Ideal free distribution of metabolic activity: Implications of seasonal metabolic-activity patterns on competitive coexistence

CrossMark

Péter Szabó *

Department of Ecology, Faculty of Veterinary Science, Szent István University, Rottenbiller utca 50, H-1077, Budapest, Hungary

ARTICLE INFO

ABSTRACT

The seasonal distribution of metabolic activity determines how much individuals experience different aspects of a periodically changing environment. Seasonal metabolic-activity patterns of coexisting species may differ significantly despite their shared environmental conditions, suggesting that interspecific diversification of this trait has a major role in the coexistence of competing species. In the present study the effect of the seasonal distribution of metabolic activity on intra- and interspecific competition is investigated in a consumer–resource model. It is shown that, in a periodically changing environment, for each environmental preference pattern there is an ideal seasonal distribution of metabolic activity, which results in maximum resource utilisation efficiency and competitive superiority. Contrary to the common interpretation of temporal niche segregation, opposing species-specific seasonal preferences are not a sufficient condition for the coexistence of two species on a population dynamical time scale. A necessary and sufficient condition for coexistence is the temporal segregation of the species via different seasonal activity distributions. However, coexistence is evolutionarily stable only if seasonal metabolic activities and preferences are positively correlated.

1. Introduction

Life is based on the metabolic activity of living organisms, during which the energy of light photons or chemical bonds is transformed into organic material. The speed of these life sustaining processes, the metabolic rate, is an important characteristic of species. From a physiological viewpoint, metabolic rate is the overall speed of energy uptake, transformation and allocation processes, which could be quantified by the respiratory or photosynthetic activity. According to the metabolic theory of Brown et al. (2004) (see also Gillooly et al., 2001; Brown et al., 2004; Savage et al., 2004), the whole-organism metabolic rate scales in general as the three-quarter power of body mass, while the mass-specific metabolic rate scales with the minus one-quarter power of body mass within larger taxonomic groups, expressing that although whole-organism metabolic rate increases, mass-specific metabolic rate decreases with body size. This tendency is reflected also in demographic properties; higher mass-specific metabolic rate of small-sized species usually implies proportionally larger potential birth rates and death rates (Yodzis and Innes, 1992).

However, the overall metabolic rate does not describe the metabolism of a given species exhaustively. Seasonal or diurnal environmental cycles are reflected in the yearly and daily distribution of metabolic activities of both plants and animals (Hall, 1832; Geiser and Ruf, 1995; Geiser, 2004). Metabolically active periods are usually associated with favourable environmental conditions, while metabolically inactive, dormant states, such as torpor or diapause, are often associated with harsh environmental conditions, like extremely cold, hot or dry seasons. However, species exhibit a large diversity in this regard; even under the same environmental conditions different species do not exhibit the same pattern of metabolic activity, but instead differ in either the metabolic peak time or the amount of seasonal metabolic variations. This raises the possibility that metabolic activity patterns are not only shaped by physiological constraints but also by other adaptive forces, such as interspecific competition. Looking from the other side, the diversification of metabolic rate patterns may promote the coexistence of species (Brown, 1989).

Temporal heterogeneity, either in the form of seasonal changes in non-regulating environmental factors, or in the form of resource abundance fluctuations, has long been known to promote coexistence (Brown, 1989; Loreau, 1989; Chesson, 1994). Chesson (2000a) distinguishes the mechanisms of relative nonlinearity and storage effect, which allow some kind of temporal niche segregation. The mechanism of relative nonlinearity is based on

* Tel.: +36 1 478 4231/8755; fax: +31 1 478 4232/8757.
E-mail address: szabo.peter@aotk.szie.hu.

fluctuations in resource abundance, irrespective of the correlations between resource abundance and non-regulating conditioning variables. It means that if species have different nonlinear responses to resource abundance, then they can coexist (Chesson, 2000a; Kisdi and Meszéna, 1993; Szilágyi and Meszéna, 2010). On the contrary, the storage effect is based on temporal fluctuations in conditioning variables. It means that if two species are adapted to the conditions of different seasons, they can coexist if they have different seasonal preferences yet can survive under the conditions of their respective unfavoured seasons by somehow storing the benefits of the favoured season (Brown, 1989; Chesson, 1994; Amarasekare, 2003). Chesson (1994) showed that this buffering effect is determined by interactive effects of the environmental conditions and the competitive impacts on population growth.

