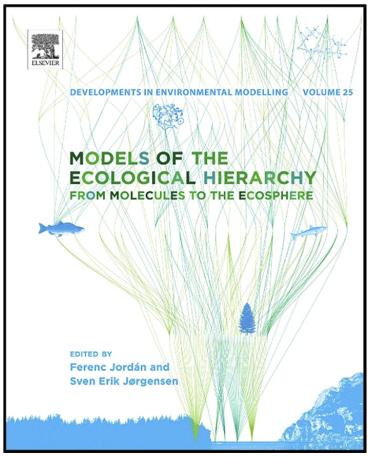

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31

Hierarchical Energy Dissipation in Populations

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This chapter is devoted to three great ecologists: Leonardo Malacalza, Eduardo Rapoport and Ramón Margalef (in memoriam). They all have been a guide, an inspiration and an example.

31.1 Introduction to Populations as Thermodynamic Systems

Biological populations are characterized by structural and demographic magnitudes such as density, age or stage structure, and growth and mortality rates. These are the typical magnitudes that are studied by ecologists, who analyze the relationships among them in terms of population dynamics. There is, however, another point of view to study biological populations, which consider them as open thermodynamic systems, i.e., systems that interchange matter and energy with their environment, and are, moreover, the units of entropy production and entropy exchange (Michaelian, 2005).

Populations are constituted by individuals, which are complex dissipative systems that remain far from thermodynamic equilibrium (Ulanowicz and Hannon, 1987). But the population is a system of a higher order of complexity: in a population, individuals born and die, also grow, and, eventually, suffer metamorphosis or changes in their reproductive stage.

The set of all interacting individuals constitute the system that we call population. It is a complex dissipative system, which is capable to regulate certain emergent properties.

If we adopt this point of view, it is clear that populations are also far from its thermodynamic equilibrium. Populations are, in general, in some stationary state characterized by a given biomass, density, age (or stage) structure, and a specific regime of energy and entropy fluxes.

In order to formalize these concepts, we must carefully define the different terms in stake.

We will focus animal populations, and start with a very imperfect analogy, considering the population like a sort of "turbine" activated by a "fall" of energy, which is sourced by

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food. Because populations are open systems, they dissipate low-quality energy (heat) and pour degraded matter to the environment. Of course, food is not the sole energy that population receives; however, we assume here that it is at thermal equilibrium and other forms of energy such as heat or light are in a stationary regime. Then, the biological work made by individuals (that is translated as demographic changes at the population level) will be supported by the chemical energy in the food.

The energetic gradient under which populations work is given by the difference of free energy between source and sink (i.e., between foods and waste). We will call this gradient $\Delta E_{SourSink}$ (see Fig. 31.1), that is, the free energy contained in the food (E_{So}) minus the energy contained in the detritus (E_{Si}). The flux of energy running throughout a population is directly proportional to this gradient.

According to Prigogine (1978), in nonequilibrium stationary states, the perturbation in the produced entropy is given by

$$\frac{1}{2}\frac{\mathrm{d}}{\mathrm{d}t}\delta^2 S = \sum(\delta J_p \delta X_p). \tag{1}$$

Here, δS is the perturbation in entropy production, the terms $\delta J_p$are the deviation in the rates of various irreversible processes, and δX_p are the deviations in the generalized forces (affinities, gradients of temperature, etc.).

The question is what happens when the system (i.e., the population) is far from equilibrium and, moreover, far from the stationary regime?

In order to tackle this problem, we propos to follow the previous analogy and consider that, like in another physical systems, when a flux that is proportional to a given gradient exists, entropy dissipation is proportional to the square of that gradient (it is non linear). We can synthesize these as follows:

$$\begin{aligned} \frac{\mathrm{d}E}{\mathrm{d}t} &\propto k_1 \Delta E_{\mathrm{SourSink}} \\ \frac{\mathrm{d}_e S}{\mathrm{d}t} &\propto k_2 (\Delta E_{\mathrm{SourSink}})^2. \end{aligned} \tag{2}$$

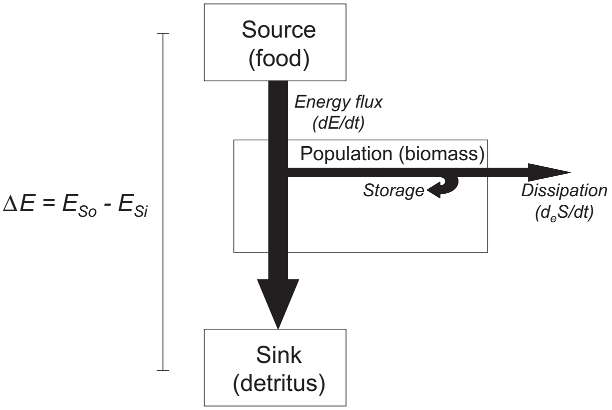

FIGURE 31.1 Conceptual representation of biological populations as dissipative systems.

