Diversity & stability

Key concepts

- Variability
- Stability
- Resilience
- Resistance

Dynamical consequences of diversity

Much of ecology concerns the factors that produce and maintain species diversity. In constrast, this chapter investigates the dynamical ecological consequences of diversity. Does the variability of net ecosystem processes – like primary production – increase or decrease with diversity? Are diverse ecosystems more or less stable or resilient to pertubrations than species poor ecosystems? Are diverse communities more resistant to invasion by new species than those with fewer members?

Figure 1: Kentucky bluegrass (*Poa pratensis*) is one of four dominant species in the experimental grasslands of the Cedar Creek Ecosystem Science Reserve in Minnesota.

Answering these questions requires experiments in which the diversity of the community can be directly manipulated. The Cedar Creek Ecosystem Science Reserve in Minnesota houses one of the longest running ecological field experiments. Before the site was used for environmental research, however, it was an agriculture facility. In 1982, fields abandoned in 1934, 1957, and 1968 were dedicated to an experimental study in which different concentrations of nitrogen were systematically added to plots and the entire ecosystem monitored to determine the ecological effects. The main finding of this experiment was that species richness declined with nitrogen deposition (Figure 2). The strength and consistency of this effect created an opportunity to study the effects of diversity on ecosystem processes experimentally. By manipulating a natural ecosystem processes (nitrogen deposition), researchers were able to look at the downstream effects of changes in species diversity on population and ecosystem dynamics.

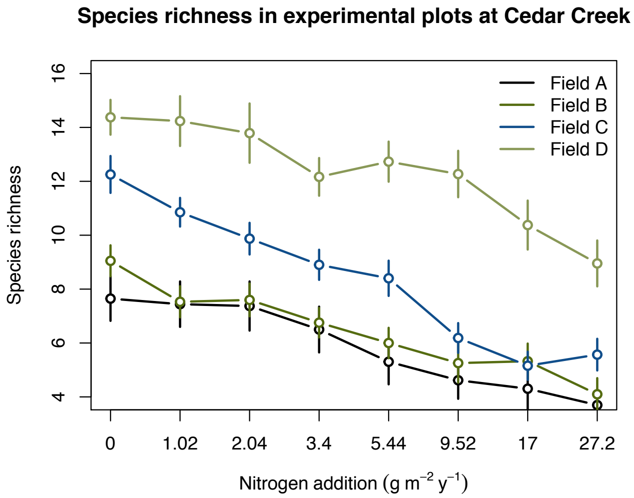

Figure 2: Average species richness by Nitrogen treatment in four old fields at the Cedar Creek Ecosystem Science Reserve. Plot shows mean ±2 standard errors.

Diversity & variability

There are several senses in which the stability of ecological communities is of interest. *Variability* refers to the magnitude of fluctuations in some aggregate property. Thus, for instance, if x_i denotes the quantity of primary production due to species i and $X = sum_i^n x_i$ is a measurement of the total primary production of the n species in the community taken together, then X may be expected to fluctuate over time. The magnitude of these fluctuations – measured, perhaps, by the coefficient of variation (the standard deviation of X divided by the mean of X) – is the variability in productivity.

Variability in productivity may decline with species richness for at least three reasons. [1]

[1]

1. *Negative covariance.* Often species will respond in opposite ways to changes in environmental conditions. Dry conditions will be good for one species while wet conditions are good for another. When such species coexist in the same location their abundances will *negatively covary* with each other due to environmental fluctuations: when one species increases in abundance the other species will decline. The result of this negative covariance is that the abundance of the two species together will be more stable than that of either species considered individually. The greater the number of species

2. *Portfolio effect.* Even if species fluctuations are independent (zero covariance rather than negative covariance) the *statistical averaging* of their fluctuations will serve to reduce the variability of the sum of their abundances.

3. *Insurance effect.* Species may also exhibit total or partial *functional redundancy*. When species overlap in their functional traits, when one species is lost to the community then another may compensate for its functional role, making use of space or other resources that would otherwise not be exploited. Thus, species that are similar to each other may provide “insurance” against the loss of decline of each other.

