

# Exergy and Information Indices: A Comparison for Use in Structurally Dynamic Models

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**Abstract:** Ecosystems are open, dynamic systems changing both their structure and their function over time. A model, which is an abstraction of the system manifest at the time of its construction, can project future dynamics so long as the fundamental structure of the system does not change. A primary modelling challenge arises when the system structure changes, i.e., internal reorganization, as a result of external perturbation. Ideally, one could include algorithms in the model to anticipate such changes, but that would entail knowing a great deal more about the system and disturbances to it than is possible. Other methods to anticipate, recognize, and adapt to changes are needed. A new modelling approach, structurally dynamic models, has been developed to address this need. Several methods have been used to implement structurally dynamic modelling; one is by optimising an ecological goal function. An ecological goal function is a macroscopic property of the system such as total system throughflow, total system cycling, residence time, or exergy. Structurally dynamic models can be constructed such that the model's parameters are continually updated –within accepted empirical bounds– to reflect values that generate the optimum value of the goal function. For example, a goal function for maximizing an exergy index has successfully modelled population dynamics. Another proposed goal function is an information index. In this paper, exergy and information indices are applied to a food web model to demonstrate and compare the usefulness of the new information metric for structurally dynamic modelling.

**Keywords:** Ecological Goal Functions, Ecological Modelling, Exergy, Fisher Information, Information Theory, Structurally Dynamic Modelling

## 1. INTRODUCTION

This paper compares two indices of dynamic systems, Exergy and Fisher Information. An exergy index has been used in many studies as an ecological organizing principle (Jørgensen 1992) including recent attempts to use it as a goal function in structurally dynamic models (Ray et al., 2001, Jørgensen et al. submitted). The expression for a Fisher Information index is based on sampling the system trajectory as it evolves in the state space. This index is sensitive to transients, and therefore, useful in detecting system ‘flips’ associated with external perturbations (Fath et al. submitted), however, there is no evidence documenting the direction of that change in regards to the functioning of that system. Its application as a goal function in structurally dynamic models depends on understanding its correlation with system behaviour. Given the success of exergy as a goal function in structurally dynamic models, a comparison would provide a useful test of the new

information based indicator. Here, the two indices are compared using three perturbation experiments on a 10-compartment food web model. Results indicate that Fisher Information and exergy indices exhibit an inverse relationship. Therefore, increasing Fisher Information may indicate decreasing system organization.

## 2. ECOLOGICAL INDICES

### 2.1 Information Indices

Information theory has been applied to ecological studies in several ways, primarily using Shannon Information (Shannon and Weaver 1949). The Shannon Information index commonly employed is an additive, global measure of system dispersion, and therefore, a useful measure of species richness such as biodiversity. Fisher Information, which has received little attention in the ecological literature, is a local measure of

dispersion. This paper uses a Fisher Information index for investigating ecological systems. Fisher Information, as developed by Ronald Fisher (1922), has been interpreted as a measure of the state of disorder of a system (Frieden 1998). This approach has recently been applied to fundamental equations of physics and problems of population genetics (Frieden 1998, Frieden et al. 2001). Fisher Information,  $I$ , for a single measurement of one variable is calculated as follows:

$$I = \int \frac{1}{P(\varepsilon)} \left( \frac{dP(\varepsilon)}{d\varepsilon} \right)^2 d\varepsilon \quad (1)$$

where  $P$  is the probability density function and  $\varepsilon$  is the deviation from the true value of the variable. Equation 1 is valid for periodic systems of one variable. The idea is that a highly disordered system has a more uniform or “unbiased” probability density function, which is broader than a highly structured system with low disorder, which shows bias to particular states. The probability of a variable taking on any given value is low in the more uniform density function, the slope of  $P$  is flatter, and this lack of predictability results in a system with low Fisher Information. Conversely, when the probability density function is steeply sloped Fisher Information is high.