In Eqn (2), $\frac{d_e S}{dt}$ represents the amount of entropy dissipated by the population to its environment per unit of time.

Energy flows (Fig. 31.1) can be associated to population dynamics and to different demographic phenomena: inputs or energy are transformed basically in work and biomass. The biological work is measurable throughout the metabolic rate of the individuals in the population and, due to the second law of thermodynamics it is in a direct correlation with a fraction of the entropy exchange between organisms and environment. The other fraction of the entropy exportation is measured by mortality.

The amount of energy that is not spent is stored as new biomass.

Finally, egestion, excretion, and other matter exchange phenomena are responsible of the remainder flux of energy (and entropy) to the detritus (the sink).

When ΔE varies abruptly, the regime of the system becomes far from the stationary state; the rapid (nonlinear) increase of the dissipated entropy allows the system to recovery the stationary regime but in a new state. In a population, this new state will be defined by a given age and size structure.

31.2 Demography and Thermodynamics

In a recent work, we have shown that several modifications in the population demography can be interpreted in a thermodynamic way (Momo et al., 2010). In fact, we can say that populations are dissipative systems because they maintain their age structure and biomass by pumping entropy to their environment.

Assuming that if populations make some kind of mechanical work, this work will be transformed finally to heat, and by analogy with other thermodynamic systems, we can postulate the following relationship:

$$\frac{dS}{dU} = \frac{1}{T} \tag{3}$$

where S is the entropy, U is the internal energy, and T is temperature. However, this relationship is incomplete for ecological purposes because dissipative systems maintain their organization by mean of fluxes of entropy and energy, and it is more accurate to write:

$$\frac{dS/dt}{dU/dt} = \frac{1}{T}. \tag{4}$$

Equation (4) represents the relationship between entropy expulsion, and the energy exchange between the system and its environment. If both fluxes are calculated, the magnitude $\tau = \frac{1}{T}$ may be interpreted as a demographic sensitivity.

Two demographic tools can be used to this approach: the first are the Leslie matrices, which represent populations divided into age classes of the same length as the time step, and that can be used to simulate the population dynamics; the second are the survival curves, which show the percent of a cohort that survives until a given age, and can be associated to different demographic traits suggesting how population allocate the available energy.

In Momo et al. (2010), we have also shown that Leslie matrices contain information about the way in which a population dissipates energy and pumps entropy outside the system, and have also shown that *r*-selected populations have higher entropic costs than *K*-selected populations, whereas populations having Type I survival curves (high survival of immature and low survival of adults) have lower entropic costs than populations with Type IV (high larvae mortality) survival curves.

Consider now a Leslie matrix (A) with three age classes, where only the last age class reproduces

$$A = \begin{bmatrix} 0 & 0 & f \\ s_1 & 0 & 0 \\ 0 & s_2 & s_3 \end{bmatrix}, \qquad (5)$$

where f is the fertility and s_i are survival rates.

In this demographic model, we can represent different trade-off, as we will show in a moment. In that work, authors assumed that $f = 1/(s_1 s_2)$ in order to have a $\lambda_1 > 1$ (growing populations); then, numerical simulations were performed considering different cases having more or less fertility combined with more or less survivals (i.e., the *r*–*K* trade-off). In addition, the relationship between s_1 and s_2 was changed in order to simulate the shift between different survival curves (from type I to IV).

Computing the demographic entropy ($H = \Sigma pi \log(pi)$) for each gradient, authors observed that both trade-offs are not equivalent and *K*-selected populations maximize their demographic entropy (Fig. 31.2).

