spent on the segment, Δt , is given by

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

where $\bar{v}(s)$ is the average speed along the path over the sub-segment. For continuous dynamic systems, in the limit as $\Delta s \rightarrow 0$ we obtain

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

where $R'(s)$ is the speed (scalar) at s (the prime denotes differentiation with respect to time), dt is now a differential in time and ds a differential in position. The time spent on the entire path over one cycle, the period T , is simply (here s is used as the variable of integration and S is the length of the closed path)

$$T = \int_0^S \frac{ds}{R'(s)}. \quad (4)$$

We define the probability density by the relation $P(s) = d[\text{cdf}(s)] = p(s) ds = A ds/R'(s)$, where cdf is the cumulative PDF, $p(s)$ is the PDF, A is a normalization constant, and $R'(s)$ is the speed at s as before. Since the system must at all times be somewhere on the closed path, it follows that

$$\text{cdf}(S) = 1 = A \int_0^S \frac{ds}{R'(s)}. \quad (5)$$

Thus, the PDF is given by

$$p(s) = \frac{A}{R'(s)} = \frac{1}{T} \frac{1}{R'(s)}. \quad (6)$$

Because there is a one to one correspondence between system evolution along the path and time, positions s along the system path are indexed to time t . Data on systems normally are collected in the form of time series, and one would thus like to calculate Fisher Information

over data collected as a function of time. We use the fact that the speed at s has to be the same at the corresponding t to write $R'(s) = R'(s(t)) = R'(t)$ and $ds = R'(s(t)) dt$ in the development leading to Eq. (6) to rewrite the probability density as

$$p(t) = \frac{1/R'(t)}{\int_0^T dt} = \frac{1}{T} \frac{1}{R'(t)}. \quad (7)$$

3.2. Fisher Information from the PDF

Now that a PDF has been determined, the Fisher Information of a dynamic system in periodic steady state can be calculated. The Fisher Information integral in Eq. (3) can be written as an integral in time by using the aforementioned relationship $d\varepsilon = ds = R'(s(t)) dt$, and by expanding the differential according to the chain rule to give

$$I = \int \frac{1}{p(t)} \left(\frac{dp(t)}{dt} \right)^2 \frac{dt}{R'(t)}. \quad (8)$$

Now, using the expression for $p(t)$ of Eq. (7) and the fact that

$$\frac{dp(t)}{dt} = -\frac{1}{T} \frac{R''(t)}{R'(t)^2},$$

we find upon simplification

$$I = \frac{1}{T} \int_0^T \frac{(R''(t))^2}{(R'(t))^4} dt. \quad (9)$$

This now gives us a scalar form of the Fisher Information for one-cycle period T . The speed and acceleration are, respectively, obtained from the n system state variables y_i by

$$R'(t) = \sqrt{\sum_{i=1}^n \left(\frac{dy_i}{dt} \right)^2}, \quad (10a)$$

$$R''(t) = \frac{1}{R'(t)} \left[\sum_{i=1}^n \frac{dy_i}{dt} \frac{d^2 y_i}{dt^2} \right]. \quad (10b)$$

Hence, the Fisher Information for a dynamic system in a periodic steady state, based on the notion of time in state, reduces to the integral of a ratio of acceleration to speed along the state-space trajectory. The integral of Eq. (9) gives a measure of the variation in the amount of time the system spends in various states along the steady-state trajectory, or equivalently, a measure of the variability in the speed along the steady-state trajectory. Systems that have a high variability in speed along their trajectories have a high bias toward particular states. These systems are, therefore, identified as having more order. Thus, for systems at equilibrium the Fisher Information is infinite (the period over which one integrates is arbitrary in this case) since the PDF is an

infinite impulse of zero width. For systems in which the system traces a closed path at constant speed we expect the Fisher Information to be zero since the PDF is flat. For closed-system trajectories on which the speed is non-zero and varies, the Fisher Information will take on values between these two extremes of zero and infinity. When calculated repeatedly as data on the system state become available, we expect the Fisher Information to be constant as long as the system is in a periodic steady state and the integration is done over an integer multiple of the system’s natural period of oscillation. If, due to a change in environmental forcing or the relationships between system elements, the system enters a transient period, the variability of the speed along its trajectory, and thus the Fisher Information, will change. Fisher Information, as we have derived it, responds to changes in system regime and transient behavior. This is the core result of our theory.

4. Illustration—ecosystem models

In order to further investigate and illustrate the utility of the Fisher Information in determining changes in system regime, we apply it to two ecosystem models of increasing complexity: a two-species predator–prey system and a ten compartment food web.

4.1. Two-species predator–prey model

The two-species Lotka–Volterra-type model equations describe a simple interaction between a prey species, y_1 , and its predator, y_2 , using four parameters: (g_1) prey growth rate, (l_{12}) prey loss rate due to predatory feeding, (g_{21}) predator feeding rate, and (m_2) predator mortality rate. Eqs. (11a, b) are standard and conveniently used adaptations of the Lotka–Volterra equations. The state of the system is defined by the population densities, i.e. the mass of a species for a given ecosystem, of the two species (prey and predator). We incorporate a logistic density-dependent term to limit growth of the prey in the absence of the predator and a function proposed by Holling to take into account predator satiation, which results in two additional parameters (k , prey density dependence, and β a predator satiation term.) This results in the following two ordinary first-order differential equations describing the dynamics of the population densities:

$$\frac{dy_1}{dt} = g_1 \left(1 - \frac{y_1}{k}\right) y_1 - l_{12} y_1 y_2 \left(\frac{1}{1 + \beta y_1}\right), \tag{11a}$$

$$\frac{dy_2}{dt} = g_{21} y_1 y_2 \left(\frac{1}{1 + \beta y_1}\right) - m_2 y_2. \tag{11b}$$

For parameters $g_1 = m_1 = 1$, $l_{12} = g_{21} = 0.01$, $\beta = 0.005$ and $k = 625$, the model has stable limit cycle behavior. Fig. 3 shows the system limit cycles for various values of k ranging from 625 to 800. The Fisher Information for each limit cycle in Fig. 3, calculated over one-cycle period using Eq. (9), is plotted in Fig. 4. Note that computing the Fisher Information requires the insertion of Eq. (11) into Eq. (10) to calculate the speed and acceleration. While a change in prey density dependence does not necessarily result in a change in Fisher Information for the steady state, the change in Fisher Information over the range of dependencies is clearly distinguishable. The Fisher Information curve in Fig. 4 starts at a relatively high value, then drops, and finally rises again as k varies from 625 to 800 in steps of 25. Recall that the Fisher Information of Eq. (9) measures the variation in the speed along the system

