



A supplementary tool to existing approaches for assessing ecosystem community structure



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ARTICLE INFO

Article history:

Received 3 February 2017

Received in revised form 3 April 2017

Accepted 3 April 2017

Available online 27 April 2017

Keywords:

Biological diversity
Community structure
Diversity indices
Fisher information
Randomization
Resampling
Shannon index
Simpson index

ABSTRACT

Measures of biological or species diversity are central to ecology and conservation biology. Although there are several commonly used indices, each has shortcomings and all vary in the relative emphasis they place on the number of species and their relative abundance. We propose utilizing Fisher Information, not as a replacement for existing indices, but as a supplement to other indices because it is sensitive to community structure. We demonstrate how Shannon's and Simpson's diversity indices quantify the diversity of two different systems and how Fisher Information can enhance the analyses by comparing, as example, body size, and phylogenetic diversity of the different communities. Fisher Information is sensitive to the order in which species are entered into the analysis, and therefore, it can detect differences in community structure. Thus, the Fisher Information index can be useful in helping understand and analyze biodiversity of ecosystems and in comparing ecological communities.

Published by Elsevier B.V.

1. Introduction

What is biodiversity? Magurran (2004) defines biodiversity as “the variety and abundance of species in a defined unit of study.” Measures of biological or species diversity are central to ecology and conservation biology (e.g., MacArthur, 1965; Magurran, 2004; Pielou, 1966; Whittaker, 1960; Williams, 1964). If appropriate conservation policies are to be implemented, then appropriate measures of community structure must continue to be developed (Butturi-Gomes et al., 2017). Buckland et al. (2005) assert that no single index can capture all aspects related to the dynamics of biodiversity. Thus, it becomes critical to develop informative, interpretable diversity measures (Jost, 2006). Whittaker (1960, 1972) defined the concepts of species diversity within and among com-

munities, and numerous indices have been proposed to capture this information (e.g., see Roy et al., 2004). Although there are several indices that attempt to capture or quantify diversity, each has shortcomings and all vary in the relative emphasis they place on the number of species and their relative abundance (Magurran, 2004; Sanjit and Bhatt, 2005). Numerous articles and books describe the different measures of biological diversity, as well as their strengths and weaknesses (e.g., Magurran, 2004; Roy et al., 2004). Although this is a subject of debate, no single index is best for all purposes (e.g., Wilson and Reeder, 2005). Nonetheless, some of the most commonly employed metrics include species richness, Shannon-Wiener index (H' , commonly referred to as Shannon index), and the inverse of Simpson's concentration ($1/D$; commonly referred to as Simpson's index; Lande, 1996).

The simplest way to describe an ecological community is by using species richness: the number of species in a defined area (e.g., Gotelli and Collwell, 2001; MacArthur and Wilson, 1967; Purvis and Hector, 2001). However, the presence of a single individual of a species carries the same weight as a population that contains numerous individuals. The Shannon index attempts to account for the relative abundance, but it is weighted towards uncommon or

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rare species (e.g., Magurran, 1988; Peet, 1974; Sanjit and Bhatt, 2005). Simpson's index (D), on the other hand, quantifies how evenly species are distributed across a community and tends to ignore rare species (Magurran, 2004; Peet, 1974). As a diversity index, $1/D$ is weighted towards the abundant species (Magurran, 2004; Peet, 1974). Another drawback of Shannon and Simpson indices is that they may not identify differences between communities when the number of species and their relative abundances are similar.

To demonstrate these drawbacks, we present two extreme examples, which result in similar values and are indistinguishable statistically by the Shannon and Simpson indices. In the first example, two communities are compared that contain entirely different species but the relative abundances are similar. Consider the following: community 1 contains 17 individuals and three species (10 of species A, 5 of species B, 2 of species C) and community 2 has 17 individuals and three species (10 of species D, 5 of species E, 2 of species F). In the second example, two communities have the same species, but the relative abundances are inverted such that community 1 has 17 individuals from three species (10 of species A, 5 of species B, 2 of species C) and community 2 has 17 individuals from three species (2 of species A, 5 of species B, 10 of species C). In these examples, the communities are equally diverse ($H' = 0.9238$ and $1/D = 0.5882$). In such simple examples, the differences in community structure are obvious. Real community comparisons are unlikely to be so straightforward and, as the number of species and individuals increases, differences may not be as readily apparent. Nonetheless, Shannon and Simpson's indices are some of the most commonly used measures of diversity (De, 2007).

