SI Materials and Methods: Discussion of NFD

This appendix was inspired by and developed with help from Bob Holt.

The term frequency dependence has been used multiple ways in ecology. To avoid confusion, here we define the precise type of frequency dependence we expect to be related to species' rarity. We are referring to frequency dependence in the population growth rate of a single species. Frequency dependence can be a direct result of processes that operate on a species' relative abundance in a location (e.g. ratio-dependent predation, frequency dependent transmission in infectious disease dynamics, predator switching) and models of these dynamics include relative abundance explicitly. This is not the type of frequency dependence to which we are referring.

We are referring to indirect frequency dependence, which ultimately stems from density dependence. As a simplified example, consider the Ricker equation for density-dependence, generalized to account for competition:

$$N_1\,(t+1) = N_1\,(t)\,\exp[r_1 - a_{11}N_1\,(t) - a_{12}N_2\,(t)],$$

$$N_2\,(t+1) = N_2\,(t)\,\exp[r_2 - a_{22}N_2\,(t) - a_{21}N_1\,(t)],$$

where r is intrinsic growth rate, and α_{ij}'s is the per capita effect of species *j* on species *i*.
To derive the equations for frequency dependence from this model, first let

$$N = N_1 + N_2,$$

$$p_1 = N_1 / (N_1 + N_2),$$

and

$$p_2 = N_2 / (N_1 + N_2)$$

respectively be total community size and the frequency of species 1 and 2. Therefore,

$$N_1 = pN,$$

and

$$N_2 = (1-p)\,N.$$

Solving for ln(growth rate) for species 1 results in:

$$\ln\frac{N_1(t+1)}{N_1(t)} = r_1 - a_{11}pN - a_{12}(1-p)N$$

If we further simplify by assuming that total community abundance N is approximately fixed, then the strength of frequency dependency for species 1 is:

$$\frac{\partial}{\partial p}\ln\frac{N_1(t+1)}{N_1(t)} = (a_{12} - a_{11})N$$

Now it is clear that the strength of negative frequency dependence can be increased in two ways. Intraspecific density dependence (a_{11}) can be increased, or interspecific density dependence (a_{12}) can be decreased. Increasing intraspecific competition could certainly make species rare, but it is unlikely to provide any population buffering from extinction. In contrast, decreasing interspecific competition directly facilitates persistence by reducing overall competitive limitation when the focal species is rare. It is not the absolute values of either interaction parameter, but their relative values, that matters for the persistence of rare species.

This definition of NFD also illustrates the reasons why we expect the effects of NFD to be asymmetric (why rare species are more likely to be disproportionately affected by competitive effects). Rare species that do not avoid interspecific competition face extremely high total competitive effects in years when common species have high abundance, despite the fact that they themselves are rare. The same would be true for a common species, but they fall to low abundance so infrequently that stochastic extinction is less of a threat.