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Separating sampling and other effects in biodiversity experiments

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As experiments testing the effects of species diversity on ecosystem processes accumulate, it becomes increasingly important to identify the mechanisms that explain the observed patterns. Different factors may cause different patterns and have very different implications for the understanding of the relationship between biodiversity and ecosystem functioning (Loreau 1998). In particular, the "sampling effect" (Aarssen 1997, Huston 1997, Tilman et al. 1997), by which productivity or other ecosystem processes increase with diversity because high-diversity plots have a higher probability of containing the most productive species by random draw from a species pool, is of a different nature than biological effects such as resource-use complementarity. Some have viewed it as a statistical artefact invalidating recent experiments (Aarssen 1997, Huston 1997); others have argued that it is a valid biodiversity effect (Tilman 1997, Tilman et al. 1997). This controversy can be resolved by noting that the sampling effect tells something about the real world to the extent that real communities assemble by sampling processes from the regional biota. This is likely to vary depending on the type of organisms, the spatial scale and the time scale considered. In any case, it seems highly desirable to separate this effect from other effects in analysing and interpreting biodiversity experiments.

Hector (1998) suggests that this may be done effectively using the relative yield total (RYT) approach borrowed from replacement series. Here I show that the RYT is only one among several possible approaches, which is appropriate for testing a particular hypothesis, and I suggest a more general strategy based on the use of proportional deviations from expected values, of which the RYT can be viewed as a special case. In what follows, I shall continue to use "yield" as an example of a measurable ecosystem process, but the same arguments may apply to many other processes.

The relative yield of species i in a mixture, RY_i, and the relative yield total of the mixture, RYT, are defined as:

$$RY_i = O_i/M_i$$

$$RYT = \sum RY_i$$

where O_i is the observed yield of species i in the mixture, and M_i is its yield in monoculture. Hector (1998) provides hypothetical examples that illustrate how the RYT can remove sampling effects; a similar illustration is provided by example 1 in Table 1. To discuss this example, let us further define p_i as the proportion of species i in the mixture, and E_i as its expected yield based on its yield in monoculture, that is:

$$E_i = p_i M_i$$

Table 1. Two hypothetical examples of expected (E) and observed (O) productivities in two-species mixtures illustrating some properties of the relative yield (RY) and the proportional deviation from expected yield (D). See text for definition of symbols.

Example

	p	M	E	O	RY	D	D_T
Species 1	0.5	800	400	600	0.75	0.5	
Species 2	0.5	200	100	50	0.25	−0.5	
Total	1	–	500	650	1	–	0.3
Average	–	500	–	–	–	0	

Example 2

	p	M	E	O	RY	D	D_T
Species 1		800	400	200	0.25	−0.5	–
Species 2		200	100	200	1	1	–
Total		–	500	400	1.25	–	−0.2
Average		500	–	–	–	0.25	–

In example 1, species 1 is the more productive species both in monoculture and in the mixture, but its observed yield in the mixture is greater than expected from its proportion of 50%. However, this increased yield is compensated for by a corresponding decrease in the RY of species 2, so that the RYT is 1. The RYT approach effectively removes the sampling effect in two ways:

(1) The yield of a mixture is compared with the yields in monoculture of those species which are present in the mixture. By so doing, it removes the effect of species identity on the results of the various mixtures and eliminates the variation that is due to differences in species composition among mixtures within each biodiversity treatment.

(2) A *RYT* value of 1 means that a proportional increase in the yield of one species is compensated for by a corresponding proportional decrease in the yield of other species. Hence the RYT removes shifts in numerical dominance among the species in a mixture. Thus, in example 1, the mixture behaves exactly as if the two species were in the ratio 75:25 instead of 50:50.

Despite these nice properties, however, the RYT does *not* allow testing for complementarity in resource use. What it does allow is testing the null hypothesis that the observed yields can be accounted for by changes in the proportional contributions of the various species in the mixture (when $RYT = 1$). But there are several alternative hypotheses to this null hypothesis, corresponding to different mechanisms by which species diversity may affect the total yield. All kinds of species interactions may affect the yield of a mixture. Complementarity in resource use is one possible effect; other common interactions include direct interference or facilitation between species. A combination of changes in numerical dominance, resource-use complementarity, interference competition and facilitation between species can produce any conceivable value of *RYT*, in principle from zero to infinity.

Example 2 in Table 1 illustrates the limitations of the RYT method. In this example, the more productive species in monoculture has a lower than expected yield in the mixture, but the other species maintains a yield similar to that in monoculture, resulting in a $RYT > 1$. Yet, clearly, nothing allows us to conclude that there is complementarity in resource use. Interference acting on the more productive species is likely, while facilitation acting on the less productive species could explain its higher than expected yield. In this case, the observed total yield is smaller than expected, and this may be regarded as more meaningful than the $RYT > 1$ value. All we can conclude from the fact that *RYT* is different from 1 is that changes in the proportional contributions of the various species are not sufficient to explain the observed yields – that is, the null hypothesis is rejected.

