Appendix A - Food Web Evenness index (FWE)

Calculation of the FWE index is a two-step process. First the expected biomass (B_{ie}) of each species (or functional group, trophospecies, depending on the aggregation level of the model) i is calculated, then an inverted dissimilarity index (Bray-Curtis, BC, or Canberra metric, C) is used to measure how close the observed biomasses of species are to their expected biomasses.

To calculate expected biomasses, we define a state of 'food web evenness' as decreasing biomasses with increasing trophic levels and equal biomasses within trophic levels. For example, if we assume that biomasses at consecutive integer trophic levels differ by a factor of 10, and total biomass at the second trophic level is B^*, then expected biomass on the third trophic level is $0.1B^*$, and on the fourth trophic level $0.01B^*$. If there are no further trophic levels, then total biomass in the community equals $(1 + 0.1 + 0.01) \cdot B^*$. Biomasses within a trophic level are expected to be equal, thus, if there are four species at trophic level 2, they are all expected to have biomasses equal to $B^*/4$.

We can generalize these relationships as follows: B_{ie} values are calculated based on the total expected biomass at the lowest ('reference') trophic level, B^*, which is estimated as a certain fraction of the observed total biomass in the community Tot_B:

$$B_{ie} = \frac{B^* \cdot \varepsilon^{-(TL_i - TL^*)}}{n_i}, \quad (1)$$

$$B^* = \frac{Tot_B}{\sum_k \varepsilon^{-(TL_k - TL^*)}} \quad (2)$$

where $\varepsilon>1$ is the biomass ratio of consecutive integer trophic levels (10 in the above example). It is the multiplicative inverse of transfer efficiency defined as the ratio of production at consecutive trophic levels. TL_i is the trophic level of i, TL^* is the reference trophic level, n_i is the number of species at the same trophic level as i, Tot_B is total biomass in the community and k is the total number of all (not only integer) trophic levels.

The vector of B_{ie} values can then be compared against observed biomasses (B_{io}) in a community using Bray-Curtis dissimilarity:

$$BC = (\textstyle\sum_i |B_{ie} - B_{io}|) / \sum_i (B_{ie} + B_{io}) \ . \quad (3)$$

The Bray-Curtis dissimilarity index is more suitable to track changes in more abundant species (Krebs, 1999), as it calculates the change in biomass in each group divided by the sum of biomass in the two compared communities. However, for many applications it is more relevant to give equal weight to less abundant higher trophic level species. In these cases the Canberra Metric (Lance and Williams, 1967) measure could be used. This one calculates change in biomass relative to the sum of observed and expected biomass, i.e. relative change compared to group biomass:

$$C = \frac{1}{s} \cdot \sum_i \frac{|B_{ie} - B_{io}|}{B_{ie} + B_{io}}, \quad (4)$$

where s is the number of species in the community.

Finally, to calculate FWE we invert BC (FWE_{BC}=1-BC) or C (FWE_C=1-C), so higher index values express higher evenness.

An advantage of the *FWE* index is that it is independent of the total biomass in the system, in the sense that if community A has two times the total biomass of community B, but the biomass fraction of each species in the two communities are the same, *FWE* index values for communities A and B are going to be the same. Thus, *FWE* only tracks relative changes in species biomasses, i.e., in the compositional diversity of the community (it's scale invariant *sensu* Tuomisto, 2012).

It has to be noted that the 'biomass pyramid' concept does not hold for the biomass relationships at the very bottom of aquatic foodwebs due to high productivity of phytoplankton and microzooplankton. Thus, for aquatic systems it is sensible to only include multicellular organisms such as macrozooplankton or higher trophic level species when calculating this index.

References

Krebs, C.J., 1999. Estimating community parameters, in: Ecological Methodology. Addison-Welsey Education Publishers, Inc., pp. 373–409.

Lance G.N., Williams W.T. (1967): Mixed-data classificatory programs, I.) Agglomerative Systems. Australian Computer Journal 1:15-20.

Tuomisto, H., 2012. An updated consumer's guide to evenness and related indices. Oikos 121, 1203–1218. doi:10.1111/j.1600-0706.2011.19897.x