## 2.2 Probability Density Function

In order to calculate Fisher Information, it is necessary to determine a probability density function for the system in question. A single probability density function for each system 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 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. A probability density function based on the amount of time the system resides in each state is given by:

$$P(t) = \frac{1}{\int_0^T d\tau} = \frac{1}{T} \frac{1}{R'(t)} \quad (2)$$

where  $R'(t)$  is the trajectory speed through phase space. Once a probability density function has

been ascertained for the system, Fisher Information can be calculated for a dynamic model. The Fisher Information integral in Equation 1 can be converted to an integral in time and by expanding the differential according to the chain rule to give:

$$I = \int \frac{1}{P(t)} \left( \frac{dP(t)}{dt} \right)^2 \frac{dt}{R'(t)} \quad (3)$$

which upon simplification yields:

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

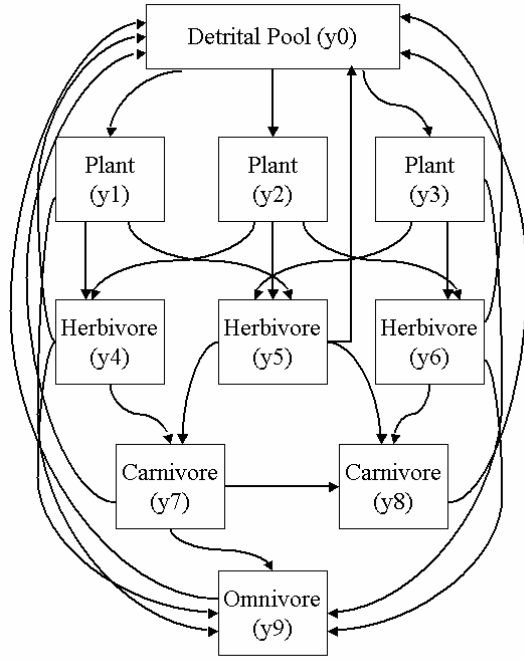
The Fisher Information for a dynamic system reduces to the integral of a ratio of acceleration to speed along the state trajectory. For a detailed description of the above derivation see Fath et al. (submitted).

## 2.3 Thermodynamic Indices

Several thermodynamically oriented properties have been proposed to describe ecosystem organization. These include the total system throughflow, total system storage, retention time and exergy (Jørgensen 1992, Fath et al. 2001). Exergy has been used successfully as a goal function in structurally dynamic models and is used here. Exergy is the amount of work that can be extracted from a system when brought into thermodynamic equilibrium with its environment. This includes both an energetic and information content embedded in the biomass, which has been estimated by the complexity of the organisms DNA. The total exergy is the sum of the compartmental biomasses each multiplied by an organism specific weighting factor. Standard values for these weighting factors are available in the literature for a variety of organisms (e.g., Marques et al. 1998). Since the Fisher Information index is a relatively new system indicator a comparison with an established goal function gives a benchmark on its behaviour. Specifically, here we compare the Fisher Information and exergy indices.

## 3. ILLUSTRATION: 10-COMPARTMENT FOOD WEB MODEL

In order to compare the two indices we apply them both to a hypothetical ten-compartment food web model. The model has three primary producers, three herbivores, two carnivores, an omnivore, and a detrital compartment (Figure 1). The primary producers are limited in growth by top-down (grazing from other compartments) and bottom-up



**Figure 2.** 10-compartment food web model. Arrows indicate direction of biomass flows. All mass recycles back to the detrital pool.