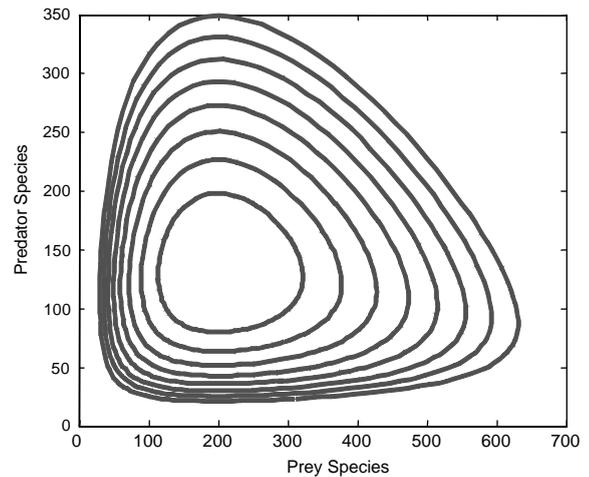


Fig. 3. Predator–prey response as k varies from 625 to 800 in steps of 25. For the largest limit cycle $k = 800$, smallest $k = 625$.

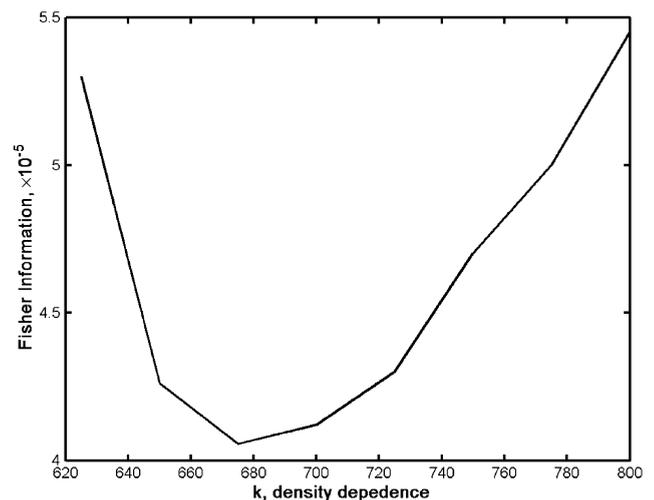


Fig. 4. Fisher Information as k varies from 650 to 800 in steps of 25. Integration window is set to period of each limit cycle.

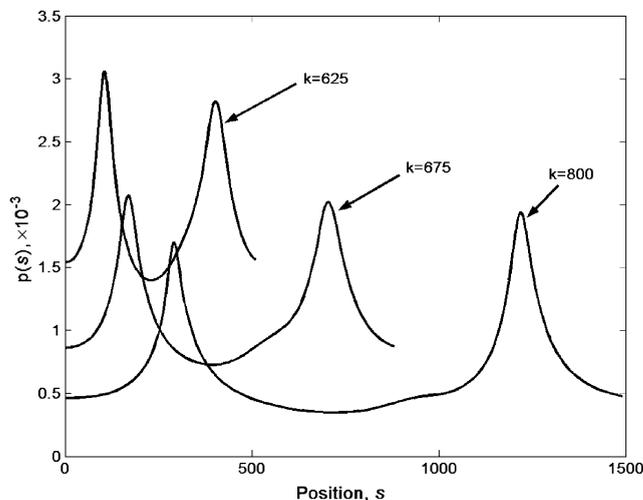


Fig. 5. Probability density as a function of the limit cycle trajectory length. Note that one is more likely to find the system in a few particular states.

state-space trajectory, which differs from one closed limit cycle in Fig. 3 to the next. Fig. 5 shows the probability densities (as given by Eq. (6)) for $k = 625$, 675 and 800. The PDF for $k = 800$ has the sharpest and the highest (relative) peaks, and thus the highest information of the three cases shown. Although it is not as obvious, the system has a higher variation in speed for $k = 625$ than for $k = 675$, and thus a higher information for $k = 625$ as well. While the level of information for two regimes can be equal, the variations that underlie these can be quite different. For example, the Information level for $k = 800$ and 625 is nearly the same but the PDFs are not. The trend shown in Fig. 4, from high to a minimum and back to high information as k is varied, is easily explained. Prior to $k = 625$, the system steady state is an equilibrium (no cycle), so the Fisher Information is infinite. As k is increased, we observe limit cycle behavior and Fisher Information drops because the speed along the cycle becomes more uniform. As k is increased further, the system spends more time in smaller portions of its trajectory (the state has a high variability in speed) and the Fisher Information is again high. These model calculations demonstrate that Fisher Information increases when the system preferentially exists in fewer states.

4.2. Ten-compartment ecological model

To further examine the response of Fisher Information to changes in model ecological systems, we developed a food web model with ten compartments: three primary producers, three herbivores, two carnivores, an omnivore, and a nutrient compartment (Fig. 6). The primary producers are limited in growth by nutrient availability and by grazing from other compartments. Again, standard Lotka–Volterra-type

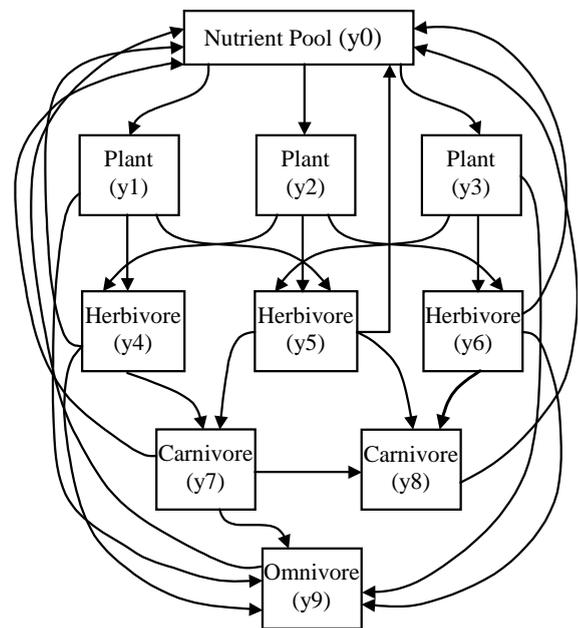


Fig. 6. Ten-compartment food web model. Arrows indicate direction of biomass flows. All mass recycles back to the nutrient pool.

equations (without density dependence or satiation terms) are used to describe the mass balance for the ten-compartment model

$$\frac{dy_i}{dt} = y_i \left(\sum_{j=0}^9 (-\varepsilon_{ij} \beta_{ij} y_j) - \alpha_i \right), \quad i = 1, \dots, 9, \quad (12)$$

where y_i is the biomass of the i th compartment, α_i is the mortality parameter, β_{ij} is the mass flow rate parameter between compartments i and j , and α_{ij} is a two-dimensional Levi–Civita symbol such that $\alpha_{ij} = 1$ and $\varepsilon_{ji} = 1$. Due to mass conservation constraints, $\beta_{ij} = \beta_{ji}$. The only exception to Eq. (12) is the first compartment ($i = 0$), which is a passive sink for nutrient storage

$$\frac{dy_0}{dt} = \sum_{j=1}^9 \alpha_j y_j - y_0 \sum_{j=1}^9 \alpha_j y_j. \quad (13)$$

