A metabolic view of the diversity–stability relationship

Julián Simón López-Villalta*

Departamento de Ecología, Universidad Autónoma de Madrid, Cantoblanco, 28040 Madrid, Spain

Abstract

A theoretical analysis of the "portfolio effect" expressed in metabolic terms indicates that the coefficient of variation of total biomass in the ecosystem is influenced by three factors: metabolic diversity, total population size and organism biomass (body mass). The contribution of these factors to ecosystem stability depends on the power scaling of population size to its temporal variance: the Tilman's z. In natural populations, $1 < z < 2$ both from a theoretical and an empirical background, and so a higher metabolic diversity, a larger population size and a bigger body mass are expected to increase ecosystem stability. The maximization of any of these factors will enhance ecosystem stability both at ecological (successional) and evolutionary timescales, which could explain a number of trends observed in ecosystems and in the history of life.
© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

The influence of diversity on ecosystem stability is a classic debate in the field of ecology (for example, Elton, 1958; Odum, 1971; MacArthur, 1955; May, 1973; see McCann, 2000 for a review) and still remains an active research field (Tilman and Downing, 1994; Tilman et al., 1996, 2001; Pfisterer et al., 2002; Doak et al., 1998; Caldeira et al., 2005; Loreau et al., 2001). The diversity–stability relationship is usually treated from the viewpoint of plant–animal species diversity, but the concept of functional diversity allows a broader point of view by referring to the variety of functional roles that species perform in ecosystems (Tilman et al., 1997; Loreau et al., 2001). This paper discusses the stabilizing effect of one kind of functional diversity that is very small in plant–animal communities: the diversity of metabolic guilds. Metabolic guilds are communities of organisms that perform the same energy metabolism (sulfate reduction, oxygenic photo-synthesis, etc.) The largest metabolic diversity is found in the ecosystem's microbial populations, because microor-ganisms, especially bacteria and archaea, represent most of

the metabolic diversity of the biosphere (Madigan et al., 2006; Pace, 1997; DeLong and Pace, 2001; Amend and Shock, 2001). On the one hand, the main phenotypic diversity of bacteria and archaea is metabolic, not morphological such as in eukaryotes; on the other, early life on Earth consisted exclusively of microorganisms, with global ecological dominance of bacteria and archaea throughout billion years (Knoll, 2003; Nisbet and Sleep, 2001; Nisbet and Fowler, 1999; Schopf, 2000). Therefore, any influence of biodiversity on ecosystem stability at the beginning of the biosphere system was probably caused by metabolic diversity. In this paper, an analysis of the diversity–stability relationship is presented in metabolic terms, which provides a theoretical insight into the stabilizing effects of three biological factors: metabolic diversity, population size and organism biomass as an indicator of metabolic rate.

2. A metabolic perspective of the "portfolio effect"

The biomass b of one metabolic guild must be expressed in terms of the collective metabolic rate. For simplicity, the assumption is made that all organisms belonging to one metabolic guild have the same biomass m. If the $\frac{3}{4}$ scaling power of biomass to metabolism is taken (West et al.,

*Tel.: +34 91 497 8010; fax: +34 91 497 8001.
E-mail address: julian.simon@uam.es

1997), a number n of organisms represents a metabolic rate of

$$r = inm^{3/4} = inm^{1-1/4} = ibm^{-1/4}. \tag{1}$$

where i is a constant. Therefore, for any metabolic guild

$$b = krm^{1/4} \tag{2}$$

being k the constant $1/i$. The theoretical approach used by Tilman (1999) to model the so-called "portfolio effect" in the species diversity–stability relationship can be adapted to explore the effect of metabolic diversity by taking metabolic guilds instead of species into account and writing biomass as a function of metabolic rate. The ecosystem's temporal stability can be measured as the coefficient of variation ($S = \mu/\sigma$) of the total biomass, that is, the ratio of the average total biomass to its standard deviation in a time series. In accordance with Tilman (1999), I am going to compare the value of S in two cases: one ecosystem with only one metabolic guild, and another with N metabolic guilds. The average total biomass, b_1, is considered in the form of Eq. (2), and the temporal variance of b_1 is

