

Diversity and scalable diversity characterizations

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Abstract

A short review of recent developments in diversity measuring is presented with a special emphasis on the evolution of these techniques. The importance of scalable diversity characterization through one-parametric diversity index families is stressed. An elementary example is also presented to demonstrate the techniques. A nature management study is discussed to reveal the usefulness of the scalable diversities through one-parametric diversity index families. Density dependent and density independent representation of diversities are also discussed.

Key words: Diversity profiles, one-parametric diversity index families, Rényi diversity, right tail sum diversity, expected number of species diversity, species accumulation plots

Introduction - motivation

The problem of index choice is well-known in the diversity literature. Thirty years ago, Peet (1974) discussed the need for a theory to facilitate choice among diversity indices. One may wish the index to be sensitive to dominant species but relatively indifferent to rare ones. The solution, as proposed by Patil & Taillie (1979), is the use of one-parametric index families that allows the diversity of an assemblage to be characterized by a diversity profile instead of a single numerical value. This is possible with the one-parametric index families, since

changing the scale parameter modifies the sensitivity of the diversity index. The change in sensitivity can then be displayed graphically by plotting the calculated diversity value against the scale parameter. The first of these techniques, the generalized entropy, was published by Rényi (1961). Today, there are a number of methods available for scalable diversity characterization (reviewed by Tóthmérész, 1995, 1998).

In the first part of the paper we review the methods stressing the evolution of these techniques; in the second part of the paper the usefulness of the methods is demonstrated by a nature management study.

Material and methods

Some notations

We frequently speak about the number of individuals of a species or about abundance generally. In formal notation, each species is represented by a positive integer. The number of individuals of the first species in the sample is denoted by n_1 . Generally, the number of individuals of the i -th species is denoted by n_i . The sum of all the individuals in all species is denoted by N . The number of species is usually denoted by S . So, the total number of individuals, N is:

$$N = n_1 + n_2 + \dots + n_i + \dots + n_S = \sum_{i=1}^S n_i$$

An assemblage A can be described by the abundance vector: $\mathbf{n}(A) = (n_1, n_2, \dots, n_S)$. For our purposes it is frequently enough to know the relative abundances of species:

$\mathbf{p}(A) = (p_1, p_2, \dots, p_S)$, where $\mathbf{p}(A)$ is the relative abundance vector and $p_i = n_i / N$. These can also be written, more simply as: $\mathbf{n} = (n_1, n_2, \dots, n_S)$ and $\mathbf{p} = (p_1, p_2, \dots, p_S)$.

Frequently we would like to know which one is the most frequent species, or the second most frequent, etc. It helps if the species are arranged in descending order, using the following notation:

$$\mathbf{p}^\downarrow = (p_{[1]}, p_{[2]}, \dots, p_{[i]}, \dots, p_{[S]})$$

where $p_{[1]}$ is the relative frequency of the most frequent species, $p_{[2]}$ is the relative frequency of the second most frequent species, ... , and $p_{[S]}$ is the relative frequency of the rarest species. The sign "[]" in the subscript means that elements of the vector is arranged in descending order. Therefore:

$$p_{[1]} \geq p_{[2]} \geq \dots \geq p_{[i]} \geq \dots \geq p_{[S]}$$

The notational conventions detailed above will be followed throughout the paper.

Simple artificial data set

We start with an elementary example in order to demonstrate that even in the simplest case

we may need sophisticated tools to characterize diversity. Consider two assemblages, denoted by C1 and C2 (Tóthmérész, 2002). There are 3 species in C1 and 4 species in C2; altogether there are 4 species. The abundance vectors (**n**) and the relative abundance vectors (**p**) are as follows:

$$\begin{aligned} \mathbf{n}(C1) &= (40, 30, 30), & \mathbf{p}(C1) &= (0.4, 0.3, 0.3), \\ \mathbf{n}(C2) &= (60, 20, 10, 10), & \mathbf{p}(C2) &= (0.6, 0.2, 0.1, 0.1) \end{aligned}$$

Basic question: Which one is more diverse?

This is a relatively simple question, which is frequently addressed in ecological studies comparing the diversity of animal assemblages.