There is an implicit and non-limiting flow of energy through the system. The system is, therefore, open to energy but closed to mass. The mass closure is expressed by

$$\sum_{i=0}^9 \frac{dy_i}{dt} = 0. \quad (14)$$

All three primary producers (y_1 , y_2 , and y_3) are also subject to a sinusoidal forcing function to represent seasonal variation in growth due to solar incidence variation. This forcing is the source of the periodic behavior for this model. Two forcing function amplitudes were used in evaluating the Fisher Information response: a strong forcing function with an amplitude of one-third of nominal; and a weak forcing function with an amplitude of one-tenth of nominal. The expression

for the forcing function with an amplitude of one-third of nominal is

$$g_i = \hat{g}_i \left[\frac{2}{3} + \frac{1}{3} \sin \left(\frac{2\pi t}{12} - \frac{\pi}{2} \right) \right]^2, \quad i = 1, 2, 3, \quad (15)$$

where g_i is the growth rate of one of three plant species (1, 2, and 3), t is time, and $\hat{g}_i = 0.25, 0.25, 0.26$ for $i = 1, 2, 3$, respectively.

After invoking mass conservation constraints there are 26 parameters in the model. Uncalibrated values for these parameters have been assigned in such a way that all the state variables remain non-zero, i.e. all compartments remained viable throughout the simulation (Table 1). This scenario is the baseline case for our work.

We present five cases to show how Fisher Information responds to gradual changes in the food web dynamics. For the ten-compartment model, the Fisher Information calculation proceeds by inserting Eq. (12) into Eq. (10) to compute the speed and acceleration. Note that Eq. (13) representing the mass balance for the nutrient compartment is not directly used in the Fisher Information calculation. The reason is that the mass of the nutrient pool is not normally a measurable variable in ecological systems. The five cases are meant to illustrate, using a model, how the Fisher Information responds to typical stresses and changes impacting ecosystems. In all cases a qualitatively similar perturbation regime was applied. The model system is in a stable regime for the first quarter of the simulation period. During the second and third quartiles, a linear increase or decrease of the specified parameter takes effect, and during the last quarter no further changes occur as the system settles to a new stable dynamic regime. This change is implemented through the function $f_i(t)$ which can represent any parameter (α_i or β_i) in the model that needs to be perturbed. Mathematically, this is defined by

$$f_i(t) = f_i^l, \quad 0 \leq t \leq t^l, \quad (16a)$$

$$f_i(t) = f_i^l + \frac{f_i^h - f_i^l}{t^h - t^l} (t - t^l), \quad t^l < t < t^h, \quad (16b)$$

$$f_i(t) = f_i^h, \quad t^h \leq t < \infty, \quad (16c)$$

where f_i^l is the constant value of the function before the perturbation starts, f_i^h is the constant value of the function after the perturbation ends, t^l is the point in time when the linear perturbation starts, and t^h is the point in time when the perturbation ends. For our studies here, we arbitrarily chose $t^l = 250$ and $t^h = 750$. Specific values for f_i^l and f_i^h for the five perturbation experiments are given in Table 2.

This type of perturbation is meant to mimic a response to changes in prevailing environmental conditions. Again, our primary interest was not in the model results *per se*, but in the response of Fisher Information to these perturbations. The five cases include increasing the growth rate of one of the plant species (y_3), increasing the growth rate of one of the herbivores (y_5), increasing the growth rate of one of the carnivores (y_8), decreasing the mortality rate of the top omnivore (y_9), and increasing the mortality rate of the top omnivore (y_9).

Table 3 shows the summary results for each perturbation experiment under both the strong and weak sinusoidal (seasonal) forcing functions. In each experiment, the same compartments were eliminated under weak and strong forcing functions. All disturbances resulted in the loss of at least one species. One herbivore, y_4 , was eliminated in four of the five experiments. The Fisher Information integral for four cycles was approximated numerically by substituting the simulated data into expressions for the speed and acceleration derived analytically from the model equations. The procedure was repeated over data windows of width equivalent to four-cycle periods in order to obtain Information values over the entire data set.

In the first case, the uptake rate of the third plant compartment (y_3) increases from 0.26 to 0.35. Figs. 7a and b show the results of the model simulation under the strong and weak forcing function conditions. The gradual increase in the growth rate of y_3 results in an increase of y_3, y_5 and y_8 , and the elimination of

Table 1
Model parameters used in the simulation to achieve results in which all compartments coexist

$\beta_{14} = 0.01$	$\beta_{25} = 0.01$	$\beta_{39} = 0.01$	$\beta_{58} = 0.01$	$\alpha_4 = 0.10$	$\alpha_9 = 0.75$
$\beta_{15} = 0.01$	$\beta_{26} = 0.01$	$\beta_{30} = 0.26$	$\beta_{68} = 0.01$	$\alpha_5 = 0.10$	
$\beta_{19} = 0.01$	$\beta_{20} = 0.25$	$\beta_{47} = 0.01$	$\beta_{69} = 0.01$	$\alpha_6 = 0.10$	
$\beta_{10} = 0.25$	$\beta_{35} = 0.01$	$\beta_{49} = 0.01$	$\beta_{78} = 0.01$	$\alpha_7 = 0.10$	
$\beta_{24} = 0.01$	$\beta_{36} = 0.01$	$\beta_{57} = 0.01$	$\beta_{79} = 0.01$	$\alpha_8 = 0.75$	

Table 2
Model parameters used in the simulation to achieve results in which all compartments coexist

	Simulation 1	Simulation 2	Simulation 3	Simulation 4	Simulation 5
f_i^l	$\beta_{30} = 0.26$	$\beta_{25} = 0.01$	$\beta_{68} = 0.01$	$\alpha_9 = 0.75$	$\alpha_9 = 0.75$
f_i^h	$\beta_{30} = 0.35$	$\beta_{25} = 0.025$	$\beta_{68} = 0.025$	$\alpha_9 = 0.50$	$\alpha_9 = 0.90$

