



## Generalized Core Functions of Maximum Entropy Theory of Ecology

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**Abstract.** Core distributions of Maximum Entropy Theory of Ecology (METE) are the Spatial Structure Function (SSF) and the Ecosystem Structure Function (ESF). SSF is a by-species prediction of the clustering of individuals over space. ESF is a kind of container function that describes the probability space of how abundances are assigned to species and how metabolic energy is partitioned over individuals in a community. In this study, these core functions of METE are generalized by deriving the corresponding functions in the Tsallis  $q$ -entropy. Derivation used the method of Lagrange multipliers. The generalized SSF and ESF are expressed in terms of the  $q$ -exponential function. Numerical examples are provided to illustrate the generalized SSF.

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### 1. Introduction

Maximum entropy framework has been utilized to construct ecological models, thus providing support to emerging ecological relationships at a broader scale [4, 10]. Maximum entropy models maximize information content from biological system while satisfying relevant constraints which are primarily composed of bioclimatic and biophysical variables. These models have extensive applications in biodiversity conservation and ecosystem management of a particular species [6, 8].

Mathematical rigor of MaxEnt models enhances the accuracy and reliability of predictions, thereby supporting ecologists in making informed choices in designing conservation

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strategies for a particular species [12]. For instance, the model may provide inputs in understanding species niche differentiation and species interactions [11], construction of food web structures [2] and establishing trophic relationships [13].

Maximum Entropy Theory of Ecology (METE) is a theoretical framework of macroecology that makes a variety of realistic ecological predictions about how species richness, abundance of species, metabolic rate distributions, and spatial aggregation of species interrelate in a given region. Underlying mathematics of METE relies on MaxEnt: the maximization of information entropy. Primary equations that regularly occur in the maximization as presented in [1] are the given in (1.1)-(1.3).

The general expression for  $K$  constraints on the mean values of the variables  $f_k(n)$ , where  $n$  follows the distribution  $p(n)$ , is expressed as

$$\sum_{n=1}^{n=N} f_k(n)p(n) = \langle f_k \rangle. \quad (1)$$

Additional constraint provides for the normalization of the probability distributions, expressed as

$$\sum_{n=1}^{n=N} p(n) = 1. \quad (2)$$

To maximize Shannon information entropy subject to the above constraints, the tools of variational calculus and the method of undetermined Lagrange multipliers will be employed. The function  $F$  to be maximized is an expression that incorporates the measure of Shannon information entropy and the constraints. That is,

$$F = - \sum_{n=N_{min}}^{N_{max}} p(n) \ln p(n) - \lambda_0 \left[ \sum_{n=N_{min}}^{N_{max}} p(n) - 1 \right] - \lambda_1 \left[ \sum_{n=N_{min}}^{N_{max}} f(n)p(n) - \langle f \rangle \right]. \quad (3)$$

On the other hand, the  $q$ -logarithm function introduced in [14] is given by

$$\ln_q x = \frac{x^{1-q} - 1}{1 - q}, \quad (q \in R, x > 0) \quad (4)$$

and the  $q$ -exponential function is given by

$$\exp_q x = \begin{cases} (1 + (1 - q)x)^{\frac{1}{1-q}}, & \text{if } 1 + (1 - q)x > 0, \\ 0, & \text{otherwise} \end{cases} \quad (5)$$

The functions  $\exp_q x$  and  $\ln_q x$  converge to  $\exp x$  and  $\log x$  as  $q \rightarrow 1$ , respectively and the following relations are true,

$$\exp_q(x + y + (1 - q)xy) = \exp_q x \exp_q y, \quad (6)$$

$$\ln_q xy = \ln_q x + \ln_q y + (1 - q) \ln_q x \ln_q y. \quad (7)$$

A new approach of handling the Lagrange multipliers involved in the extremization process leading to Tsallis' statistical operator was presented in [9]. To understand this new approach, the following discussion taken from [9] is provided.