Former studies on coexistence in periodically fluctuating environments have expressed coexistence conditions in terms of interspecific differences in a resource-uptake function, which however involves differences in both metabolic activities and environmental preferences. Expressing coexistence conditions in terms of metabolic activity and seasonal preference separately could be useful, because the seasonal distribution of metabolic activity is a clear expression of temporal segregation, without implying any kind of competitive superiority or inferiority in itself (as opposed to environmental preference). Understanding the implications of seasonal metabolic-activity distributions on coexistence requires expressing the relative strength of intra- and interspecific competition in terms of metabolic rate. To this end, in the present study, metabolic-rate dependence was incorporated into a general resource–consumer model. MacArthur's model (MacArthur, 1969, 1970; May, 1974) was a suitable starting point, because it expresses competition explicitly, based on resource consumption, but also describes the relationship between resource utilisation functions and intra- and interspecific competition coefficients. In the following, after briefly reviewing the original version of the MacArthur model, its modified version is presented, which expresses demographic parameters in terms of species-specific seasonal metabolic activities, leading eventually to an expression of coexistence conditions in terms of seasonal metabolic activities and seasonal environmental preferences.

2. Model

2.1. The MacArthur model

The original resource–consumer model of MacArthur describes scramble competition between species that consume the same, shared resources (MacArthur, 1969) (see also Chesson, 1990 for a detailed discussion). We consider the case of one resource and many consumers, for which the model is given by the equations

$$\frac{dp_i}{dt} = c_i p_i (u_i R - T_i) \tag{1a}$$

$$\frac{dR}{dt} = gR\left(1 - \frac{R}{K}\right) - \sum_i u_i p_i R \tag{1b}$$

where p_i is the population density of species i, and R is the abundance of the resource. The population dynamical parameters of the species are u_i, T_i and c_i; u_i is the rate at which an individual of species i encounters and eats a given unit of resource, T_i is a threshold resource-uptake rate, while c_i quantifies the conversion from resource to individuals. The dynamics of the resource is parameterised by its natural rate of increase g and the habitat carrying capacity for the resource K. Assuming that the dynamics of the resource is much faster than that of the consumers, the equilibrium resource level can be expressed as

$$R^* = K - \sum_i \frac{K}{g} u_i p_i. \tag{2}$$

Substituting R^* into Eq. (1a) yields the familiar Lotka–Volterra competition model

$$\frac{dp_i}{dt} = c_i p_i \left[\underbrace{u_i K - T_i}_{k_i} - \frac{K}{g} \sum_j \underbrace{u_i u_j}_{a_{ij}} p_j \right] \tag{3}$$

which gives an explicit expression for the maximal growth rates $k_i c_i$ and the competition coefficients a_{ij}.

MacArthur (1969) has shown that the condition for the population dynamical equilibrium is equivalent to minimising the weighted square of the unused production added to twice the threshold food requirements, defined as:

$$Q = \frac{K}{g}\left(g - \sum_i u_i p_i\right)^2 + 2\sum_i T_i p_i. \tag{4}$$

This quantity, which expresses the inefficiency of resource utilisation is actually the Lyapunov function of the MacArthur model (Gatto, 1990; Loreau, 2010), which means that this function is always positive and its time derivative is always negative, except at equilibrium where it is zero.

Efficiency can increase either by decreasing the amount of minimal resource requirement (T_i) or by increasing the total resource uptake until it reaches the amount of available resources. Hence, low and high Q corresponds to high and low efficiency, respectively. This quantity will play an important role also in the present analysis.

2.2. Introducing metabolic rate dependence

Let us define metabolic activity m_i, as the respiratory activity of species i. Also, let us replace variables u_i and T_i by the products

$$u_i = m_i u_i' \tag{5a}$$
$$T_i = m_i T_i', \tag{5b}$$

where u_i' and T_i' are the metabolic rate-specific resource consumptions and threshold resource-uptake levels, respectively. Applying these changes, and following the lines of the derivation of the original model yields

$$\frac{dp_i}{dt} = c_i p_i \left[\underbrace{m_i u_i' K - m_i T_i'}_{k_i} - \frac{K}{g} \sum_j \underbrace{u_i' u_j' m_i m_j}_{a_{ij}} p_j \right]. \tag{6}$$

Notice that, unlike the conversion rate c_i, the metabolic rate terms m_i and m_j affect the carrying capacities and the competition coefficients differently, therefore they affect not only the overall speed of the dynamics, but also the relationship between intraspecific and interspecific competition terms, revealing that their actual value may have important implications on the outcome of competition. In the following, $K = g = 1$ is assumed and, for notational convenience, u_i and T_i will denote metabolic rate-specific resource consumptions and threshold resource-uptake levels. Since the focus of the present study is the effect of interspecific differences in the temporal distribution of metabolic activity, other species-specific traits are set equal ($c_i = 1$ and $u_i = 1$), yielding the temporally homogeneous version of the investigated model

$$\frac{dp_i}{dt} = p_i m_i \left[1 - T_i - \sum_j m_j p_j \right]. \tag{7}$$

Therefore, considering two species ($i = 1, 2$), the parameters of this version of the model are the vectors $\mathbf{m} = [m_1, m_2]$ and