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Fisher Information and dynamic regime changes in ecological systems

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ABSTRACT

Ecosystems often exhibit transitions between multiple dynamic regimes (or steady states), such as the conversion of oligotrophic to eutrophic conditions and associated aquatic ecological communities, due to natural (or increasingly) anthropogenic disturbances. As ecosystems experience perturbations of varying regularity and intensity, they may either remain within the state space neighborhood of the current regime or "flip" into the neighborhood of a regime with different characteristics. An increasingly integral aspect of many ecological, economic, and social decisions is their impact on the sustainability of particular dynamic regimes of ecosystems. Sustainability entails a human preference for one particular regime versus another, and the persistence of that regime with regard to the human and natural perturbations exacted on the system.

Information theory has significantly advanced our ability to quantify the organizational complexity inherent in systems despite imperfect observations or 'signals' from the source system. Fisher Information is one of several measures developed under the theme of estimation theory. Fisher Information can be described in three ways: as a measure of the degree to which a parameter (or state of a system) can be estimated; as a measure of the relative amount of information that exists between different states of a system; as a measure of the disorder or chaos of a system. Fisher Information may be a useful measure to identify the degree to which a system is at risk of "flipping" into a different dynamic regime. We developed a Fisher Information index for dynamic systems in a periodic steady state and applied it to a simple, two species Lotka–Volterra predator–prey model. Changes in the carrying capacity (size) of the system resulted in different stable steady states establishing themselves, each with a characteristic Fisher Information. By repeatedly calculating Fisher Information over time, transitions or "flips" between steady states were identified with changes in Fisher Information. We then examined data collected from four ecological systems (of increasingly large spatial and temporal scale) that have demonstrated regime transitions: the Bering Strait/Pacific Ocean food web; the western Africa savanna; the Florida (USA) pine–oak system; the global climate system. These datasets are noisy and reflect several to many cycles that are out of phase, which complicates the identification of both dynamic regimes and transitions. If transition phases between regimes can be detected early enough, human activity suspected of contributing to regime changes can be altered (or continued if the resultant steady state is desirable, such as in ecosystem restoration efforts).

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1. Introduction

Ecosystems are complex, dynamic systems that often display characteristic regimes of behavior dictated by their internal dynamics and the disturbances that act on them (Scheffer et al., 2001). A regime is characterized by a particular multidimensional neighborhood or set of values within which the system state fluctuates. Each set forms a basin of attraction about a particular steady state, meaning that, starting in the set and absent any change in outside forcing, the system will remain in the same neighborhood of the steady state. Here we are not referring to a steady state in a thermodynamic sense, where equilibrium would infer a dead system (all living systems exist far from thermodynamic equilibrium), but rather a steady state in the dynamic systems sense of system behavior. However, real systems may not always reach a steady state or remain in a regime for long, as disturbances constantly perturb the system, making the identification of regimes difficult (and therefore the concept may be controversial for some). A disturbance that is greater in intensity or duration than some background level can cause the system to flip from one regime to another, although intrinsic characteristics of the system also influence the impact these disturbances can have (Holling, 1973; Ellner and Turchin, 1995). For example, changes in phosphorus input can cause lakes to switch between oligotrophic and eutrophic regimes, and grazing and fire ultimately determine whether a valley is dominated by grassland or forest regimes (Carpenter et al., 2001). The size of disturbance that can be tolerated by an ecosystem before a change in regime occurs is a measure of the ecosystem's resilience to disturbances. The same system features that affect resilience also determine the degree to which an ecosystem can move from one regime to another (Holling, 1973, 1996; Pimm, 1984; Gunderson, 2000). Although ecosystems may naturally pass through many regimes, the functions and services that ecosystems can provide human societies under these can vary (Wardle et al., 2000; Portela and Rademacher, 2001). In this respect, some regimes may be more desirable to humans than others.

Sustainability has become an increasingly desirable goal for human interactions with ecosystems, one that requires the preservation of ecosystem structures and functions for current and future generations (World Commission on Environment and Development, 1987; National Research Council, 1999). These ecosystem structures and functions are those that are most often desirable from a human perspective. Therefore, human societies have an interest in detecting when an ecosystem is in transition from one regime to another, and whether it is moving from a desirable to an undesirable regime (e.g., deterioration) or from an undesirable to a desirable regime (e.g., restoration; Carpenter and Cottingham, 1997). Theoretically, this would entail monitoring all of the ecosystem variables (such as species abundances, nutrient cycling, and disturbances) relevant to the regime flip of interest, and then detecting a characteristic pattern of change. However, even if the relevant variables were known, detecting meaningful change over many variables can be difficult (and knowing all relevant variables may be impossible for even artificially simplistic ecosystems, given the potential need for variables that describe self-organizing properties; Peterson, 2001). An index or proxy variable that responds appropriately to the collective behavior of all the pertinent variables is essential.

We postulate that systems at or near a stable dynamic regime have a characteristic variability in the values of their state variables. Changes in regime are manifest as changes in the established pattern of variability. By measuring the variation experienced by variables in an ecosystem over sequential periods in time, we may be able to identify the onset of transition between dynamic regimes. To this end, we use information theory, in particular, Fisher Information to collapse the variability of many state variables into one index that measures the overall system variation. We describe how this index is derived, illustrate the behavior of the index with a simple, two-variable predator–prey system model, and demonstrate its application to complex ecosystems with many state variables, for which a shift was detected between alternative regimes despite noisy data (Scheffer et al., 2001).

