entropart, an R Package to Measure and Partition Diversity

Eric Marcon AgroParisTech UMR EcoFoG Bruno Hérault Cirad UMR EcoFoG

Abstract

entropart is a package for R designed to estimate diversity based on HCDT entropy or similarity-based entropy. It allows calculating neutral, phylogenetic and functional entropy and diversity, partitioning them and correcting them for estimation bias.

Keywords: point patterns, spatial structure, R.

1. Introduction

Diversity measurement can be done through a quite rigorous framework based on entropy, *i.e.* the amount of uncertainty calculated from the frequency distribution of a community (Patil and Taillie 1982; Jost 2006; Marcon, Scotti, Hérault, Rossi, and Lang 2014). Tsallis entropy, also known as HCDT entropy (Havrda and Charvát 1967; Daróczy 1970; Tsallis 1988), is of particular interest (Jost 2006; Marcon *et al.* 2014) namely because it includes the number of species, Shannon (1948) and Simpson (1949) indices of diversity into a single framework. Interpretation of entropy is not straightforward but one can easily transform into Hill numbers (Hill 1973) which have many desirable properties (Jost 2007): mainly, they are the number of equally-frequent species that would give the same level of diversity as the data.

Marcon and Hérault (2014) generalized the duality of entropy and diversity, deriving the relation between phylogenetic or functional diversity (Chao, Chiu, and Jost 2010) and phylogenetic or functional entropy (we will write *phylodiversity* and *phyloentropy* for short), as introduced by Pavoine, Love, and Bonsall (2009). Special cases are the well-known PD (Faith 1992) and FD (Petchey and Gaston 2002) indices and Rao's (1982) quadratic entropy. The same relation holds between Ricotta and Szeidl entropy of a community (Ricotta and Szeidl 2006) and similarity-based diversity (Leinster and Cobbold 2012).

The **entropart** package for R (R Development Core Team 2014) enables calculation of all these measures of diversity and entropy and their partitioning.

Diversity partitioning means that, in a given area, the γ diversity D_{γ} of all individuals found may be split into within (α diversity, D_{α}) and between (β diversity, D_{β}) local assemblages. α diversity reflects the diversity of individuals in local assemblages whereas β diversity reflects the diversity of the local assemblages. Marcon *et al.* (2014) derived the decomposition of Tsallis γ entropy into its α and β components, generalized to phyloentropy by Marcon and Hérault (2014).

Estimators of diversity are biased because of unseen species and also because they are not linear functions of probabilities (Marcon et al. 2014). α and γ diversities are underestimated by naive estimators (Chao and Shen 2003; Dauby and Hardy 2012). β diversity is severely biased too when sampling is not sufficient (Beck, Holloway, and Schwanghart 2013). Biascorrected estimators of phylodiversity have been developed by Marcon and Hérault (2014). The package includes them all.

The successive sections of this paper presents the package features, illustrated by worked examples based on the data included in the package.

2. Package organization

2.1. Data

Most functions of the package calculate entropy or diversity of a community or of a metacommunity. Community functions accept a vector of probabilities or of abundances for species data. Each element of the vector contains the probability or the number of occurrences of a species in a given community. Meta-community functions require a particular data organization in a MetaCommunity object described here.

A MetaCommunity is basically a list. Its main components are \$Nsi, a matrix containing the species abundances whose lines are species, columns are communities and \$Wi, a vector containing community weights. Creating a MetaCommunity object is the purpose of the MetaCommunity function. Arguments are a dataframe containing the number of individuals per species (lines) in each community (columns), and a vector containing the community weights. The following example creates a MetaCommunity made of three communities of unequal weights with 4 species. The weighted average probabilities of occurrence of species and the total number of individuals define the meta-community as the assemblage of communities.

A meta-community is partitioned into several local communities (indexed by i = 1, 2, ..., I). n_i individuals are sampled in community i. Let s = 1, 2, ..., S denote the species that compose the meta-community, n_{si} the number of individuals of species s sampled in the local community i, $n_s = \sum_i n_{si}$ the total number of individuals of species s, $n = \sum_s \sum_i n_{si}$ the

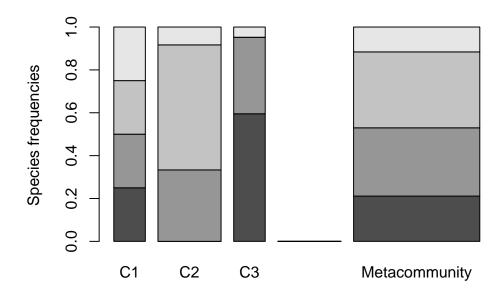


Figure 1. Plot of a MetaCommunity. Communities (named C1, C2 ad C3) are represented in the left part of the figure, the metacommunity to the right. Bar widths are proportional to community weights. Species abundances are represented vertically (4 species are present in the meta-community, only 3 of them in communities C2 and C3.