First, we would like to demonstrate a trichotomy: C1 can be more diverse than C2, they can be equally diverse, or C1 can be less diverse than C2. An easy calculation shows that the Shannon diversity of C1 is:

$$HS(C1) = 0.4 \log 0.4 + 2 \cdot (0.3 \log 0.3) = 1.0899 \quad \text{and} \quad HS(C2) = 1.0899.$$

The quadratic or Simpson diversity is

$$DQ(C1) = 1 - (0.4^2 + 2 \cdot 0.3^2) = 0.66 \quad \text{and} \quad DQ(C2) = 0.58.$$

The numerical results are contrasted in Table 1.

Table 1. The trichotomy of diversity for the assemblages C1 and C2.

	C1		C2
Number of species	3	<	4
Shannon diversity	1.0889	=	1.0889
Quadratic diversity	0.66	>	0.58

Even in such a simple situation we can get all three possible outcomes. Obviously, such ambiguity can emerge in complex situations as well. This is a common problem emerging from the use of traditional diversity indices.

Evolution of the methods of diversity characterizations

The number of species

The number of species is the oldest and the most traditional measure of diversity. However, it depends on the number of individuals in the sample and/or the area to be sampled. This is the basic motivation for the standardizations: the number of species can be divided by the number of individuals or by the area sampled (e.g. plot size). This leads to the diversity ratios.

Diversity ratios

These indices are based on the ratio of the number of species and the number of individuals. The number of species does not increase linearly with the number of individuals, but (usually) with the logarithm of the number of individuals. It is better to use the ratio of linearly related quantities. Therefore, a more correct expression is obtained by dividing the number of species by the logarithm or by the square root of the number of individuals. A few diversity ratios are listed below:

$$\begin{aligned} dsr &= S / N, & dlr &= S / \log N, \\ dsqr &= S / \sqrt{N}, & dslr &= (S - 1) / \log N. \end{aligned}$$

These simple, richness-type measures of diversity may be useful in many cases, when the abundance is not known for each species, only the total abundance. They do not take into account the abundance-dominance structure of the assemblages. This shortcoming is overcome by the traditional diversity indices, like the Shannon diversity or the quadratic diversity. These methods utilize the information about the relative frequencies of the species of the assemblages. We call them traditional diversity statistics.

Traditional diversity statistics

The most frequently used diversity statistics is the Shannon index of diversity:

$$HS = - \sum_{i=1}^S p_i \log p_i .$$

This index was proposed by Claude Shannon as a measure of information (Shannon, 1948; Shannon & Weaver, 1949), and now it is also used as a measure of diversity in ecology. Sometimes it is mentioned as Shannon-Weaver or Shannon-Wiener diversity, even though the publication priority of Shannon is inevitable.

The other frequently used classical diversity statistic is based on a measure of concentration, C (Pielou, 1975):

$$C = - \sum_{i=1}^S p_i^2 .$$

It measures the un-evenness of the relative abundances. It is evident that the concentration receives its minimum when $p_i = 1/S$ for all $i = 1, \dots, S$.

Diversity is the opposite of concentration. There are, however, at least three different ways to create an opposite measure. One of them, resulting in the quadratic or Simpson diversity, DQ , is the following:

$$DQ = 1 - \sum_{i=1}^S p_i^2 .$$

A less frequently used possibility is based on the logarithmic function:

$$HR(2) = -\log \sum_{i=1}^S p_i^2 = \log \frac{1}{\sum_{i=1}^S p_i^2} .$$

It is related to the one-parametric Rényi diversity index family (Tóthmérész, 1998), discussed later on in the paper. The third possibility is producing a measure of effective number of species, discussed in the next section.

The effective number of species

The diversity statistics introduced in the previous section reflect the abundance-dominance structure of an assemblage. These are producing numerical figures without direct ecological meaning. A diversity value, for example 0.58, has no evident meaning. A diversity characterization that has straightforward biological meaning would be advantageous. Such an index is the effective number of species. The number of species has a direct and important ecological message. The effective number of species is defined as the number of species, all with the same number of individuals, that produces the same diversity value as the one under study (Pielou, 1975). This therefore equals the number of species in a hypothetical assemblage of perfect evenness that would have the same diversity as the assemblage whose diversity is to be characterized.

For the Shannon diversity index the effective number of species is defined as

$$SHS = \exp \{HS\} ,$$

where *exp* is the exponential function. Shannon diversity reaches its maximum when all the species are present with the same number of individuals. In this case the diversity is

$$\max \{HS\} = \log S .$$

Therefore, the effective number of species is exactly *S* (i.e, the actual number of species) for an assemblage in which all species are equally abundant, while less than *S* for any other assemblage.

