TESTS FOR MORPHOLOGICAL COMPETITIVE DISPLACEMENT: A REASSESSMENT OF PARAMETERS

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Pleasants (1990) compared the relative power of tests based on several parameters to detect morphological competitive displacement. He concluded that tests based on "community-wide" parameters such as Mean (the average distance between adjacent species in a logarithmic size gradient), Poole and Rathcke's (1979) Var (the variance of these distances), and Min (the shortest distance between any two adjacent species) are more reliable than those based on the G parameters (ratios of distances between adjacent species) developed by Simberloff and Boecklen (1981). Here I show that Pleasants' (1990) observations are flawed because he concentrated on two extreme cases, ignoring intermediate arrangements that provide a better test for the parameters under consideration.

Pleasants (1990) analyzed a hypothetical community of four species arranged in a gradient of size ranging from 1.0 to 19.0 arbitrary units. The scale was logarithmic, so distances in the gradient actually measured body-size ratios. In what I will call his first example, Pleasants (1990) maximized morphological segregation by assigning values of 1.0, 7.0, 13.0, and 19.0 to the species. In the second example, he analyzed a contrasting case in which three of the species had the same size (values were 1.0, 19.0, 19.0, and 19.0). The first example is a community in which displacement is evident, whereas the second one presents obvious clumping of species.

When he compared the G parameters for his first example with the distributions of G parameter values for 1000 randomly generated communities, Pleasants (1990) obtained nonsignificant ($P > .05$) results for two of the three G parameters and concluded that estimates of such parameters did not provide a reliable basis for detecting competitive displacement. Using his second example, he claimed that the use of $G_{1(n-1)}$ may produce a Type I error by suggesting displacement when species

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are in fact clumped. Upon close examination of the results, I found two shortcomings in Pleasants' methodology: (1) the use of a discrete scale of sizes and (2) the use of observed values as limits for the size gradient.

Pleasants (1990) simulated the communities by generating random integers from 1.0 to 19.0 (J. Pleasants, *personal communication*), restricting the set of possible values to 19 integers instead of an infinite number of continuous values. A consequence of a finite number of values is that the set of possible distances is reduced, and the probability of getting two distances with the same magnitude is increased. This increased probability impairs the tests based on the G parameters because the probability of getting distance ratios of 1.0 (and thus values of $G = 1.0$) is also increased.

I replicated Pleasants' (1990) first example, but allowed species in the random communities to acquire any continuous value between 1.0 and 19.0. In 10 replicates of 1000 simulations each, null hypotheses were invariably rejected ($P = .0$ for all parameters in all replicates). Clearly, Pleasants' (1990) alleged lack of power of tests based on the G parameters in this case is due to the use of a discrete scale.

The use of a discrete scale also increases the probability of getting two or more species with the same size simply by chance. For example, the probability of getting at least two species with exactly the same size in a random sample of four values from a set of 19 possible integers (assuming sampling with replacement) is 0.286 (Appendix, A), whereas the same probability using an infinite set of continuous variables is 0.0. If two species have the same size, $G_{1x} = 0.0$ for any x. Therefore, Pleasants' (1990) simulations had an inflated number of random communities with $G_{1x} = 0.0$, so the probability of values for $G_{1x} \geq$ the observed value was reduced, and the probability of incorrectly claiming segregation was increased.

As most authors have done, Pleasants (1990) set the limits for the morphological scale to the two extreme observed values. In his first example, however, such procedure limits the usefulness of Mean. This parameter is calculated as the average of the distances between adjacent species, that is, the summation of distances divided by their number. However, for points arranged in a line, the summation of such distances equals the distance between the extreme points. Therefore, the value of Mean is determined by the position of only two species in the community (the smallest and the largest), so it is not a community-wide parameter as defined by Pleasants (1990). Admittedly, if species are evenly spaced, the distance between the two extreme species would tend to be long, but the same distance could be the result of pure chance. In Pleasants' (1990) first example, Mean = 6.0 implies that the extreme species are separated by 18.0 units, regardless
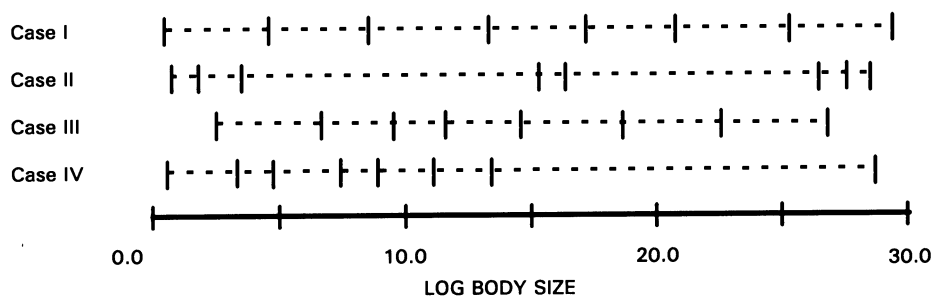
FIG. 1. Four eight-species hypothetical communities showing complete segregation of sizes (Case I), clumped distribution of sizes (Case II), size displacement with one exception (Case III), and size displacement with one outlier (Case IV). Scale is an arbitrary measure of body size.

