Supplemental information for Ecological Theory Provides Insights into Evolutionary Computation

I. Equivalence between coexistence criteria in fitness sharing and ecology

A. Fitness sharing

Deb and Goldberg describe the rules for coexistence between two genotypes (1 and 2) on different fitness peaks (f_1 and f_2, respectively) with the following equation (one of three possible forms of equation 13 from [1]):

$$Sh_{12} < \frac{1}{\gamma} \tag{1}$$

In this equation, Sh_{12} is the value of the sharing function (equation 1 from the main body of our paper) between genotypes 1 and 2. f_1, the peak that genotype 1 sits on, is the higher fitness peak. γ in the above equation is the ratio of these two fitness peaks: $\frac{f_1}{f_2}$. Note that because genotype 2 has the lower fitness, failure to coexist would necessarily mean genotype 2 going extinct.

B. Ecology

The criteria for stable coexistence under modern coexistence theory in ecology are described by equation 2 from [2]:

$$\rho < \frac{k_2}{k_1} < \frac{1}{\rho} \tag{2}$$

Where ρ is a value between 0 and 1 that describes the amount of overlap in the niches of species 1 and 2. k_1 and k_2 are the average fitnesses of these two species. The two inequalities in this equation come from the fact that it is actually a combination of two independent equations:

$$\rho < \frac{k_1}{k_2} \tag{3}$$

and

$$\rho < \frac{k_2}{k_1} \tag{4}$$

Together, these equations describe what is known as the "mutual invasibility criterion". Essentially, for two species to coexist, each one needs to be able to invade a population of the other. This criterion makes sense because each species will be at its fittest when it is rare (since individuals will have less competition from other members of that species). As that species becomes more plentiful, its fitness will decrease. Thus, for any given pair of species that meet the mutual invasibility criterion, there will be a stable attractor in the space of possible densities each species could have in the population.

In equations 3 and 4, the dominant species in the population corresponds to the denominator (e.g. k_2 in equation 3) and the species invading the population corresponds to the numerator (e.g. k_1 in equation 3).

C. Common ground

With a trivial amount of algebra and reasoning, we can see that these equations are in fact the same. Sh_{12} and ρ are functionally identical. Both range from 0 to 1, with 0 indicating no niche overlap and 1 indicating complete niche overlap. Although Deb and Goldberg do make some assumptions about the sharing function when deriving this equation, those assumptions will not effect this equivalency.

The only other term is the fitness ratio. In fitness sharing, it is described as $\frac{1}{\gamma}$ which is equivalent to $\frac{f_2}{f_1}$ (the reciprocal of γ). Coexistence theory also involves a fitness ratio term ($\frac{k_2}{k_1}$) but it's important to carefully consider whether they have the same meaning.

A potentially important difference is that, in fitness sharing, we said that f_1 is always the higher fitness peak. This requirement is necessary in equation 1, because it only contains a lower bound on the fitness ratio. Thus, it only tells us about genotype 2's ability to stably persist in the population, which is only sufficient when genotype 2 is the one at the disadvantage.

The modern coexistence theory equations make no assumptions about which fitness is higher. Doing so would be unnecessary, because the fitness ratio is bounded on both sides. These turn out to be two equivalent approaches to satisfying the mutual invasibility criterion. Thus, if we add an upper bound to the fitness sharing equation, we can safely drop the requirement that f_1 be greater than or equal to f_2.

The other possible distinction between the fitness ratios is what the fitnesses themselves represent. In fitness sharing, f_1 and f_2 are the fitnesses of the two genotypes before we add the fitness sharing adjustment (Deb and Goldberg define them as the height of the fitness peaks, but in reality the very top of a fitness peak may not be found). In modern coexistence theory, k_1 and k_2 are the "average fitnesses" of a species; in biology, it would be impossible (and somewhat non-sensical) to separate the fitness of an individual from its environment. However, in practice, dealing with the average fitness will cancel out the effects of competition.

Thus, we can conclude that the fitness ratio terms in these two equations are indeed measuring the same underlying quantity. As such, equations 1 and 2 are completely equivalent.

References

[1] K. Deb and D. E. Goldberg, "An Investigation of Niche and Species Formation in Genetic Function Optimization," in *Proceedings of the 3rd International Conference on Genetic Algorithms*. San Francisco, CA, USA: Morgan Kaufmann Publishers Inc., 1989, pp. 42–50. [Online]. Available: http://dl.acm.org/citation.cfm?id=645512.657099

[2] P. Chesson and J. J. Kuang, "The interaction between predation and competition," *Nature*, vol. 456, no. 7219, pp. 235–238, Nov. 2008. [Online]. Available: http://www.nature.com/articles/nature07248