Table 3
Simulation results before and after perturbations: average system states (unforced equilibria)

	y_1	y_2	y_3	y_4	y_5	y_6	y_7	y_8	y_9	y_{10}
<i>Strong forcing function</i>										
Initial value	14.59	32.89	13.76	9.16	37.50	11.47	26.03	25.19	11.46	7.93
1. β_{30} increase	0.00	0.00	58.85	0.00	58.85	7.64	8.52	40.32	8.52	7.30
2. β_{25} increase	0.00	0.00	57.57	0.00	57.58	0.00	17.43	30.13	17.43	9.85
3. β_{68} increase	0.00	27.62	45.56	0.00	45.56	0.00	29.44	33.73	1.82	6.25
4. α_9 decrease	0.00	51.34	0.00	13.17	38.18	16.16	20.67	20.67	20.67	9.13
5. α_9 increase	23.92	8.95	38.24	0.00	47.14	1.95	25.91	35.19	1.95	6.72
<i>Weak forcing function</i>										
Initial value	14.64	22.65	29.06	4.01	47.71	6.33	20.97	35.39	6.33	2.92
1. β_{30} increase	0.00	0.00	61.15	0.00	61.15	6.46	7.39	43.76	7.39	2.69
2. β_{25} increase	0.00	0.00	60.68	0.00	60.68	0.00	14.31	36.37	14.31	3.63
3. β_{68} increase	0.00	23.54	49.48	0.00	49.48	0.00	25.52	37.50	1.98	2.49
4. α_9 decrease	0.00	53.64	0.00	14.32	39.32	13.86	21.82	21.82	21.82	3.39
5. α_9 increase	19.27	4.17	47.33	0.00	51.53	2.12	21.35	39.42	2.11	2.70

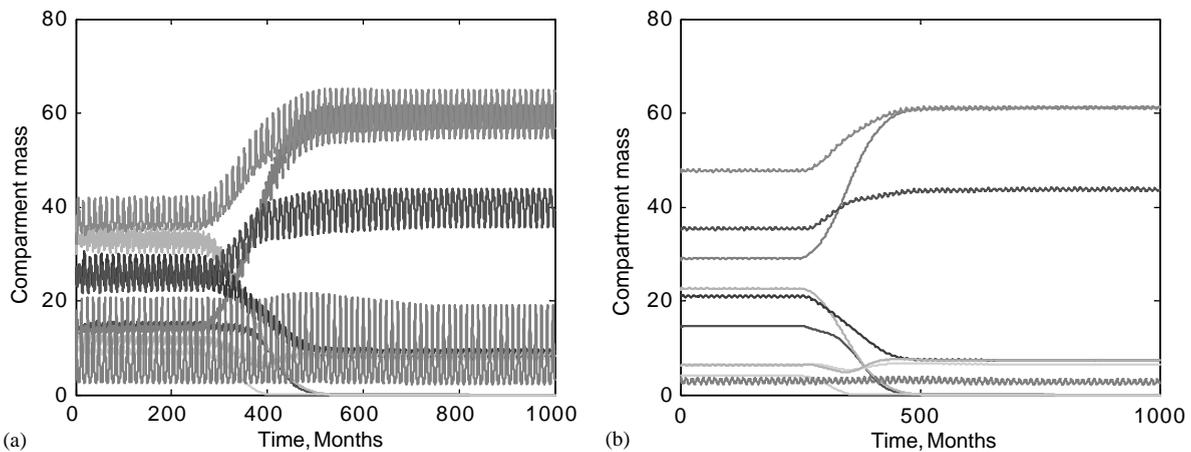


Fig. 7. (a) Food web dynamics of the ten-compartment model with a strong sinusoidal forcing function. The growth parameter of y_3 experiences a linear increase from 0.26 to 0.35 between $t = 250$ and 750. (b) Same perturbation with a weak sinusoidal forcing function.

compartments y_1 , y_2 and y_4 . The level of y_7 decreases sharply (Table 3). Fig. 8 shows the response of the Fisher Information for the same case, with an integration window of 48 months (this same window is again used in all cases, and is four times the period of the forcing function). All ten states are used in the calculation. Strictly speaking, the Fisher Information Theory that we have developed is applicable to systems in steady cyclic dynamic regimes, and it is not well defined for transient dynamics. However, for this system the forcing function provides a constant period cycle at steady state before and after the disturbance. The transient then shows up as a smooth transition between one constant Fisher Information value and another. For both the strong and weak forcing functions, the Fisher Information shows a marked drop over the transient. The Fisher Information under the weak forcing function is higher and the drop proportionately higher since the

system variation about equilibrium is smaller. While interpretation of our Fisher Information calculations around transient regimes is difficult for the aforementioned reasons, we hypothesize that the Fisher Information decreases during the transition between steady regimes when the transition is dominated by a relatively disordered regime where many different states of the system are more or less equally preferred.

In the second case, the uptake rate of the second herbivore compartment (y_5), increases from 0.01 to 0.025 (Fig. 9). Mass in compartments y_1 , y_2 , y_4 and y_6 goes to zero. This was the only simulation of the five where four compartments were eliminated. Fig. 10 shows the Fisher Information. The transient is easily distinguished in the Fisher Information plot. In this case, the Fisher Information clearly shows the transition between steady dynamic regimes for both strong and weak forcing, but it goes through a minimum only for

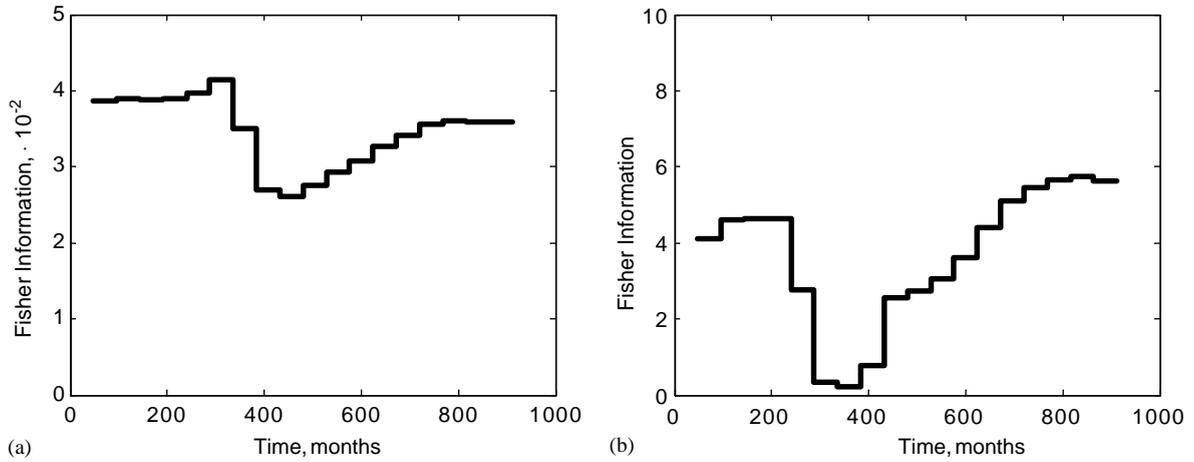


Fig. 8. Fisher Information (integration window of 48 months) of the ten-compartment model in which the growth parameter of y_3 experiences a linear increase from 0.26 to 0.35 between $t = 250$ and 750. (a) strong forcing function and (b) weak forcing function.