Despite the interest of this approximation, it is strongly limited because the relationship shown in Eqn (3) is only true under linear and near to equilibrium conditions, and the demographic entropy considered in the model is only a measurement of the relative abundance of individuals of different ages; so, it is not a true entropy in a thermodynamic sense, and it does not represent a flux. In consequence, it is necessary to deepen in the problem in order to catch the complete picture including nonlinear and far from equilibrium regimes and energy and entropy fluxes.

31.3 Body Size and Metabolic Rate

The metabolic rate is the fundamental biological rate, because it is a measure of energy uptake, transformation, and allocation (Brown et al., 2004). Metabolic rate is linked to the rates of many other biological activities at various hierarchical levels of organization (Brown et al., 2004; Glazier, 2005). Moreover, studies of metabolism are useful tools for understanding the patterns of energy flow in populations and ecosystems (Glazier, 1991; Doyle and Momo, 2009; Doyle et al., 2012).

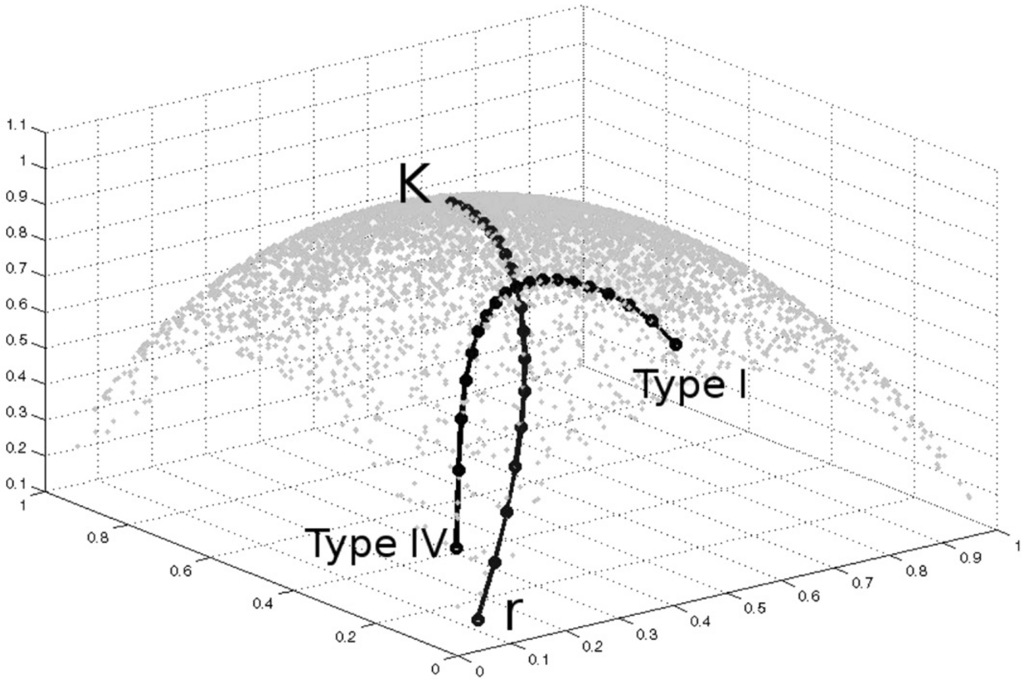

FIGURE 31.2 Phase space of populations following *r*–*K* or Type IV—Type I trade-offs. Horizontal axis are percent of ages 2 and 3; the vertical axis indicates the entropy. Points indicate the level of demographic entropy.

Several variables influence the metabolic rate of organisms; among these, temperature and body size (generally understood as body weight) are the most important (Gillooly et al., 2001).

Temperature is the dominant abiotic factor that affects metabolic rate in ectothermic organisms, and its effect on metabolic rate is due to the thermodynamic nature of the kinetics of chemical reactions and enzyme conformational changes (Hill et al., 2004). In ectothermic animals, metabolic rate increases exponentially with temperature within a certain range up to a maximum value, and further increase in temperature produces a decrease in metabolic rate (Schmidt-Nielsen, 1997). The acute response of metabolic rate to temperature is due to the thermodynamic nature of the kinetics of chemical reactions and enzyme conformational changes (Hill et al., 2004).

