

Estimating sustainability of a simple human society and its associated ecosystem using resilience and Fisher Information

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Abstract: Sustainability applies to integrated systems comprising humans and the rest of nature. To be considered sustainable, human components (society, economy, law, etc.) that interact with ecosystems cannot decrease the resilience of the ecosystem structures and functions (trophic linkages, biodiversity, biogeochemical cycles, etc.) upon which the human components depend. A mathematical theory embodying these concepts would be immensely valuable in humanity's efforts to determine the effects of human activity on the resilience of the ecosystems. However, resilience of ecosystems can be very difficult to measure when only data collected in the field are available. We propose that indicators based on Information Theory can be used to develop measures that bridge the natural and human systems and make sense of the disparate state variables of the system. Fisher Information measures the variation of a dynamic steady state based on the probability density function it generates. We investigate the relationship between ecosystem resilience and Fisher Information using a simple, deterministic ecosystem model. This model is formed by a series of differential Lotka-Volterra equations, and includes 10 species arranged in 5 trophic levels, in addition to two resource pools, one of which is only accessible to two of the four plant species. The human society is modeled as one of the 10 species, and in proportion to its population size can increase the growth rate of three domesticated species, and decrease the mass transfer between other species. We create perturbations in the system to explore its resilience to these perturbations, and the relationship between resilience and Fisher Information. Since Fisher Information tracks the variation in a system, we hypothesize its use as an index of ecosystem resilience, and therefore sustainability.

Keywords: *Resilience; Fisher Information; Sustainability; Modeling*

1. INTRODUCTION

A sustainable interface between ecosystems and human systems requires that ecosystems be able to maintain the structures and functions that provide critical products and services to humans, despite the human system (Daily and Ehrlich 1996). Ecosystem products and services such as food and fiber, water retention and filtration, carbon sequestration and pollination of crops would be very expensive (if not impossible) to replace on a large scale with solely man-made systems (Costanza et al. 1997). Detecting when critical ecosystem structures and functions are threatened is important in determining whether human activities are sustainable.

From a dynamic systems perspective, the multiple behaviors often manifest in the biotic and abiotic components of ecosystems (such as oligotrophic versus eutrophic states in lakes, Scheffer et al.

1993) are characteristic of systems with distinct attractor regimes. Ecosystems may shift between several regimes due to natural disturbance, although the products and services that these different regimes can provide to humans may differ considerably (Wardle et al. 2000, Portela and Rademacher 2001). Using a simple ecosystem model, we demonstrate the use of Fisher Information and resilience to differentiate between time periods when an ecosystem is in a stable, dynamic regime, and periods of transition between regimes. By integrating a rudimentary human society into the ecosystem, we can then begin to examine the relationship between Fisher Information, resilience and sustainability when describing ecosystem regimes. We note, however, that while Fisher Information and resilience provide necessary conditions that must be met for a system to be sustainable, there are likely to be many other conditions that are equally important.

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2. FISHER INFORMATION AND RESILIENCE

Ronald Fisher (1922) developed the statistical measure of indeterminacy called Fisher Information. This index 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 as a measure of the state of order of a system (Frieden 1998). Fisher Information, I , for a single measurement of one variable is calculated from:

$$I = \int \frac{1}{p(e)} \left(\frac{dp(e)}{de} \right)^2 de \quad (1)$$

where $p(e)$ is the probability density as a function of the deviation, e , from the true value of the variable. Fath et al. (in press) have developed a Fisher Information index for dynamic systems with a periodic attractor, which reduces to the integral of a ratio of powers of acceleration to speed along the state-space trajectory:

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

where t is time, T is the cycle period, $R''(t)$ is the tangential acceleration, and $R'(t)$ is the tangential speed. We expect the Fisher Information given by equation 2 to be constant as long as the system is in a periodic steady state and the integration time coincides with the cycle period. The integral takes on values between zero (for systems in which the state traces a closed path at constant speed), and infinity (for systems at equilibrium, with the period of integration arbitrary). Fisher Information is thus an indicator of the uniformity of variability of the steady state and the degree of order in the system regime. A system that shows preference for particular states has high Fisher Information, and a system that has no preference for any states has low Fisher Information.

One way to characterize the status of ecosystems is to measure their resilience. Two definitions of resilience have been used: the recovery time of a system back to a regime after being perturbed away from it (Pimm 1984); and the ability of a system to absorb perturbations and remain in the same regime (Holling 1973, 1996, Gunderson 2000). Although both of these characteristics are important aspects of the resilience of a regime, here we use only the second measure of resilience due to the way in which we define our regime boundaries. We define a regime for our system as the set of parameter values over which the system maintains the same number of extant species. Therefore there is no recovery from a regime in

which one species is zero, because no species can recover from extinction.