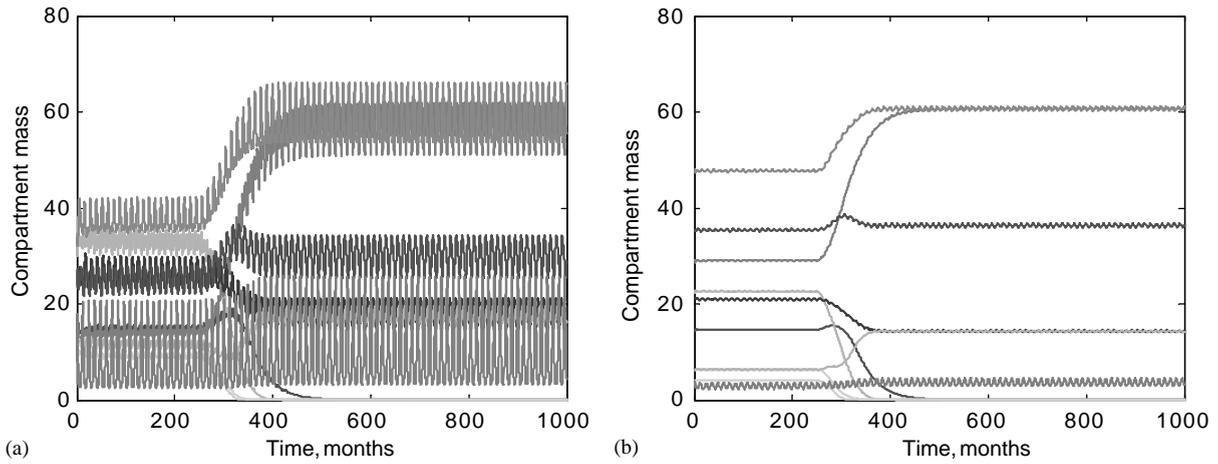


Fig. 9. (a) Food web dynamics of the ten-compartment model with a strong sinusoidal forcing function. The uptake from y_2 to y_5 experiences a linear increase from 0.01 to 0.025 between $t = 250$ and 750. (b) Same perturbation with a weak sinusoidal forcing function.

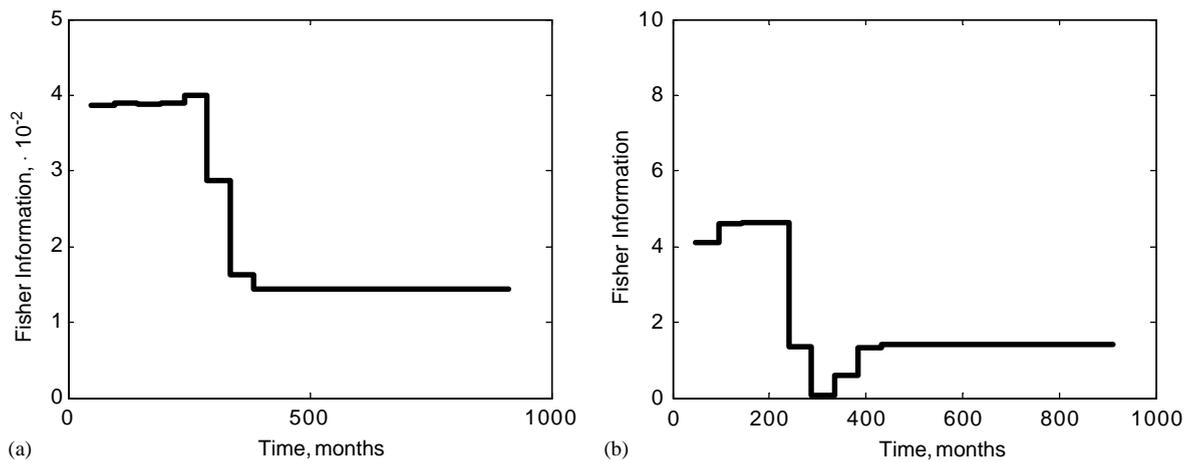


Fig. 10. Average Fisher Information (over 48 time steps) of the ten-compartment model in which the uptake from y_2 to y_5 experiences a linear increase from 0.01 to 0.025 between $t = 250$ and 750. (a) strong forcing function and (b) weak forcing function.

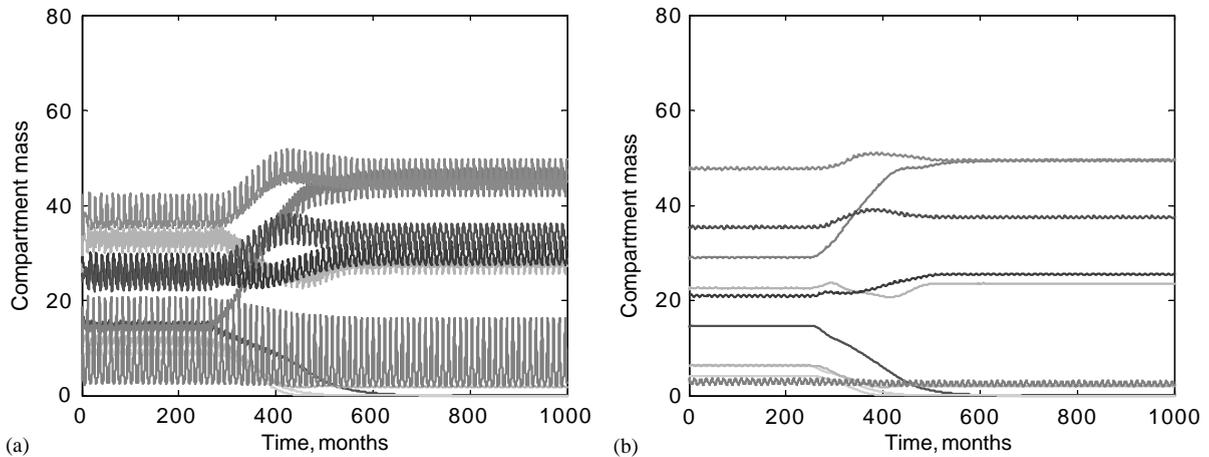


Fig. 11. (a) Food web dynamics of the ten-compartment model with a strong sinusoidal forcing function. The uptake from y_6 to y_8 experiences a linear increase from 0.01 to 0.025 between $t = 250$ and 750. (b) Same perturbation with a weak sinusoidal forcing function.