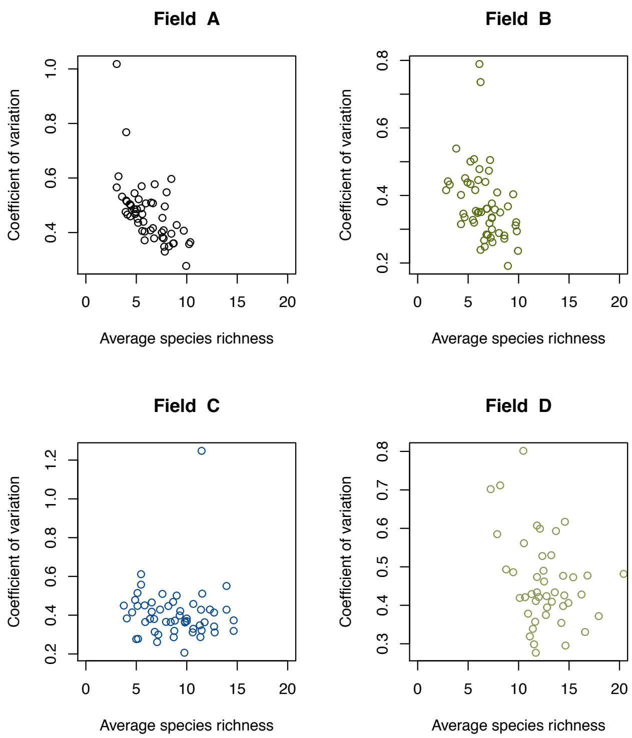

Figure 3: The coefficient of variation in total primary productivity declined with average species richness in old fields at the Cedar Creek Ecosystem Science Reserve. Spearman rank-order correlation tests show this effect to be strong and significant in three out of the four fields (A, B, and D). Field A: $\rho = -0.59$, $p < 0.001$; Field B: $\rho = -0.39$, $p = 0.004$; Field D: $\rho = -0.88$, $p = 0.023$.

These results suggest that the variability in productivity did decrease with species richness at Cedar Creek. There is a problem with this result, however. Because species richness was itself a response to nitrogen addition, it is impossible to tell if the observed pattern is a result of species richness or the effect of nitrogen. Indeed, because nitrogen increases productivity on average – and because average productivity is in the denominator of the coefficient of variation – it’s plausible that the effect has nothing to do with species richness at all.

To separate the effects of fertilization and species richness, a second experiment was performed in which the number of species in each plot was directly manipulated, first by planting with pre-determined combinations of species, followed by weeding to remove encroaching colonizers.

No evidence for an effect of species richness on coefficient of variation.

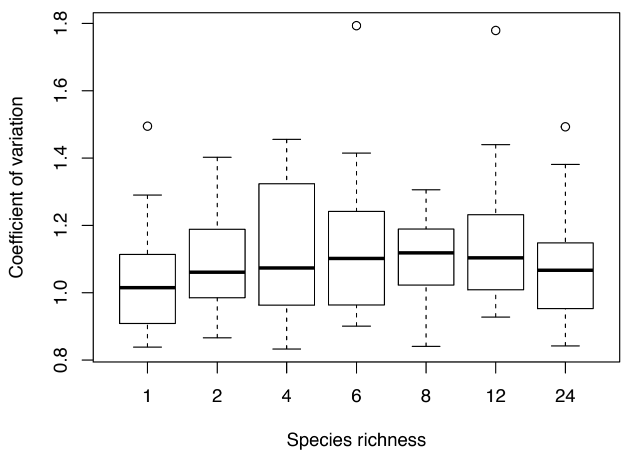

Figure 4: There was no effect of species richness on the coefficient of variation in total primary productivity in old fields at the Cedar Creek Ecosystem Science Reserve in an experiment in which species richness was experimentally varied and not manipulated by nitrogen addition..