For the quadratic diversity, an opposite of the concentration also can be created in the following way

$$SDQ = \frac{1}{\sum_{i=1}^S p_i^2} ,$$

which is a measure of the effective number of species. *SDQ* can be used for measuring the effective number of species related to the quadratic diversity. *SDQ* is closely related to *HR(2)*, because $SDQ = \exp\{HR(2)\}$. *SHS* and *SDQ* are also strongly related, because they are related to the Rényi diversity index family (Tóthmérész, 1998). Each member of the Rényi diversity index family can be used in the form of an effective number of species, similarly to the diversity indices discussed above.

Scalable diversity by one-parametric diversity index families

In the case of one-parametric diversity index families, a number of diversity values is used to characterize the diversity of an assemblage. The one-parametric diversity indices may be portrayed graphically by plotting diversities against a (scale) parameter (Fig. 1). This curve is frequently mentioned as the diversity profile of the assemblage (Patil & Taillie, 1979, 1982). Members of a one-parametric diversity index family have varying sensitivities to the rare and abundant species as the scale parameter changes. There exists a large family of one-parametric diversity functions (see Tóthmérész, 1993, 1995). The Rényi diversity is a typical member of the generalized entropy functions. Each of the generalized entropies includes the Shannon diversity as a special case.

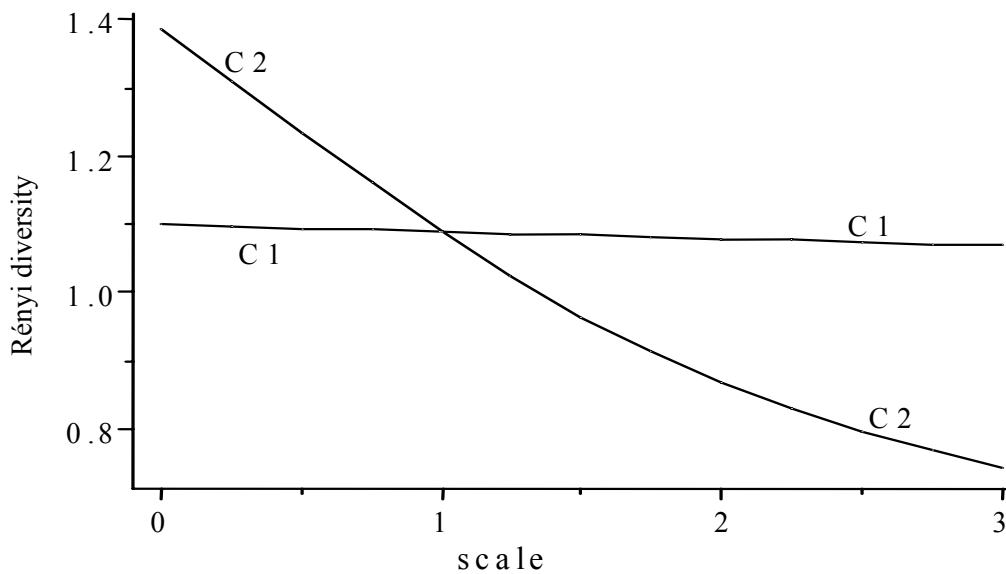


Figure 1. Rényi diversity profiles of the C1 and C2 assemblages.

Diversity profiles are used for scalable diversity comparisons of assemblages. This is also termed diversity ordering. Using diversity profiles, the diversity ordering of assemblages is defined in the following way: assemblage A is more diverse than assemblage B ($A > B$) when the diversity profile of A is above or equal to the diversity profile of B over the entire range of the scale parameter. It can be shown that diversity ordering is a partial order: if $A > B$ and $B > C$, then $A > C$. However, it is not true that for every assemblages A and B, either $A > B$ or $B > A$; the curves of two diversity profiles may intersect, as illustrated in Fig. 1 for C1 and C2. This situation may reflect important ecological processes and therefore needs to be interpreted carefully. For these two assemblages, the intersection of the diversity profiles means that the assemblage C1 is more diverse than C2 for the rare species, while assemblage C2 is more diverse than C1 for the frequent species.

