Biological age from the viewpoint of the thermodynamic theory of ecological systems

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ABSTRACT

Not all ecosystems are in a steady-state or approaching it. Some of them merely pass through the life-cycle stages. The best example is the forest ecosystems formed by even-aged forest stands, where ecosystem properties and functions are related to the stand age. The relationship is not strict, however, and so the stand age is not a general measure of ecosystem state. We propose and theoretically justify a thermodynamic measure for ecosystem state, which is named here as ecosystem biological age and defined as the period of time that some reference ecosystem needs to accumulate the same amount of exergy as the ecosystem under concern. The use of the concept is illustrated by analyzing the 30-year observations of larch stands growth.

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1. Introduction

The founder of *Ecological Modelling*, Sven Jørgensen, once said, "Ecological Modelling and systems ecology are inseparable" (Joergensen, 1999). Since "a model cannot give the details of an ecosystem but only describe it in the system level" (Joergensen, 1999), to develop an original ecosystem model one should first conceptualize ecosystem features as system properties. The system analysis starts from drawing a boundary between the ecosystem and its environment (Fath, 2014). A modeller should select the objects that form an ecosystem and define how they interact with each other. There are no strict rules for defining the objects. Each component of the ecosystem could be considered as an object. It could be a large group of organisms like autotrophs and heterotrophs, or even individual organism. For example, the individual-based models (Judson, 1994; Grimm, 1999; DeAngelis and Mooij, 2005; Shuman et al., 2013) are focused on system-level phenomena emerging from individual traits of organisms and their interactions with other organisms and 'ecosystem environment'.

Interaction between an organism and its environment is a traditional field of ecological researches (Amano, 2012). The effect of environmental conditions on organism growth and development is often considered in ecological models (Usoltsev et al., 2002; O'Neill and Nigh, 2011; Kindermann et al., 2013; Anyomi et al., 2012; Maclean et al., 2012; Armstrong and Brooks, 2013; Rasche et al., 2012; Bellassen et al., 2010; Shanin et al., 2013). Most models reflect the wide-spread opinion that environmental conditions can be categorized into more favorable and less favorable. The most favorable conditions are said to be optimal.

If the conditions of growth deviate from the optimal, the organisms grow slower – that is, they need more time to reach a given weight, or height, or size (there is a number of biometric indicators that are used to characterize the growth). The biometric differences between organisms could be thus expressed in terms of delay in development. For example, if the growth is measured by a single biometric indicator, then the organisms which are "smaller" in sense of this indicator may be considered as biologically "younger".

The estimate of the age derived from a biometric indicator is said to be the "biological age" of the organism. The notion of biological age is used in biomedical studies to characterize the difference between the "biometric portrait" of an individual and that of its age cohort (Bourlier, 1970; Mitnitski et al., 2002).

Similar notion could be used to characterize the differences between forest ecosystems of the same age. The forests which are managed using even-aged silvicultural systems consist of even-aged stands, that is, patches of forest vegetation that are reasonably homogeneous in terms of age and species composition. In the ideal case thus regulated forest makes up a "shifting mosaic" of stands (Remmert, 1991) that differ in age. The stand age does not exceed the rotation age, an important management parameter which is set at the point where forest stand achieves the quality that makes it ready for harvest. Since the age at which the stand achieves the required quality depends on the conditions of growth, the rotation age is raised under non-optimal conditions.

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Notation

γ	is the coefficient in the Kostizyn–von Bertalanffy equation, Eq. (1), that characterizes the organism shape
ϕ	is the coefficient that characterizes the specific energy of the organism in Eq. (6)
ψ	is the feeding area of an individual tree, Eq. (9)
N	is the number of trees per hectare
N^*	is the asymptotic value of N
p	denotes the coefficient characterizing the specific rate of energy consumption in Eq. (1) and the site productivity in Eq. (9)
$\tilde{p}$	is the coefficient characterizing the specific rate of energy outflow in Eq. (4)
r	is the coefficient characterizing the specific rate of metabolism in Eqs. (1)–(9)
$\tilde{r}$	is the coefficient characterizing the specific rate of entropy production in Eq. (4)
S	is the entropy of a living organism, Eq. (4)
T_R	is a reference temperature, Eq. (6)
t_{max}	is the age, at which exergy is equal to zero
V	denotes the organism volume in Eqs. (1)–(8) and the wood volume of individual tree in Eqs. (9)–(22)
V_{max}	denotes the asymptotic value of the organism volume in Eq. (1) and that of wood volume in Eq. (9)

In this paper we interpret the notion of biological age from the viewpoint of the Jørgensen–Svirezhev theory (Jorgensen and Svirezhev, 2004), assuming that exergy could be used as a generic indicator of ecosystem state, propose a definition for "ecosystem biological age", and illustrate the use of this concept by analyzing 30-year observations on larch stands growth published by the Hokkaido Research Center of the Forestry and Forest Product Research Institute (Ishibashi et al., 1995).

