OLM12.2. The relationship between species- and community-level variation in biomass

The phenomenon recurring in many habitats that the biomass production of a community fluctuates less than that of the species it is composed of (Figure 12.22) was explained by the portfolio effect known from investment theory (Ch12.2, p. 261). We have also made the – thus far unproven – statement that „the more diverse our investment portfolio is, the less its total value fluctuates in time" (TBE, p.263). We present a mathematical proof to this statement here.

The fluctuations in the biomass production of a species or a community are usually expressed in terms of the deviations in proportion to the "average" value, i.e., the variation coefficient (CV: Eq.(2.4), p. 119). Therefore, we will discuss the topic as the relation between CV values calculated on a species and on a community basis, showing that on the community level the fluctuations are typically smaller.

Let us denote the expected value and the variance of species *i* with μ_i and σ_i , and let the same characteristics of the entire community be denoted by μ_{com} and σ_{com} . Since the total biomass of the community is the sum of the biomasses of the constituent species, we may apply the familiar expressions for the expected value and variance of the sum of random variables:

$$\mu_{com} = \sum_i \mu_i \qquad (12.2.1)$$

$$\sigma_{com}^2 = \sum_i \sigma_i^2 + \sum_i \sum_{j \neq i} cov_{ij} \qquad (12.2.2)$$

where cov_{ij} is the covariance of the biomasses of species *i* and *j*. It takes a value of 0 if the species biomasses change independently and it takes its maximum $\sigma_i\sigma_j$ if all species change biomass in synchrony. We will discuss these special cases next.

For maximally correlated changes in species biomasses,

$$\sigma_{com}^2 = \sum_i \sum_j cov_{ij} = \sum_i \sum_j \sigma_i \sigma_j = (\sum_i \sigma_i)^2 \qquad (12.2.3)$$

The variation coefficient of the biomass of the community is

$$CV_{com} = \frac{\sigma_{com}}{\mu_{com}} = \frac{(\sum_i \sigma_i)}{\mu_{com}} \qquad (12.2.4)$$

We can replace the species-level standard deviations in Eq.(12.2.4) by the product of their variation coefficient and expected value:

$$CV_{com} = \frac{\sum_i \mu_i CV_i}{\mu_{com}} \qquad (12.2.5)$$

Denote the proportion of species *i* within the total biomass by $p_i = \mu_i / \mu_{com}$:

$$CV_{com} = \frac{\sum_i \mu_{com} p_i CV_i}{\mu_{com}} = \sum_i p_i CV_i \qquad (12.2.6)$$

Thus we obtain that under the given conditions the coefficient of variation for the community is the weighted average of the species CV-s. If the biomasses of the species do not change in perfect synchrony, then σ_{com} , and thus also CV_{com}, will be smaller.

Now let us turn to the other case that can be handled analytically, i.e., the one in which species biomasses change independently of each other. Then the coefficient of variation for the community is

$$CV_{com} = \frac{\sigma_{com}}{\mu_{com}} = \frac{\sqrt{\sum_i \sigma_i^2}}{\mu_{com}} \qquad (12.2.7)$$

Also in Eq. (12.2.7) we can substitute the species standard deviations by the products of their variation coefficients and expected values, and make use of their relative biomasses (p_i):

$$CV_{com} = \frac{\sqrt{\sum_i \mu_i^2 CV_i^2}}{\mu_{com}} = \frac{\sqrt{\sum_i \mu_{com}^2 p_i^2 CV_i^2}}{\mu_{com}} = \sqrt{\sum_i p_i^2 CV_i^2} \qquad (12.2.8)$$

If the coefficients of variation are the same (CV_{sp}) for all the species, the formula becomes even simpler:

$$CV_{com} = CV_{sp}\sqrt{\sum_i p_i^2} = CV_{sp} \Big/ \sqrt{\frac{1}{\sum_i p_i^2}} = \frac{CV_{sp}}{\sqrt{^2D}} \qquad (12.2.9)$$

where $^2D = \frac{1}{\sum_i p_i^2}$ is Hill's diversity at a value 2 of the scaling factor (Jost 2007; for all species equally abundant ^2D is equal to the number of species; it is smaller than that otherwise, but not smaller than 1).

According to Eq. (12.2.9), at a given species-level CV the community-level CV is smaller in communities of higher diversity. If the coefficients of variation are different for different species but independent of their relative frequencies, then CV_{sp} has to be replaced by the quadratic mean (square root of the mean of the squares) of the variation coefficients for the relation to remain true.

The relations derived thus far could be used in their same forms in an economy textbook just as well, re-interpreting "community" as "portfolio", "species" as "investment assets", and "biomass production" as "yield". This is the analogy that explains the name "portfolio effect".

There is, however, an important difference between an investment portfolio and a community: the fluctuations in the price of investment assets is independent of the number of assets in a portfolio, but the fluctuations of species biomass productions is not independent of the diversity of the community. Figure 10.22 shows, for example, that the fluctuations of the relative abundance of rare species is larger than that of more frequent ones. Knowing this we expect that in very diverse communities (in which the average frequency of species is smaller) the species-level fluctuations should be larger. That is, the portfolio effect explains why the fluctuations of the total biomass of a community is smaller than that of the constituent species, but is not in itself sufficient to predict the effect of increasing the diversity of the community on its stability.

References

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. *Ecology*, 88(10): 2427–39.