The Tsallis' generalized entropy will be defined as follows,

$$\frac{S_q}{k} = - \sum_{i=1}^{\omega} p_i \ln_q p_i, \quad (8)$$

where  $k \equiv k(q)$  tends to the Boltzmann constant  $k_B$  in the limit  $q \rightarrow 1$  [14] subject to the constraints

$$\sum_{i=1}^w p_i = 1, \quad (9)$$

$$\frac{\sum_{i=1}^w p_i^q O_j^{(i)}}{\sum_{i=1}^w p_i^q} = \langle\langle O_j \rangle\rangle_q, \quad (10)$$

where the  $p_i$  is the probability assigned to the microscopic configuration  $i$  ( $i = 1, 2, \dots, w$ ) and the  $O_j^{(i)}$  denote the  $n$  relevant observables whose generalized expectation values  $\langle\langle O_j \rangle\rangle_q$  are a priori known.

Following the generalization in [3], the second generalized Tsallis' entropy that will be used is defined by

$$\frac{S_q}{k} = - \sum_{i=1}^{\omega} p_i^q \ln_q p_i. \quad (11)$$

The method of Lagrange multipliers requires to maximize the function

$$F = \frac{S_q}{k} - \lambda_0 \left( \sum_{i=1}^w p_i - 1 \right) - \sum_{j=1}^s \lambda_j \left( \frac{\sum_{i=1}^w p_i^q O_j^{(i)}}{\sum_{i=1}^w p_i^q} - \langle\langle O_j \rangle\rangle_q \right). \quad (12)$$

The new approach replaces (12) by

$$F = \frac{S_q}{k} - \alpha_0 \left( \sum_{i=1}^w p_i - 1 \right) - \sum_{j=1}^s \alpha_j \sum_{i=1}^w p_i^q (O_j^{(i)} - \langle\langle O_j \rangle\rangle_q), \quad (13)$$

which will yield the same  $p_i$  and the relation of the Lagrange multipliers  $\lambda_j$  and  $\alpha_j$  is given by

$$\lambda_j = \alpha_j \sum_{i=1}^w p_i^q. \quad (14)$$

The core distributions of METE are the Spatial Structure Function (SSF) and the Ecosystem Structure Function (ESF). The SSF is a by-species prediction of the clustering of individuals over space. The ESF is a kind of "container function" that describes the probability space of how abundances are assigned to species and how metabolic energy

is partitioned over individuals in a community. These core functions of the MaxEnt were derived in [1] using the Shannon entropy. A phase space entropy model of ecosystems was developed in [7] and ecosystem equilibria was specified by conservation of biomass and total metabolic energy. A new proof of the theorems on the maximum entropy principle in Tsallis statistics without using the Lagrange multipliers method was presented in [3]. Analysis of the climate fluctuations in past deuterium records corresponding to the last glacial period was done in [5] using nonadditive entropy on which nonextensive statistical mechanics is based.

In this paper, core functions of METE are generalized by deriving the corresponding functions in the Tsallis  $q$ -entropy given in (8) and (11). The ecological state variables introduced in [1] namely,  $A$ ,  $H$ ,  $N$ , and  $E$ , representing respectively, total area, total number of species, total abundance and total metabolic energy of an ecological system will be used in the discussion below.

## 2. Generalization of Spatial Structure Function

Spatial Structure Function (SSF) also called "Pi Distribution" [1], is defined as the probability that  $n$  individuals of a species are found in a cell area  $A$  if it has  $n_0$  individuals in the total area  $A_0$  under consideration. The variables involved in the function are  $A$  and  $n$  which is the abundance of a single species at the total spatial scale.

