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Statistical performance of a multicomparison method for generalized species diversity indices under realistic empirical scenarios



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ABSTRACT

The Pallmann-Scherer test is a promising multicomparison procedure to test statistical hypotheses regarding generalized diversity/entropy indices, such as Tsallis family and Hill numbers (S_q and H_q , respectively), which represent alternative ways of profiling species diversity along a gradient of emphasis on species richness versus evenness in abundance distributions. Given the pressing importance of reliably comparing diversity across ecological communities, and since only a few of such procedures are currently available, knowing its statistical performance under realistic ecological scenarios is of strategic importance. In this paper, we evaluated the performance of the Pallmann-Scherer test using computer simulations of communities following different species-abundance distributions, spatially aggregated as widely observed empirically, and sampled by a commonly used quadrat procedure. We found that the test is very conservative for both S_q and H_q , leading to biased significance levels, with low probabilities of type-I error but high probabilities of type-II error (i.e., low statistical power). Although it should be acknowledged that the current method represents an important starting point, further improvements must be made in order to enhance its power and meet the required standards in comparative studies of diversity.

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1. Introduction

Species diversity indices are among the most important and commonly used indicators in ecological studies (Magurran, 2004; Magurran and McGill, 2011). Although a large number of indices have been proposed to date, they are all aimed to combine information on species richness and relative abundances into a single value, differing on how much emphasis is given to each one of these two components (Gotelli and Chao, 2013; Ricotta, 2005). For instance, the most commonly used diversity indices, (i) species richness s – and its jackknife version for quadrat samples as in

Kosickia and Chylareckib (2014) –, (ii) the Shannon-Wiener H' (Shannon, 1948), and (iii) the Gini-Simpson $1 - D$ (Simpson, 1949), differ markedly on how much importance is given to rare versus dominant species in a community: s gives the same importance to all species, irrespective of abundance, whereas $1 - D$ is strongly affected by dominant species, with H' occupying an intermediate position along this richness-evenness spectrum. In any application of a diversity index, the overall expectation is that more diverse communities will be those with a larger number of species and a more even distribution of abundances. However, due to the aforementioned differences, the same communities can be ranked differently or counterintuitively with respect to diversity depending on which one of these indices are being used, which makes the a priori choice of individual indices a complicated issue as Hoffmann and Hoffmann (2008) and Hurlbert (1971) pointed out (but see Jost (2009) and Tuomisto (2011) for a different perspective).

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Despite the historical importance of these classical indices, there has been considerable theoretical and practical efforts in providing generalizations of diversity indices, known as diversity profiles (Chao et al., 2014; Chao and Jost, 2015; Jost, 2006; Patil and Taillie, 1979, 1982; Tóthmérész, 1995), which manage to solve the index choice dilemma and its ecological interpretation under certain circumstances (Ricotta, 2003). The diversity profiles explicitly represent diversity along a continuum of emphases on richness versus evenness, allowing for a more comprehensive assessment of the differences in diversity between ecological communities (see Chao et al. (2012), for instance). They are usually based on modifications or adaptations for ecological purposes of generalized entropies as the Rényi entropy (Rényi, 1961) and the Boltzmann-Gibbs entropy (Tsallis, 1988). The ecological modification of the namely entropies are, respectively, the Hill numbers (Hill, 1973) – H_q Eq. (1) and the Tsallis family (Keylock, 2005) – S_q Eq. (2), given by

$$H_q = \left(\sum_{i=1}^s p_i^q \right)^{\frac{1}{1-q}} \quad \text{and} \quad (1)$$

$$S_q = \frac{1 - \sum_{i=1}^s p_i^q}{q - 1} \quad (2)$$

where s is the number of observed species in the sample, p_i is the relative frequency of species and q is an *a priori* positive constant set to balance between richness and evenness: if $q < 1$, H_q and S_q are more strongly affected by rare species, emphasizing richness, whereas if $q > 1$, H_q and S_q are more strongly affected by dominant species, emphasizing evenness (see Mendes et al. (2008)). Both H_q and S_q include as special cases the three classical indices (or functions of them): for $q = 0$, $H_q = H_0 = s$ and $S_q = S_0 = s - 1$; for $q \rightarrow 1$, $H_q \rightarrow H_1 = \exp H'$ and $S_q \rightarrow S_1 = H'$; and for $q = 2$, $H_q = H_2 = 1/D$ and $S_q = S_2 = 1 - D$. For further information on the choice and use of either H_q or S_q , we refer to the works of (Jost, 2006, 2007) and of Tuomisto (2010), since we do not intend to favor neither H_q nor S_q . Such a choice is still subject to discussion in the literature (e.g., see Hoffmann and Hoffmann (2008) and Jost (2009)) and it is out of the scope of this paper.