(resource availability) constraints. Standard Lotka-Volterra type equations describe the mass balance for the 10-compartment model:

$$\frac{dy_i}{dt} = y_i \left( \sum_{j=1}^n (-\varepsilon_{ij} \beta_{ij} y_j) - \alpha_i \right) \quad i=1, \dots, 9 \quad (5)$$

where  $y_i$  is the biomass of the  $i$ th compartment,  $\alpha_i$  is the mortality parameter,  $\beta_{ij}$  is the mass flow rate parameter between compartments  $i$  and  $j$ , and  $\varepsilon_{ij}$  is a two-dimensional Levi-Civita symbol such that  $\varepsilon_{ij}=1$  and  $\varepsilon_{ji}=-1$ . Due to conservation constraints,  $\beta_{ij}=\beta_{ji}$ . The only exception to this is the first

compartment ( $i=0$ ), which is a passive sink for biomass storage.

$$\frac{dy_0}{dt} = \sum_{j=1}^n \alpha_j y_j - y_0 \sum_{j=1}^n \alpha_j y_j \quad (6)$$

The three primary producers ( $y_1$ ,  $y_2$ , and  $y_3$ ) are subject to a sinusoidal forcing function to represent seasonal variation in growth, which gives the model periodic, limit cycle behaviour. Parameter values have been assigned such that all state variables remain non-zero throughout the simulation, but this model has not been calibrated. This scenario is the baseline case.

Three modifications to this baseline are presented to compare the how Fisher Information and exergy respond to gradual changes in the food web dynamics. In all cases a qualitatively similar perturbation regime was applied. The model system is at steady state 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 re-establishes steady state. The three cases include increasing the growth rate of one of the plant species ( $y_3$ ), decreasing the mortality rate of the omnivore ( $y_9$ ), and increasing the mortality rate of the omnivore ( $y_9$ ).

Table 1 shows the summary results for each perturbation experiment. All disturbances resulted in the loss of at least one species. One plant ( $y_1$ ) and one herbivore ( $y_4$ ) were eliminated in two of the three experiments. Fisher Information was calculated using the exact speed and acceleration by differentiating model equations. Exergy is calculated by multiplying a weighting factor by the amount of biomass in each compartment. Values for the weighting factor values, based on Marques et al. (1998), are given in Table 2.

Table 1. Simulation results before and after perturbations.

	$y_1$	$y_2$	$y_3$	$y_4$	$y_5$	$y_6$	$y_7$	$y_8$	$y_9$	$y_0$
Initial value	14.60	24.70	25.84	5.12	46.56	7.50	22.51	32.98	7.28	2.91
1. $\beta_{30}$ increase	0.00	0.00	60.45	0.00	61.85	6.83	7.78	42.88	7.56	2.69
2. $\alpha_9$ decrease	0.00	52.94	0.00	14.38	40.12	14.64	22.08	21.24	21.20	3.39
3. $\alpha_9$ increase	20.04	5.25	45.34	0.00	51.51	2.16	22.69	38.27	2.09	2.64

Table 2. Exergy weighting factors.