2. Methods

2.1. *Information theory and the Fisher Information index*

Information theory provides a quantitative framework by which to describe processes that admit only partial knowledge. Shannon and Weaver (1949) developed what has become known as Shannon entropy in the context of communication networks. Networks with low noise transmit with few 'outlying' signals, making it a relatively simple task to recover the original input. Such signals are considered to have high information content. In contrast to communication networks, ecological systems with high biodiversity or redundancy (i.e., many 'outlying' species or degrees of freedom) are deemed desirable for a variety of reasons (Tilman et al., 1996; McGrady-Steed et al., 1997; Naeem and Li, 1997; Yachi and Loreau, 1999; Balvanera et al., 2001; but see Pfisterer and Schmid, 2002). The most common application of information theory in ecology thus has been the use of Shannon entropy, H, as a measure of biodiversity (Ricklefs, 1979; Krebs, 2001). Given a probability density function (PDF; $p(\varepsilon)$), the Shannon entropy is given by:

$$H = -\int p(\varepsilon)\ln p(\varepsilon)\,\mathrm{d}\varepsilon \tag{1}$$

Shannon entropy is a measure of the 'global' smoothness in $p(\varepsilon)$, in the sense of being invariant to changes in the ordering of probability density values with respect to the independent variable. 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).

Fisher (1922) developed a statistical measure of indeterminacy now called Fisher Information. Fisher Information can be variously interpreted as a measure of the ability to estimate a parameter, as the amount of information that can be extracted from a set of measurements (the 'quality' of the measurements), and also as a measure of the state of disorder of a system or phenomenon (Frieden, 1998). Essentially, the

Shannon index is the inverse of the Fisher Information index; where Shannon entropy decreases with a skewed distribution of abundances among species, Fisher Information increases with a skewed distribution of time among states. This form of information has not made its way into the ecological literature to date (with the exception of Cabezas and Fath, 2002 and Fath et al., 2003).

Fisher Information, I, for a single measurement of one variable is calculated as follows:

$$I = \int \frac{1}{p(\varepsilon)} \left(\frac{dp(\varepsilon)}{d\varepsilon} \right)^2 d\varepsilon \tag{2}$$

Here, $p(\varepsilon)$ is the probability density as a function of the deviation, ε, from the true value of the variable. In contrast to Shannon entropy, Fisher Information takes into account the changes in the probability density shape that result from a re-ordering over the independent variable since it involves a derivative term. This sensitivity can be useful for situations in which there is a notion of ordering. Such a situation arises in dynamic systems, for which time is a natural ordering variable.

2.2. Fisher Information development

In order to calculate Fisher Information, it is necessary to determine a probability density function 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 is in a periodic steady state. We identify a single PDF that is based on the probability of finding the system in a given state from within a set of possible states. In general, the longer a system is in a specific state, the more likely one is to find it in that state when sampling. The time spent in each state is calculated from the system acceleration and velocity in phase space. When normalized over the entire space of possibilities, a probability density function for the states of the system results.

For example, consider a dynamic system of dimension n whose steady state trajectory forms a cyclical (closed) path in state space. Fig. 1 shows a predator–prey system, $n = 2$, as an example. We divide the trajectory into a finite number, m, of sub-segments of length Δs. The variable s denotes the position of each sub-segment along the path relative to an unknown initial position, s^*. Because the variable s is indexed relative to s^*, if we treat s^* as the 'true' position of the system, s is exactly the deviation from that true position ($\varepsilon = s$). The periodicity of the system and our indexing scheme make our choice of s^* arbitrary.

An observed deviation, s, maps to particular values of the state variables and has a speed associated with it as determined by the time evolution of the system. The probability of observing a particular deviation is thus related to the amount of time the system state spends in the sub-segment corresponding to that deviation. 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:

$$\Delta t(s) = \frac{\Delta s}{\bar{v}(s)} \tag{3}$$

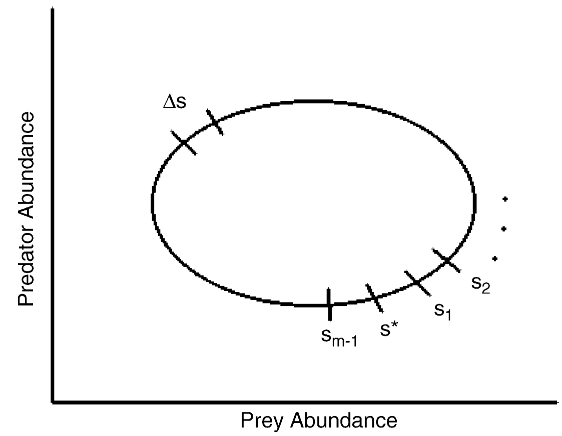

Fig. 1 – Two-dimensional phase space plot of a predator–prey system, with *m* sub-segment states. The time spent in a state depends on sub-segment length, Δs, and the velocity of the system over this length.

where $\bar{v}(s)$ is the average speed for that segment. In the limit as $\Delta s \to 0$, we obtain

$$dt(s) = \frac{ds}{R'(s)} \tag{4}$$

where $R'(s)$ is the speed (scalar) at s (the prime denotes differentiation with respect to time). The time spent on the entire closed path, the period T, is simply (here, τ is used as the variable of integration and S is the length of the closed path):

$$T = \int_0^S \frac{d\tau}{R'(\tau)} \tag{5}$$

We define the probability density by the relation $d\mathrm{cdf}(s) = p(s)\,ds = A\,dt(s)$, where A is a normalizing constant (or scaling factor) and cdf is the cumulative probability density function. Since at any given time the system must be somewhere on the closed path, it follows that:

$$\mathrm{cdf}(s) = 1 = A \int_0^S \frac{d\tau}{R'(\tau)} \tag{6}$$

The probability density is thus given by:

$$p(s) = \frac{\frac{1}{R'(s)}}{\int_0^S \frac{d\tau}{R'(\tau)}} = \frac{1}{T}\frac{1}{R'(s)} \tag{7}$$