Generalized entropies

Rényi (1961) extended the concept of Shannon entropy by defining the entropy of order α or Rényi diversity ($\alpha \geq 0, \alpha \neq 1$):

$$HR(\alpha) = \frac{1}{1-\alpha} \left(\log \sum_{i=1}^S p_i^\alpha \right).$$

This is the first published family of diversity indices. In the original definition the base of the logarithm was 2; in ecological applications, natural logarithm is more frequently used.

It is important to know some special cases of diversity index families to interpret the result of diversity orderings. For the Rényi index family the following relations are valid:

(i) When the value of the scale parameter is zero ($\alpha=0$), then the value of the Rényi diversity is the logarithm of the number of species of the assemblage; i.e.

$$HR(0) = \log S.$$

In this case the method is extremely sensitive to the contribution of the rare species to the diversity of the assemblage. At this point, the C2 assemblage is more diverse than the C1.

(ii) When the value of the scale parameter approaches 1 (as there is a division with α - see above- $\alpha \neq 1$; but it can take a value infinitely close to 1), then the Rényi diversity is identical to the Shannon diversity:

$$HR(\alpha \rightarrow 1) = -\sum_{i=1}^S p_i \log p_i.$$

In this case the HR value is sensitive to the rare species, although less so than at $\alpha=0$. The diversities of the C1 and C2 assemblages are now identical (Fig. 1).

(iii) When $\alpha = 2$, the Rényi diversity is related to the quadratic diversity:

$$HR(2) = \log \frac{1}{\sum_{i=1}^S p_i^2}.$$

In this case the index starts to be more sensitive to the frequent species than to the rare ones, and assemblage C1 is more diverse than assemblage C2 (Fig. 1).

(iv) When the value of the scale parameter is large (i.e. $\alpha \rightarrow \infty$) the Rényi diversity is related to the Berger-Parker dominance index that is determined only by the relative abundance of the most common species (Southwood & Henderson, 2000):

$$HR(\alpha \rightarrow \infty) = \log \frac{1}{\max \{p_i; i = 1, \dots, S\}}.$$

Cumulative relative abundance plots

RTS diversity (Right-Tail-Sum diversity) also plays a central role in scalable diversity characterizations (Patil & Taillie, 1979; Solomon, 1979). *RTS* diversity is a typical member of the cumulative relative abundance plots, defined as follows (Tóthmérész, 1993, 1998):

$$RTS(i) = p_{[i+1]} + \dots + p_{[S]},$$

where $p_{[1]}, \dots, p_{[S]}$ are the relative abundances of the species arranged in descending order.

The integer i , is the rank of a species, and may be interpreted as a scale parameter. $RTS(i)$ is the sum of the relative abundances of the rarest ($S-i$) species, or the sum of relative abundances remaining after eliminating the i most frequent species. Cumulative relative abundance plots are very different from the generalized entropy curves. A diversity profile produced by a generalized entropy function is a continuous curve, usually defined on the $[0, \infty]$ or $[-1, \infty]$ range. Cumulative relative abundance plots are discrete functions defined for the integers $i=1, \dots, S$. Traditionally, the discrete values are joined by lines to help in the visual comparison of diversity profiles. Therefore, cumulative relative abundance plots are displayed as a polygon, as demonstrated for the data set of the field study in Fig. 3.

Species accumulation plots

There is a long tradition of species-area and species-counts (number of species – number of individuals) *curves* in biology (Engen, 1978; Fisher *et al.*, 1943). We prefer to mention them as *species-accumulation plots*. These curves also can be used for scalable diversity characterization (Patil & Taillie, 1979), and they are defined as follows:

$$ES(m) = S - \sum_{i=1}^S (1 - p_i)^m.$$

This is the expected number of species present when m individuals are drawn at random from an infinitely large population. Conceptually m is an integer, but real values also make mathematical sense. $ES(m)$ is also referred to as expected species-individual diversity.

An important property of $ES(m)$ is that here the scale parameter has a direct biological interpretation: it is the number of species in a sub-sample of size m . When m is small, rare species have a very low probability of appearing in the sub-sample, so $ES(m)$ is small. When the sub-sample size is increased, the expected number of species also increases. Plotting $ES(m)$ against m produces a diversity profile that is essentially a species-individual curve. It is well known that the number of species depends on the number of individuals in the sample in a non-linear manner. This motivates the proposal of plotting $ES(m)$ against $\log m$, although sometimes it is natural to plot the expected number of species against the sampling units (e.g., number of traps, or the area to be sampled).