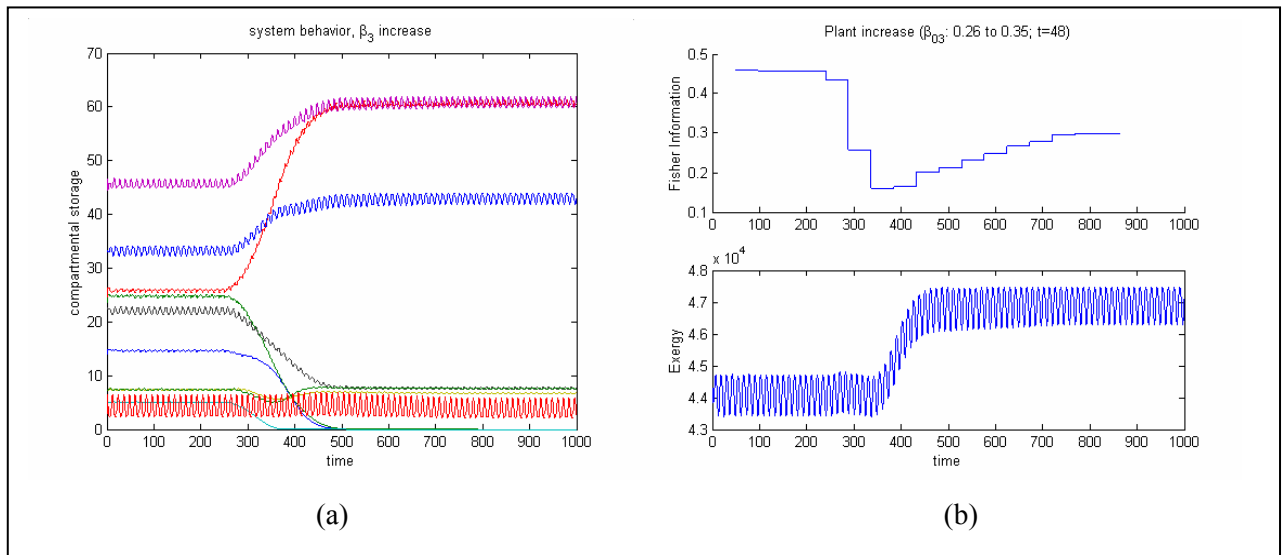
	plant t ( $y_1$ )	plant t ( $y_2$ )	plant t ( $y_3$ )	herbivor e ( $y_4$ )	herbivor e ( $y_5$ )	herbivor e ( $y_6$ )	carnivor e ( $y_7$ )	carnivor e ( $y_8$ )	omnivor e ( $y_9$ )	detritu s ( $y_0$ )
Weightin g Factor	30	60	90	150	200	250	350	450	740	1

#### 4. RESULTS

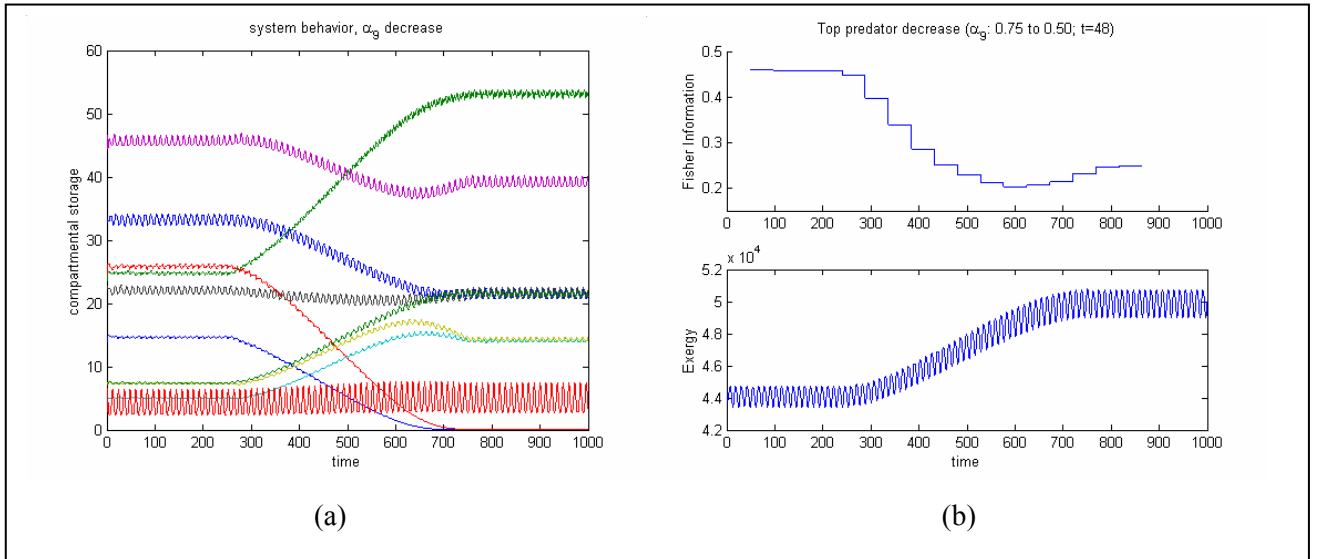
In the first case, the uptake rate of the third plant compartment ( $y_3$ ) increases from 0.26 to 0.35. Figure 2a shows the simulation results of the ten compartments. The gradual increase in the growth rate of  $y_3$  results in an increase of  $y_3$ ,  $y_5$  and  $y_8$ , and the elimination of compartments  $y_1$ ,  $y_2$  and  $y_4$ . The level of  $y_7$  decreases sharply (Table 1). Figure 2b shows the response of the Fisher Information and exergy indices. Since the Fisher Information index is based on the probability of sampling the system in a particular state, it must be calculated over a given period. In this case it is averaged over 48 time steps (months), which is four times the period of the annual forcing function. Fisher Information shows a marked drop over the transient before steadying off at a level about midway between the initial maximum value and minimum value during the transient. Exergy is calculated at each time step, and therefore, displays the influence of the seasonal sinusoidal forcing function. However, in addition to this short-time transient is a long-term trend in which the exergy index increases sharply during the perturbation in the second quartile as a result of the increase in the growth parameter for compartment  $y_3$ . Clearly, exergy and Fisher Information respond in opposite directions to the perturbation.