Because we are dealing with a dynamic system, s is indexed with time. Thus, using the fact that $ds = R'(s(t))\,dt$ (and a slight abuse of notation), we re-write the probability density as:

$$p(t) = \frac{\frac{1}{R'(t)}}{\int_0^T d\tau} = \frac{1}{T}\frac{1}{R'(t)} \tag{8}$$

Returning to the development of Fisher Information, we can use the fact that $d\varepsilon = ds = R'(s(t))\,dt$ and expand the integrand in (2) according to the chain rule to give:

$$I = \int_0^T \frac{1}{p(t)} \left(\frac{dp(t)}{dt} \right)^2 \frac{dt}{R'(t)} \quad (9)$$

Now, using the expression for $p(t)$ of Eq. (8) we find, upon simplification:

$$I = \frac{1}{T} \int_0^T \frac{(R''(t))^2}{(R'(t))^4} dt \quad (10)$$

Eq. (10) is a scalar form of the Fisher Information for one cycle period. In the notation of component vectors this is:

$$I = \frac{1}{T} \int_0^T \frac{((\mathbf{x}'(t))^T \mathbf{x}''(t))^2}{||\mathbf{x}'(t)||^6} dt \quad (11)$$

since

$$R'(t) = ||\mathbf{x}'(t)|| \quad \text{and} \quad R''(t) = \frac{dR'(t)}{dt} = \frac{(\mathbf{x}'(t))^T \mathbf{x}''(t)}{||\mathbf{x}'(t)||}$$

Under the above PDF development, the Fisher Information of Eq. (10) or (11) is interpreted as a measure of the variability in the time the system state spends in the various sections of its steady state trajectory (or, since time and speed are inversely related, variation in the speed of the state over its steady state trajectory). A system steady state with a uniform speed would have zero information, as one is equally likely to observe the state at all locations on the path. By the same token, for equilibrium systems the information is infinite, since we are assured of observing the system in only one state. Connections to the estimation and the measurement 'quality' interpretation of Fisher Information also can be made.

2.3. *Fisher Information evaluation*

We now turn to the evaluation of the Fisher Information given by Eq. (10) or (11) using time series data (see Appendix A for a detailed algorithm). This involves estimating the state speed and acceleration along the trajectory, and performing a numerical integration over the system period. We assume the data are sampled from a continuous system for which the phase space coordinate position is given by a (vector) function of time, $\mathbf{f}(t)$. The data may or may not be sampled at even time intervals, but this is not necessary for velocity and acceleration estimation. However, we find evenly spaced data to be easier to handle when using numerical integration since such data can be more easily converted to the period of integration. For this purpose, interpolation will create data that are evenly spaced in time.

In order to estimate the speed and acceleration from time series data, we employ a central difference scheme. A 'central' data point at time t and a point on either side at $t - \Delta t_p$ and at $t + \Delta t_a$ are considered. We relate the time interval on either side of the central point by $\alpha\,\Delta t_a = \Delta t_p$, where α is the ratio of the time step after (Δt_a) to the time step prior (Δt_p) to a given data point. The velocity $\mathbf{f}'(t)$ is then given by:

$$\mathbf{f}'(t) = \frac{\alpha^2 \mathbf{f}(t + \Delta t_a) - (\alpha^2 - 1)\mathbf{f}(t) - \mathbf{f}(t - \alpha\,\Delta t_a)}{(\alpha^2 + \alpha)\,\Delta t_a} \quad (12)$$

and the acceleration $\mathbf{f}''(t)$ is given by:

$$\mathbf{f}''(t) = \frac{\alpha \mathbf{f}(t + \Delta t_a) + \mathbf{f}(t - \alpha\,\Delta t_a) - (\alpha + 1)\mathbf{f}(t)}{(\alpha^2 + \alpha)\,\Delta t_a^2/2} \quad (13)$$

These reduce to the forms expected for evenly spaced data ($\alpha = 1$).

The speed along the path system trajectory is the magnitude of the velocity vector, and we take the path acceleration to be the component of the acceleration vector tangent to the path. The acceleration must have the proper sign to account for reversals in velocity direction, i.e., when there is an instant of zero velocity but non-zero acceleration along the trajectory.

Numerical estimation of velocity and acceleration is subject to noise and other data artifacts. We address these through the use of a two-point average of the calculated speed values, rather than the speed values derived from Eq. (12), in the numerical integration of Fisher Information. In order to preserve the original number of estimated velocity points, the very first speed data point is averaged with speed calculated as a simple difference of the first two raw data points. In addition, the integration in the expression of Fisher Information (Eqs. (10) and (11)) itself averages outlying values of the speed and acceleration to some extent.

In addition to noise, unknown periodicity of the steady state is also a difficult issue when dealing with real-world data. When the integration window is not matched to the period of the system, Fisher Information will appear to fluctuate as the calculation is repeated over time even if the data are not noisy (see Section 2.3). The dominant system period can be estimated using fast Fourier transform techniques (FFTs), or determined using knowledge about the specific system (such as external forcing effects to which it is subject). However, Fisher Information also can appear 'noisy' when data do not represent a periodic steady state, when the real system is non-periodic, or when the steady state changes periodicity following disturbance. Strictly speaking, the Fisher Information development of Section 2.1 applies to systems that have reached a periodic steady state. Thus, while the calculation described by Eqs. (10) and (11) can be applied to systems undergoing transient or other non-periodic behavior, ecological interpretation of the resulting values is difficult under the current development. Nonetheless, many systems do achieve some sort of periodic, or near periodic steady state. For these systems, the onset of transient behavior can be easily detected.