$$\sigma_1^2 = cb_1^z \tag{3}$$

with c being a constant and z a scaling power. Under the previous assumptions, biomass is a linear function of the population size n, and thus z is the scaling power used by Tilman (1999) for species populations. Finally, for an ecosystem with only one metabolic guild, the coefficient of variation of total biomass is

$$S_1 = b_1/\sigma_1 = krm^{1/4}/c^{1/2}b_1^{z/2} = Cr^{1-z/2}m^{(2-z)/8}, \tag{4}$$

where C is a constant. Using Eq. (1), an equivalent expression of Eq. (4) is

$$S_1 = C(nm)^{1-z/2}. \tag{5}$$

In this expression, it is remarkable that the coefficient of variation is a function of the number of organisms and of organism biomass, both factors being influenced by the power scaling z. As will be discussed later, this relationship has interesting ecological implications concerning how to maximize ecosystem stability.

In the second case, for an ecosystem with N metabolic guilds, the following assumptions are made to better compare with the previous case: all the organisms have the same biomass m, all the metabolic guilds have the same average population and therefore the same average biomass and metabolic rate r, as in Eq. (1). Let the total biomass of the N metabolic guilds be b_N; then for any metabolic guild, the average biomass is b_N/N, or $r\,m^{1/4}\,N^{-1}$ in the form of Eq. (2). In this situation the temporal variance of the average biomass of any ith metabolic guild is

$$\sigma_i^2 = c(b_N/N)^z = Cr^z m^{z/4} N^{-z} \tag{6}$$

with c and C being two new constants. Assuming for simplicity no covariance between the biomasses of metabolic guilds, the variance of total biomass, σ_N^2, is the sum of the N variances σ_i^2, that is

$$\sigma_N^2 = N\sigma_i^2 = Cr^z m^{z/4} N^{1-z} \tag{7}$$

and the coefficient of variation of total biomass, S_N, is

$$S_N = b_N/\sigma_N = krm^{1/4}/C^{1/2}r^{z/2}m^{z/8}N^{(1-z)/2}$$
$$= kC^{-1/2}r^{1-z/2}m^{(2-z)/8}N^{(z-1)/2}. \tag{8}$$

Replacing r by $i\,n\,m^{3/4}$ (Eq. (1)) and rearranging, S_N depends again on $(nm)^{1-z/2}$ as was the case in Eq. (5), with the only difference that now n represents the average total number of organisms in the N metabolic guilds.

Finally, the ratio of the coefficients of variation in the two cases is

$$S_N/S_1 = cN^{(z-1)/2} \tag{9}$$

with c being one constant. The dependence on both the number of organisms and the organism biomass has disappeared. The only stability difference between the metabolically rich and poor situations is a function of the number of metabolic guilds. As a large coefficient of variation indicates more stability, in the previous expression, a metabolically diverse ecosystem is more stable than a metabolically nondiverse one if $S_N/S_1 > 1$. The factor N will contribute to this condition if its scaling power is positive, that is if $z > 1$.

3. Discussion

It is interesting to note that when $z > 1$, both species diversity (Tilman, 1999) and metabolic diversity contribute to stabilize the community. Plant and animal species in natural communities present z values above one (Tilman, 1999), and Murdoch and Stewart-Oaten (1989) found that $1 < z < 2$ from both a theoretical and an empirical viewpoint. Therefore, for natural populations, metabolic diversity is expected to be a stabilizing factor. However, the lack of data for microbial populations shows the need for future research in this area.

The influence of metabolic diversity on ecosystem stability raises the ecological role of bacteria and archaea in stabilizing the biosphere. Prokaryotes demonstrate an astonishing variety of fermentations, anaerobic respirations, anoxygenic photosynthesis and chemosynthesis (Madigan et al., 2006; Pace, 1997). Most visible eukaryotes only respire aerobically, and, if photosynthetic, undertake oxygenic photosynthesis, but even among macroscopic eukaryotes some remarkable and poorly known metabolic diversity exists. For example, with its aerobic sulfide-oxidizing mitochondria (Powell and Somero, 1986), the bivalve *Solemya reidi* can live as a chemolithotrophic animal. Some fungi oxidize organic carbon through nitrate reduction (Shoun and Tanimoto, 1991; Kobayashi et al., 1996), and in anoxia, certain fungi undertake ammonia fermentation (Zhou et al., 2002). Other fungi might respire organic matter by iron reduction (Ottow and von Klopotek, 1969; unpublished personal data), but this

has not been confirmed (Ehrlich, 2002). Among the microbial eukaryotes, cells ferment, producing hydrogen with special organelles: the hydrogenosomes (Muller, 1993; Biagini et al., 1997). Such a metabolic diversity deserves attention from the viewpoint of the diversity–stability debate of ecology as a probable promoter of ecosystem stability.