Body size is the most biotic factor that regulates metabolic rate, and it has been recognized like that since the seminal work of Kleiber (1932). More recently, the books by Peters (1983) and Schmidt-Nielsen (1984) have summarized some regularities relating the body size with the physiological and population parameters, including metabolic rate. Knowledge of the relationship between body size and metabolic rate has multiple applications in ecology; for instance, it is possible to estimate the whole respiration of a population from its body size distribution. In an animal population, size distribution is a measure that can be obtained easily, and thus the whole respiration of the population can be estimated with a relatively low survey effort (LaBarbera, 1989; Han and Straškraba, 2001).

The expected relationship between metabolic rate (MR) and body weight (W) is an allometric scaling:

$$\mathrm{MR} = a \cdot W^{b}. \tag{6}$$

The constant a is a proportionality parameter whose value is equal to the metabolic rate of an individual having a unit body weight; the parameter b is known as the scaling exponent. The metabolic rate per unit of biomass or specific metabolic rate (SMR) can be similarly calculated as:

$$\mathrm{SMR} = a \cdot W^{b-1}. \tag{7}$$

It is clear that the metabolism of a given size class in the population can be calculated by multiply Eqn (7) by the abundance of the class.

31.4 Going Further: Thermodynamic Regime of Populations

Let us go back to the Prigogine (1978) approximation: if a population is in a stationary state, its amount of internal (structural) entropy remains roughly constant. If it is assumed that the system is near the equilibrium, we can expand the function of entropy as follows:

$$S = S^{*} + \delta S + \frac{1}{2}\delta^{2} S, \tag{8}$$

were S^* denotes the entropy in the stationary state, and δS is the fluctuation in entropy around that stationary value. Because $\delta^2 S$ can be considered a Lyapunov function of the system (Jørgensen and Svirezhev, 2004), a given state will be stable (in both the thermodynamics sense and the Lyapunov sense) if it is verified that $\delta S = 0$, $\delta^2 S < 0$, and $\frac{\mathrm{d}}{\mathrm{d}t}(\delta^2 S) > 0$. In this condition, biomass, density, and age structure of the population remain constant, while $\frac{\mathrm{d}_i S}{\mathrm{d}t} = \frac{\mathrm{d}_e S}{\mathrm{d}t}$, and the total amount of internal entropy of the population remains constant. Hence, the mortality rate, integrated through all ages, equals the birthrate of the population.

However, populations rarely are near to the equilibrium and therefore these relationships ought to be different, because the entropy pumping to the environment grows nonlinearly with the energy gradient as is shown in Eqn (2). The distance from equilibrium can be measured by mean of one of the classic magnitudes used in the literature, among which *exergy* is one which has been most widely used (Jørgensen and Svirezhev, 2004). Meysman and Bruers (2007) have proposed the use of the disequilibrium between resource and waste products as a meaningful measure of the distance from equilibrium of an ecological system. In the context of this chapter, this last approximation is a good way to relate the forcing variable (the energetic cascade) with the response variable (the rate of entropy exportation) and, moreover, the state variable of the population (its structural entropy). We will assume that, under realistic conditions, the energetic distances between food and detritus are large, and the population has a very low probability to be near to the thermodynamic equilibrium.

In a far from equilibrium condition, populations fight against the Second Law in order to maintain not only their biomass, but their organization. In this regime, higher-order interaction terms in the relationship between forces and fluxes are not negligible.

31.5 Symmetry Breaking and Hierarchical Responses of Population

We postulate that, when the difference of free energy between the source (food) and the sink (detritus) starts to grow, the exportation of entropy to the environment ($\mathrm{d}_e S/\mathrm{d}t$) starts to vary according to the power relation shown in Eqn (2). One might ask, however, what is exactly $\mathrm{d}_e S/\mathrm{d}t$? We consider here that this rate is composed by two terms: the first represents the metabolic dissipation of all individuals in the population, and the second represents the mortality of every age or stage class.

The metabolic rate of a given individual, as previously exposed, is mainly determined by its body size and environmental temperature. As a consequence, the amount of entropy exchanged by each size class in the population will be given by the product between the mean body size of the class, the SMR for that size, and the relative abundance of the stage; all these magnitudes are multiplyed by a constant to adjust units and divided by T, the absolute temperature.

Mortality rates are also determined by the body size, but affect the relative abundance of each stage.