**Theorem 2.1.** *The generalized Spatial Structure Function (SSF), denoted by  $\Pi(n, q)$ , is given by*

$$\Pi(n, q) = \frac{\exp_q(\alpha_1(n - \mu_q))}{\sum_{n=1}^{N_0} \exp_q(\alpha_1(n - \mu_q))}. \quad (15)$$

*Proof.* The generalization of the Spatial Structure Function is obtained using the Tsallis'  $q$ -entropy (11) subject to the normalization constraint which is given by

$$\sum_{n=1}^N \Pi(n) = 1, \quad (16)$$

and the second constraint comes from the measurement of the average value of the per-species abundance which is given by

$$\frac{\sum_{n=1}^N n \Pi(n)^q}{\sum_{n=1}^N \Pi(n)^q} = \mu_q. \quad (17)$$

The function to be maximized is

$$F = \frac{S_q}{k} + \alpha_0 \left( \sum_{n=0}^N \Pi(n) - 1 \right) + \alpha_1 \left( \sum_{n=0}^N \Pi(n)^q (n - \mu_q) \right), \quad (18)$$

where  $\alpha_0$  and  $\alpha_1$  are the Lagrange multipliers. Taking the derivative of  $F$  with respect to  $\Pi(n)$  and setting it equal to 0,

$$\begin{aligned} 0 &= -1 - q\Pi(n)^{q-1} \ln_q \Pi(n) + \alpha_0 + \alpha_1(n - \mu_q)q\Pi(n)^{q-1} \\ 0 &= -1 - \frac{q}{1-q} + \alpha_0 + \left( \frac{q}{1-q} + \alpha_1(n - \mu_q)q \right) \Pi(n)^{q-1}. \end{aligned}$$

Solving for  $\Pi(n)$ ,

$$\begin{aligned} \Pi(n) &= \left( \frac{q}{1 - (1-q)\alpha_0} \right)^{\frac{1}{1-q}} \{1 + (1-q)\alpha_1(n - \mu_q)\}^{\frac{1}{1-q}} \\ &= \left( \frac{q}{1 - (1-q)\alpha_0} \right)^{\frac{1}{1-q}} \exp_q(\alpha_1(n - \mu_q)). \end{aligned} \tag{19}$$

Applying the normalization constraint will give

$$\left( \frac{q}{1 - (1-q)\alpha_0} \right)^{\frac{1}{1-q}} \sum_{n=1}^{N_0} \{1 + (1-q)\alpha_1(n - \mu_q)\}^{\frac{1}{1-q}} = 1. \tag{20}$$

Let

$$Z_q = \sum_{n=1}^{N_0} \exp_q(\alpha_1(n - \mu_q)). \tag{21}$$

Now, with  $\Pi(n)$  being a function of  $q$ , we can write  $\Pi(n) = \Pi(n, q)$ . Hence,

$$\Pi(n, q) = \frac{\exp_q(\alpha_1(n - \mu_q))}{Z_q}.$$

### 3. Generalization of Ecosystem Structure Function

Ecosystem Structure Function (ESF) denoted by  $R(n, \epsilon)$  is a joint probability distribution, with  $R(n, \epsilon)d\epsilon$  by definition being the probability that a randomly selected species has abundance  $n$ , and that a randomly selected individual from any species with abundance  $n$  has metabolic requirement in the interval  $\epsilon, \epsilon + d\epsilon$ . The normalization constraint is given by

$$\sum_{n=1}^N \int_{\epsilon=1}^E R(n, \epsilon)d\epsilon = 1. \tag{22}$$

The additional constraints are aggregated measures of variables  $n$  and  $n\epsilon$ . With  $f_1(n) = n$ , and  $f_2(n)\epsilon = n\epsilon$ , the corresponding means of the data sets are respectively,

$$\left\langle f_1(n) \right\rangle = N/H \quad , \quad \left\langle f_2(n\epsilon) \right\rangle = E/H. \tag{23}$$

These give the pair of constraints,

$$\sum_{n=1}^N \int_{\epsilon=1}^E nR(n, \epsilon)d\epsilon = \frac{N}{H}, \tag{24}$$

$$\sum_{n=1}^N \int_{\epsilon=1}^E n\epsilon R(n, \epsilon)d\epsilon = \frac{E}{H}. \tag{25}$$