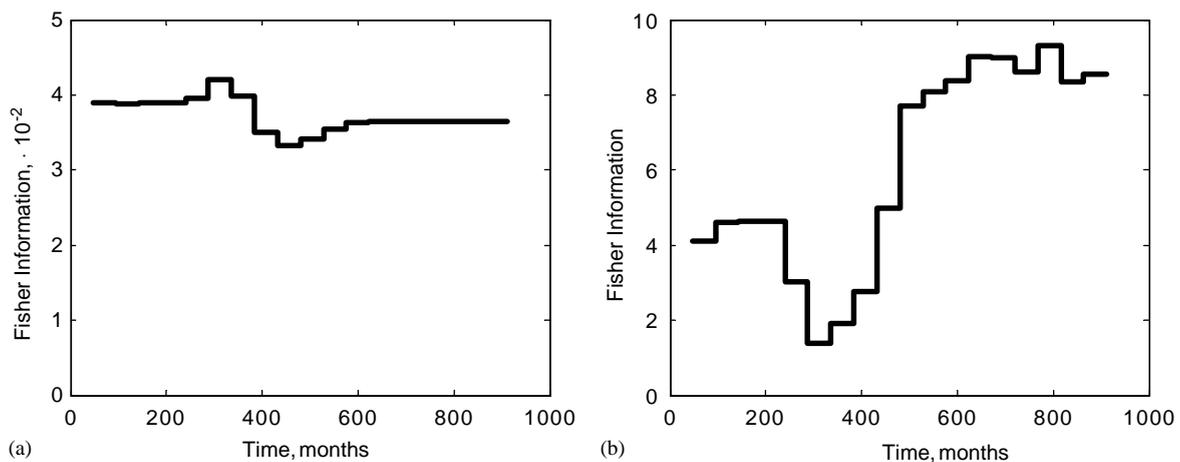


Fig. 12. Average Fisher Information (over 48 time steps) of the ten-compartment model in which the uptake from y_6 to y_8 experiences a linear increase from 0.01 to 0.025 between $t = 250$ and 750. (a) Strong forcing function and (b) weak forcing function.

the weak forcing function (Fig. 10b). For the strong forcing function case (Fig. 10a) the transition is orderly from one regime to another.

In the third case, one carnivore feeding rate, β_{68} , increases from 0.01 to 0.025 (Fig. 11). Three compartments are eliminated, y_1 , y_4 and y_6 . Fig. 12 shows the Fisher Information calculations. Again, the interesting aspect of this measure is not either the initial or final value, but the fact that the transient is clearly shown by the Fisher Information calculations. In both of these cases, the Fisher Information exhibits a minimum through the transition between the two steady dynamic regimes. We again hypothesize that the minimum in information reflects the temporary loss of order as the system moves from one steady regime to another.

In the fourth case, the top omnivore mortality rate decreased from 0.75 to 0.50 (Fig. 13). Note that the transient is much longer than in the previous cases. This seems to indicate that changes that occur at the top of the food chain take longer to propagate through the

model system than changes at the bottom, e.g. primary producers or plants. Only two compartments were eliminated in this simulation, plant compartments, y_1 and y_3 . Fig. 14 shows the Fisher Information response, which again clearly shows that a change in steady regime has occurred. For the case of strong forcing (Fig. 14a), the transition between steady regimes is again orderly. A minimum in the information during the transition is visible only for the case of weak forcing (Fig. 14b). Note that the changes in information are not sharp reflecting a long transition period between steady regimes.

In the fifth and final case, the top omnivore mortality rate increased from 0.75 to 0.90 (Fig. 15). Only one carnivore, y_4 , goes extinct. This transition period is extremely long and probably spans longer than the 1000 simulated months shown, and the transient does not appear to have settled out by the end of the simulation. This can be seen from the Fisher Information plot (Fig. 16). The case of weak forcing shows a Fisher Information plot that has not reached a steady dynamic

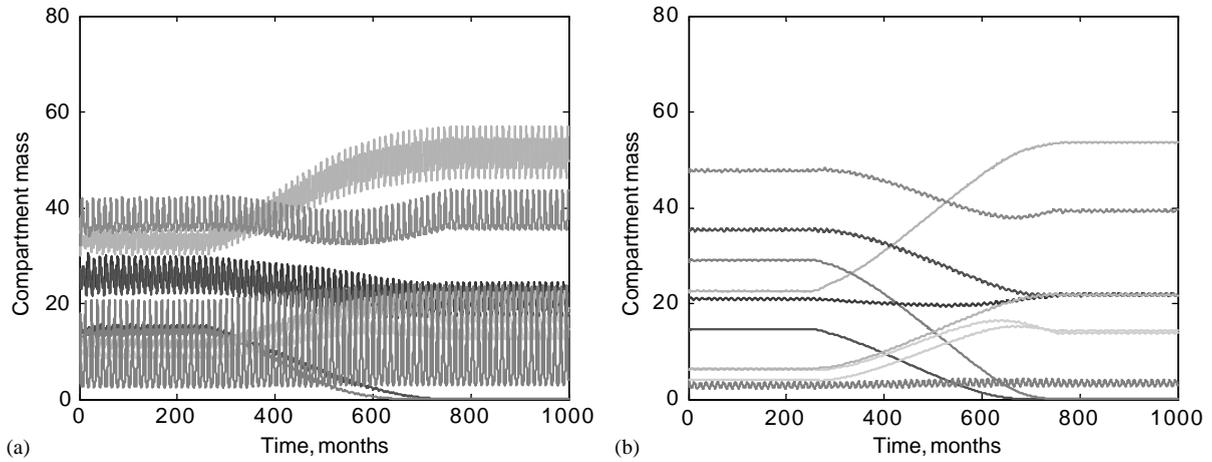


Fig. 13. (a) Food web dynamics of the ten-compartment model with a strong sinusoidal forcing function. The top omnivore, y_9 , mortality rate decreases from 0.75 to 0.50 between $t = 250$ and 750. (b) Same perturbation with a weak sinusoidal forcing function.