Shannon and Simpson's indices are unable to represent structural information embodied in a community or ecosystem (Brooks, 2003; Roy et al., 2004); the reason they do not identify differences in the above examples is evident in their respective mathematical formulas:

$$H' = -\sum_{i=1}^s p_i \log(p_i) \quad (1)$$

where s is the number of species and p_i is the proportion of the i^{th} species at each site and where

$$D_s = \sum_{i=1}^s \frac{n_i(n_i - 1)}{N(N - 1)} \quad (2)$$

the diversity index equals $\frac{1}{D}$, and where n_i = number of individuals of species i and $N = \sum n_i$ (Solow, 1993). Because the proportions are added, the order in which species are entered is irrelevant.

To enhance information obtained from H' and $1/D$ (and other possible indices), we propose utilizing Fisher Information (FI) as supplement to other indices of community structure. Information theory has been used before in ecology and, in fact, Shannon index is based on information theory (e.g., Ulanowicz, 2001). The strength of FI is that it is highly dependent on how groups (e.g., species) are ordered, and the order of species can be varied based on the question being asked. For instance, species in a community can be ordered by rank of abundance, with species of greatest abundance listed first followed by subsequent numbers of other species. In an example of comparing communities, species also could be ordered by body mass to test community assembly rules (e.g., Allen et al., 2006; Levin et al., 2001; White et al., 2007), by trophic or functional groups to compare energy flow (e.g., Blackburn et al., 2005; Dauby et al., 2001; Downing and Leibold, 2002; Petchey et al., 2004; Tilman, 2001), or by phylogeny to compare phylogenetic diversity (e.g., Inagaki et al., 2003; Kelly et al., 2008; Martin, 2002; Nehring and Puppe, 2004). In all the above cases H' and $1/D$ would be the same for a given community irrespective of how the species are ordered. FI, on the other hand, is sensitive to community structure and its value would depend on how the species are ordered. There-

fore, we suggest FI as a structure sensitive tool to augment, not replace, existing diversity indices. We will demonstrate the utility of FI by comparing it with Shannon and Simpson indices.

2. Materials and methods

2.1. Fisher information

Ronald Fisher developed Fisher Information as a measure of indeterminacy, and the Fisher Information concept has been used as a unifying principle of physical laws (Frieden, 2004). A specific formulation of Fisher Information has been used as a measure of order in dynamic complex systems such as ecosystems (Fath et al., 2003; Karunanithi et al., 2008). We propose using Fisher Information based on proportional observed relative abundance (p_i) as a new index of community structure. Fisher Information is formally given for discrete data by,

$$FI = \sum_{i=1}^s \frac{1}{p_i} \left[\frac{\Delta p_i}{\Delta i} \right]^2 \equiv \sum_{i=1}^s \frac{1}{p_i} [\Delta p_i]^2 \quad (3)$$

Here, $p_i = \frac{n_i}{N}$ where, n_i is the number of individuals of species i , and N is the total number of individuals in the community (i.e., $N = \sum n_i$). The ratio $\Delta p_i / \Delta i$ represents the slope of proportions (i.e., capturing local fluctuations in species proportions) between adjacent species, and s is the number of species in the community. We have simplified Eq. (3) by noting that $\Delta i = 1$ for adjacent species, and by replacing the proportion p_i with the amplitude q_i defined by $q_i^2 \equiv p_i$, to give

$$FI = 4 \sum_{i=1}^s \Delta q_i^2 \approx 4 \sum_{i=1}^s [q_i - q_{i+1}]^2 \quad (4)$$

This expression has the benefit of eliminating the division by p_i , which can be numerically problematic if p_i happens to be a small number. If you compare Eqs. (1), (2) and (4), you see that Eqs. (1) and (2) are additive indices of species proportions (and hence they are not sensitive to the order in which the species are arranged) whereas Eq. (4) is an additive index of slopes of proportions between adjacent pairs of species (and, hence, it is sensitive to the order in which the species are arranged; Fig. 1). Thus, FI is a useful index when combined with Shannon and Simpson indices for comparing and analyzing community structure.

Using existing data sets, we compared two vastly different sets of small mammals: one from the grasslands of North America and one from the jungles of Borneo. We demonstrate how Shannon's and Simpson's diversity indices quantify the diversity of the two systems, and how FI can enhance the analyses by comparing body size and phylogenetic diversity of each. Our goal is not to delve into alpha, beta, or gamma diversity, but to demonstrate how FI can be used to augment some commonly used diversity indices, and reveal information on community structure.

2.2. Small mammal communities

Data came from two different published studies of small mammals. The first dataset (hereafter referred to as Hays) came from Hopton and Choate (2002), in which they examined the effect of an interstate highway on movement of small mammals between the triangles of median vegetation at exit/entrance ramps and the adjacent roadside vegetation in North American mixed-grass prairie. The second dataset (hereafter referred to as Borneo) came from Wells et al. (2004), in which they investigated how space is partitioned by small mammals in a Borneo forest by comparing use of terrestrial and arboreal space. Both studies provided species lists and abundance data (Hopton and Choate, 2002; Wells et al., 2004).

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