The total number of organisms and the organism biomass influences ecosystem stability as shown in Eq. (5). This relationship is independent of metabolic diversity because it is the same in Eq. (8). In Eq. (5), a positive power scaling implies that ecosystem stability increases with a larger population size and a bigger body size per organism. Therefore, it is easy to see that a large population and a high organism biomass stabilize the ecosystem if $z < 2$, and, as discussed, species are expected to be found in this case. Therefore, population size and body mass are expected to be stabilizing factors in natural populations, and thus in ecosystems. Furthermore, an intrinsic stabilizing effect of biomass in ecological communities is implicit in Eqs. (5) and (8) because of the presence of *nm*, and then an expression linking total biomass with the ecosystem's temporal stability can be obtained

$$S = Cb^{1-z/2}. \tag{10}$$

A summary of the stabilizing effects of metabolic diversity, population size, organism biomass and total biomass is shown in Table 1.

A number of trends of ecological succession can be explained looking at Table 1 and assuming $1 < z < 2$. During ecological succession, ecosystem stability increases simply due to the principle of "prevalence of the stable." This principle can be considered as the extended form of natural selection (Lotka, 1922), applied to complex systems with a large number of interacting elements subjected to an energy flux that drives them to a stationary state. The prevalence of stable components indicates that, as complex systems, ecosystems tend to gain stability with time by maximizing stabilizing variables. At least from a theoretical viewpoint, the present analysis points to an increase of metabolic diversity, total population size, body mass and total biomass that contributes to ecosystem stability. From empirical studies, it is known that metabolic diversity increases during development of a microbial mat through the generation of anoxic to suboxic habitats for anaerobic

metabolisms (Van Gemerden, 1993; Des Marais, 2003), and, during ecological succession, the substitution of species with small individual biomass (r strategy) by others with a large body size (K strategy; see Pianka, 1970) is clearly observed, together with an increase of total biomass (Odum, 1969; Odum, 1971; Margalef, 1963). Furthermore, the reduction of energy flux per unit biomass *(E/B*, see Odum, 1969) could also be explained since the ratio of metabolic rate to organism biomass is $m^{3/4}/m = m^{-1/4}$. Being negative, the power scaling E/B decreases with an increase of body mass, and, as the latter is a stabilizing factor, the former is expected to decrease during ecosystem organization.

Looking beyond ecosystem assembly to the timescale of evolution, during the history of life on Earth, the same principles would apply with higher biosphere stability as a result. In fact, the trend towards a larger body mass (Cope's Rule) has been confirmed at least for North American fossil mammals (Alroy, 1998), and is supported by a number of works (see Hone and Benton, 2005, for a review). In summary, the stabilizing nature of ecosystem self-organization implies that four trends can be expected in ecological succession as well as in biological evolution: higher metabolic diversity, larger average total population, bigger body size and bigger total biomass. At least for ecological succession, this seems to be the case.

4. Conclusion

From a theoretical analysis of the "portfolio effect" in the diversity–stability relationship, if, as expected, $1 < z < 2$ in natural populations, then a higher metabolic diversity, a larger population size, a bigger body size and a bigger total biomass would increase the temporal stability of ecosystems both at ecological (successional) and evolutionary timescales.

Table 1
Effects of metabolic diversity, population size, body size and total biomass on the temporal stability of ecosystems, according to Eqs. (5), (9) and (10)

Variable	Stabilizing threshold	Natural values $1 < z < 2$
Metabolic diversity	$z > 1$	
Population size		Stabilizing
Organism biomass (body size)	$z < 2$	
Total biomass		

References

Alroy, J., 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science 280, 731–734.

Amend, J.P., Shock, E.L., 2001. Energetics of overall metabolic reactions of thermophilic and hyperthermophilic archaea and bacteria. FEMS Microbiol. Rev. 25, 175–243.

Biagini, G.A., Finlay, B.J., Lloyd, D., 1997. Evolution of the hydrogenosome. FEMS Microbiol. Lett. 155, 133–140.