total number of sampled individuals. Within each community i, the probability p_{si} for an individual to belong to species s is estimated by $\hat{p}_{si} = n_{si}/n_i$. The same probability for the meta-community is p_s . Communities have a weight w_i , satisfying $p_s = \sum_i w_i p_{si}$. The commonly-used $w_i = n_i/n$ is a possible weight, but the weighting may be arbitrary (e.g. the sampled areas). The components of a MetaCommunity object satisfy these conditions: \$Ps for example contains the probability of occurrence of each species in the meta-community:

R> MC\$Ps

A MetaCommunity can be summarized and plotted (Figure 1).

The package contains an example dataset containing the inventory of two 1-ha tropical forest plots in Paracou, French Guiana (Marcon, Hérault, Baraloto, and Lang 2012):

```
R> data(Paracou618)
R> summary(Paracou618.MC)
```

Meta-community (class 'MetaCommunity') made of 1124 individuals in 2 communities and 425 species.

Its sample coverage is 0.92266748426447

Community weights are:

Paracou618.MC is a meta-community made of two communities named "P006" and "P018", containing 425 species (their name is *Family_Genus_Species*, abbreviated to 4 characters). The values of the abundance matrix are the number of individuals of each species in each community. Sample coverage will be explained later.

The dataset also contains a taxonomy and a functional tree. Paracou618.Taxonomy is an object of class phylog, defined in ade4 (Dray and Dufour 2007), namely a phylogenetic tree. This example data is only a taxonomy, containing family, genus and species levels for the sake of simplicity. Paracou618.Functional is an object of class hclust containing a functional tree based on leaf, height, stem and seed functional traits (Hérault and Honnay 2007; Marcon and Hérault 2014). The package accepts any ultrametric tree of class phylog or hclust. Paracou618.dist is the distance matrix (actually a dist object) used to build the functional tree.

2.2. Utilities

The deformed logarithm formalism (Tsallis 1994) is very convenient to manipulate entropies. The deformed logarithm of order q is defined as:

$$\ln_q x = \frac{x^{1-q} - 1}{1 - q} \tag{1}$$

It converges to ln when $q \to 1$, see figure 2.

The inverse function of $\ln_q x$ is the deformed exponential:

$$e_q^x = [1 + (1 - q)x]^{\frac{1}{1 - q}}$$
 (2)

Functions of the packages are lnq(x, q) and expq(x, q).

3. Neutral diversity

3.1. Community functions

HCDT entropy

Neutral HCDT entropy of order q of a community is defined as:

$${}^{q}H = \frac{1 - \sum_{s} p_{s}^{q}}{q - 1} = -\sum_{s} p_{s}^{q} \ln_{q} p_{s}$$
(3)

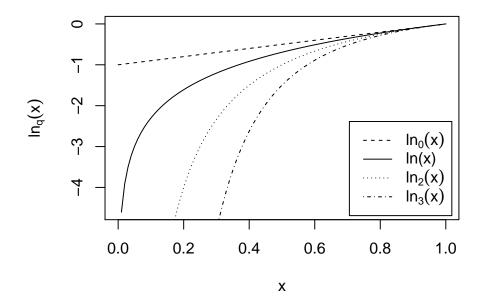


Figure 2. Curves of $\ln_q x$ for different values of q between 0 and 4 $(\ln_1 x = \ln x)$.

q is the order of diversity (e.g.: 1 for Shannon). Entropy can be calculated by the **Tsallis** function. Paracou meta-community entropy of order 1 is:

R > Tsallis(Ps = Paracou618.MC\$Ps, q = 1)

[1] 4.736023

For convenience, special cases of entropy of order q have a clear-name function: Richness for q = 0, Shannon for q = 1, Simpson for q = 2.

R> Shannon(Ps = Paracou618.MC\$Ps)

[1] 4.736023

Sample coverage

A useful indicator of sampling quality is the sample coverage (Good 1953; Chao, Lee, and Chen 1988; Zhang and Huang 2007), that is to say the probability for a species of the community to be observed in the actual sample. It equals the sum of the probability of occurrences of all observed species. Its historical estimator is (Good 1953):

$$\hat{C} = 1 - \frac{S^1}{n} \tag{4}$$

 S^1 is the number of singletons (species observed once) of the sample, and n is its size. The estimator has been improved by taking into account the whole distribution of species (Zhang and Huang 2007). The Coverage function calculates it, allowing to choose the estimator (Zhang and Huang's by default):

R> Coverage(Ns = Paracou618.MC\$Ns)

[1] 0.9220438

The sample coverage cannot be estimated from probability data: abundances are required.