3. ECOSYSTEM MODEL

3.1 Model description

Using Lotka-Volterra differential equations, we developed a twelve-compartment model system that mimics a general ecosystem with a very rudimentary social system. This system represents the flow of “mass” (which is meant to loosely characterize biomass, nutrients, water and other resources) within a system closed to mass (i.e., the cumulative mass is constant, Figure 1). The model is not intended to be an accurate representation of any particular ecosystem or society, but rather an abstract model of relationships between compartments that mimics the influence of human activities on the system as a whole. In Figure 1, solid arrows represent transfers of mass that are not influenced by the human compartment. Dashed arrows represent transfers of mass from the nutrient pool to the inaccessible nutrient pool that occur as a by-product of human activity (unintentional) in the domestic branch, e.g., landfills, pavement, etc., necessary to support domesticated agriculture and product distribution. Dotted arrows represent mass transfers that can be intentionally increased or decreased by humans.

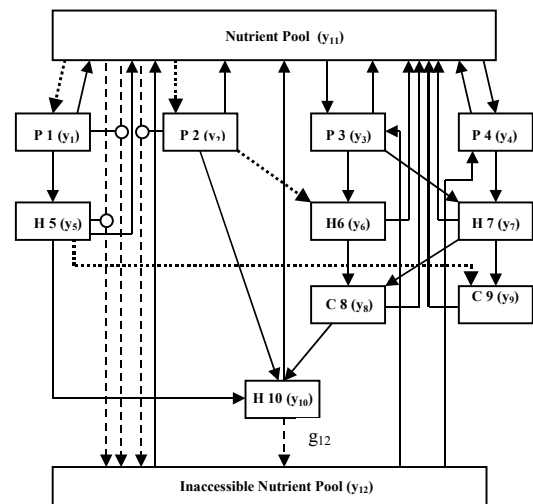


Figure 1. Diagram of model system with plants (P1, P2, P3, P4), herbivores (H5, H6, H7), carnivores (C8, C9), and humans (H10). Arrows represent mass flows. P1, P2 and H5 are domesticated and consumed by humans. P3, H6 and C8 are non-domesticated and consumed by humans (e.g., hunting and gathering). Detritivores function within the Nutrient Pool (y_{11}).

The ecosystem model is divided vertically into two characteristic branches, with a domestic branch representing agricultural and livestock activities, and a non-domestic branch that represents hunting, gathering, and species that are not directly used by humans. The model has four trophic levels (plants, herbivores, carnivores and a top omnivore, representing humans), and two resource pools, one of which (an “inaccessible” nutrient pool) has a much slower rate of mass transferred out of it than from the other resource pool. Although the human compartment does not receive mass directly from the non-domestic branch, this branch supplies ecosystem functions critical to the survival of the entire system through “recycling” of the mass in the inaccessible nutrient pool back into the rest of the system. If the mass in the non-domestic branch falls to zero, mass only transfers from the inaccessible to the accessible nutrient pool at a relatively low rate. If this rate is too low to support the growth rates of the remaining compartments, the remaining compartments will collapse. The flow of mass from one compartment to another is dictated by the following equations:

$$y'_1 = y_1 (G_1 (y_{10})y_{11}-g_5y_5-m_1) \quad (3)$$

$$y'_2 = y_2 (G_2 (y_{10})y_{11}-G_{26}(y_{10})y_6-g_{102}y_{10}-m_2) \quad (4)$$

$$y'_3 = y_3 (g_3y_{11}+r_3y_{12}-g_{37}y_7-g_6y_6-m_3) \quad (5)$$

$$y'_4 = y_4 (g_4y_{11}+r_4y_{12}-g_7y_7-m_4) \quad (6)$$

$$y'_5 = y_5 (g_5y_1-G_{59}(y_{10})y_9-g_{105}y_{10}-m_5) \quad (7)$$

$$y'_6 = y_6 (g_6y_3+G_{26}(y_{10})y_2-g_8y_8-m_6) \quad (8)$$

$$y'_7 = y_7 (g_7y_4+g_{37}y_3-g_{78}y_8-g_9y_9-m_7) \quad (9)$$

$$y'_8 = y_8 (g_8y_6+g_{78}y_7-g_{108}y_{10}-m_8) \quad (10)$$

$$y'_9 = y_9 (g_9y_7+G_{59}(y_{10})y_5-m_9) \quad (11)$$

$$y'_{10} = y_{10} (g_{102}y_2+g_{105}y_5+g_{108}y_8-g_{12}-m_{10}) \quad (12)$$

$$y'_{11} = m_1y_1+m_2y_2+m_3y_3+m_4y_4+m_5y_5+m_6y_6+m_7y_7+m_8y_8+m_9y_9+m_{10}y_{10}+m_{11}y_{11}-y_{11}(G_1(y_{10})y_1+G_2(y_{10})y_2+g_3y_3+g_4y_4+W_1(y_{10})y_1+W_2(y_{10})y_2+W_5(y_{10})y_5) \quad (13)$$