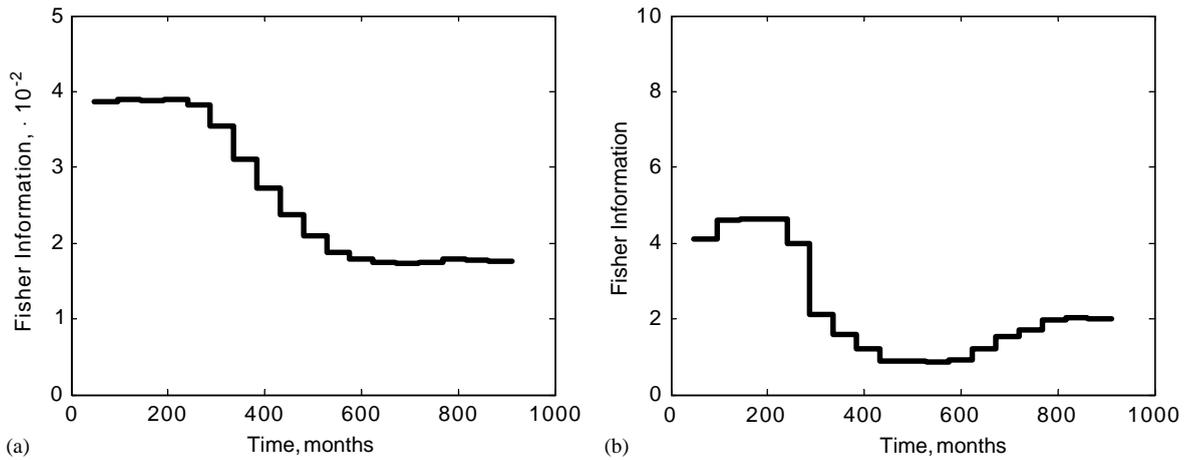


Fig. 14. Average Fisher Information (over 48 time steps) of the ten-compartment model in which the mortality rate of the top omnivore, y_9 , experiences a decrease from 0.75 to 0.50 between $t = 250$ and 750. (a) Strong forcing function and (b) weak forcing function.

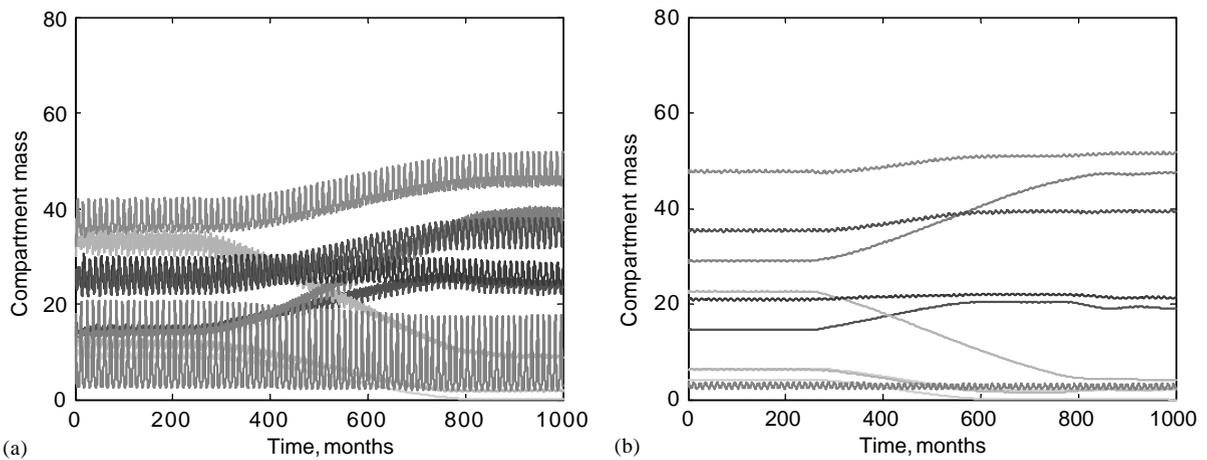


Fig. 15. (a) Food web dynamics of the ten-compartment model with a strong sinusoidal forcing function. The top omnivore, y_9 , mortality rate increases from 0.75 to 0.90 between $t = 250$ and 750. (b) Same perturbation with a weak sinusoidal forcing function.

regime by the end of the simulation. In the case of strong forcing (Fig. 16a), the Fisher Information surprisingly shows a maximum during the transition. We hypothe-

size that this implies that in moving between the two steady states, the system falls into a dynamic regime that gives preference to a small number of states giving high

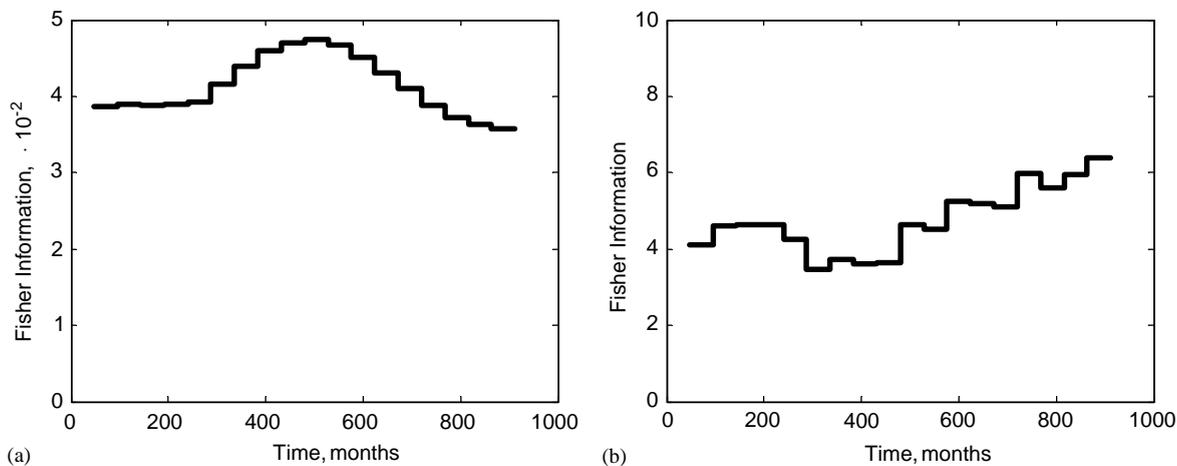


Fig. 16. Average Fisher Information (over 48 time steps) of the ten-compartment model in which the mortality rate of the top omnivore, y_9 , experiences an increase from 0.75 to 0.90 between $t = 250$ and 750. (a) Strong forcing function and (b) weak forcing function.

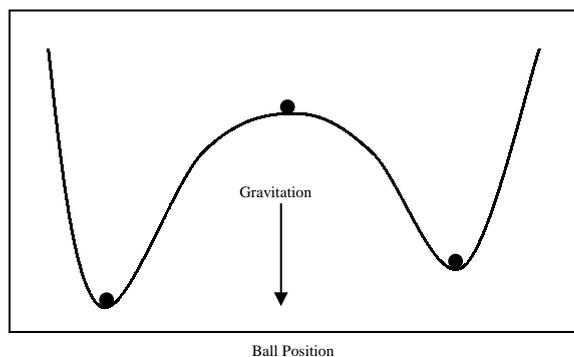


Fig. 17. Illustrative example of a ball oscillating between two valleys through a relatively flat hill under gravitational attraction. For some combinations of ball mass and specific strength and frequency of the force pushing the ball out of the valleys, the ball can spend a large amount of time transitioning over the hill.

information, but where the dynamic regime itself is not stable. Very roughly, this is similar to the situation of a ball oscillating between two valleys through a relatively flat hill (Fig. 17). In this mechanical case, depending on the strength and frequency of the oscillating force pushing the ball out of the valleys, it is conceivable that the ball could move in and out of the valleys quickly while moving slowly over the top of the hill in between. For such a case, our Fisher Information calculation would show higher information for the transition over the hill as the system ‘slows down’.