In the case of a finite population, where the total number of individuals is N , the minimum variance unbiased estimator for $ES(m)$ is (Smith and Grassle, 1977):

$$\widehat{ES}(m) = S - \sum_{i=1}^S \binom{N-n_i}{m} / \binom{N}{m},$$

where $\binom{N}{m}$ denotes the binomial coefficients.

Density dependent and density independent representations of species accumulation plots

The expected number of individuals in an area is proportional to the size of the area. We can calculate the *expected species-area curve* using the relationship:

$$m = N \cdot \frac{\text{size of the area}}{\text{total area}}.$$

Specialists of different sub-disciplines of ecology traditionally use different representations. In samples from pitfall traps, the estimation of the species richness is based on the number of individuals in the traps. This may be mentioned as a density-dependent representation, because there are different number of individuals in the traps. In plant ecology, density dependent representation of the species richness is also used since field surveys use plots of the same size, yet they usually contain different number of individuals. In other cases, a density-independent representation of the species richness is used. In algology, species number is often determined by identifying 100 (or 400) individuals. A similar technique is frequently used to determine species richness in samples of soil invertebrates. Both of these are density independent representations of the number of species. Tóthmérész (1993, 1998) stressed the distinction between these two representations of the species accumulation curves, because they may produce strikingly different ecological interpretations.

Which one to use?

Each of the diversity profiles of the one-parametric diversity families shows the same ordering guaranteed by mathematical theorems for the density independent representations (e.g. Patil and Taillie, 1982). The reason to use different kinds of one-parametric diversity index families is that they reveal different aspects of the data set. *RTS* diversity is useful only for species poor assemblages, because it is effective in demonstrating the ordering relations regarding the dominant species (Tóthmérész, 1995). The *RTS* diversity is important from a theoretical rather than practical point of view: it can be used to prove important mathematical theorems (Patil & Taillie, 1982). This may explain why Patil & Taillie (1979) proposed that an assemblage is intrinsically more diverse when its *RTS* diversity is larger for all i ($i=1, \dots, S$) than that of another assemblage. The *RTS* diversity profile can conveniently be pictured in the form of a logarithmic dominance plot (Tóthmérész, 1993, 1995). The Rényi diversity is generally useful for most assemblages and can be used very effectively in ecological studies (Tóthmérész, 1995, 1998). Species accumulation plots provide the most sophisticated tools to reveal diversity relationships; the density dependent and density independent representation makes them especially useful (Tóthmérész, 1998, 2002).

Why we speak about scaling?

In the case of generalized entropies and cumulative relative abundance plots, the scale parameter is related to the abundance-dominance structure of the studied assemblage. The interpretation of relative abundance plots is straightforward; for $i=1$ we eliminate the relative abundance of the most frequent species, for $i=2$ we eliminate the second most frequent, etc. For generalized entropy plots (especially in the case of Rényi's diversity), the interpretation is indirect because of the sensitivity properties of $HR(0)$, $HR(1)$, $HR(2)$, and $HR(+\infty)$. For the species accumulation plots it is evident that m may be interpreted as a scale parameter; for small m (small sample) the expected number of species is also small and only the frequent species have a real chance to be present. For large m (large sample) the rare species also contribute to the total number of species.

Computing possibilities

Tóthmérész (1993) provided a DOS based computer program to calculate and plot diversity profiles. Recently in R, which is a programming environment for data analysis and graphics (Ihaka and Gentleman, 1996) a package is implemented to calculate one-parametric diversity index families (Tóthmérész, 2005). Oksanen (2004), in his package, called 'vegan', written in the R program language, also provides a function to calculate the Rényi diversity.

A field study: Management of a non-native spruce plantation

To illustrate the possibilities and approaches by scalable diversity comparisons, a ground beetle study from Hungary is used (Magura *et al.*, 2000). Pitfall catches of carabids from native oak-hornbeam forest were compared with those from managed spruce plantation to examine the effect of management on the diversity of ground beetles.

Study area and sampling

The sampling area was located in the North Hungarian Mountain Range. In this region the typical native forest association was oak-hornbeam, which was the most extensive forest type on this territory. We compared carabids in a native deciduous oak-hornbeam forest and a Norway spruce plantation, where gaps were created as a management practice. The Norway spruce plantation was planted after clear-cutting the native forest stand. The spruce was dominant with 70% cover in the tree layer. The presence of native species in the canopy was due to thinning of the spruce that resulted in a re-invasion of native trees, herbs and shrubs, and produced relatively thick leaf litter patches spreading over the 75% of the soil surface. In the native forest the shrub and herbaceous layer were moderate and the leaf litter layer was thick. Beetles were sampled during the main activity period of the species using unbaited pitfall traps (diameter 100 mm, volume 500 ml) containing ethylene-glycol as a killing-preserving solution (details are in Magura *et al.*, 2000).

