Is competition structuring this ancient ecosystem?

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This exercise is based on Casey Hermoyian and colleagues' (2002) work testing the hypothesis that competition helped structure a community of four strophomenid brachiopods. Hermoyian. *et al* (2002) tested Robert MacArthur's (1972) predictions that past competition would be recognized by (1) non-overlapping resource use by former competitors, but with (2) very small differences between that nonoverlapping use. (See Figs. 1 and 2 below.)

Students use the same protocols and procedure used by Hermoyian *et al* (2002) on a collection of middle Paleozoic brachiopods to test the same hypothesis. We use brachs from the Middle Devonian Onondaga Limestone from western New York, but different brachs from different times could certainly be used.

There are several goals for the exercise. First, students learn about some of paleoecology's abilities and limits. The exercise also reinforces the ecological concepts of competition and niche partitioning.

Students also practice (1) honing observation skills as they must sort through a pile of different brachs and separate them into groups, (2) collecting and analyzing data with statistical techniques, (3) testing hypotheses, (4) using computer spreadsheets, (5) synthesizing results, and (6) providing clear and cogent results in abstract form.

The exercise may also be a lesson in negative results, as there's no guarantee they'll get a positive result; more than likely there *won't* be evidence for competition. Either way, the results are interesting.

This is a stand-alone exercise, but dovetails well with lecture units on paleoecology, competition, and testing hypotheses, as well as part of continuing practice on synthesizing results and summarizing material in abstract form.

Hermoyian, C.S., L.R. Leighton, and P. Kaplan. 2002. Testing the role of competition in fossil communities using limiting similarity. *Geology* 30:15-18.

MacArthur, R.H. 1972. *Geographical Ecology*. Princeton University Press, Princeton, NJ, 269 p.

GEO 290—Paleontology
Is Competition Structuring this Ancient Ecosystem?

Objective: In this lab we will analyze a brachiopod community to determine whether competition was responsible for structuring the community.

Paleoecology encompasses a wide variety of research questions, ranging from the reconstruction of ancient environments and the environmental preferences of single species (**autecology**) to the analyses of assemblages of organisms as a whole, looking for relationships among them (**synecology**).

Many paleoecologists are interested in competition. This interest is logical because most biologists believe that competitive interaction among organisms is an important force in natural selection. (I have to put in my knee-jerk disclaimer here, I can't help it: Beware using competition to explain everything. Done.) Testing whether competition played an important role in shaping the patterns we see in the fossil record is one way of resolving knee-jerk complaints. With a tool for answering this question, we could wonder about whether competition is important in most or only a few communities, whether it is equally important at all moments in time, or whether it is particularly strong in some environments and weak in others. *The problem is that even in the modern world, where we can watch the organisms interact, recognizing competition is notoriously difficult*. For example, it has been suggested that zebra mussels and native unionid mussels compete for living space in Seneca Lake. How would you tell whether they are, in fact, competing? One possibility is to see whether populations of zebra mussels displace unionids over time. This might (or might not) suggest superior competitive ability on the part of the zebra mussels, but you couldn't tell *for what* they were competing…or even whether competition caused the disappearance of unionids.

Ecologists working with living organisms solved the problem theoretically. G. Evelyn Hutchinson (1959) defined the **niche** of an organism as an n-dimensional hypervolume with the axis of each dimension being the range of the organism's tolerance or requirement for one environmental parameter. For example, the niche of an elephant might include one dimension (or axis) describing a range of temperatures it tolerates, one dimension describing a range of required food resources, one dimension with home range size, *etc.* Hutchinson (1959) went on to argue that when organisms competed, one of two things would eventually happen. Either one of the partners would disappear (the species would no longer compete because they no longer live together) or natural selection would adjust the resource requirements of one or both competitors so that their descendents use slightly different resources (they no longer compete). He called this latter possibility **resource** or **niche partitioning**. Either way, the species no longer compete.

Robert MacArthur (1972) (of island biogeography fame) took this idea one step farther. MacArthur homed in on one or a few aspects of the co-occurring organisms' environment over which they might be competing. For example, two lizard species living together might compete for prey of a given size. To test this, one could record the size of prey caught by each species and plot these data as a frequency distribution (Fig. 1). In this example, the two lizard species eat prey of different sizes, with no overlap. This suggests that they are not, in fact, competing for a food resource because each has specialized on a specific size of prey, exclusive of that preferred by the other lizard species.