2. Theory

According to the Jørgensen–Svirezhev theory (JST) the growth of an organism could be described by the generalized Kostizyn–von Bertalanffy equation:

$$\frac{dV}{dt} = pV^{\gamma}\left(1 - \frac{V^{1-\gamma}}{p/r}\right); \quad V(0) = V_0 \tag{1}$$

where V is the organism volume, γ characterizes the organism shape, r characterizes specific rate of metabolism (per unit of volume), and p characterizes the specific rate of energy consumption (per unit of surface).

This equation results from the law of energy conservation, when energy input is proportional to the organism surface and the energy output is proportional to the organism volume. Consider, for example, an organism having a spherical shape. The surface area is proportional to the square of the radius, and the volume is proportional to the cube of the radius. The surface area in such case is proportional to the two-third power of the volume, and thus $\gamma = 2/3$.

Eq. (1) where $\gamma = 2/3$ is commonly referred to as Bertalanffy growth equation. This equation generates three-parameter family of growth curves. Each growth curve that satisfies Bertalanffy growth equation is determined by three parameters: p, r, and V_0. If we assume that organisms of the same species growing in similar environment have the same specific rate of metabolism and the same specific rate of energy consumption, then their growth curves will form one-parameter family: $V_i(t) = V(t; V_{0i})$. Each growth curve $V_i(t)$ in such case is determined by V_{0i}.

The difference in initial volume can be also expressed in terms of delay in development. Let us consider two growth curves: $V_1(t)$ and $V_2(t)$, where $V_{01} > V_{02}$. Both curves approach the same maximum value, $V_{max} = (p/r)^3$. ($dV/dt = 0$ when $V = (p/r)^3$, and so V cannot grow further.) Therefore, the second curve will pass the level of V_{01} at some moment u. Denoting $t - u$ as τ, we come to the equation for V_2 which is identical to the equation for V_1:

$$\frac{dV_2}{d\tau} = pV_2^{2/3}\left(1 - \frac{V_2^{1/3}}{p/r}\right); \quad V_2(0) = V_{01} \tag{2}$$

Hence,

$$V_2(t) = V_1(t - u) \tag{3}$$

when $t \geqslant u$.

Eq. (1) reflects the most important aspect of organism growth and development – energy balance. Another important aspect is the entropy balance. If entropy production is proportional to the organism volume and entropy outflow is proportional to the organism surface, as it is assumed in JST, the entropy balance could be described by the equation:

$$\frac{dS}{dt} = \tilde{p}V^{\gamma}\left(\frac{V^{1-\gamma}}{\tilde{p}/\tilde{r}} - 1\right); \quad S(0) = S_0 \tag{4}$$

where V is the organism volume as calculated by using Eq. (1), $\tilde{r}$ characterizes specific rate of entropy production (per unit of volume), and $\tilde{p}$ characterizes the specific rate of entropy outflow (per unit of surface).

Since $V(t)$ is known,

$$S(t) = S_0 + \int_0^t \tilde{p}V^{\gamma}\left(\frac{V^{1-\gamma}}{\tilde{p}/\tilde{r}} - 1\right)dt \tag{5}$$

The entropy of a living organism is much lower than the entropy of the "inorganic soup" that that could be "cooked" from the organism. Hence the entropy may help us to answer the question: how far is the organism from such *reference state*? JST suggests that *exergy* could be even more helpful in answering this question.

The exergy is defined as the amount of work that a system can perform when it is brought into thermodynamic equilibrium with its environment. In the case we are considering here, the exergy can be calculated as

$$Ex(t) = \phi V(t) - T_R S(t) \tag{6}$$

where ϕ characterizes the specific energy of the organism (per unit of volume), and T_R is the reference temperature.

The exergy increases in course of organism development, peaks at the time when the organism reaches maturity (i.e., at the stage of reduced growth rate), and approaches zero when the organism is brought into thermodynamic equilibrium with its environment (Fig. 1). The descending branch of the exergy graph, or shortly the ageing curve, represents the process of ageing in terms of exergy loss.

The age, t_{max}, at which $Ex(t_{max}) = 0$ determines the thermodynamical life span of the organism. One may find t_{max} by solving the following equation:

$$S_0 + \int_0^{t_{max}} \tilde{p}V^{\gamma}\left(\frac{V^{1-\gamma}}{\tilde{p}/\tilde{r}} - 1\right)dt = \frac{\phi}{T_R}V_{max} \tag{7}$$

The value of t_{max} may depend on V_0. Let us consider again two growth curves: $V_1(t)$ and $V_2(t)$, where $V_2(t) = V_1(t - u)$, and the volume of the second organism reaches V_{01} at the moment u ($V_2(u) = V_{01}$). Since the entropy of the second organism does not