Briefly, we can write the following:

$$\frac{\mathrm{d}_e S}{\mathrm{d}t} = \frac{k_3 n}{T} \sum_{i=1}^{m} \mathrm{SMR}_i p_i \overline{B}_i + k_4 n \sum_{i=1}^{m} \mu_i p_i, \tag{9}$$

where $p_i = n_i/n$ is the relative abundance of the i-stage, $\overline{B}_i$ is the mean body biomass of the i-stage, and μ_i is its mortality rate.

Considering that ΔE is growing, the flux of entropy must vary over time and we can write:

$$\frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{\mathrm{d}_e S}{\mathrm{d}t}\right) = \frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{k_3 n}{T} \sum_{i=1}^{m} \mathrm{SMR}_i p_i \overline{B}_i + k_4 n \sum_{i=1}^{m} \mu_i p_i\right). \tag{10}$$

If we expand Eqn (10), under isothermal conditions and assuming that $\overline{B_i}$ are constant, we obtain the following expression:

$$\begin{aligned}\frac{\mathrm{d}_e^2 S}{\mathrm{d}t^2} = {} & \frac{\mathrm{d}n}{\mathrm{d}t}\left(\frac{k_3}{T}\sum_{i=1}^{m}\mathrm{SMR}_i p_i\,\overline{B}_i + k_4\sum_{i=1}^{m}\mu_i p_i\right)+ \\ & +n\left\{\frac{k_3}{T}\left[\sum_{i=1}^{m}\left(\frac{\mathrm{d}p_i}{\mathrm{d}t}\mathrm{SMR}_i\,\overline{B}_i\right)+\sum_{i=1}^{m}\left(p_i\overline{B}_i\frac{\mathrm{dSMR}_i}{\mathrm{d}t}\right)\right]+k_4\left(\sum_{i=1}^{m}\left(\frac{\mathrm{d}p_i}{\mathrm{d}t}\mu_i\right)+\sum_{i=1}^{m}\left(p_1\frac{\mathrm{d}\mu_i}{\mathrm{d}t}\right)\right)\right\}\end{aligned} \tag{11}$$

We can see that the first term in Eqn (11) represents the effect of the population density variation. In the second term, we have the effect of the whole population metabolism given by the variation in the relative abundances of stages: $\frac{k_3}{T}\left[\sum_{i=1}^{m}\left(\frac{\mathrm{d}p_i}{\mathrm{d}t}\mathrm{SMR}_i\,\overline{B}_i\right)\right]$. Similarly, the whole population metabolism can be modified by changes in the specific metabolic rate of each size class: $\frac{k_3}{T}\left[\sum_{i=1}^{m}\left(p_i\overline{B}_i\frac{\mathrm{dSMR}_i}{\mathrm{d}t}\right)\right]$. The remaining terms indicate the variations in the flux of entropy that depend on total mortality, influenced by relative abundances and group mortalities variations. All these effects are summarized in Table 31.1.

As the difference between source and sink is increasing ($\mathrm{d}\Delta E/\mathrm{d}t > 0$), the flux of entropy to the environment also increases. When the ratio between this rate and the energy flow rises the critical values, symmetry can break, in consequence the population rises a new stationary state (i.e., it becomes a new dissipative structure) characterized by a particular amount of structural entropy.

However, the different terms of Eqn (11) change with a particular timing. The first effect in be apparent is the physiological one (term C of Table 31.1) because individuals

Table 31.1 Mean of the Components of the Eqn (11) (Changes in the Rate of Entropy Exchange Between Population and Environment)

A	$\frac{\mathrm{d}n}{\mathrm{d}t}\left(\frac{k_3}{T}\sum_{i=1}^{m}\mathrm{SMR}_i\,p_i\overline{B}_i + k_4\sum_{i=1}^{m}\mu_i p_i\right)$	Is the global effect produced by the change in the population density
B	$n\frac{k_3}{T}\left[\sum_{i=1}^{m}\left(\frac{\mathrm{d}p_i}{\mathrm{d}t}\mathrm{SMR}_i\,\overline{B}_i\right)\right]$	Represents the changes in the total metabolism of the population given by changes in the relative abundances of the different size classes
C	$n\frac{k_3}{T}\left[\sum_{i=1}^{m}\left(p_i\overline{B}_i\frac{\mathrm{dSMR}_i}{\mathrm{d}t}\right)\right]$	Is the change in metabolism produced by the variation in the SMR of each size class. It represents the physiological effect of modifying the energetic quality and quantity of food
D	$nk_4\left[\sum_{i=1}^{m}\left(\frac{\mathrm{d}p_i}{\mathrm{d}t}\mu_i\right)\right]$	Is the change in total mortality given by the modification of the relative abundances of size classes
E	$nk_4\left[\sum_{i=1}^{m}\left(p_1\frac{\mathrm{d}\mu_i}{\mathrm{d}t}\right)\right]$	Is the change in the mortality effect due to the modification in stage-specific rates of mortality