Result of diversity analysis

There were a combined total of 20 ground beetle species captured in the two habitats; 19 versus 17 species in the native oak-hornbeam forest and in the managed spruce plantations, respectively. There was also a remarkable difference in the number of captured individuals between the managed spruce plantation and the native forest (Table 2). Using traditional diversity statistics, the native forest was more species rich (number of species) and more diverse for the Shannon diversity, while the managed spruce plantation was more diverse using the quadratic or Simpson diversity and the Berger-Parker index of dominance (Table 2).

Table 2. Some statistics for the assemblages of the native oak-hornbeam forest and the spruce plantations.

	<i>native forest</i>		<i>spruce plantations</i>
Number of individuals	1199	>	826
Number of species	19	>	17
Shannon diversity	1.75	>	1.72
Quadratic diversity	1.29	<	1.38
Berger-Parker index	0.89	<	1.92

The Rényi diversity profiles of the two carabid assemblages cross each other and the native forest is more diverse considering the rare species, while the plantation is more diverse considering the dominant species (Fig. 2). Using the *RTS*-diversity we can locate the change in the diversity order. The *RTS*-diversity profiles cross each other between the 3-rd and 4-th species (Fig. 3).

Using a density independent representation of the diversity relationships of the native forest and managed plantation by the *ES(m)* diversity we receive the diversity profiles shown in Fig. 4. For a small (sub)sample, which includes only a few captured individuals, the managed plantation is more species rich than the native plantation. For a larger (sub)sample including approximately 20 or more captured individuals, the native forest is more species rich.

Using the density dependent representation of the *ES(m)* diversity the diversity profiles of the native forest and the managed spruce plantation do not cross each other. The carabid fauna of the native forest is more species rich over the whole range of the scale parameter (Fig. 5). Therefore, they can be unequivocally ordered according to their diversity: the native forest is more diverse than the managed plantation.

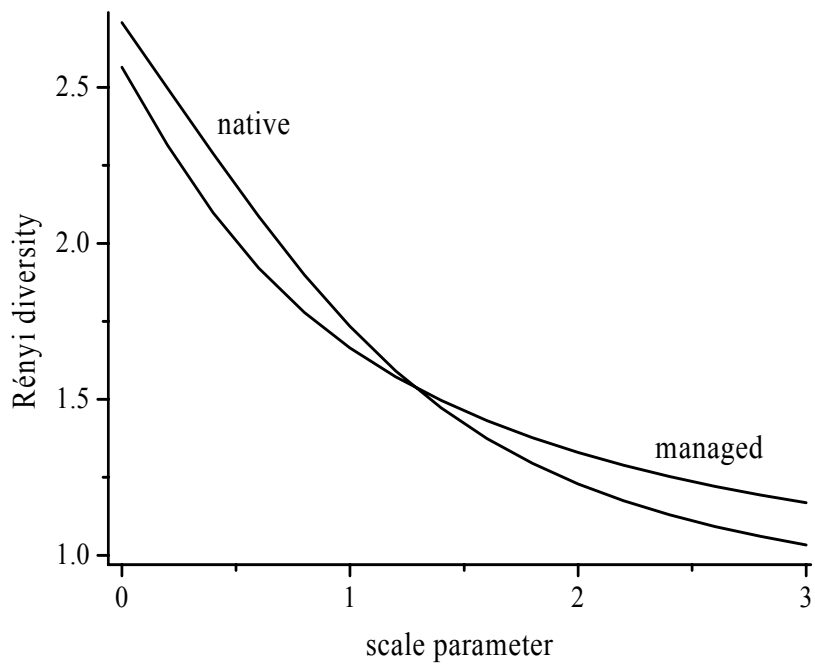


Figure 2. Diversity profiles of the assemblages by the one-parametric Rényi diversity index family.