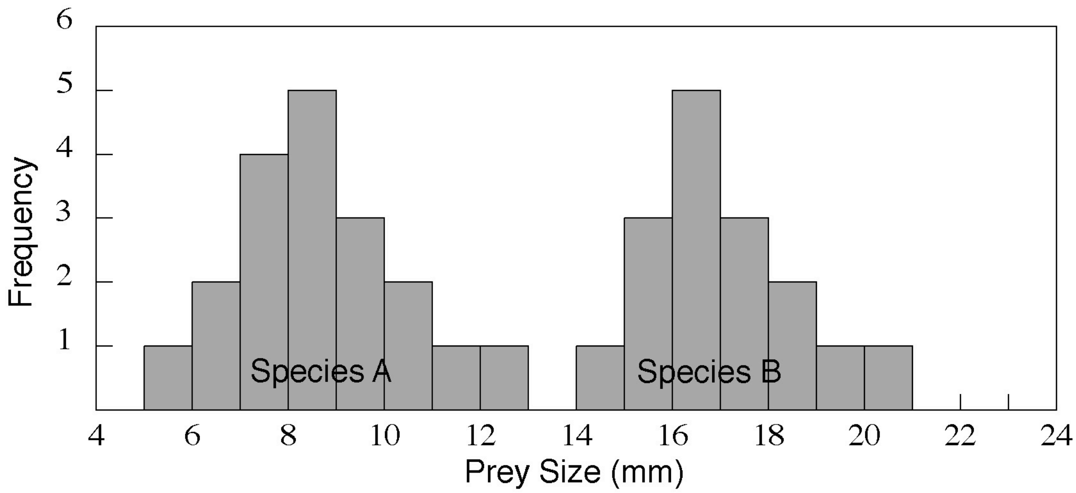


Fig. 1. Prey size preferences for two species of co-occurring lizards.

MacArthur (1972) went on to suggest that this type of distribution, where species co-exist using non-overlapping resources, showed that competition *in the past* had shaped the resource use of each species. He called this the "ghost of competition past". Furthermore, if natural selection driven by past competition had, indeed, shaped this pattern, one would expect only very small differences between the ranges of prey size preferences among the lizards. After all, once competition had been relieved by partitioning the resources, selection would cease and no more change in prey size preference would occur.

Casey Hermoyian and colleagues (2002) performed a similar analysis with fossil brachiopods. The first challenge was to think of the resources for which articulate brachiopods might have competed. Given that brachiopods are sessile filter feeders, space and food were the most likely candidates. Next, they had to find some feature on the fossil brachiopod that would correlate with the feeding and space requirement of the living brachiopod. Required space was easy. This would correspond with the size of the brachiopod shell. For feeding ability, they approximated the size of the brachiopod's feeding organ, the lophophore, by measuring the outline of the shell from hinge to hinge (SOL in Fig. 2). This works because the lophophore is a curved organ that rests just inside the shell following the line of the commissure.

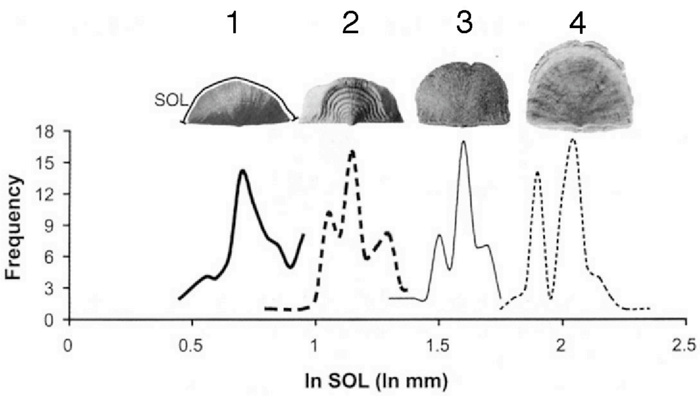


Fig. 2. Frequency distributions of ratio sums of the strophomenid outline length (SOL) for four brachiopods from the Liberty Member, Dillsboro Fm., Upper Ordovician of Indiana (Hermoyian et al., 2002). Note little overlap and small gaps between distributions, suggesting resource partitioning produced by natural selection in a competitive environment.