**Theorem 3.1.** *The generalized Ecosystem Structure Function (ESF)  $R(n, \epsilon, q)$  is given by*

$$R(n, \epsilon, q) = \alpha_2(2 - q) \frac{\exp_q(\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2}))}{\sum_{n=1}^N \frac{1}{n} [(\exp_q u_E)^{2-q} - (\exp_q u_1)^{2-q}]}, \tag{26}$$

where  $u = \alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2})$ ,  $u_E = u(\epsilon = E)$ ,  $u_1 = u(\epsilon = 1)$ .

*Proof.* The generalization for the Ecosystem Structure Function is obtained using (11). Following [9], the normalization constraint (22) will be kept while the constraints (24) and (25) will be replaced respectively, by

$$\frac{\sum_{n=1}^N \int_{\epsilon=1}^E nR^q(n, \epsilon)d\epsilon}{\sum_{n=1}^N R^q(n, \epsilon)} = \mu_{q,1}, \tag{27}$$

$$\frac{\sum_{n=1}^N \int_{\epsilon=1}^E n\epsilon R^q(n, \epsilon)d\epsilon}{\sum_{n=1}^N R^q(n, \epsilon)} = \mu_{q,2}, \tag{28}$$

where  $R^q(n, \epsilon) = [R(n, \epsilon)]^q$ . The function to be maximized is

$$F = \frac{S_q}{k} + \alpha_0 \left[ \sum_{n=1}^N \int_{\epsilon=1}^E R(n, \epsilon)d\epsilon - 1 \right] + \alpha_1 \left[ \sum_{n=1}^N \int_{\epsilon=1}^E R^q(n, \epsilon)d\epsilon(n - \mu_{q,1}) \right] + \alpha_2 \left[ \sum_{n=1}^N \int_{\epsilon=1}^E R^q(n, \epsilon)d\epsilon(n\epsilon - \mu_{q,2}) \right]. \tag{29}$$

Taking the derivative of  $F$  with respect to  $R := R(n, \epsilon)$ ,

$$\frac{\delta F}{\delta R} = - \sum_{n=1}^N \int_{\epsilon=1}^E \left( 1 + qR^{q-1} \frac{R^{1-q} - 1}{1 - q} \right) d\epsilon + \alpha_0 \sum_{n=1}^N \int_{\epsilon=1}^E d\epsilon + \alpha_1 \left[ \sum_{n=1}^N \int_{\epsilon=1}^E q(n - \mu_{q,1})R^{q-1}(n, \epsilon)d\epsilon \right] + \alpha_2 \left[ \sum_{n=1}^N \int_{\epsilon=1}^E q(n\epsilon - \mu_{q,2})R^{q-1}(n, \epsilon)d\epsilon \right]. \tag{30}$$

Setting (30) equal to zero and solve for  $R(n, \epsilon)$ ,

$$0 = - \left( 1 + \frac{q}{1 - q} - \frac{q}{1 - q} R^{q-1} \right) + \alpha_0 + \alpha_1 q(n - \mu_{q,1})R^{q-1} + \alpha_2 q(n\epsilon - \mu_{q,2})R^{q-1}$$

$$1 + \frac{q}{1-q} - \alpha_0 = \left( \frac{q}{1-q} + \alpha_1 q(n - \mu_{q,1}) + \alpha_2 q(n\epsilon - \mu_{q,2}) \right) R^{q-1}$$

$$\frac{1 - \alpha_0(1-q)}{q} R^{1-q} = 1 + (1-q) \{ \alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2}) \}.$$

Solving for  $R = R(n, \epsilon)$ ,

$$R(n, \epsilon) = \left( \frac{q}{1 - \alpha_0(1-q)} \right)^{\frac{1}{1-q}} (1 + (1-q)(\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2})))^{\frac{1}{1-q}}. \quad (31)$$