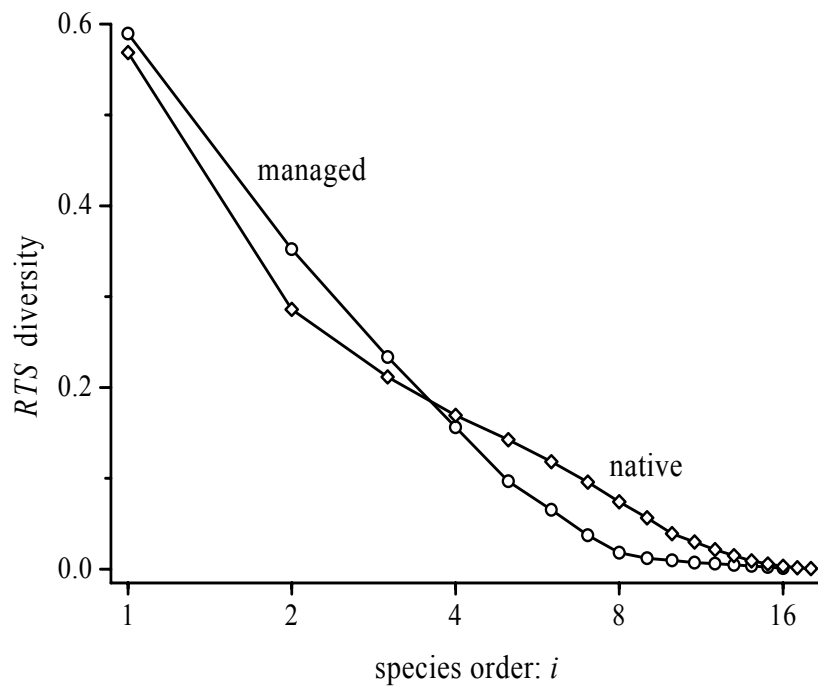


Figure 3. Diversity profiles of the assemblages by the one-parametric *RTS* diversity index family.

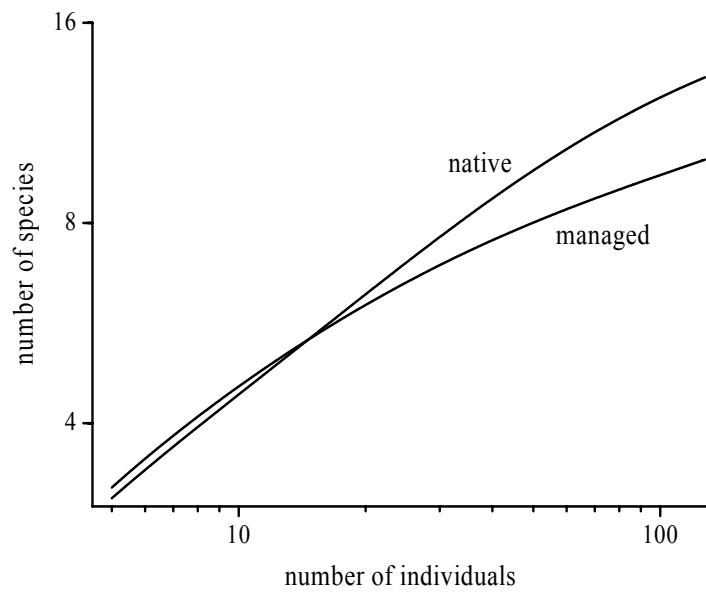


Figure 4. Density independent representation of the expected number of species or $ES(m)$ -diversity profiles.

