* 1. **Negative Frequency dependency (NFD) method**

The most commonly used empirical method to measure *per capita* competition coefficients (*α*) is the negative frequency method (Adler et al. 2007, Levine andHilleRisLambers 2009). The idea of NFD method is that assuming a community is saturated so all the resources or niche are being occupied by either the focal species *i* or it competitor *j*. Under this assumption, decreasing the frequency of the focal species *i* frees the resources for its competitor. Therefore, decreasing the frequency of focal species *i* means the focal species *i* are competing with less individuals of its own kind than individual of the competitor. On one hand, if the focal species *i* is more limited by its own than by its competitor, i.e. the intra-specific competition coefficient is greater than the inter-specific competition coefficient, decreasing relative frequency of the focal species *i* should increase its own *per capita* growth rate. The frequency should thus be negative. On the other hand, if inter-specific competition is greater, frequency dependency should be positive as the *per capita* growth rate of the focal species *i* increase with its own frequency. Given this rationale, we argue that negative frequency is to be expected when the focal species *i* limits itself more than it limits its competitor, i.e. intra-specific competition coefficient is greater than inter- specific competition coefficient. Therefore, as long as the frequency dependency is negative, species should be guaranteed to stably coexistence. Adler *et al* 2007 show that if NFD is constant across all focal species’ frequency, this slope and the difference in intercepts can be used to estimate whether both species have a positive per capita growth rate when at rare. When this condition is satisfied, two species are mutually invasible and should coexist.

However, we argue that there are two issues associated with the NFD method. First, the magnitude of negative frequency dependency (the slope) is not equivalent to either intra- or inter-specific competition coefficients but a rather complex combination between both. Second, while the NFD method is consistent with Chesson’s requirement that coexisting species are mutually invasible, we argue that the assumption that NFD is constant across frequencies is problematic in practice.

First, to show that NFD slope is a complex combination of intra- and inter specific competition coefficients, we attempt to calculate the NFD slope based on the the Lotka-Volterra model. Conceptually, when the per capita growth rate is being plotted against the frequency of the focal species, the NFD slope is actually the ”per %” impact on the per capita growth rate. To show that negative frequency dependency (NFD) metrics cannot be used directly to measure competition coefficients (*α*), we attempt to derive the NFD metrics from the Lotka-Volterra model. We found that, the NFD metrics cannot be readily derived from the Lotka-Volterra model without making further assumptions. First, there is only density term but no frequency term in the Lotka-Volterra model. Only when the community density is fixed, the density dependency, *αij*, is equivalent to density dependency (Adler et al. 2007). In addition, since the density dependency, *αij*, is modeled in *per capita* fashion, one-to-one conversion between the focal species *i* and its competitor also needs to be assumed. By doing so, the Lotka-Volterra competition model can be rewritten as followed.

(2)

In equation 2, *B* is the fixed community density and one unit decrease of *Ni* will lead to one unit increase of *Nj*. Note that this *B* is an arbitrarily defined constant describing a fixed community density and has nothing do to with the equilibrium of any of the species. To calculate the negative frequency dependency (NFD) metrics, we take derivative of equation 6 in terms of Ni/B.

(3)

This equation 3 describe the change of species *i*’s *per capita* growth rate with respective to the change of its own frequency in a community (Fig. 1). From equation 3 the NFD depends on a combination of *per capita* growth rate (*ri*) and the fixed community density (*B*) in addition to the intra- and inter-specific competition coefficients. From this equation, we first see that NFD is negative as long as the intra-specific competition (*αii*) is greater than the inter-specific competition (*αij*). Additionally, higher *per capita* growth rate of a species and higher community density (e.g. in the later more mature stage of the community) would lead one to estimate stronger frequency dependency (Fig. 1). Most importantly, although NFD metrics has been used to estimate species coexistence empirically for annual plant communities (e.g. Godoy et al. 2014), NFD should be interpreted with caution as it is related but not equivalent to the competition coefficients (*αii* and *αij*) and thus should not be directly used to calculate ND and RFD, and to predict species coexistence.

Second, in practice, intra- and inter specific competition coefficients do not necessarily be constant so that the NFD might not be constant across frequencies of the focal species. To demonstrate that non-constant intra- and inter specific competition coefficients can lead to non-constant NFD slope and incorrect prediction of species coexistence, we did simulation using Tilman’s consumer resource model. From the simulation experiment based on this model, we see that the slope of NFD is not constant across all frequencies (Figure SXXX). Because the purpose of the NFD method is to estimate whether both species would have positive growth rates when invading from rare, we argue that directly measuring growth rates at low frequency is preferred over relying upon the slope of NFD at point. If, however, an empiricist is unable to attain growth rates at low frequency, they would need to extrapolate from the observed frequencies and risk inaccurate predictions.