Hill's diversity: a general framework to address marine biodiversity management issues.

Grégoire Certain(1) and Benjamin Planque(2).
(1) Institute for Coastal Research, SLU, Öregrund, Sweden. Gregoire.Certain@slu.se
(2) Institute for Marine Research, Tromsø, Norway. Benjamin.Planque@imr.no

Introduction

How much species diversity do we have in a system, and how is it expected to change through space and time? How does taxonomic, phylogenetic or functional diversity relates to each other? How vulnerable is a community to a given pressure? All these questions are central issues in marine management and all can be addressed using a single mathematical framework rooted in biodiversity statistics. Hill (1973) proposed a general mathematical formulation of diversity indices that encompassed many of the well-known diversity indices used in ecology. However, this general formulation has rarely been used in biodiversity studies of marine ecosystems where "simpler" measures such as species richness or Shannon index are often preferred. A key aspect of diversity studies is the partitioning into α- and β- diversity (Whittaker 1972), which explicitly separates measures of biodiversity levels (α-diversity) from measures of biodiversity change (β-diversity). Such biodiversity change can be expressed in space, in time, or across a nested succession of hierarchical levels representing sampling units, regions, and various time periods. As reviewed by Tuomisto (2010), α- and β- taxonomic diversities can be generally expressed as Hill numbers. Biodiversity is often measured in terms of taxonomical variations only, but other species-specific sources of information can be used to account for species similarity or differences. Leinster & Cobbold (2012) proposed a slight modification of Hill's formula to account additional information such as phylogeny or functional trait. In this contribution, we briefly review the methodological core of these developments and present several recent applications for the Barents Sea (Certain et al. 2014, 2015a&b).

Method

Suppose a community dataset consisting of N samples where individuals are divided into S categories. Diversity can be partitioned into α-diversity, the diversity of categories represented within a sample, and β-diversity, the diversity of sample types. **Alpha-diversity** is noted $^qD_\alpha$ and is calculated as a weighted average of relative abundances of species:

$$(1) \quad ^qD_\alpha = \left(\sum_{j=1}^{N} w_j \sum_{i=1}^{S} p_{i|j}^q \right)^{\frac{1}{(1-q)}}$$

where i and j are the categories and sample indices respectively, $p_{i|j}$ is the proportional abundance of the ith species in the jth sample, and w_j is the proportional abundance of the jth sample relatively to the entire dataset. **Total diversity** in the dataset, $^qD_\gamma$, is calculated as:

$$(2) \quad ^qD_\gamma = \left(\sum_{i=1}^{S} p_i^q \right)^{\frac{1}{(1-q)}}$$

where p_i is the proportional abundance of the ith species in the whole dataset. From there, **β-diversity** $^qD_\beta$ is obtained by $^qD_\gamma / {}^qD_\alpha$. The above equations partition diversity as follows: the α component provides a diversity measure at the sample level, the γ component provides a diversity measure at the dataset level, and the β component scales the diversity measure from the sample to the dataset level. Considering further levels result in the addition of level-specific β components. In practice, level-specific $^qD_\alpha$ are computed from the first equation by aggregating the diversity samples at the level under focus, $^qD_\gamma$ is computed from the second equation, and the level specific $^qD_\beta$ are deduced

accordingly. In both equations, the parameter q controls the influence of abundant over rare species on the diversity metric. As q increases, the diversity measure becomes more sensitive to the abundant species and less sensitive to the rare ones. The parameter q varies in the interval $[0, +\infty[$. As it does, $^qD_\alpha$ equals species richness ($q=0$), the exponential of the Shannon index ($q=1$), and the reciprocal of the Simpson index ($q=2$). When q tends toward $+\infty$, $^qD_\alpha$ tends toward the reciprocal of the relative abundance of the most abundant species. A common practice is to measure $^qD_\alpha$ along a range of q values. This is called a diversity profile and it highlights how the diversity measure changes when the relative influence of rare and abundant species is gradually reversed (Hill 1973). Slopes of diversity profiles reflect unevenness in species abundance distribution: the steeper the profile, the larger the differences in the frequencies between the abundant and rare species.

A third methodological step is required to include further species-specific information such as phylogenetic position or functional traits. Leinster & Cobbold (2012) modified the classical estimate of Hill's diversity (Hill 1973) to take into account **species similarity**:

$$(3) \quad {}^qD^Z = \left(\sum_{i=1}^{S} p_i \left(Z_p \right)_i^{q-1} \right)^{\frac{1}{(1-q)}}$$

where $(Z_p)_i$ is a measure of the similarity between an individual of the ith species and an individual taken at random in the community; $(Z_p)_i$ is expressed between 0 (completely dissimilar) and 1 (identical) and it is usually measured through a set of traits for each species, as in classical functional diversity studies. This formula equals Hill diversity when $(Z_p)_i = p_i$. The use of $(Z_p)_i$ instead of p_i gives more weight to the highly dissimilar species, whereas in classical Hill diversity more weight is simply given to the most abundant species. $^qD^Z$ can be viewed as either a functional or phylogenetic diversity index, depending on which information has been used to compute $(Z_p)_i$.

Result & Discussion

The three equations provided here can be used as the core of an extensive framework for measuring species diversity, based on Hill's numbers. Using various combinations of these equations, all questions stated at the beginning of our introductory section can be addressed. Equation (2) at the sample level in combination with an extensive environmental covariate dataset can be used to predict the fate of ecological communities facing climate change (Certain et al. 2014). Equations (1) and (2) can be used to quantify changes in biodiversity in space and time as exemplified by Certain et al. (2015a). Equations (3) allows shifting from taxonomic to other type of diversity, depending on what information has been used to compute $(Z_p)_i$. For example, Certain et al. (2015b) used information on species vulnerability to compute $(Z_p)_i$ and transformed the diversity index into a community vulnerability measure. Given its flexibility and wide applicability, a more systematic use of Hill's framework in marine systems could provide more consistent tools for measuring, comparing and ultimately support management of marine species diversity.

References

Certain, G., Dormann, C. F., and Planque, B. 2014. Choices of abundance currency, community definition and diversity metric control the predictive power of macroecological models of biodiversity. Global Ecology and Biogeography, 23: 468–478.

Certain G. and Planque B. 2015. Biodiversity Baseline for Large Marine Ecosystems: An example from the Barents Sea. ICES journal of marine science, 72(6) : 1756-1768.

Certain G., Jørgensen L., Christel I., Planque B., and Bretagnolle V. 2015. Mapping the vulnerability of animal community to pressure in marine systems: disentangling pressure types and integrating their impact from the individual to the community level. ICES journal of marine science, 72(5) : 1470-1482.

Hill, M. O. 1973. Diversity and Evenness : A Unifying Notation and Its Consequences. Ecology, 54: 427–432.

Leinster, T., and Cobbold, C. 2012.Measuring diversity: the importance of species similarity. Ecology, 93: 477–489.

Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1.Defining beta diversity as a function of alpha and gamma diversity. Ecography, 33: 2–22.

Whittaker, R. H. 1972. Evolution and Measurement of Species Diversity. Taxon, 21: 213–251.