Estimation-bias corrected estimators

Estimation-bias correction is used to improve the estimation of entropy despite unobserved species. Bias-corrected estimators (often relying on sample coverage) are returned by functions whose names are prefixed by bc, such as bcTsallis. They are similar to the non-corrected ones but they use abundance data and propose several bias-correction techniques to select in the Correction argument. A "Best" correction is calculated by default, detailed in the help file of each function.

R> bcTsallis(Ns = Paracou618.MC\$Ns, q = 1)

[1] 4.898061

The best correction for Tsallis entropy follows Marcon *et al.* (2014). bcSimpson returns Lande's correction (Lande 1996) and bcShannon returns the very efficient correction by Chao, Wang, and Jost (2013), so their results are different (and more accurate) than those of the general bcTsallis function.

R> bcShannon(Ns = Paracou618.MC\$Ns)

[1] 4.892159

Effective numbers of species

Entropy should be converted into "true diversity" (Jost 2007), *i.e.* effective number of species equal to Hill (1973) numbers:

$${}^{q}D = \left(\sum_{s} p_{s}^{q}\right)^{\frac{1}{1-q}} \tag{5}$$

This can be done by the deformed exponential function, or using directly the Diversity or bcDiversity functions (equal to the deformed exponential of order q of Tsallis or bcTsallis)

 $R > \exp(Simpson(Ps = Paracou618.MC$Ps), q = 2)$

[1] 68.7215

R > Diversity(Ps = Paracou618.MC\$Ps, q = 2)

[1] 68.7215

 \mathbb{R} > expq(bcTsallis(Ns = Paracou618.MC\$Ns, q = 2), q = 2)

[1] 73.19676

R > bcDiversity(Ns = Paracou618.MC\$Ns, q = 2)

[1] 73.19676

3.2. Meta-community functions

Meta-community functions allow partitioning diversity according to Patil and Taillie's concept of diversity of a mixture (Patil and Taillie 1982), *i.e.* α entropy of a meta-community is defined as the weighted average of community entropy, following Routledge (1979):

$${}^{q}H_{\alpha} = \sum_{i} w_{i} {}^{q}_{i} H_{\alpha} \tag{6}$$

 $_{i}^{q}H_{\alpha}$ is the entropy of community i:

$${}_{i}^{q}H_{\alpha} = \frac{1 - \sum_{s} p_{si}^{q}}{q - 1} = -\sum_{s} p_{si}^{q} \ln_{q} p_{si}$$
 (7)

Jost's (2007) definition of α entropy is not supported explicitly in the package since it only allows partitioning of equally weighted communities. In this particular case, both definitions are identical.

 γ entropy of the meta-community is defined as α entropy of a community. β entropy, the difference between γ and α , is the generalized Jensen-Shannon divergence between the species distribution of the meta-community and those of communities (Marcon *et al.* 2014):

$${}^{q}H_{\beta} = {}^{q}H_{\gamma} - {}^{q}H_{\alpha} = \sum_{s} p_{si}^{q} \ln_{q} \frac{p_{si}}{p_{s}}$$

$$\tag{8}$$

 β entropy should be transformed into diversity, i.e. an effective number of communities:

$${}^{q}D_{\beta} = e_q^{\frac{q_{H_{\beta}}}{1 - (q - 1)^{q_{H_{\alpha}}}}} \tag{9}$$

Basic meta-community functions

These values can be estimated by the meta-community functions AlphaEntropy, AlphaDiversity, BetaEntropy, BetaDiversity. They accept a Metacommunity and an order of diversity q as arguments, and return an MCentropy or MCdiversity object which can be summarized and plotted. GammaEntropy and GammaDiversity return a number. Estimation-bias corrections are applied by default:

```
R> e <- AlphaEntropy(Paracou618.MC, q = 1)
R> summary(e)

alpha Entropy of order 1 of MetaCommunity Paracou618.MC
with correction: Best

Entropy of communities:
    P006    P018
4.403435    4.673620
Average entropy of the communities:
[1] 4.519057
```