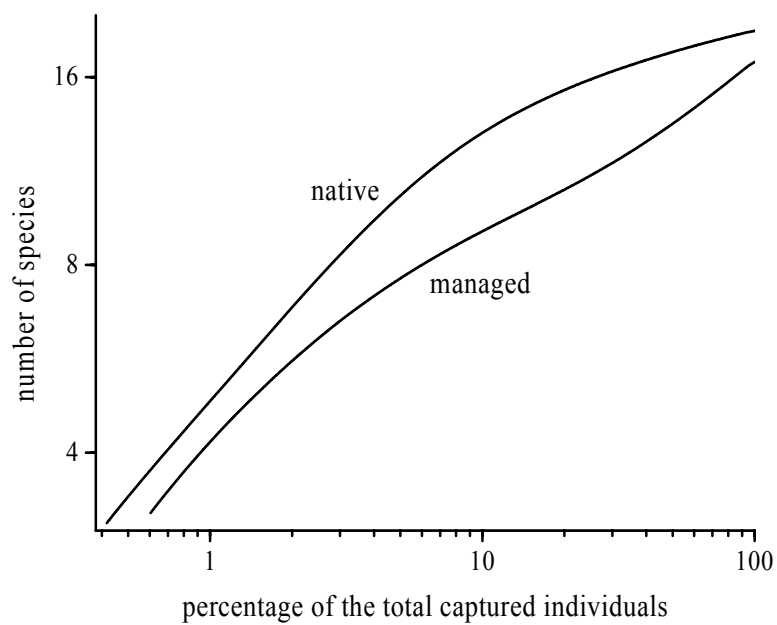


Figure 5. Density dependent representation of the expected number of species diversity or $ES(m)$ -diversity profiles.

Discussion of diversity comparison of the native forest and managed spruce plantation

Using traditional diversity statistics, the results were confusing (Table 2). This ambiguity is visible on the Rényi diversity profiles (Fig. 2). The profiles cross each other, indicating different relationships at different scale parameter values. Using the *RTS*-diversity profile we can locate the reversal in the diversity ordering: the *RTS*-diversity profiles cross each other between the 3rd and the 4th most frequent species (Fig. 3). Ecologically this phenomena, i.e. the lack of the unequivocal diversity order of the carabid assemblages because of the crossing over of the diversity profiles, occurs because generalist and forest generalist species were more frequent in the managed plantation than in the native forest. There were more rare and/or moderately frequent forest specialist carabids in the native forest causing an increased diversity for this part of the diversity profile.

The usual *ES(m)*-diversity profile revealed that using a small (sub)sample (small number of individuals), the managed forest was more diverse: more species occurred in a small (sub)sample than in a (sub)sample of the same size from the native forest. However, with sample sizes larger than 20, the native forest proved more diverse than the managed plantation. This is the usual, density independent representation of the *ES(m)*-diversity profile. Each of the diversity profiles produced by the previous methods (Fig. 2 - Fig. 4) resulted in the same diversity relationship.

The number of species in a sample depends on the size of that sample (Gleason, 1922; Fisher *et al.*, 1943). The total number of captured individuals was larger by one-third in the native forest than in the spruce plantation. Therefore, collecting the beetles in a unit area, there were more carabid individuals in the native forest than in the managed plantations. When there are m individuals in a unit of the sampled area in the plantation, there are $1199/826 \cdot m \approx 2.9/2 \cdot m \approx 3/2 \cdot m$ individuals in the same area in the native forest. Therefore, a density dependent representation of the *ES(m)*-diversity profile is reasonable. Using a density dependent representation of the diversity relationships of the native forest and the managed plantation by the *ES(m)*-diversity profile we obtain the diversity profiles shown in Fig. 5. An important difference between the two representations is that in the density dependent representation the curves of the diversity profiles do not cross each other. Therefore, when taking into account differences in density, the two assemblages can be ordered unambiguously according to their diversity. The native forest is more diverse than the managed plantation over the whole range of the scale parameter.

The analysed management practice increased the diversity of the carabid beetles, although there were important and subtle differences that were highlighted by the scalable one-parametric diversity index families. An important difference revealed by the scalable one-parametric diversities that the managed plantation is more diverse for the most frequent or dominant species, which were forest generalist species. The native forest was still more species rich, because of the presence of rare and moderately frequent forest specialist carabid species. In the case of species accumulation plots or *ES(m)*-diversity profiles there is an

additional benefit besides the scalable comparison. It is the density independent and/or density dependent representation of the diversity profiles. The carrying capacity of the habitat, reflected by density, is frequently an important characteristic of a habitat. In the studied case, the natural forest supported higher density of carabids than the managed plantation. The usual density independent representation of the diversity does not take into account this difference. Using a density dependent representation, we could conclude that the native forest is more diverse than the managed plantation.

We would like to stress that this kind of nature management practice, which encourages the recolonization of herbs, shrubs and trees of the native vegetation by thinning the spruce and especially by creating gaps in the spruce stand is very useful. Advantageous effects of the nature management practice were manifested in the carabid assemblage of the managed plantation. There were subtle differences in the diversity of the native forest and the managed plantation, which were reflected better by the density dependent representation. We do not suggest that the density dependent representation is always automatically more desirable from an ecological point of view than the usual density independent representation. The latter ignores the differences in the densities of the compared assemblages but this is not always important. An appropriate representation should be carefully chosen.

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