$$y'_{12} = g_{12}y_{10}+y_{11}(W_1(y_{10})y_1+W_2(y_{10})y_2+W_5(y_{10})y_5)-y_{12} (r_3y_3+r_4y_4+m_{12}) \quad (14)$$

where y_i represents the mass in compartment i , g_i represents the growth rate for compartment i , m_i is a parameter representing the mortality rate of compartment i , g_{ij} is a parameter representing the transfer of mass from compartment i to

compartment j , and g_{12} represents the proportion of mass transferred from the human compartment to the inaccessible nutrient pool (or the “wastefulness” of the humans). Hence, g_{102} , g_{105} and g_{108} represent transfers from compartments 2, 5 and 8 to the top omnivore, g_{37} is the proportion of mass transfer from compartment 3 to 7 and g_{78} the proportion of mass transfer between compartments 7 and 8. The term m_{12} is the proportion of mass transferred from the inaccessible nutrient pool to the “accessible” nutrient pool by natural non-biological processes, e.g., erosion. Finally, the terms r_3 and r_4 represent the proportion of mass in the inaccessible nutrient pool that is recycled by P3 and P4, respectively. Note that the domestic branch cannot recover inaccessible mass, and that most transfers of mass are also proportional to mass in the compartments involved.

The symbols G_i and W_i represent variable growth and waste generation functions based on human activity. If the inter-compartment mass transfer (functions G_1 , G_2 , G_{26} , G_{59} , W_1 , W_2 , W_5 in equations 3 to 21) are constant, then this compartment functions essentially as a top omnivore animal that does not manipulate the system. When these functions are conditional on the mass of the human compartment (representing an available labor force), this is a primitive representation of a human society that encourages growth of some plants and herbivores (agriculture), builds “fences” around some compartments (H5 to C9 and P2 to H6) to regulate mass flow between one branch and another, and changes the efficiency of production methods and consumption. In Figure 1 dotted arrows represent mass transfers that are functions of the mass in the human compartment according to:

$$G_1(y_{10})=g_1y_{10} \quad (15)$$

$$G_2(y_{10})=g_2y_{10} \quad (16)$$

$$G_{26}(y_{10})=g_{26}/(1+y_{10}) \quad (17)$$

$$G_{59}(y_{10})=g_{59}/(1+y_{10}) \quad (18)$$

where G_{26} represents the rate at which H6 consumes P2 under ‘cultivation’, and G_{59} represents the rate at which C9 consumes H5. The functions in equations 17 and 18 indicate that, with a larger human population, there is more opportunity to invest in fences and to hunt to reduce the impact of herbivore 6 and carnivore 9 on P2 and H5.

The dashed arrows in Figure 1 that go through circles represent direct transfers from the accessible nutrient pool to the inaccessible nutrient pool, based on the mass in the

compartment to which the circle is connected. These represent the degree of “wastefulness” of the agricultural activities and are functions of the mass in the omnivore compartment:

$$W_1(y_{10})=w_1y_{10} \quad (19)$$

$$W_2(y_{10})=w_2y_{10} \quad (20)$$

$$W_5(y_{10})=w_5y_{10} \quad (21)$$

where W_i represents the rate of mass transfer from the accessible to the inaccessible nutrient pool in proportion to the mass in compartment i and the mass in the human compartment y_{10} . As the mass in the human compartment grows, more infrastructure is necessary and more waste is produced.

In addition to equations 3 through 21, there is an implicit and non-limiting flow of energy through the system. Hence, the system is open to energy but closed to matter. The mass closure constraint is:

$$\sum_i^{12} y_i' = 0 \quad (22)$$

All four plants ($y_1, y_2, y_3,$ and y_4) are subject to a cyclic forcing function to represent seasonal variation in their intrinsic growth rate. This forcing is the source of the periodic behavior for the model. The expression for the forcing function is:

$$g_i(t) = g_i \left[1 + \frac{1}{3} \sin \left(\frac{2\pi t}{12} - \frac{\pi}{2} \right) \right]^2 \quad (23)$$

where t is time, and g_i is the mean growth rate for plant i . We use MATLAB² software to simulate and explore the system behavior.