Diversity Partition of a metacommunity

The DivPart function calculates everything at once. Its arguments are the same but bias correction is not applied by default. It can be, using the argument Biased = FALSE, and the correction chosen by the argument Correction. It returns a DivPart object which can be summarized (entropy is not printed by summary) and plotted:

```
R > p \leftarrow DivPart(q = 1, MC = Paracou618.MC, Biased = FALSE)
R> summary(p)
Diversity partitioning of order 1 of MetaCommunity Paracou618.MC
 with correction: Best
Alpha diversity of communities:
     P006
               P018
 81.73115 107.08473
Total alpha diversity of the communities:
[1] 91.74905
Beta diversity of the communities:
[1] 1.460828
Gamma diversity of the metacommunity:
[1] 134.0296
R> p$CommunityAlphaEntropies
    P006
             P018
4.403435 4.673620
```

Diversity Estimation of a metacommunity

The DivEst function decomposes diversity and estimates confidence interval of α , β and γ diversity following Marcon *et al.* (2012). If the observed species frequencies of a community are assumed to be a realization of a multinomial distribution: they can be drawn again to obtain a distribution of entropy.

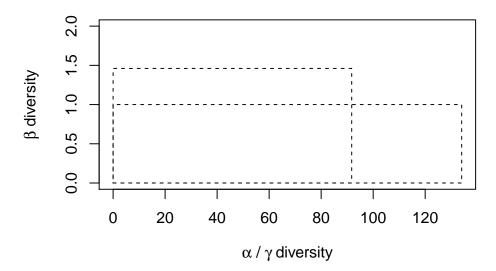


Figure 3. Plot of the diversity partition of the meta-community Paracou618.MC. The long rectangle of height 1 represents γ diversity, equal to 134 effective species. The narrower and higher rectangle has the same area: its horizontal size is α diversity (92 effective species) and its height is β diversity (1.46 effective communities).

R > de < - DivEst(q = 1, Paracou618.MC, Biased = FALSE, Correction = "Best",

```
Simulations = 1000)
R> summary(de)
Diversity partitioning of order 1 of MetaCommunity MC
 with correction: Best
Alpha diversity of communities:
     P006
               P018
 81.73115 107.08473
Total alpha diversity of the communities:
[1] 91.74905
Beta diversity of the communities:
[1] 1.460828
Gamma diversity of the metacommunity:
[1] 134.0296
Quantiles of simulations (alpha, beta and gamma diviersity):
                10%
                                     10%
       0%
                          50%
                                               25%
                                                          50%
                                                                    75%
                     91.91839
                               87.02291
                                          89.24340 91.91839 94.34100
 79.37784
           87.02291
                           99%
      90%
                95%
                                    100%
           97.89250
 96.60530
                     99.91433 103.85602
              10%
                       50%
                                 10%
                                                   50%
                                                             75%
      0%
                                          25%
1.392408 1.430387 1.461703 1.430387 1.444735 1.461703 1.476975
```

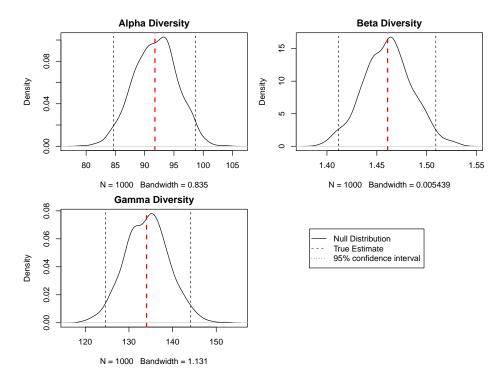


Figure 4. Plot of the diversity estimation of the meta-community Paracou618.MC. α , β and γ diversity probability densities are plotted, with a 95% confidence interval.

The result is a Divest object which can be summarized and plotted (Figure 4).

Diversity Profile of a metacommunity

 ${\tt DivProfile}$ calculates diversity profiles, *i.e.* the value of diversity against its order (Figure 5). The result is a ${\tt DivProfile}$ object which can be summarized and plotted.

R> dp <- DivProfile(seq(0, 2, 0.2), Paracou618.MC, Biased = FALSE)R> summary(dp)

Diversity profile of ${\tt MetaCommunity}\ {\tt MC}$

with correction: Best

Diversity against its order:

		,				
	Order	Alpha Diversit	y Beta	Diversity	${\tt Gamma}$	Diversity
[1,]	0.0	205.8422	6	1.441996		296.82368
[2,]	0.2	181.6381	1	1.424471		258.73825
[3,]	0.4	157.3527	7	1.413780		222.46224

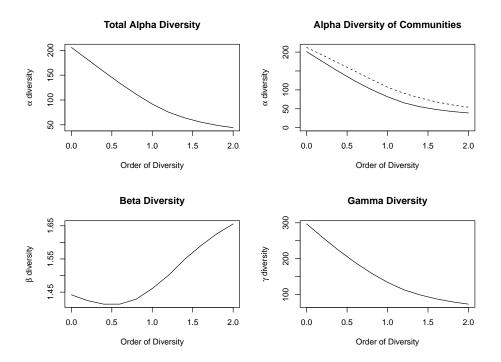


Figure 5. Diversity profile of the meta-community Paracou618.MC. Values are the number of effective species (α and γ diversity) and the effective number of communities (β diversity). α and γ diversity decrease from q=0 (number of species) to q=2 (Simpson diversity) by construction.