of the position of the two intermediate species. Assuming random sampling with replacement, the probability of getting the smallest and largest species in a sample of four from a set of 19 is 0.030 (Appendix, B), which is close to the value reported by Pleasants (1990) for the expected probability of Mean (0.031).

TABLE 1. One-tailed P-level probabilities for six parameters of competitive displacement. Probabilities are the average for five replicates of 1000 simulations for each case. For G parameters and for Min, probabilities are for values $\geq$ those observed. For Mean and Var, probabilities are for values $\leq$ those observed.

	Expected probabilities		
Parameter	Four species	Six species	Eight species
Case I			
Mean	.523	.606	.038
Var	.000	.000	.000
Min	.020	.001	.000
G_{1n}	.000	.000	.000
G_{2n}	.047	.000	.000
$G_{1(n-1)}$	.011	.000	.000
Case II			
Mean	.441	.845	.137
Var	.840	.291	.956
Min	.665	.246	.130
G_{1n}	.780	.199	.204
G_{2n}	.890	.527	.607
$G_{1(n-1)}$	.353	.059	.268
Case III			
Mean	.445	.392	.461
Var	.608	.024	.001
Min	.454	.010	.130
G_{1n}	.587	.002	.002
G_{2n}	.145	.000	.000
$G_{1(n-1)}$	.849	.022	.091
Case IV			
Mean	.487	.263	.083
Var	.610	.166	.969
Min	.334	.002	.002
G_{1n}	.418	.005	.151
G_{2n}	.778	.090	.412
$G_{1(n-1)}$	.237	.000	.000

The Min parameter is also affected by the selection of the limits for the scale. With limits set to 1.0 and 19.0, the only combination that can produce a Min = 6.0 is Pleasants' (1990) first example. The probability of getting this particular combination is <.001 (Appendix, C). Pleasants (1990) reported one such combination in his 1000 simulations; I did not observe it in any of my simulations. Using a wider scale, the probability of getting Min = 6.0 is increased, and the power of tests based on this parameter to detect segregation is reduced.

To show the effect of limits, I replicated Pleasants' (1990) first example, but extended the upper limit to 30.0 and gave the species the values 6.0, 12.0, 18.0, and 24.0, leaving a space of 6.0 units between the extreme species and the limits. Average test P values for 10 replicates of 1000 simulations each were $P = .492$ for Mean, $P = .016$ for Min, and $P = .0$ for all other parameters. The Min parameter still was able to show segregation, but the power of tests based on the Mean parameter was clearly reduced by the wider limits.

Pleasants' (1990) examples are the two extreme cases of possible species arrangement, and they do not test the performance of the parameters in intermediate cases, where segregation or clumping is not so obvious. I designed four cases to test the performance of the parameters in intermediate cases (Fig. 1). I started with a morphological space with a range from 0.0 to 30.0 units. In the first community (case I) species were arranged evenly from 1.0 to 29.0, with a 4.0-unit space between each pair (this case is equivalent to the first example of Pleasants [1990]). To avoid using integers, each value was modified by adding a random number in the range (−0.5, 0.5). In this way species retained their relative positions, but values were continuous instead of discrete. Similar procedures were used to create a community with clumped species (case II, Fig. 1). For case III, I started with a community of seven evenly spaced species, and then positioned the eighth species in a randomly selected point along the gradient. This case simulates a community structured by com-

petitive displacement in which only one species breaks the pattern. A real case could be the presence of an accidental or transient species in an otherwise highly organized community. In case IV, seven of the species are evenly distributed and the eighth is an outlier, being much larger than the rest of the species in the community. These four cases were replicated for assemblages of four and six species. To allow comparison with Pleasants' (1990) results, the pool for my simulations had a log-uniform frequency distribution instead of a log-normal one, as advised by several authors (Colwell and Winkler 1984, Schoener 1984, Tonkyn and Cole 1986, Eadie et al. 1987, Losos et al. 1989, but see Boecklen and NeSmith 1985).