In order to detect transients, the Fisher Information integral can be calculated in one of two ways. The first is to simply evaluate the integral using the data over the equivalent of one cycle period, assigning the resulting Fisher Information value to the entire time interval, and then moving to the next 'window' of time/data. We call this a 'block average'. As long as the system is at steady state, the Fisher Information resulting from this calculation will remain constant over each integration period. Changes in the steady state show up as changes in Fisher Information, but the resulting plots mask details of transitions because they are 'blocky'. As an alternative, one can evaluate the Fisher integral as a 'moving average', a single point at a time. In this mode, the Fisher integral is evaluated using a 'window' of data points of a size equivalent to the period, centered on the given point. The Fisher Information value is then assigned to that point (in time), and the evaluation 'window' is moved over the next data point. Again, the Fisher Information is constant for systems in steady state; however, the resulting plots are less blocky, allowing changes in Fisher Information to become more apparent.

3. Results

3.1. *Fisher Information: application to a simple model*

We first develop a simple predator–prey system to demonstrate the use of the Fisher Information calculation for multivariable systems. The two-species Lotka–Volterra model equations given in Eqs. (13a) and (13b) describe a simple interaction between a prey species, x_1, and its predator, x_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. The state of the system is defined by the population densities of the two species (prey and predator). We incorporated a logistic density-dependent term to limit growth of the prey in the absence of the predator and a predator satiation term (Holling, 1965), which provides two additional parameters (k density dependence and β satiation).

$$\frac{dx_1}{dt} = g_1\left(1 - \frac{x_1}{k}\right)x_1 - l_{12}x_1x_2\left(\frac{1}{1+\beta x_1}\right) \tag{13a}$$

$$\frac{dx_2}{dt} = g_{21}x_1x_2\left(\frac{1}{1+\beta x_1}\right) - m_2x_2 \tag{13b}$$

For parameter values $g_1 = m_1 = 1$, $l_{12} = g_{21} = 0.01$, $\beta = 0.005$, and $k = 6.25$, the model has stable limit cycle behavior.

Fig. 2 shows the results of a numerical experiment in which the density dependence, k, is varied linearly from 650 to 800. This figure highlights the issues surrounding the Fisher Information integration as discussed in Section 2.2. The plot in Fig. 2a shows Fisher Information calculated repeatedly using the period of the initial steady state limit cycle ($k = 650$) as the integration widow and applying the 'block average' method. As expected, the value initially is flat and steady. When the density dependence changes, starting at $t = 100$, the Fisher Information first drops and then settles to a varying pattern around the steady state value previously calculated for $k = 800$. The variation in the final steady state Fisher Information value can be attributed to a mismatch between the integration window (114 steps, each step 0.1 units of time) and the period of the final steady state (131 steps). Indeed, when the integration window is increased to 131 steps, the situation is reversed. In Fig. 2b, the final Fisher Information value is steady and the initial varies about the steady state value previously calculated for $k = 650$.

Fig. 2c shows the Fisher Information calculated over the entire time period before the transient, during the transient, and after the transient, i.e., with a single integration window for each (1000, 600, and 2400 time steps each, respectively). For this calculation, we take advantage of the fact that we know when the transient behavior of the system state begins and (approximately) when it ends. Before and after the transient, the system is in steady state. The steady state values of Fisher Information during these steady states matches those calculated in (a) and (b). This method of calculation circumvents two problems. First, it eliminates the necessity of knowing a priori the system periodicity. Second, by calculating the Fisher Information over a single integration window, the contribution of noise, extraneous data, slight non-periodicities, etc., to the Fisher Information are minimized—we essentially average these effects out by integrating over multiple system periods. Note that while we can calculate a value for Fisher Information for transient behavior, we cannot interpret the result under our current theory. However, we give the calculated value over such known periods because transient phenom-

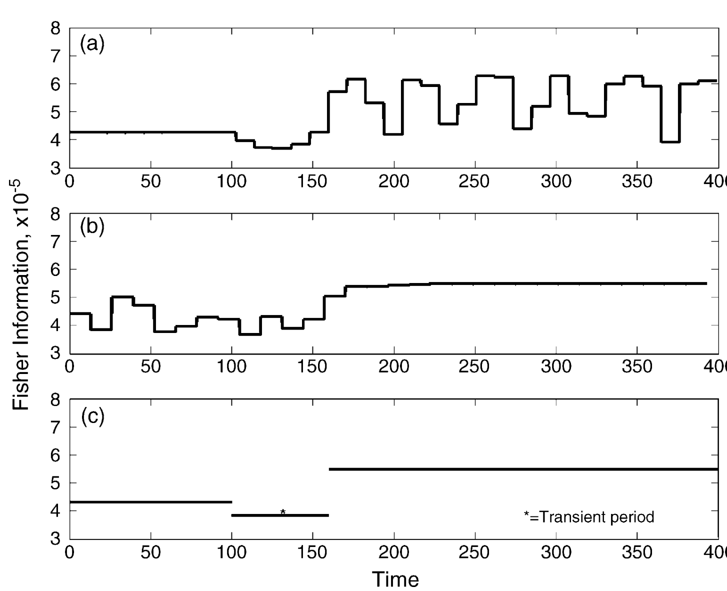

Fig. 2 – Fisher Information as k is increased from 650 to 800 over $100 < t < 150$. Integration window is 114 steps for (a) and 131 steps for (b). The results shown use the 'block averaged' Fisher Information calculation, not the moving average. Fisher Information is averaged for each regime and transient period in (c), where the transient period is from 100 to 160 time steps.

ena are nonetheless real and we do not want to 'average them out'. This possibility becomes more likely when the timing of steady state versus transient periods is not exactly known.