Substitution to (22),

$$\sum_{n=1}^N \int_{\epsilon=1}^E \left( \frac{q}{1 - \alpha_0(1-q)} \right)^{\frac{1}{1-q}} (1 + (1-q)(\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2})))^{\frac{1}{1-q}} d\epsilon = 1,$$

which will give

$$\left( \frac{q}{1 - \alpha_0(1-q)} \right)^{\frac{1}{1-q}} = \frac{1}{\sum_{n=1}^N \int_{\epsilon=1}^E \exp_q(\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2})) d\epsilon}. \quad (32)$$

Let

$$Z_q = \sum_{n=1}^N \int_{\epsilon=1}^E \exp_q(\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2})) d\epsilon. \quad (33)$$

Now, with  $R(n, \epsilon)$  being a function of  $q$ , we can write  $R(n, \epsilon) = R(n, \epsilon, q)$ . Hence,

$$R(n, \epsilon, q) = \frac{\exp_q(\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2}))}{Z_q}. \quad (34)$$

The expression in (34) will be called the  $q$ -ESF denoted by  $R(n, \epsilon, q)$  and  $Z_q$  given in (33) is the corresponding partition function. Solving the integral involved in the partition function,

$$\int_{\epsilon=1}^E \exp_q(\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2})) d\epsilon$$

$$= \int_{\epsilon=1}^E (1 + (1-q)\{\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2})\}) d\epsilon$$

$$= \frac{1}{\alpha_2 n(2-q)} (\exp_q^{2-q}(u_E) - \exp_q^{2-q}(u_1)),$$

where  $u = \alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2})$ ,  $u_E = u(\epsilon = E)$ ,  $u_1 = u(\epsilon = 1)$ . Then

$$Z_q = \frac{1}{\alpha_2(2-q)} \sum_{n=1}^N \frac{1}{n} [(\exp_q u_E)^{2-q} - (\exp_q u_1)^{2-q}], \quad (35)$$

and

$$R(n, \epsilon, q) = \alpha_2(2-q) \frac{\exp_q(\alpha_1(n - \mu_{q,1}) + \alpha_2(n\epsilon - \mu_{q,2}))}{\sum_{n=1}^N \frac{1}{n} [(\exp_q u_E)^{2-q} - (\exp_q u_1)^{2-q}]}.$$

#### 4. Examples

In this section, examples are provided to illustrate the generalized SSF.

Example 1. To be able to give an example for (15), the values of  $q$ ,  $\mu_q$ , and  $n$  must be specified. Taking  $q = \frac{1}{2}$ ,  $\mu_{\frac{1}{2}} = 2$  and  $n = 1, 2, 3$ , the partition function (21) is

$$Z_q = \sum_{n=1}^3 \exp_{1/2}(\alpha_1(n - \mu_{1/2})) = \sum_{n=1}^3 \left(1 + \frac{1}{2}\alpha_1(n - 2)\right)^2 = 3 + \frac{(\alpha_1)^2}{2}.$$

The probability function (15) becomes

$$\Pi(n, 1/2) = \frac{\exp_{1/2}(\alpha_1(n - 2))}{3 + \frac{\alpha_1^2}{2}} = \frac{\left(1 + \frac{1}{2}\alpha_1(n - 2)\right)^2}{3 + \frac{\alpha_1^2}{2}}.$$