In the second case, the omnivore mortality rate decreases from 0.75 to 0.50 (Figure 3a). The perturbation influences the system more gradually as seen by the much longer transient. In this simulation two plant compartments were eliminated,  $y_1$  and  $y_3$ . The remaining plant compartment ( $y_2$ ) increases sharply as does the omnivore itself. Figure 3b shows the Fisher Information and exergy responses. As before, the Fisher Information decreases in response to the perturbation and the exergy index increases.

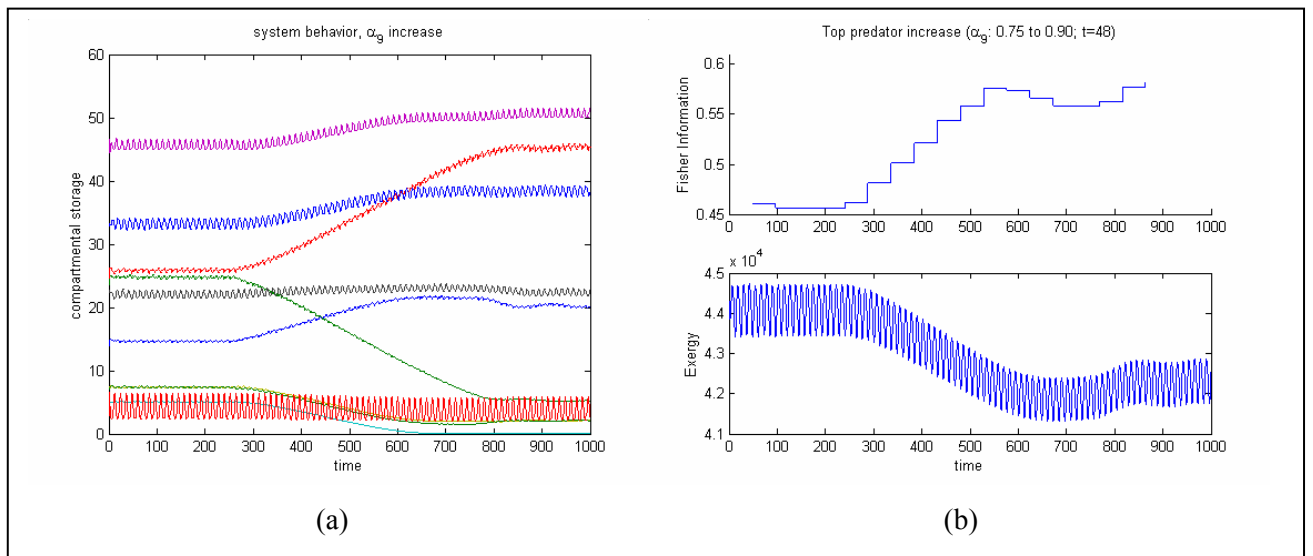
In the final case, the omnivore mortality rate increases from 0.75 to 0.90 (Figure 4a). Only one compartment, herbivore  $y_4$ , is eliminated. The transient has not completely settled by the end of the simulation, but no other compartments are headed to extinction. One plant compartment ( $y_2$ ) and the omnivore also experience sharp declines, whereas one plant compartment ( $y_3$ ) experiences the greatest gain in biomass. Figure 4b shows that in this scenario Fisher Information increases in response to the perturbation, however, the exergy index decreases in response to the perturbation. The inverse relationship between exergy and Fisher Information occurs in all three perturbation experiments.