[4,]	0.6	133.77507	1.413903	189.14504
[5,]	0.8	111.70847	1.428705	159.59848
[6,]	1.0	91.74905	1.460828	134.02961
[7,]	1.2	75.51773	1.500587	113.32093
[8,]	1.4	63.95522	1.549024	99.06819
[9,]	1.6	55.37376	1.590012	88.04495
[10,]	1.8	48.97244	1.626123	79.63520
[11,]	2.0	44.21244	1.655569	73.19676

Alternative functions

Beta entropy can also be calculated by a set of functions named after the community functions, such as TsallisBeta, bcTsallisBeta, SimpsonBeta, etc. which require two vectors of abundances or probabilities instead of a MetaCommunity object: that of the community and the expected one (usually that of the meta-community). Bias correction is currently limited to Chao and Shen's correction. The example below calculates the Shannon β entropy of the first community of Paracou618 and the meta-community.

R> ShannonBeta(Paracou618.MC\$Psi[, 1], Paracou618.MC\$Ps)

[1] 0.3499358

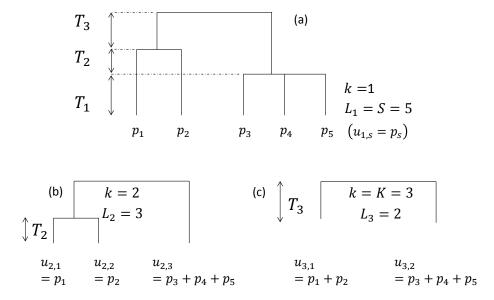


Figure 6. Hypothetical ultrametric tree. (a) The whole tree contains three slices, delimited by two nodes. The length of slices is T_k . (b) Focus on slice 2. The tree without slice 1 is reduced to 3 leaves. Frequencies of collapsed species are $u_{k,l}$. (c) Slice 3 only.

These functions are available for particular uses, when a MetaCommunity is not available or not convenient to use (e.g. simulations). Meta-community functions are preferred for current use.

4. Phylogenetic diversity

Phylogenetic or functional diversity generalizes HCDT diversity, considering the divergence between species (Marcon and Hérault 2014). Here, all species take place in an ultrametric phylogenetic or functional tree (Figure 6). The tree is cut into slices, delimited by two nodes. The first slice starts at the bottom of the tree and ends at the first node. In slice k, L_k leaves are found. The probabilities of occurrence of the species belonging to branches that were below leaf l in the original tree are summed to give the grouped probability $u_{k,l}$. HCDT entropy can be calculated in slice k:

$${}_{k}^{q}H = -\sum_{l} u_{k,l}^{q} \ln_{q} u_{k,l} \tag{10}$$

Then, it is summed over the tree slices. Phyloentropy can be normalized or not. We normalize it so that it does not depend on the tree height:

$${}^{q}\overline{H}\left(T\right) = \sum_{k=1}^{K} \frac{T_{k}}{T} {}^{q}_{k} H \tag{11}$$

Unnormalized values are multiplied by the tree height, such as ${}^{q}PD\left(T\right)$ (Chao et al. 2010).

Phyloentropy is calculated as HCDT entropy along the slices of the trees applying possible estimation-bias corrections, summed, possibly normalized, and finally transformed into diversity:

$${}^{q}\overline{D}\left(T\right) = e_{q}^{q}\overline{H}(T) \tag{12}$$

4.1. Community functions

PhyloEntropy and the estimation-bias-corrected bcPhyloEntropy are the phylogenetic analogs of Tsallis and bcTsallis. They accept the same arguments plus an ultrametric tree of class hclust or phylog, and Normalize, a boolean to normalize the tree height to 1 (by default).

Phylogenetic diversity is calculated by PhyloDiversity or bcPhyloDiversity, analogous to the neutral diversity functions Diversity and bcDiversity.