Next, Hermoyian and colleagues (2002) had to ask the question: Do we see evidence of niche partitioning, likely shaped by competition? Remember, MacArthur's theory offered two predictions. First, that the distribution of resource use wouldn't overlap among the species; and second that there would be only small differences between adjacent species on the resource gradient. They tested the first part of this prediction by plotting the frequency of SOL measurements for each species against ln SOL (Fig.2). As you can see, the resource use curves overlap very little. The second prediction turns out to be more challenging. The curves seem close together as predicted by MacArthur. The important question is, how close is close enough to conclude that competition was at work? In other words, is this pattern similar to or different from a pattern you might expect from a random sample of four brachiopod species? If this pattern could be produced by a random sample, then it is unlikely that it was shaped by competition, which would create a non-random pattern. They phrased their question like this:

Null hypothesis: The ratio sum of the four brachiopod species in the study is similar to that expected from four randomly selected brachiopod species.

Alternative hypothesis: The ratio sum of the four brachiopod species in their study is smaller than[1] that expected from four randomly selected brachiopod species.

The ratio sum quantitatively reflects the collective differences among the resource use gradients. It is calculated by summing the absolute value of the difference between ratios of all possible combinations of the four species, as follows (Hermoyian et al., 2002).

$$\text{ratio sum} = \left|\frac{\text{SOL sp. 2}}{\text{SOL sp.1}} - \frac{\text{SOL sp. 3}}{\text{SOL sp. 2}}\right| + \left|\frac{\text{SOL sp. 2}}{\text{SOL sp.1}} - \frac{\text{SOL sp. 4}}{\text{SOL sp. 3}}\right| + \left|\frac{\text{SOL sp. 4}}{\text{SOL sp.3}} - \frac{\text{SOL sp. 3}}{\text{SOL sp. 2}}\right|$$

The next question is, what do we expect by random chance? Hermoyian and colleagues (2002) measured SOL for all of the strophomenid brachiopods in the *Treatise on Invertebrate Paleontology*. Then, they wrote a computer program to randomly sample four species from this list and calculate the ratio sum. After repeating the calculation 100,000 times, they plotted the frequency distribution of these randomly selected combinations and compared the ratio sum of the four brachiopods in their study against the random sample. It turned out that the ratio sum

[1] In this case, we're just thinking about the case where the study sample is smaller than expected because our hypothesis of competition predicts small differences between resource distributions.

for their brachiopods was much smaller than that likely to be produced by chance alone, suggesting to the authors that competition had been at work.

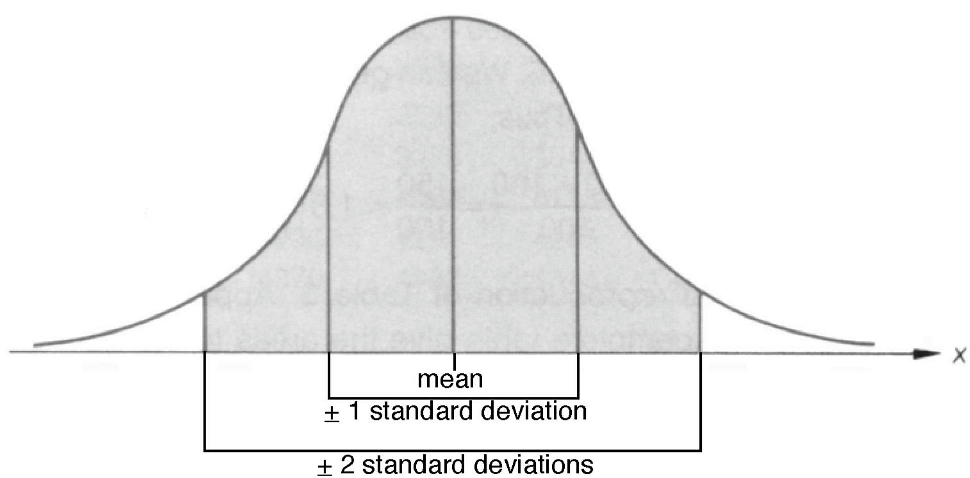
In this lab, you will be performing a similar analysis on four species of brachiopods collected from the Middle Devonian Moorehouse Member of the Onondaga Formation at the Oaks Corners quarry, near Geneva, New York[2].

1. Double check that the brachiopods have been sorted by species correctly. Remove all specimens that are broken or damaged such that SOL could not be confidently measured.
2. Measure SOL in millimeters (see Fig. 2) on the remaining specimens of each species. Measure SOL by carefully running a string along the commissure of the brachiopod and measuring the string length with a ruler. With each species as its own column, record the SOL for each individual in Excel. Calculate SOL means for each species.