3.2. *Fisher Information: application to real datasets*

A true measure of the utility of the Fisher Information index is its ability to identify transitions (or periods of high variability) between regimes in datasets characterized by a great deal of noise, such as that evident in data collected from field studies of real ecosystems. We used data from four ecosystems, for which regime flips had been detected by other means, to determine whether the calculation of Fisher Information could be used to detect these flips. In the Bering Strait region of the Pacific Ocean, two shifts have occurred, one in 1977 and the other in 1989 (Hare and Manuta, 2000). At a much larger scale, the global climate on Earth has rapidly flipped between warm and wet interglacial periods and cool, dry glacial periods, all recorded in ice core data from Antarctica. Regime flips can occur regionally as well. The ecosystem of the western African continent experienced extreme shifts, from a humid and forested regime to a desert regime, driven by ocean currents and other regional climate patterns (deMenocal et al., 2000). Finally, pollen records from the state of Florida in the southeastern United States also demonstrated regime shifts from humid pine forest to dry oak savanna, due to regional climate conditions. We shall discuss some background of these systems and the data, and then illustrate the capacity of Fisher Information to distinguish regime flips.

3.2.1. *Pacific Ocean ecosystem*

From 1976 to 1977, and again in 1989, the marine ecosystem of the Bering Strait region in the northern Pacific Ocean experienced shifts in both climate and biological components pronounced enough to be considered regime shifts (Miller et al., 1994; McGowan et al., 1998; Hare and Manuta, 2000, and references therein). Hare and Manuta (2000) gathered time series data for 100 environmental and biological variables that had been monitored in this region for the past 30 years. Some of the 31 environmental variables surveyed characteristics such as sea surface temperatures and coastal upwelling, while the 69 biological variables included the recruitment of fish species such as Chinook and coho salmon, zooplankton biomass, and jellyfish population surveys. Because these variables were all measured using different units and scales, each series was normalized based on its mean and standard deviation, but the data were not smoothed (Hare and Manuta, 2000). Many of the variables demonstrated either a significant increase or decrease in either 1976 or 1989, and some variables displayed shifts in both years. Differences in behavior among these 100 variables may have been due to variability in the way these variables respond to two or more inter-decadal climate oscillations that affect the Pacific Ocean (Hare and Manuta, 2000).

Although these two regime shifts are apparent in some of the time series variables, they were not confirmed until several years after the event because of the high number of measured variables involved and the inherent variability in the data (Hare and Manuta, 2000). By using this variability to track changes in the overall system, Fisher Information may greatly improve the ability to identify these shifts. We used

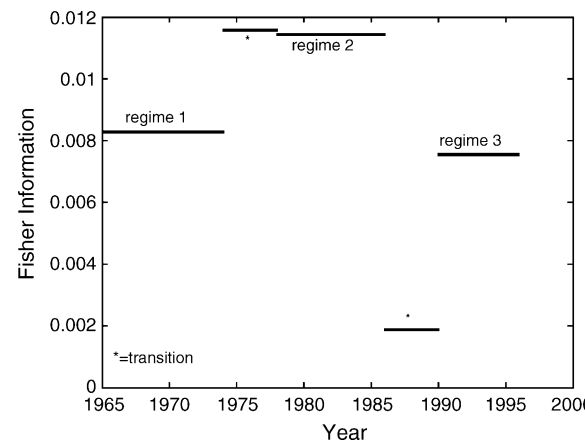

Fig. 3 – Fisher Information integrated over the duration of each regime, and over each transition period, for 65 complete time series variables measured in the Pacific Ocean ecosystem. Transitions represent 4 years over which the transition period was identified (Hare and Manuta, 2000).

65 of the 100 variables that had complete or near-complete time series data to calculate Fisher Information. We used the periods over which each regime was identified, as well as the transition periods between them, to calculate five values of Fisher Information (one for each regime, and one for each transition). Fisher Information clearly changed between regimes and over-transition periods. The 1989 shift may have been more pronounced, as the information for this period is substantially different from the rest of the periods (Fig. 3), and Hare and Manuta (2000) suggested that the 1977 and 1989 transitions were ecologically distinct from one another. In addition, the interim stable regime (2) between the 1977 and 1989 shifts may be characteristically different from the regimes before and after these periods, although the ecological interpretation of these differences is not entirely clear (Mantua, 2004).

3.2.2. *Global climate changes*

The global climate has flipped between warm and cold periods frequently for at least the past several million years, as evidenced by pollen, ocean sediment, and ice core data. Ice cores around the world have documented the dramatic shifts from warm and cold periods on Earth, some back to more than 200,000 years in the past (Taylor et al., 1997; Taylor, 1999). Carbon dioxide, methane, and deuterium are trapped in air pockets or as part of the ice itself as ice accumulates, and are particularly useful indicators of such change, as these three variables are highly correlated with the overall temperatures on Earth (Manabe and Stouffer, 1993). These variables indicate that within the past 160,000 years there have been three transitions: from a cold period to a warm period around 140 thousand years before present (kyear BP); back to a cold period around 115 kyear BP; another transition (around 12 kyear BP) to the warm period at present. All of these shifts occurred rapidly, over only a few decades (Taylor, 1999; Adams et al., 1999).

We performed a Fisher Information calculation on time series data for carbon dioxide, methane, and deuterium measured from the Antarctic–Vostok ice core (Lorius et al., 1985; Barnola et al., 1987; Jouzel et al., 1987, 1993, 1996; Chappellaz et al., 1990). Because measurements were taken at different depths (and therefore at different times) for the three variables, we interpolated all three to develop a uniform data series with one datapoint every 50 years, using a linear interpolation. Fisher Information responded to all of the transitions between the warm and cold regimes (Fig. 4). In this case, Fisher Information decreased for all of the transition periods. The substantial difference in Fisher Information between the two warm periods may indicate the cyclic pattern in the time series data for the warm period occurring about 12,000 years before present is substantially different from the more recent period, or that the data for the recent warm period does not cover a complete cycle, therefore resulting in a different (low) Fisher Information.