It can be verified that  $\sum_{n=1}^3 \Pi(n, 1/2) = 1$ . To determine  $\alpha_1$ , impose the second constraint (17) to yield

$$\begin{aligned} \sum_{n=1}^3 n\Pi(n, 1/2)^{\frac{1}{2}} &= 2 \sum_{n=1}^3 \Pi(n, 1/2)^{\frac{1}{2}} \\ &\quad - \Pi(n, 1/2)^{\frac{1}{2}} + \Pi(3, 1/2)^{\frac{1}{2}} = 0, \end{aligned}$$

from which  $\alpha_1 = 0$ . Thus, the desired probability function is the uniform distribution,

$$\Pi(n, 1/2) = \frac{1}{3}, \quad n = 1, 2, 3.$$

Example 2. As a second example for (15), take  $q = \frac{2}{3}$ ,  $\mu_{2/3} = 2$ ,  $n = 1, 2, 3, 4, 5$ . The partition function (21) is

$$\begin{aligned} Z_{2/3} &= \sum_{n=1}^5 \exp_{2/3}(\alpha_1(n - 2)) \\ &= \sum_{n=1}^5 \left(1 + \frac{1}{3}\alpha_1(n - 2)\right)^3 = 5 + 5\alpha_1 + 5\alpha_1^2 + \frac{35}{27}\alpha_1^3. \end{aligned}$$

To determine  $\alpha_1$ , impose the second constraint (17)

$$\sum_{n=1}^5 n\Pi(n, 2/3)^{\frac{2}{3}} = 2 \sum_{n=1}^5 \Pi(n, 2/3)^{\frac{2}{3}},$$

which will yield the equation

$$45 + 90\alpha_1 + 35\alpha_1^2 = 0.$$



The two solutions to the preceding equation obtained using Wolfram alpha equation solver are  $\alpha_1 = \frac{-3}{7}(3 + \sqrt{2})$ , and  $\alpha_1 = \frac{3}{7}(\sqrt{2} - 3)$ . The second value for  $\alpha_1$  will give the desired probability function. In particular, for  $n = 1, 2, 3, 4, 5$  the values of the probability function are:

$$\begin{aligned} \Pi(1, 2/3) &= 0.527, & \Pi(1, 2/3) &= 0.28571, & \Pi(3, 2/3) &= 0.132, \\ \Pi(4, 2/3) &= 0.048, & \Pi(5, 2/3) &= 0.0094. \end{aligned}$$

**Remark 4.1.** *Owing to the complexity of (26) no example will be provided for the generalized ecosystem structure function.*

## 5. Conclusion and Recommendation

This paper has delved into the theoretical framework of METE, specifically focusing on the development of  $q$ -generalizations for its two core functions. METE, or the Maximum Entropy Theory of Ecology, is a fundamental framework used to understand the structure and dynamics of ecological systems. By introducing  $q$ -generalizations, the paper extends the applicability of METE to systems exhibiting non-trivial behavior, potentially offering deeper insights into ecological patterns and processes.

In the context of this study, the  $q$ -generalizations were elucidated with regards to the Spatial structure function, which plays a crucial role in characterizing the spatial distribution of species within an ecosystem. Through illustrative examples, the paper provided sample probability functions for the  $q$ -Spatial structure function, showcasing how these generalized formulations can be applied in practical scenarios.

However, a notable gap exists in the paper's treatment of the  $q$ -ecosystem structure function. Despite the detailed exploration of the  $q$ -Spatial structure function, no corresponding example was provided for the  $q$ -ecosystem structure function. This omission leaves a significant aspect of METE unaddressed, limiting the comprehensiveness of the study. Furthermore, the paper did not extend its analysis to encompass physical applications of the derived generalized functions. While theoretical developments are valuable, their utility often lies in their practical applicability. By demonstrating how these  $q$ -generalizations can be applied to real-world ecological data or modeling scenarios, researchers can validate their effectiveness and enhance their relevance to ecological studies.

In light of these considerations, it is recommended that future research endeavors focus on bridging these gaps. Specifically, efforts should be directed towards exploring sample probability functions for the  $q$ -ecosystem structure function, thereby completing the theoretical framework. Additionally, researchers should actively seek out opportunities to apply these generalized functions in physical contexts, such as ecological modeling or data analysis. By doing so, we can advance our understanding of METE and its relevance to the study and management of ecological systems.

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