In this model, regimes were characterized by ranges of parameters over which the compartment masses settle to non-zero cycles. When the mass in a species compartment drops to zero, the species is not recoverable, even if parameters are changed back to those characteristic of the regime in which the species is persistent. Therefore, our measure of resilience does not include a return time, but rather only measures the range over which a parameter can vary without the loss of a species. We began the simulation at a value for the “wastefulness” parameter (g_{12}) within the regime in which all species are non-zero under the forcing. At specific timesteps, we increased g_{12} to the threshold at which a species is lost, and simultaneously measured the Fisher Information

of the system. We raised g_{12} three more times until three species disappeared and terminated the simulation.

3.1. Results

We began the simulation at $g_{12} = 0.15$, and ran the system for 5000 timesteps. Parameter g_{12} can vary as much as 0.1863 before a compartment mass falls to zero (Table 1). Resilience of this regime is therefore 0.1863. Fisher Information is 0.7 for $g_{12}=0.15$ (Figure 2a and 2b). We then raised g_{12} to $= 0.15+0.18631=0.33631$, and H5 was lost. The resilience for this second regime is 0.65369, and Fisher Information is approximately 1.0. At timestep 65000, we increased g_{12} to 1.0, and P1 was lost. For this regime with two less species, the resilience increases to 0.9, and Fisher Information increases to roughly 7.0. We increased g_{12} one last time to 2.0 at timestep 80000, and C8 was then lost from the system. The resilience of this regime is roughly 1.0, and the Fisher Information increases to 20.0. Fisher Information did not increase linearly with resilience, and therefore these two measures may rely on slightly different behavior when characterizing the system.

Table 1. Regime boundaries (as defined by changes in g_{12}), resilience (range over which g_{12} can change within the regime), Fisher Information (FI) and the species lost from each regime as g_{12} is increased.

Regime	resilience	FI	Species lost
$g_{12}=0.15-0.33630$.1863	0.7	None
$g_{12}=0.33631-0.99$.65369	1.0	H5
$g_{12}=1.0-2.0$	0.9	7.0	H5 & P1
$g_{12}=2.0+$	1.0	20.0	H5, P1 & C8

Fisher Information peaked during the transient periods following instantaneous changes in g_{12} , indicating that mass flows between compartments may have dramatically slowed or “stalled”. Indeed, the amount of variation (amplitude in the cycles) in mass in some of the compartments decreases as species are lost from the system, coinciding with an increase in Fisher Information (Figure 2a).

² Citation is for clarity only and does not imply approval or endorsement by the U.S. Environmental Protection Agency.