3.2.3. *Sahara and Florida ecosystems*

In addition to ice cores, sediment cores from lakes and oceans also can often reveal the past history of regional ecosystems. The regions of western Africa and Florida have experienced similar climatic changes from humid to dry conditions. These changes are measurable in several variables, such as increases in terrestrial dust in oceanic sediment, blown off of the desert ecosystem existing in arid periods in Africa, and increased pine pollen in lake sediments from the spread of pine forests during humid periods in Florida. In both systems, these regime flips occurred on the scale of several decades. Unlike the Pacific Ocean system, there are fewer time series data available, and the correlation between these variables and the regime flips that have occurred in the system has not been made clear. However, the time series data available for both of these systems suggest that the distinction between regime and transition periods is great enough to serve as an interesting case study for Fisher Information.

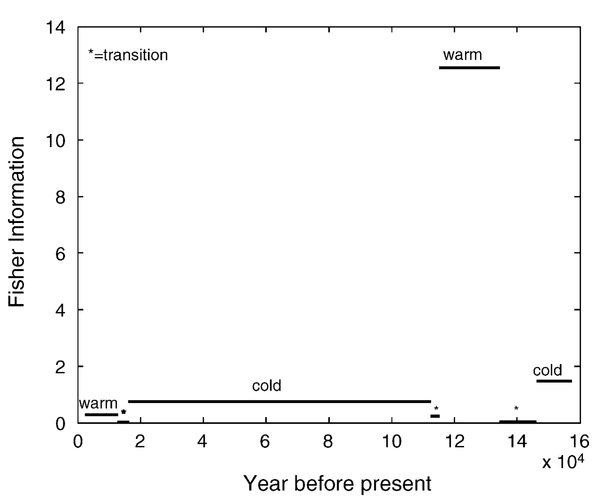

Fig. 4 – Fisher Information calculated for the global climate time series data over the periods in which the regimes and transitions occurred. Major transitions between warm and cold regimes were delineated by changes in the CO_2 concentration, where concentrations below 250 ppm indicate cold regimes, and concentrations above indicate warm regimes (Taylor, 1999).

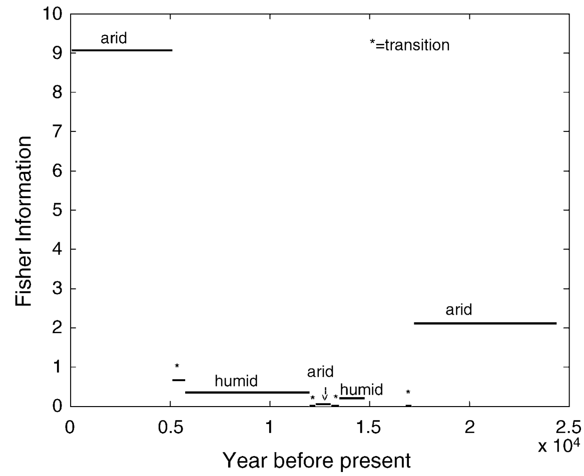

Fig. 5 – Fisher Information calculated for the Sahara climate time series data over the periods in which the regimes and transitions occurred. Transitions between humid and arid periods were identified using trends observed in the percentage of terrigenous dust time series data (deMenocal et al., 2000). The empty period between 1.5 kyear BP and about 1.7 kyear BP indicates a hiatus in the sedimentation record, possibly due to erosion or lack of sedimentation processes.

Over the past 15,000 years, the Sahara ecosystem experienced two major flips, from an arid period (prior to 14.5 kyear BP) to a humid period (5.5–14.5 kyear BP, with a brief arid period around 1.3 kyear BP), and back to an arid climate from about 5.5 kyear BP to present (Gasse et al., 1990; Gasse and Van Campo, 1994; Lamb et al., 1995). We combined data on the concentration of terrestrial-originated dust and biogenic opal, $CaCO_3$, and warm sea surface temperatures from ocean sediment core data off the west coast of Africa (deMenocal et al., 2000). We interpolated the data so that a value for each variable was calculated every 20 years. Again, changes in Fisher Information corresponded to changes in data variation between regimes and transitions (Fig. 5). Fisher Information was lower on average during the shift than during the regimes, and the arid periods exhibited a higher Fisher Information than the humid periods, with the exception of the brief arid period around 13,000 years BP. The ecosystem may not have established a stable regime during this brief arid period, and therefore the data may be more characteristic of a transition period than a steady state. The similarity in Fisher Information between the two transition periods on either side may support the supposition.

Florida plant communities have experienced several regime flips in the past 50,000 years, from a dry, oak savanna regime (dominated by *Quercus* and *Ambrosia* species) to humid pine forests during Heinrich events (Heinrich, 1988; Bond et al., 1993), dominated by *Pinus* species (Grimm et al., 1993). We combined the percent dominance of several plant genera (*Pinus*, *Quercus*, *Ambrosia*, and species in the family Poaceae; Grimm et al., 1993), with $d^{18}O$ from the GISP2 ice core from Greenland (Grootes et al., 1993; Meese et al., 1994; Steig et al., 1994; Stuiver et al., 1995; Grootes and Stuiver, 1997). Again, to ensure a uniform dataset, we linearly interpolated these