Results are either a PhyloDiversity or a PhyloEntropy object, which can be plotted (Figure 7) and summarized.

```
R> phd <- bcPhyloDiversity(Paracou618.MC$Ns, q = 1, Tree = Paracou618.Taxonomy,
+     Normalize = TRUE)
R> summary(phd)
```

alpha or gamma phylogenetic or functional diversity of order 1 of distribution Paracou618.MC\$Ns

with correction: Best

Phylogenetic or functional diversity was calculated according to the tree Paracou618.Taxonomy

Diversity is normalized

Diversity equals: 55.13383

The AllenH function is close to PhyloEntropy: it also calculates phyloentropy but the algorithm is that of Allen, Kon, and Bar-Yam (2009) for q=1 and that of Leinster and Cobbold (2012) for $q \neq 1$. It is much faster since it does not require calculating entropy for each slice of the tree but it does not allow estimation-bias correction. ChaoPD calculates phylodiversity according to Chao et al. (2010), with the same advantages and limits compared to PhyloDiversity.

For convenience, PDFD and Rao functions are provided to calculate unnormalized phyloentropy of order 0 and 2.

4.2. Meta-community functions

DivPart, DivEst and DivProfile functions return phylogenetic entropy and diversity values instead of neutral ones if a tree is provided in the arguments.

```
R> dp <- DivPart(q = 1, Paracou618.MC, Biased = FALSE, Correction = "Best",
+ Tree = Paracou618.Taxonomy)
R> summary(dp)
```

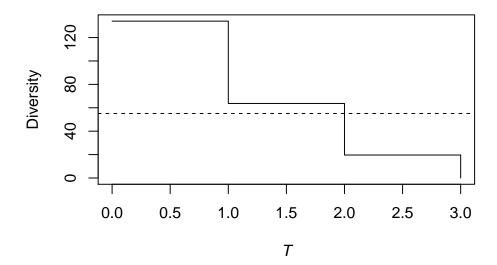


Figure 7. Plot of the γ phylodiversity estimation of the meta-community Paracou618.MC. The effective number of taxa of Shannon diversity is plotted against the distance from the leaves of the phylogenetic tree. Here, the tree is based on a rough taxonomy, so diversity of species, genera and families are the three levels of the curve.

```
Diversity partitioning of order 1 of MetaCommunity Paracou618.MC with correction: Best
Phylogenetic or functional diversity was calculated according to the tree Paracou618.Taxonomy
```

Diversity is normalized

```
Alpha diversity of communities:
P006 P018
37.22132 51.31045
Total alpha diversity of the communities:
[1] 42.70238
Beta diversity of the communities:
[1] 1.291119
Gamma diversity of the metacommunity:
[1] 55.13383
```

Other meta-community functions, such as AlphaEntropy behave the same way:

```
R> summary(BetaEntropy(Paracou618.MC, q = 2, Tree = Paracou618.Taxonomy, + Correction = "None", Normalize = FALSE))
```

```
beta Entropy of order 2 of MetaCommunity Paracou618.MC with correction: None
```

Phylogenetic or functional entropy was calculated according to the tree Paracou618.Taxonomy

```
Entropy is not normalized
Entropy of communities:
P006 P018
0.04117053 0.02325883
Average entropy of the communities:
[1] 0.03350547
```

Compare with Rao's divc computed by ade4:

```
R> library(ade4)
R> divc(as.data.frame(Paracou618.MC$Wi), disc(as.data.frame(Paracou618.MC$Nsi),
+ Paracou618.Taxonomy$Wdist))
```

diversity Paracou618.MC\$Wi 0.03350547

5. Similarity-based diversity

Leinster and Cobbold (2012) introduced similarity-based diversity of a community ${}^qD^Z$. A matrix **Z** describes the similarity between pairs of species, defined between 0 and 1. A species ordinariness is its average similarity with all species (weighted by species frequencies), including similarity with itself (equal to 1). Similarity-based diversity is the reciprocal of the generalized average of order q (Hardy, Littlewood, and Pólya 1952) of the community species ordinariness.

The Dqz function calculates similarity-based diversity. Its arguments are the vector of probabilities of occurrences of the species, the order of diversity and the similarity matrix **Z**.