3. On graph paper, plot frequency distributions for SOL values for each species. The easiest way to do this is to sort your values in Excel before you begin plotting. Do you see the pattern of non-overlapping resource distributions predicted by the competition hypothesis?

4. Using the average SOL values for each species, calculate the ratio sum of the Moorehouse Member brachiopods using the formula discussed above. Now compare the Moorehouse Member ratio sum to that expected from a random sample of brachiopods.

When you take a large random sample (like the 100,000 random ratio sums described above), your results graph into a **normal distribution** like that in Fig. 3. The high point of the curve is the mean or average value. From this distribution you can calculate the standard deviation, which expresses the variation of values around the mean in your random sample. Typically, 68% of the values in the random sample will occur within one standard deviation of the mean; 95% will be within two standard deviations of the mean. By convention, any value outside of this 95% is considered statistically different from a value you might expect through random processes alone.



[2] Thanks to Nadine Acquisto, Dewey Price, Andy Goldman, Michelle Rinaldi, Steve Domber, Susan Butts, Janine Witte, Ann Isley, Don Woodrow and Evie Krasnow for these collections.

Fig. 3. A normal distribution with the mean and range of values included in one and two standard deviations noted. Sixty-eight percent of the values of this parameter will fall within one standard deviation of the mean; 95% of values in this distribution will fall within two standard deviations. Any values of this parameter larger or smaller than two standard deviations (white areas) are considered statistically different from a value expected by random chance alone.

Following the procedure described by Hermoyian and colleagues (2002), we calculated 100,000 ratio sums for randomly selected groups of four species of strophomenid brachiopods. The mean is 3.769 and the standard deviation is 2.898. If the Moorehouse Member ratio sum is smaller than two standard deviations below this mean, then we reject the hypothesis that the pattern we observe in the Moorehouse Member was produced at random, and accept the alternative that some process, in this case, competition, influenced the ratio sum of the Moorehouse brachiopods. Obviously, two standard deviations below the mean would be a negative number, which doesn't have a physical meaning. Therefore, we want to figure out what is the probability that the Moorehouse Member value is not due to random chance. To do this, we first calculate a **z-statistic** for the Moorehouse Member ratio sum. The z-statistic is a standardization of the ratio sum on a z-distribution. The z-distribution is useful because it always has a mean of 0 and a standard deviation of 1. Calculate the z-statistic as follows:

$$z = \frac{\text{Morehouse Mb. ratio sum} - \text{mean}}{\text{standard deviation}} = \frac{x - 3.769}{2.898}$$

Note that this number will probably be negative. Now consult a statistical table to find the area under the normal distribution corresponding to this z-statistic. The p-value, or probability of your ratio sum being the result of a random selection of four brachiopods (null hypothesis) is calculated as follows:

$$1 - [(area) \times 2] = \text{p - value}$$

5. As a general rule, p-values of 0.05 or less are considered statistically significant. This means that there is only a 5% chance that your ratio sum is derived from a random selection of brachiopods. Is your result statistically significant? If your p-value > 0.05, you **fail to reject your null hypothesis** that your brachiopods are a random assemblage, not influenced by competition-induced niche partitioning.

ABSTRACT

Write an abstract, similar to one you might submit to a scientific conference[3], describing your analysis. Your abstract *may not exceed 200 words*, and should include the following elements:

- Title (maximum 70 characters including spaces) that tells the main idea of the research.
- Background information that explains the context of the research and poses the research question.

[3] Check out the abstract volume from a recent meeting of the Geological Society of America for examples of how scientific abstracts in geology are composed.

- Method that gives the main idea of the procedure you followed.
- Results. Was your result statistically significant?
- Interpretation of the results and the primary conclusion of the analysis.

Questions for Further Thought

1. What sources of error can you find in this method? Consider its basic idea (e.g., the theoretically predicted consequence of competition), the design of the analysis (e.g., the resources considered and how resource use is reconstructed from fossils), and execution of the method (e.g., what you actually did).

Note: Nan Crystal Arens originated the idea for this exercise and has kindly allowed me to develop it.

References

Hermoyian, C.S., L.R. Leighton, and P. Kaplan. 2002. Testing the role of competition in fossil communities using limiting similarity. *Geology* 30:15-18.

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