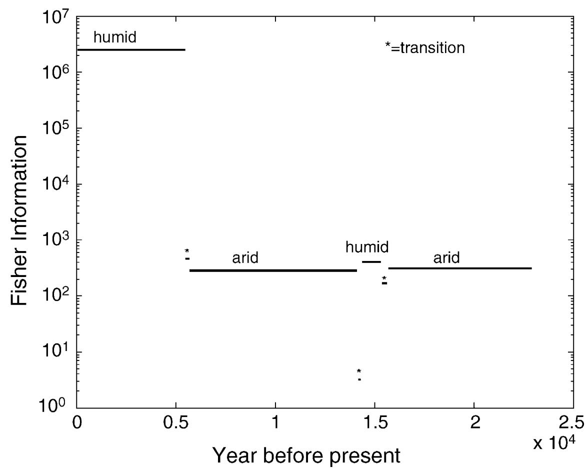

Fig. 6 – Fisher Information calculated for the Florida pollen time series data over the periods in which the regimes and transitions occurred. Transition zones between humid and arid periods were identified using the percent of pine pollen recovered in the sediment core; a large proportion of pine pollen indicates a humid climate (Grimm et al., 1993).

data to obtain values every 20 years. When Fisher Information was calculated over each of the regime and transition periods, the transition periods were noticeably different from the established regimes, and the two arid regimes had strikingly similar values for Fisher Information (Fig. 6). Again, the brief period around 1.5 kyear BP may have been too short to establish steady state behavior, and therefore is different in Fisher Information than the most recent humid period. In fact, the recent humid period is three orders of magnitude higher than any of the other regimes and transition periods, suggesting that this regime is characterized by state variables that have little noise or low variability associated with them.

4. Discussion

We have developed a measure of system variability using the concept of Fisher Information. A system in a periodic steady state has a characteristic Fisher Information, which captures the variability in the time the system spends over different sections of the steady state trajectory. Repeated calculation of the Fisher Information permits the identification of periods of transient behavior, and ultimately to transitions between steady states, if these occur. In idealized system models, this application of Fisher Information easily picks out such transitions if the steady state periodicity before or after the transient is known. For real data on real systems, the utility of the method outlined here is complicated by the difficulty in choosing an appropriate integration window matched to the system cycles, as this methodology requires the system to be in a periodic steady state. A mismatch between integration period and the system period, or data that do not reflect a periodic steady state would lead to Fisher Information plots that are difficult to interpret. However, for every dataset included here, Fisher Information calculated over the entire time of existence of each steady state regime was different, implying that the pattern of variability in the measured data during these time periods is distinct.

Although changes in Fisher Information can signal the onset of a transient period, this may not necessarily mean that a ‘flip’ is in the process of occurring—ecosystems often undergo prolonged transient behavior without ‘flipping’ to different regimes. The ecosystems examined here operate at a range of spatial and temporal scales, and our knowledge about these systems, their characteristic variables and the underlying feedbacks and forces that drive them, is imperfect. The Pacific Ocean time series data represent a system for which many variables have been measured, but over which a variety of forces (that cycle over a span of several different timescales) may have influence. Indeed, the changes observed in the biological variables over the time period represented in the data may not only have been influenced by environmental or climate changes (Lehman and Keigwin, 1992), but also by cascade effects throughout the food web (Chen and Cohen, 2001), variations in anthropogenic pressure (such as fishing), or demographic stochasticity (Shaffer, 1981). The less that is known about the system and the number of possible regimes to which the system (or parts of the system) can flip, the less useful Fisher Information becomes (as interpretation is more difficult).

In this respect, interpretation of Fisher Information for global and regional climate time series data may be more straightforward. The shifts in climate are relatively more pronounced, there are fewer major state variables to enter into the calculation, and the transitions occur over at least several decades, as opposed to 1 or 2 years in the Pacific Ocean system. In addition, these global and regional datasets cover longer time periods, increasing the probability that near periodic behavior of a system will be captured. For all of the systems examined, when the timing of the shifts is known, Fisher Information could be calculated over the regime and transition periods individually, producing a single Fisher Information value (Figs. 3–6). Fisher Information calculated over these known time periods produced distinct values between transitions from one regime to another, suggesting that some regimes are characteristically different from each other. However, this method of calculation not only obscures other flips that may be important, but also may not be as useful to determine how the system is behaving in the present, or what can be expected in the near future. As all of the empirical ecosystem data here demonstrate, some knowledge of the system, the possible regimes, and the relationship between those regimes and the state variables must be available. If variables extraneous to the system are entered into the Fisher Information calculation, the index loses much of its diagnostic capability.

The development of Fisher Information and its use on real world datasets is clearly not complete. First, a methodology needs to be developed to determine the appropriate time period over which Fisher Information should be integrated. We suspect this period would be related either to the time period over which transitions occur, or the periodicity of the system due to environmental or climatic forcing functions. Second, Fisher Information clearly responds to system behaviors that are unidentified at present, and we are unclear as to what differing values for Fisher Information might mean for real ecosystems. High Fisher Information is characteristic of systems for which the state variables exhibit low variation in time (they spend long periods of time at the same values), and we suspect that the same holds for systems that vary little over the state space (they vary over a very small range of values). Here we have developed a particular probability density on which to apply the Fisher Information. Other interpretations might be developed that could prove more useful, such as an interpretation that explicitly considers transient behavior or a-periodic systems, for example. Modeled ecosystems with varying levels of noise and complexity (i.e., more state variables) will undoubtedly help clarify some of these issues, although Fisher Information as we have applied it here will never be useful as a sole index for ecosystem behavior. Rather, it will be of high utility when paired with one or more other ecosystem indices and knowledge about the system (such as, what flips are possible and what they portend for human society).