5. Discussion

The results shown here demonstrate that on these model-generated data sets for ecological models exhibiting characteristic periodic system behavior, the Fisher Information form that we have developed provides a clear signal that the system has undergone a transition from one steady dynamic regime to another, i.e. the

Fisher Information can be shown to closely track changes in dynamic regime. Note that although we have used our knowledge of model dynamics to calculate the Fisher Information in these examples, a model is not necessary. We are currently working to apply Fisher Information using experimentally determined or field measured time-series data for biological populations and other abiotic variables. All that our theory requires for computing the Fisher Information is the time derivatives of the state variables of the system (Eq. (10)) which can be obtained from a model (Eqs. (11) or (12) and Eq. (13)) or from experimental or field data in the form of time series. Computation of the Fisher Information does not depend on knowledge of system structure, feedbacks or causality. In this sense, the Fisher Information gives us a ‘black box’ approach to the generation of signals from data. However, subsequent application certainly will require situation-specific interpretation and intimate knowledge of the dynamics of the system on which the measure is applied in order to determine the direction and potential extent of change, and what must be done to stem or reverse detected changes if so desired. This work offers a means of detecting when associated system changes in dynamic regime are in the process of occurring, but it does not shed light on the factors that contribute to system resilience or buffer capacity.

In addition to this theoretical interest, there are ecological reasons for proposing the use of Fisher Information in the manner discussed here. Ecosystems have observable, measurable properties, and one sign of an underlying system organization is a characteristic manner in which measurable properties or state variables vary. This may be due to homeostatic mechanisms, as observed in many ecosystems. For example, Liebig’s Law of the Minimum and Shelford’s Laws of Tolerance set upper and lower resource constraints on the effects of environmental variables

upon organisms. Given a set of time-series data for these state variables in an ecological system, whether model-generated or field measured, the Fisher Information gives an overall measure of the consistency of variability, and therefore, of the consistency of the system organization that generated the data. An ecological system in a stable periodic regime has a characteristic variability and a characteristic Fisher Information. This system, if experiencing a perturbation, will typically show a change in the variability of its measurable variables and a corresponding change in Fisher Information. This change in Fisher Information is reflective of transient behavior, which may represent a change in the dynamic regime of the system or a change in the organization between system elements. Although not directly measured, we hypothesize that it may be possible to infer the system resilience or buffer capacity by the change in Fisher Information. A persistent organization is especially important for human exploitation of ecosystems, as it is a source of predictable future behavior in the presence of disturbances.

When the system is moving from one steady regime to another, there seem to be two prototypical behaviors for the Fisher Information (Figs. 8, 10, 12, 14 and 16) during the transition: (1) a loss of information and (2) a gain of information. The typical loss of information behavior is illustrated by Fig. 8b, and the typical gain of information behavior is shown in Fig. 16a. As already discussed, we hypothesize that the information loss is due to the system moving through a disordered regime during the transient where there is no preference for any particular set of states. We have also hypothesized that the gain in information is due to the system moving through an ordered regime during the transient where a particular set of states is preferred, although the regime itself is not stable. The latter was illustrated with an example of a ball moving between valleys (Fig. 17). It is important to note that the actual transition between one steady regime and another can occur through a combination of these two prototypical behaviors. Hence, we see that in many cases (Figs. 8a, b, 10b, 12a, b and 14b) there is a small rise in the Fisher Information followed by a drop during the transition as the system settles to a new steady regime. We suspect that these are cases where the system first moves through an ordered regime (information rise) followed by a disordered regime (information loss). In some of these cases (Fig. 12a), the information gain and the information loss appear to be approximately equal. There are still other cases where the transition is smooth (Figs. 10a and 14a), with perhaps a small rise followed by a drop. We suspect that these are cases where the order in the transition regime is lower than that of the initial regime but higher than that of the final regime. Hence, the seemingly complex behavior exhibited by the Fisher Information in these examples may be due to

combinations of a few prototypical behaviors. Recall, however, that the theory developed here is strictly applicable to steady cyclic dynamic regimes, not transient behavior. Thus, the discussion above represents our hypothesis and an opportunity for further research.

There are still many questions that remain to be addressed. For example, what is the effect of noise on the Fisher Information calculation? Because estimation of speed and acceleration from real data is sensitive to noise, we expect this to be an important issue. Furthermore, the results shown use a fixed integration window for the Fisher Information, which is then moved (in time) a single window width at a time to generate a Fisher Information versus time plot. This is appropriate here since the characteristic period of the system is known. However, in other systems, if the period changes or is otherwise not known, or when the system steady state is not periodic, alternative methods may be needed. A more significant challenge which currently being researched is developing a Fisher Information concept that is valid for transient as well as steady state behavior. Although here we limit our discussion to the presentation of this new methodology and to the utility of it as an indicator of regime change, further work may also shed light on a biophysical interpretation of the quantitative level of the observed Fisher Information. These questions and others provide directions for future research.

The overarching goal is to link Fisher Information to concepts such as ecosystem resilience, ecological buffer capacity, and ultimately, sustainability. In order to link Fisher Information to sustainability, we must: (1) be able to identify the direction of system change at the onset of transient behavior; (2) be aware of the existence of different system regimes; and (3) understand the nature of the system organization that gives rise to any new regime that becomes established and whether or not it can sustain ecosystem function. While we are currently far from having this knowledge, Fisher Information offers a powerful and theoretically sound approach to investigate transient behavior and changes in dynamic regime, a fundamental understanding of which is necessary to gauge the long-term persistence of sustainable ecosystem function.

6. Conclusion

We present a new application of Fisher Information in conjunction with the dynamics of ecological systems. The Fisher Information that we have developed is a measure of the state of order or organization, as compared to Shannon and Gini-Simpson Information. Shannon and Gini-Simpson Information are appropriate as biodiversity indices, whereas, the Fisher index is adept at revealing changes in system order which

generally correspond to changes in dynamic regime. A derivation is provided which gives a probability density function for the chance of observing a dynamical system in any one of its accessible states. The resulting Fisher Information expression is given in terms of ratios of speed and acceleration of the system over its state-space trajectory. The application of the Fisher Index to two examples is given: a two-species predator–prey model and a ten-compartment food web model. Fisher Information closely tracks changes in regime for these model systems.

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