Diversity indices are widely used in different fields of applied Ecology and two distinct scenarios arise whenever one applies hypotheses tests regarding these measures. The first one incorporates a specific diversity index into more complex statistical models as intrinsic, independent (co)variables; the second one focus on the diversity index itself, treating it as a dependent (response) variable in such a model. Examples of the former include the recent studies of Azevêdo et al. (2015), Betbeder et al. (2015), Santos et al. (2015), Zhang et al. (2015) and of Zhu et al. (2015), although we are more interested in the latter. Hypotheses tests based on analysis of variance or simple linear regression models, whereas frequently used (Bevilacqua et al., 2012; Jaunatre et al., 2013; Lane et al., 2011; Miller and Chamberlain, 2008), are seldom recommend for diversity indices without some sort of robust inference approach. Since the assumptions made in these models do not hold for most classical diversity indices, the ecological implications and conclusions for conservation and management may be compromised.

Thus, a solution for such apparently controversial situation would be the use of *ad hoc* procedures to directly test hypotheses regarding diversity indices, though rare as they are. The modified t -test of Hutcheson (1970) for the Shannon-Wiener index H' (Shannon, 1948) and the t -test using the variance formulae given by (Simpson, 1949), for the Gini-Simpson $1 - D$ are examples of specific methods. Both of these methods are limited by (i) a 2-sample case and by (ii) the exclusive use of their respective indices. It is possible to overcome (i) using a Bonferroni correction for the significance level; but (ii) is trickier, since correlations between H' and

$1 - D$ will always be found and neglecting such structures may lead to conflicting results of the hypotheses tests.

The procedure of Pallmann et al. (2012), herein referred to as Pallmann-Scherer test, is said to solve issues (i) and (ii) altogether, extending its use to H_q – based diversity profiles. The performance of their procedure is the core interest of our study.

Although Pallmann et al. (2012) claim that a small simulation study was carried out to evaluate if the effective level of significance of the test (probability of rejecting the null hypothesis when it is true) meets its nominal level, it is unclear whether or not the study was carried out in ecological realistic scenarios. Also, the evaluation of the relative frequency of type-II errors (probability of not rejecting the null hypothesis when it is false) is still a pending study, to the best of our knowledge. We will refer to the probability of type-I error as α_{eff} in contrast to α_{nom} , the nominal significance level chosen by the investigator. The probabilities of type-II error will be represented here by β and its complement $1 - \beta$, which stands for the empirical power of the test.

We ask the following questions under realistic scenarios of sampling designs, sampling efforts, species-abundance distributions, and spatial aggregation of populations: (i) how conservative or liberal the Pallmann-Scherer test is (i.e., how α_{eff} compares to α_{nom}) and (ii) how does the power of the test raise with increases in actual diversity differences between and among communities.

2. Methods

2.1. The Pallmann-Scherer test for diversity indices

The Pallmann-Scherer test can be briefly described as a multicomparison adjustment method for p-values based on Westfall et al. (1993) general formulae for linear models (but see also Westfall and Troendle (2008) for more details). The diversity indices, calculated on the basis of a chosen number of q values, are computed for each sample and then they are treated as the response variables in an one-way ANOVA model, whose factor term (predictor) is the community label. Each sample represents a list of species with their respective relative abundances, and each community must be composed by two or more samples in order to allow estimating the residual (within community) variation in diversity. The test proceeds with a nonparametric bootstrap (Efron and Tibshirani, 1993) to construct stratified samples from the model residuals within communities assuming homoscedasticity (equal residual variance for all communities). Finally, the test statistic is computed, according to a contrast matrix. There are basically three types of contrast matrices of particular importance, namely “Tukey”, if one is interested in testing all pair-wise combinations of communities; “Dunnet” if a “control” community is available and all the other communities should be compared to the former; and “Grand Mean” if one is interested in testing whether all communities can be described by their diversity average. Also, it is possible to specify a user-defined contrast matrix, as long as its rows sum up to zero.

The test procedure for H_q -based indices is implemented in R language and is available in the package ‘simboot’ (Scherer and Pallmann, 2014), through the ‘mcpHill’ function (Pallmann et al., 2012), which, in turn, depend on the packages ‘mvtnorm’ (Genz et al., 2016) and ‘boot’ (Canty and Ripley, 2016). Since H_q and S_q are related, as in the formula given by Jost (2006) $H_q = [1 - (q - 1)S_q]^{1/(1-q)}$, and we do not intend to favor using one index over another, we considered a minor modification in the ‘mcpHill’ function to allow for S_q -based indices testing as well, which is described in the next section.

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