Our hope is that Fisher Information will be useful in the delay or even prevention of catastrophic shifts in ecosystems that are the result of human activity and would prove to be harmful to human concerns. (Likewise, Fisher Information could help with ecosystem restoration, in which a shift from one regime to the "restored" regime would be desirable.) Fisher Information might be used to detect patterns in data indicating the start of a transition phase, before this phase is obvious from monitored variables themselves or the system as a whole. Advanced warning of regime shifts (or "ecological forecasting"; Clark et al., 2001), especially those of the global climate (Zwiers, 2002), would be a great benefit to enhance the sustainability of human activities. However, accurate forecasting requires knowledge of the characteristics of the regime into which the system is transitioning. The possibility arises that potential ecosystem regimes exist that humans have not experienced, and warning of the system entering a transition phase, if it is recognized at all, will provide little aid in terms of adaptation to the new regime. Such new regimes are most likely to appear in ecosystems in which many species extinctions and/or many invasions by species exotic to the system have occurred, or in which conditions arise that are theoretically possible (and modeled) but have not been observed in the past (Marotzke and Willebrand, 1991; Broecker, 1997).

5. Conclusion

Fisher Information represents a novel way to illustrate the behavior of multidimensional systems, especially systems for which multiple possible dynamic steady state regimes are possible. Transitions between these regimes are detected, provided that these regimes are periodic, and that their periodicity is known or can be estimated. Although our Fisher Information index presented promising results with modeled and real world systems, a greater knowledge of the system dynamics, along with an improved interpretation of Fisher Information behavior, is needed. When calculated using a non-integer multiple of the system cyclic period, Fisher Information appears highly variable and is extremely difficult to interpret. As developed, Fisher Information is hypersensitive to deviations from cyclic behavior, and further work on the effects of noise, simultaneous cycles, and integration issues will be required. However, this index represents a promising tool for ecological management, restoration and forecasting efforts, and is widely applicable to abiotic systems as well.

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Appendix A

Here we outline the calculation of Fisher Information. We assume that we have time series data for one cycle of the system, comprising a column vector of (absolute) times ($\mathbf{t}$) at which data were taken, size $[n \times 1]$, and a matrix ($\mathbf{x}$) of data points, size $[n \times m]$. A column in the data matrix represents a variable's values over the n time points, and a row represents the m variable values at a particular point in time. Since we are considering one cycle, $\mathbf{x}(1) = \mathbf{x}(n)$.

Prior to the Fisher Information calculation, the data must fit several conditions. First, there can be no missing data points; missing data should not be given a default code such as −99 or 0, as this would be interpreted by the calculation as a real point. Instead, interpolation should be used to fill in these data points. Second, if the variables are measured in different units, the data must be normalized to make the potential contribution of each variable to the FI calculation roughly the same. For example, if the mass (in kilograms) of 20 different species of fish is measured, no normalization is necessary even if the weight measurements may differ by an order of magnitude between species. However, if these data are combined with sea surface temperature (in degree centigrade) that typically varies only by several degrees, all variables should be normalized. For model generated data, the relative sizes of the variables are taken as given; we assume the scaling embedded in the model captures the relative significance of system variables on system behavior.

Once the data are ready for analysis, we proceed as outlined below. The calculation has been written in a stylized pseudo-code form. The reader will need to adapt this pseudo-code to their computer programming language of choice.

```
%Calculate vector velocity and acceleration using Eqs. (12) and (13), row by row
%(starting at row i = 2, and ending at row i = n − 1, since these are three-point calculations).
%Below, x(i) is a row vector [1 × m] representing the data at time t(i), rprime_vector(i) is
%the velocity vector [1 × m] at data point i, and rdblprime_vector(i) is the acceleration
%vector [1 × m] at data point i, and alpha is the ratio of time steps about the current data
%point i.

for i = 2:n
   alpha = (t(i) − t(i − 1))/(t(i + 1) − t(i))
   rprime_vector(i) = ((x(i + 1)*alpha^2 − (alpha^2 − 1)*x(i) −
x(i − 1))/((t(i + 1) − t(i))*(alpha^2 + alpha)))
   rdblprime_vector(i) = ((x(i + 1)*alpha − (alpha + 1)*x(i) +
x(i − 1))/((t(i + 1) − t(i))^2*(alpha^2 + alpha)/2))
   if i == n
      alpha = (t(i) − t(i − 1))/(t(2) − t(1))
      rprime_vector(i) = ((x(2)*alpha^2 − (alpha^2 − 1)*x(i) −
x(i − 1))/((t(2) − t(1))*(alpha^2 + alpha)))
      rdblprime_vector(i) = ((x(2)*alpha − (alpha + 1)*x(i) +
x(i − 1))/((t(2) − t(1))^2*(alpha^2 + alpha)/2))
end

%The (scalar) speed required for the calculation is then determined, by taking the
%Euclidean norm of the velocity vector at each data point i:
   rprime_scalar(i) = (rprime_vector(i)*(rprime_vector(i))^T)^1/2
%The tangential acceleration (scalar) at point i, rdblprime_tangent_scalar(i), is
%determined by the scalar (dot) product of vector acceleration to normalized velocity:
   rdblprime_tangent_scalar(i) =
      rprime_vector(i)*(rdblprime_vector(i))^T/rprime_scalar(i)
%Here the superscript T stands for transpose
end

%We are now ready to calculate the FI integral of Eq. (10) (equivalent to Eq. (11)). We
%first calculate the differential Fisher Information, and then sum and divide by the total
%time to obtain the result:
for i = 1:n − 1
   dFI(i) = (rdblprime_tangent_scalar(i))^2/rprime_scalar(i)*(t(i) −
t(i + 1))
end
   FI = sum(dFI)/((t(n) − t(1))
%end of calculation of FI for data representing one cycle.
```

Notes:

I. Because of our three point differencing scheme, we have $n - 1$ speed and acceleration points, whereas there are n original data points.
II. If the velocity is found to be zero, this is either because the system is truly stationary (zero velocity and zero acceleration) or because there is a change in direction (i.e., zero velocity and non-zero acceleration). In the latter case, we use the convention that the tangential acceleration is positive and take its magnitude to be the usual Euclidean norm of the acceleration vector.

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