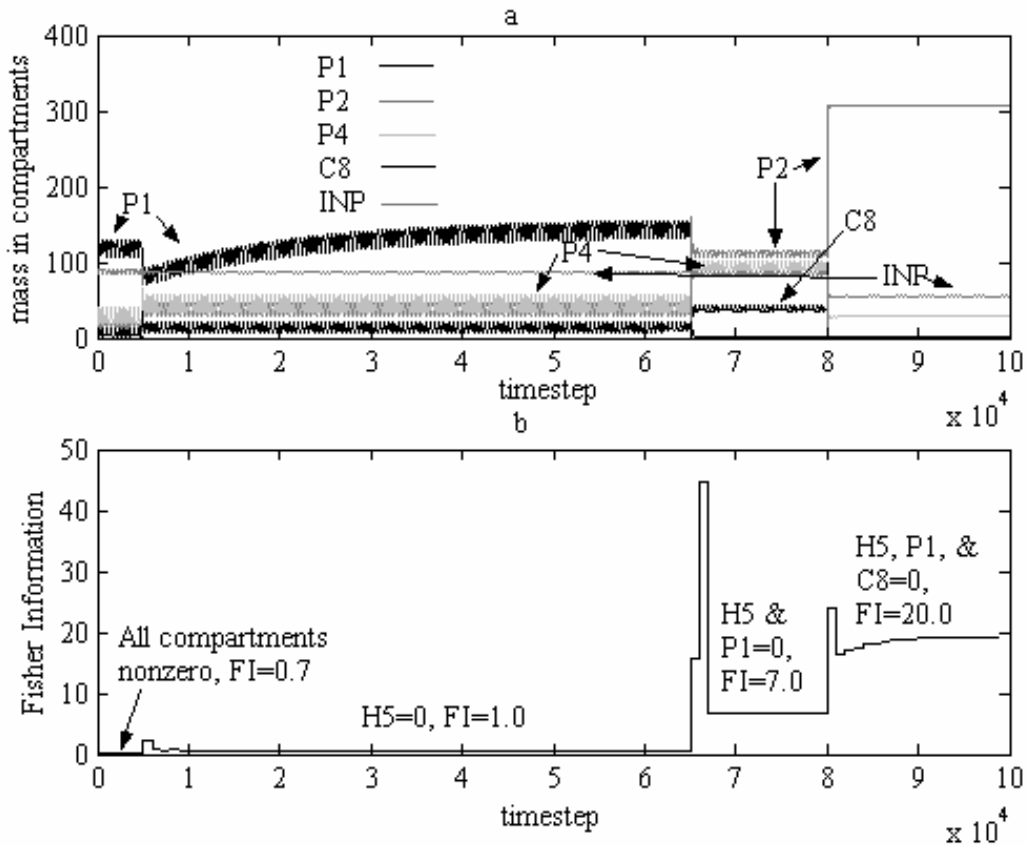


Figure 2. Simulation increasing wastefulness of human population (a), leading to a loss of species and an increase in resilience and Fisher Information (b). Only compartments that displayed an observable response to a change in g_{12} are displayed in (a) (e.g., the mass in the human compartment remains small throughout the simulation). At timestep 65000, mass in P2 drops to near zero, and from timestep 0 to 65000, mass in P2 and P4 are relatively equal.

3.2. Discussion

In this model, resilience (defined as the amount by which a parameter must be changed before a species is lost) increased as species were lost from the system (at least until 3 species were lost). Resilience is probably closely related to the conservation of mass attribute of this model. When the same amount of mass is divided between fewer and fewer compartments, the range over which a parameter can change and not trigger a species to fall to zero increases. In this respect the model, being closed to mass, is a poor mimic of many natural conditions, as local ecosystems are generally open systems. The Earth as a whole, however, is closed to mass, neglecting atmospheric losses and meteorites.

The increase in Fisher Information that here goes along with a decrease in viable compartments may be due to the decline in connectivity in the system, which decreases complex mass cycling. As this complexity is lost, the system shows preference for fewer states and Fisher Information

increases. Indeed, a “dead” system at equilibrium would have infinite Fisher Information. This occurs when all of the species go “extinct” and the mass ends up in the resource pools. Mass flows between the two pools at a fixed rate, and once equilibrium is reached the mass distribution between the two pools remains constant.

When g_{12} is changed gradually from one regime to another, Fisher Information is not steady but rather fluctuates as the mass cycling changes through the compartments. On average, however, Fisher Information increased as species were lost from the system. Fisher Information behaves differently when other parameters are altered, depending upon the manner in which those parameter changes cause the extinction of particular compartments.

In natural systems, we might also expect Fisher Information to increase with resilience, but not for the reason illustrated here. Systems that are able to maintain regular cycling (whether in population sizes, nutrient flows, etc.) after experiencing a perturbation would probably display a higher

preference for certain states, and therefore would be characterized by a higher Fisher Information than those systems that are more substantially disrupted. As we begin to understand the relationship between resilience and Fisher Information based on simple models, the use of these measures on complex models that more closely mimic real ecosystems and on data from real systems will become more straightforward. In addition, these indices may predict an approaching regime shift since, in response to perturbations, system variables can display an increase in variability. In natural systems, increased variability of the system variables generally indicates a loss of preference for the particular states of the system characteristic of the present regime, and generally this indicates the approach of a regime change. The Fisher Information form that we have constructed should have the capacity to detect this change, although whether it would respond by increasing or decreasing remains to be examined.

4. CONCLUSIONS

Although the model here is a caricature of a real system with known regime boundaries, the link between Fisher Information and resilience can be explained using real processes. In combination, Fisher Information and resilience can increase our ability to detect regimes and shifts between regimes, and can aid restoration, management, and sustainability efforts. More importantly, these measures are scale-independent, and can be used on a variety of ecosystems from small lakes to the global climate (Mayer et al. 2002). Fisher Information can be used on any system regardless of size or resolution or coverage of data, and data collected at disparate scales can be combined into this one index. As humans impact ecosystems over increasingly larger spatial and temporal scales, scale-independent measurements and methods to monitor sustainability become increasingly important (Patten 1998).

5. ACKNOWLEDGEMENTS

The authors thank Dr. Roy Frieden of the University of Arizona, Tucson for advice on the use of Fisher Information. In particular we appreciate the support and encouragement of Dr. Subhas K. Sikdar, the director of the Sustainable Technology Division.

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