Given these limitations of the RYT approach, are there any other approaches we could use to address the problem? In an experimental study of the effect of species diversity on litter decomposition rates, Wardle et al. (1997) used comparisons between observed and expected values based on the following index:

$$D_T = \frac{O_T - E_T}{E_T}$$

where

$$O_T = \sum O_i \quad \text{and} \quad E_T = \sum E_i$$

are the observed and expected values, respectively, of the total "yield" (or other relevant ecosystem variables) of a mixture. D_T measures the proportional deviation of the observed total yield from its expected value, and offers a convenient standardised way to compare the overall performance of a mixture with its expectation in the absence of species interactions (Table 1). Jolliffe (1997) proposed another measure, the relative land output (RLO), for the same purpose. This measure is more specific because it assumes a particular spatial structure in the monoculture plots. Otherwise, ignoring this difference in spatial structure, the RLO can be written in the above formalism as:

$$RLO = \frac{O_T}{E_T} = D_T +$$

which shows that it has equivalent properties to those of D_T.

One advantage of the proportional deviation from the expected value is that it is both easy to interpret and easy to generalise to any kind of comparison between observed and expected values. In particular, it can be applied to individual species in a mixture. Define the proportional deviation of species *i*'s yield from its expected value, D_i, as:

$$D_i = \frac{O_i - E_i}{E_i}$$

This measure reveals the sign and magnitude of the net effect on each species of the interactions with the other species in a mixture (Table 1). Because it is standardised by the expected value, it can also be used in comparisons among mixtures that differ in both composition and diversity.

Further define the (weighted) average proportional deviation from the expected yield in a mixture as:

$$\bar{D} = \sum p_i D_i$$

It is easy to prove that this average is related to the RYT by the following identity:

$$RYT = \bar{D} +$$

Thus, $\bar{D} = 0$ is strictly equivalent to $RYT = 1$, so that $\bar{D}$ provides the same potential as RYT for testing the null hypothesis that the observed yields can be accounted for by changes in the proportional contributions of the various species in the mixture (Table 1).

Note that positive values of either D_T or $\bar{D}$ alone do not suffice to provide unambiguous evidence for a positive effect of species interactions on the yield of a mixture after removal of the sampling effect. This is because these two measures aggregate various species-specific effects which may have opposite signs. In such a case, they may even lead to contradictory results, as illustrated by the two examples of Table 1, because they aggregate these species-specific effects differently. These potential problems can be mitigated, and our confidence in the results of these measures correspondingly increased, when the two measures provide congruent results, and when they are averaged across species combinations for each species richness treatment, as they should in randomised biodiversity experiments.

It is also possible to identify more stringent conditions that provide fully unambiguous evidence for a positive effect of species interactions on the yield of a mixture, whether by complementarity in resource use or direct facilitation. The first of these conditions is overyielding, as mentioned by Hector (1998). Overyielding can also be tested using the above formalism by defining:

$$D_{Max} = \frac{O_T - Max(M_i}{Max(M_i)}$$

Overyielding occurs when $D_{Max} > 0$. The second condition is when all species in a mixture have a higher than expected yield, i.e., $D_i > 0$ for all i. Either of these conditions (which do not necessarily coincide) is sufficient to unambiguously assert that a mixture performs better than the corresponding monocultures.

In conclusion, given the multitude of potential interspecific effects in mixed communities, no single measure is likely to be satisfactory for all purposes. Instead I suggest a mixed strategy based on the use of proportional deviations from expected values as a simple unified methodological framework to control for sampling effects in biodiversity experiments. A combination of D_T, $\bar{D}$, D_{Max} and D_i can be used to analyse experimental results at several levels:

(1) D_T can be used as a rough tool to analyse the effect of biodiversity on total ecosystem processes. This aggregated measure already allows one to remove the effect of species identity in comparisons between mixtures, thus reducing undesirable variations due to different species compositions within each diversity treatment.

(2) $\bar{D}$ can be used to perform a more specific test of the null hypothesis that the observed yields can be accounted for by shifts in numerical dominance among species in each mixture.

(3) D_{Max} can be used to test for overyielding, which is a sufficient (but stringent) condition to unambiguously assert that a mixture performs better than the corresponding monocultures.

(4) In the last analysis, any effect of biodiversity on ecosystem processes is to be viewed as the aggregated result of a large number of species interactions in the ecosystem. Since different species are likely to be affected differently by changes in the composition and diversity of mixed communities, D_i can be used to analyse these species-specific effects. For instance, the average D_i across mixtures at each level of diversity could be plotted against diversity for a species i to detect if variations in diversity have a consistent effect on that particular species. The D_i's also provide an alternative sufficient condition to unambiguously assert that a mixture performs better than the corresponding monocultures.

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