Tests based on all parameters except Mean correctly detected displacement in case I for the three sample sizes ($P < .05$, Table 1); tests based on Mean did indicate segregation when $n = 8$ ($P = .038$), but this was because the extreme species were close to the limits. This failure to detect segregation even in the extreme case clearly shows that Mean is not a good indicator of competitive displacement.

For case II, all tests correctly indicated no displacement (all $P > .05$). For case III and $n = 8$, tests based on Mean, Min, and $G_{1(n-1)}$ failed to detect displacement in the community, but the last two correctly detected it for $n = 6$. All parameters failed to show displacement when $n = 4$. In case IV, only parameters Min and $G_{1(n-1)}$ detected displacement for $n = 8$ and $n = 6$. All tests failed when $n = 4$.

Results of my simulations show that tests based on the Mean parameter are not reliable in detecting competitive displacement. Tests based on Min, Var, and Simberloff and Boecklen's (1981) Gs have much more power, but no single parameter is reliable under all circumstances. Tests based on parameters Min and $G_{1(n-1)}$ perform well in detecting displacement despite the presence of an outlier (case IV) but are unreliable in case III. Tests based on Var, G_{1n}, and G_{2n} are effective in detecting displacement in situations like case III, but can produce incorrect results if an outlier is present. All tests have little power for small sample sizes, except in cases with obvious segregation.

In conclusion, when testing communities for competitive displacement, no single parameter will provide the correct result in all cases. A combination of tests using different parameters would be the best way to avoid Type II errors. It is also apparent that when the community is very small ($n < 6$) displacement will not be detected unless species are almost perfectly segregated.

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APPENDIX

A) Assuming sampling with replacement, there are n^r ways of arranging n objects in groups of r ($r \leq n$) elements, and $_nP_r$ possible arrangements in which all r elements are different. ($_nP_r = n!/(n - r)!$, where the symbol "!" indicates factorial, is the number of possible permutations of subsets of r elements from a set of n elements). Therefore, the probability of getting a sample with all elements different is:

$$P(\text{all different}) = \frac{_nP_r}{n^r},$$

and the probability of getting samples with at least two identical elements is:

$$P(\text{at least two elements identical}) = 1 - \frac{{}_nP_r}{n^r}.$$

For samples of four elements from a set of 19, the probability of getting at least two identical elements is:

$$P = 1 - \frac{{}_{19}P_4}{19^4} = 1 - \frac{19!}{15! \cdot 19^4} = .2862.$$

B) Under the same sampling conditions as in A, and defining A and B as the events of getting the numbers a and b in a sample from a set of n numbers, the probability of getting both numbers in the sample can be expressed as:

$$P(A \cap B).$$

It can be shown (Freund and Walpole 1987) that:

$$P(A \cap B) = 1 - P(A') - P(B') + P(A' \cap B'),$$

where $P(A') = 1 - P(A)$ and $P(B') = 1 - P(B)$. Consequently, the probability of getting two given numbers in a sample of r elements from a set of n is:

$$P(A \cap B) = 1 - \frac{(n-1)^r}{n^r} - \frac{(n-1)^r}{n^r} + \frac{(n-2)^r}{n^r}, \quad \text{or:}$$

$$P(A \cap B) = 1 - \frac{2(n-1)^r - (n-2)^r}{n^r}.$$

If $n = 19$ and $r = 4$:

$$P(a \text{ and } b) = 1 - \frac{2 \times 18^4 - 17^4}{19^4} = .02985$$

C) There are 4! ways of arranging four elements in groups of four. Consequently, the probability of getting four particular numbers from a sample of 19 is:

$$P = \frac{4!}{19^4} = .000184.$$

The results of calculations using these formulas were confirmed numerically by generating the 19^4 possible permutations and tallying the successes in each case.