This example calculates the γ diversity of the meta-community Paracou. First, the similarity matrix is calculated from the distance matrix between all pairs of species as 1 minus normalized dissimilarity.

```
R> DistanceMatrix <- as.matrix(Paracou618.dist)
R> Z <- 1 - DistanceMatrix/max(DistanceMatrix)
R> Dqz(Paracou618.MC$Ps, q = 2, Z)

[1] 1.472353

If Z is the identity matrix, similarity-based diversity equals HCDT diversity:
R> Dqz(Paracou618.MC$Ps, q = 2, Z = diag(length(Paracou618.MC$Ps)))

[1] 68.7215
```

```
R> Diversity(Paracou618.MC$Ps, q = 2)
```

[1] 68.7215

The similarity-based entropy of a community ${}^qH^Z$ (Leinster and Cobbold 2012; Ricotta and Szeidl 2006) has the same relations with diversity as HCDT entropy and Hill numbers. The Hqz function calculates it:

```
R> Hqz(Paracou618.MC$Ps, q = 2, Z)

[1] 0.3208152

R> lnq(Dqz(Paracou618.MC$Ps, q = 2, Z), q = 2)

[1] 0.3208152
```

6. Advanced tools

The package comes with a set of tools to realize frequents tasks: running Monte-Carlo simulations on a community, quickly calculate its diversity profile, applying a function to a species distribution along a tree, and manipulation of meta-communities.

6.1. Entropy of Monte-Carlo simulated communities

The EntropyCI function is a versatile tool to simplify these simulations. Its arguments are an entropy function (any entropy function of the package accepting a vector of species abundances, such as bcTsallis), the number of simulations to run and the observed species frequencies. The result is a numeric vector containing the entropy value of each simulated community. Entropy can be finally transformed into diversity but it is not correct to use a diversity function in simulations because the average simulated value must be calculated (and only entropy can be averaged).

This example shows how to use the function. First, the distribution of the γ HCDT entropy of order 2 (Simpson entropy) of Paracou meta-community is calculated and transformed into diversity. Then, the actual diversity is calculated and completed by the 95% confidence interval of the simulated values.

```
R> SimulatedDiversity <- expq(EntropyCI(FUN = bcTsallis, 
+ Simulations = 1000, Ns = Paracou618.MC$Ns, q = 2), 
+ q = 2)

R> bcDiversity(Paracou618.MC$Ns, q = 2)

[1] 73.19676
```

R> quantile(SimulatedDiversity, probs = c(0.025, 0.975))

2.5% 97.5% 63.07206 107.44083

6.2. Diversity or Entropy Profile of a community

This function is used to calculate diversity or entropy profiles based on community functions such as Tsallis or ChaoPD. It is similar to DivProfile but does not require a Metacommunity for argument. It returns a list which can be plotted, see the help page of the function for an example.

6.3. Applying a Function over a Phylogenetic Tree

The PhyloApply function is used to apply an entropy community function (generally bcTsallis) along a tree.

6.4. Manipulation of meta-communities

Several meta-communities, combined in a list, can be merged two different ways: the MergeMC function simplifies hierarchical partitioning of diversity: it creates a new meta-community whose communities are the original meta-communities aggregated data. The α entropy of the new meta-community is the weighted average γ entropy of the original meta-communities.

MergeC combines the communities of several meta-communities to create a single meta-community containing them all. Last, ShuffleMC randomly shuffles communities across meta-communities to allow simulations to test differences between meta-communities.

7. Conclusion

The entropart package allows estimating biodiversity according to the framework based on HCDT entropy, the correction of its estimation-bias (Grassberger 1988; Chao and Shen 2003) and its transformation into equivalent numbers of species (Hill 1973; Jost 2006; Marcon et al. 2014). Phylogenetic or functional diversity (Marcon and Hérault 2014) can be estimated, considering phyloentropy as the average neutral diversity over slices of a phylogenetic or functional tree (Pavoine et al. 2009). We believe it is a complete toolbox for ecologists who need to estimate the diversity of actual, undersampled communities and to partition it.

Similarity-based diversity is also considered even though neither estimation-bias correction nor decomposition are available yet.