Caldeira, M.C., Hector, A., Loreau, M., Pereira, J.S., 2005. Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. Oikos 110, 115–123.

DeLong, E.F., Pace, N.R., 2001. Environmental diversity of bacteria and archaea. Syst. Biol. 50, 470–478.

Des Marais, D.J., 2003. Biogeochemistry of hypersaline microbial mats illustrates the dynamics of modern microbial ecosystems and the early evolution of the biosphere. Biol. Bull. 204, 160–167.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D., 1998. The statistical inevitability of stability–diversity relationships in community ecology. Am. Nat. 151, 264–276.

Ehrlich, H.L., 2002. Geomicrobiology. Marcel Dekker, New York.

Elton, C.S., 1958. The ecology of invasions by animals and plants. Methuen, London.

Hone, D.W.E., Benton, M.J., 2005. The evolution of large size: how does Cope's rule work? TREE 20, 4–6.

Knoll, A.H., 2003. Life in a Young Planet: The First Three Billion Years of Evolution on Earth. Princeton University Press, Princeton, NJ.

Kobayashi, M., Matsuo, Y., Takimoto, A., Suzuki, S., Maruo, F., Hirofumi, S., 1996. Denitrification, a novel type of respiratory metabolism in fungal mitochondrion. J. Biol. Chem. 271, 16263–16267.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.

Lotka, A.J., 1922. Natural selection as a physical principle. Proc. Natl. Acad. Sci. 8, 151–154.

MacArthur, R., 1955. Fluctuations of animal populations, and a measure of community stability. Ecology 36, 533–536.

Madigan, M.T., Martinko, J.M., Parker, J., 2006. Brock Biology of Microorganisms, 11th ed. Prentice-Hall, Englewood Cliffs, NJ.

Margalef, R., 1963. On certain unifying principles in ecology. Am. Nat. 97, 357–374.

May, R.M., 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ.

McCann, K.S., 2000. The diversity–stability debate. Nature 405, 228–233.

Muller, M., 1993. The hydrogenosome. J. Gen. Microbiol. 139, 2879–2889.

Murdoch, W.W., Stewart-Oaten, A., 1989. Aggregation of parasitoids and predators: effect on equilibrium and stability. Am. Nat. 134, 288–310.

Nisbet, E.G., Fowler, C.M.R., 1999. Archaean metabolic evolution of microbial mats. Proc. R. Soc. London B 266, 2375–2382.

Nisbet, E.G., Sleep, N.H., 2001. The habitat and nature of early life. Nature 409, 1083–1091.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Odum, E.P., 1971. Fundamentals of Ecology. W.B. Saunders Company, Philadelphia.

Ottow, J.C.G., Von Klopotek, A., 1969. Enzymatic reduction of iron oxide by fungi. Appl. Microbiol. 18, 41–43.

Pace, N.R., 1997. A molecular view of microbial diversity and the biosphere. Science 276, 734–740.

Pfisterer, A.B., Schmid, B., 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. Nature 416, 84–86.

Pianka, E.R., 1970. On r- and K-selection. Am. Nat. 102, 592–597.

Powell, M.A., Somero, G.N., 1986. Hydrogen sulfide oxidation is coupled to oxidative phosphorylation in mitochondria of *Solemya reidi*. Science 233, 563–566.

Schopf, J.W., 2000. Solution to Darwin's dilemma: discovery of the missing precambrian record of life. Proc. Natl. Acad. Sci. 97, 6947–6953.

Shoun, H., Tanimoto, T., 1991. Denitrification by the fungus *Fusarium oxysporum* and involvement of cytochrome P-450 in the respiratory nitrite reduction. J. Biol. Chem. 266, 21078–21082.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80, 1455–1474.

Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. Nature 367, 363–365.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302.

Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379, 718–720.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. Science 294, 843–845.

Van Gemerden, H., 1993. Microbial mats: a joint venture. Mar. Geol. 113, 3–25.

West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of allometric scaling laws in biology. Science 276, 122–126.

Zhou, Z., Takaya, N., Nakamura, A., Yamaguchi, M., Takeo, K., Shoun, H., 2002. Ammonia fermentation, a novel anoxic metabolism of nitrate by fungi. J. Biol. Chem. 277, 1892–1896.