**Figure 2** 10-compartment model simulation in which the growth rate of the primary producer,  $y_3$ , experiences an increase from 0.25 to 0.35 between  $t=250$  and  $t=750$ ; a) System behavior, b) Average Fisher Information (over 48 time steps) and exergy.



**Figure 3.** 10-compartment model simulation in which the mortality rate of the omnivore,  $y_9$ , experiences a decrease from 0.75 to 0.50 between  $t=250$  and  $t=750$ ; a) System behavior, b) Average Fisher Information (over 48 time steps) and exergy.



**Figure 4.** 10-compartment model simulation in which the mortality rate of the omnivore,  $y_9$ , experiences an increase from 0.75 to 0.90 between  $t=250$  and  $t=750$ ; a) System behavior, b) Average Fisher Information (over 48 time steps) and exergy.

## 5 CONCLUSIONS

The purpose here was to investigate the use of a Fisher Information index as a goal function in structurally dynamic models. One may ask why develop a structurally dynamic model at all and not simply build a larger, higher-order model (HOM) to explicitly incorporate the factors

believed to underlie system variation. One reason is that an open system, which is embedded in and influenced by the external environment, must have boundaries as an object of study. In addition, it is not only practically impossible to build a HOM which includes all potential relevant factors, but theoretically impossible as well. Kauffman (2000) describes system behaviour as a transition into the

“adjacent possible”. The adjacent possible comprises all possible states reachable from the current position. Two important considerations follow: First, the adjacent possible is indefinitely expandable; and second, it is impossible to prestate the configuration space of the system. Therefore, it is impossible to state all relevant properties in a larger HOM because there is no finite description of a simple physical object *in its context*. Kauffman uses an example of a coffee table. Specific dimensions of the object (coffee table) are stateable: length, width, height, material, color, texture, four legs, etc. In context there are an infinite number of properties: it is two feet from the sofa, eight feet from the door, 4.3 light years from Alpha Centauri, etc., and that behaviour may be influenced by any of these relations. When an object is defined by its relations, context is the important concept. Although Kauffman does not explicitly state it, context is the environment a system experiences beyond its boundary. This provides motivation for using ecological goal functions since they measure the system response in its context. Organization of the system components is continually being updated by the influences of environment and goal functions give a holistic way to track those influences. Ultimately, the aim of modelling is to gain insight into the behaviour of the ecosystem which using goal functions allows.

In conclusion, a 10-compartment food web model is used to demonstrate and compare the response of two system-level indices following a perturbation. Three different scenarios were investigated, and in all cases the Fisher Information and exergy indices exhibited an inverse relationship. The exergy index, which has already been shown to track system organization, is a good test for the Fisher Information index, which until now has been used to detect transient behavior without any indication of the direction of the behavior. Fisher Information may be a suitable goal function in structurally dynamic models; however, based on its comparison to exergy, these examples indicate that the Fisher Information index decreases with increased system organization. Also, the exergy index is a more practical measure since it is considerably easier to compute. Nonetheless, this was an important comparison in order to better understand the response of the Fisher Information index. The next step is to further compare the indices utilizing calibrated ecosystem models. However, the simple heuristic model presented here provides a good starting place for evaluating the Fisher Information index and its potential role as a goal function in structurally dynamic models.

## 6. ACKNOWLEDGEMENTS

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