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References

- Allen B, Kon M, Bar-Yam Y (2009). "A New Phylogenetic Diversity Measure Generalizing the Shannon Index and Its Application to Phyllostomid Bats." *American Naturalist*, **174**(2), 236–243.
- Beck J, Holloway JD, Schwanghart W (2013). "Undersampling and the measurement of beta diversity." *Methods in Ecology and Evolution*, 4(4), 370–382.
- Chao A, Chiu CH, Jost L (2010). "Phylogenetic diversity measures based on Hill numbers." *Philosophical Transactions of the Royal Society B*, **365**(1558), 3599–609.
- Chao A, Lee SM, Chen TC (1988). "A generalized Good's nonparametric coverage estimator." Chinese Journal of Mathematics, 16, 189–199.
- Chao A, Shen TJ (2003). "Nonparametric estimation of Shannon's index of diversity when there are unseen species in sample." *Environmental and Ecological Statistics*, **10**(4), 429–443.
- Chao A, Wang YT, Jost L (2013). "Entropy and the species accumulation curve: a novel entropy estimator via discovery rates of new species." *Methods in Ecology and Evolution*, 4(11), 1091–1100.
- Daróczy Z (1970). "Generalized information functions." Information and Control, **16**(1), 36–51.
- Dauby G, Hardy OJ (2012). "Sampled-based estimation of diversity sensu stricto by transforming Hurlbert diversities into effective number of species." *Ecography*, **35**(7), 661–672.
- Dray S, Dufour AB (2007). "The ade4 package: implementing the duality diagram for ecologists." *Journal of Statistical Software*, **22**(4), 1–20.
- Faith DP (1992). "Conservation evaluation and phylogenetic diversity." *Biological Conservation*, **61**(1), 1–10.
- Good IJ (1953). "On the Population Frequency of Species and the Estimation of Population Parameters." *Biometrika*, **40**(3/4), 237–264.
- Grassberger P (1988). "Finite sample corrections to entropy and dimension estimates." *Physics Letters A*, **128**(6–7), 369–373.
- Hardy G, Littlewood J, Pólya G (1952). Inequalities. Cambridge University Press.
- Havrda J, Charvát F (1967). "Quantification method of classification processes. Concept of structural a-entropy." *Kybernetika*, **3**(1), 30–35.
- Hill MO (1973). "Diversity and Evenness: A Unifying Notation and Its Consequences." *Ecology*, **54**(2), 427–432.
- Hérault B, Honnay O (2007). "Using life-history traits to achieve a functional classification of habitats." *Applied Vegetation Science*, **10**(1), 73–80.
- Jost L (2006). "Entropy and diversity." Oikos, 113(2), 363–375.

- Jost L (2007). "Partitioning diversity into independent alpha and beta components." *Ecology*, **88**(10), 2427–2439.
- Lande R (1996). "Statistics and partitioning of species diversity, and similarity among multiple communities." Oikos, **76**, 5–13.
- Leinster T, Cobbold C (2012). "Measuring diversity: the importance of species similarity." *Ecology*, **93**(3), 477–489.
- Marcon E, Hérault B (2014). "Decomposing Phylodiversity." *HAL*, hal-00946177 (version 1).
- Marcon E, Hérault B, Baraloto C, Lang G (2012). "The Decomposition of Shannon's Entropy and a Confidence Interval for Beta Diversity." *Oikos*, **121**(4), 516–522.
- Marcon E, Scotti I, Hérault B, Rossi V, Lang G (2014). "Generalization of the partitioning of Shannon diversity." *PLOS One*, **9**(3), e90289.
- Patil GP, Taillie C (1982). "Diversity as a concept and its measurement." *Journal of the American Statistical Association*, **77**(379), 548–561.
- Pavoine S, Love MS, Bonsall MB (2009). "Hierarchical partitioning of evolutionary and ecological patterns in the organization of phylogenetically-structured species assemblages: Application to rockfish (genus: Sebastes) in the Southern California Bight." *Ecology Letters*, 12(9), 898–908.
- Petchey OL, Gaston KJ (2002). "Functional diversity (FD), species richness and community composition." *Ecology Letters*, **5**, 402–411.
- R Development Core Team (2014). "R: A Language and Environment for Statistical Computing."
- Rao C (1982). "Diversity and dissimilarity coefficients: a unified approach." *Theoretical Population Biology*, **21**, 24–43.
- Ricotta C, Szeidl L (2006). "Towards a unifying approach to diversity measures: Bridging the gap between the Shannon entropy and Rao's quadratic index." *Theoretical Population Biology*, **70**(3), 237–243.
- Routledge R (1979). "Diversity indices: Which ones are admissible?" *Journal of Theoretical Biology*, **76**(4), 503–515.
- Shannon CE (1948). "A Mathematical Theory of Communication." *The Bell System Technical Journal*, **27**, 379–423, 623–656.
- Simpson EH (1949). "Measurement of diversity." Nature, 163(4148), 688.
- Tsallis C (1988). "Possible generalization of Boltzmann-Gibbs statistics." *Journal of Statistical Physics*, **52**(1), 479–487.
- Tsallis C (1994). "What are the numbers that experiments provide?" Química Nova, 17(6), 468–471.

Zhang Z, Huang H (2007). "Turing's formula revisited." Journal of Quantitative Linguistics, 14(2-3), 222-241.

Affiliation:

Eric Marcon AgroParisTech Campus agronomique, BP 316 97310 Kourou, French Guiana E-mail: eric.marcon@ecofog.gf

Bruno Hérault Cirad Campus agronomique, BP 316 97310 Kourou, French Guiana E-mail: bruno.herault@ecofog.gf