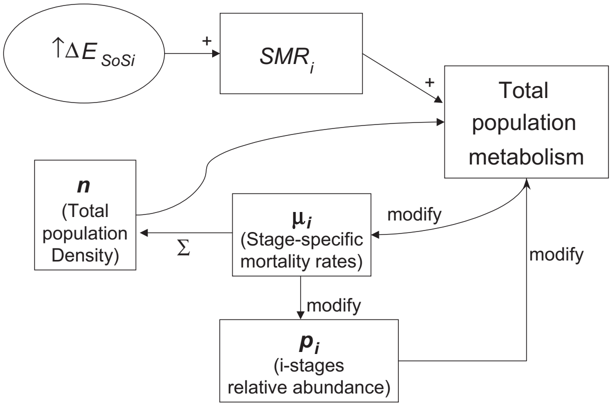

FIGURE 31.3 Conceptual relationships between the different components of the entropy flux variation.

respond to a better input of food. The well-known effect of food on metabolic rates is the reason by which standard measurement of metabolism are made in fasted animals, and has a characteristic time scales of hours to days. Moreover, a trend to higher metabolic rate with increasing potential food availability, a related but different phenomenon operating at larger time scales, has been observed in several invertebrates (Brockington, 2001; Brockington and Peck, 2001; Fraser et al., 2002; Doyle et al., in press).

This change produces in a second instance a modification in the survival probability for each size class; if the food is better, all stages have lower mortality rates but the effect is mediated by the allometric dependence of the size. In consequence, term E is the second in be modified and causes a shift in relative abundances of stages (term D). Changes in relative abundances produce modifications in the total metabolism of the population (term B).

Finally, the population density (term A) changes until the biomass rises a new state stage. These phenomena are summarized in Fig. 31.3.

In this way, a sort of "cascade" of effects is caused by a change in energy flow throughout the population. This succession of changes can be detected experimentally by the measurement of the metabolic rate of the population and the Shannon entropy of size classes (stages or ages), that is, the demographic entropy *sensu* (Demetrius et al., 2004, 2009). If we plot these magnitudes versus the energetic difference between food and detritus, the phase transitions will be apparent by abrupt changes in the slope of each curve (Fig. 31.4).

31.6 Concluding Remarks

Ecological populations involve a set of nested biological phenomena, from physiological to demographic ones. This hierarchical structure constraints and determinates the thermodynamic response to changes in the flux of energy. Each biological process has

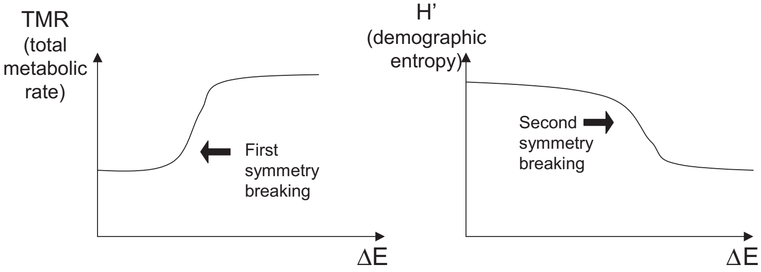

FIGURE 31.4 Phase diagrams of the symmetry breaking in metabolism and size structure. When the energetic skip is high, the final stable state of the population is given by a higher metabolic rate and a lower diversity of sizes.

a characteristic velocity of response to environmental changes, so there is a successive group of responses in the population.

The consideration of nonlinear effects in thermodynamic processes allows us to predict some general timing in the responses and, in this way, it is possible to test experimentally the validity of our model and hypotheses. First of all, the metabolic rate of individuals should show changes under an increment of energy availability. In a second phase, we should see differential changes in the mortality rates of the different size classes. Finally, the size structure of the population should change together with its density.

Experiments that investigate these predictions will be very important in order to continue building a strong thermodynamic theory of ecological systems.

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