



Biodiversity analysis: issues, concepts, techniques

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Abstract: The paper responds to the question: *How should one go about designing the statistical analysis of biodiversity if it had to be done across scales in time and space?* The conceptual basis of the design is the definition of biodiversity as a convolution of two community components. One of the components is richness, the product of species evolution, and the other structure, the consequence of environmental sorting (biotic, physical). The method of choice takes information in the manner of frequency distributions, and decomposes the associated total diversity into additive components specific to the deemed sorting factors. Diversity quantities are supplied by the analysis by which the relative importance of sorting factors can be measured and the dynamic oscillations which they generate in diversity can be traced. Examples support the *a priori* idea that the velocity of compositional change in the community during the late quaternary period has co-varied closely with the specific components of Kolmogorov-type complexity, Anand's structural complexity and Rényi's entropy of order one. The paper explains what is involved and why is it important.

1. Introduction¹

We are addressing biodiversity analysis under the assumption that it is performed in the presence of broad spatial and temporal scales within a natural environment. It is assumed also that geographic extent, period length, and time step are matters of choice. We fully recognise that the problem area has global dimensions, and for this reason we consider it desirable to frame the discourse within the broader terms of the global biodiversity issue. This is highlighted in Appendix A.

What is "biodiversity"? Writing in S. A. Levin's *Encyclopaedia of Biodiversity* (2001, p. XXV, and references), E. O. Wilson defines biodiversity as "... inherited variation of all forms of life". Definition in such terms is useful to us to set bounds within which the discourse should remain. We see specific technical utility of emphasising attributes such as *range*, *number* and *type*, as the authors of Microsoft's *Encarta World Dictionary* have done. Involvement of *structure* and *function* (Izsák and Papp 1994), and reference to statistical models with focus

on cause/effect relations within a dynamic multi-scale environment, further enhances a definition's technical utility.²

We take biodiversity as a convolution of two attributes (*richness*, *structure*) and a class of feedback relations (*cause/effect/cause...*):

1) *Richness*. This implies the numerousness of community components. What first comes to mind when mentioning community components is "organism type", most likely a population of common inheritance, such as a "species". Of course, inheritance is one of the many criteria for recognising populations. Particularly important of the others is linked directly with organismal function. Changing from inheritance to function, the taxa recognised will likely be other than "species" (see Fekete and Lacza 1970, Mueller-Dombois and Ellenberg 1974, Orlóci 1991a, Pillar and Orlóci 1993, and references therein).

2) *Structure*. If we equate *richness* with the numerousness of the organism types, it should make sense to think of

1 A major part of this paper is based on the plenary lecture presented by L.O. at the V. Congresso de Ecologia do Brasil, "Ambiente e Sociedade", Universidade Federal do Rio Grande do Sul, Porto Alegre, November 2001. The paper's contents are augmented with results on biocomplexity (M. Anand) and specific experimental results on late Holocene dynamics (V. Pillar).

2 Having dynamics involved, Margalef's (1989) vortex idea is interesting, albeit the choice of laminar flow and turbulence for analogues is better (see Orlóci 2000, Anand 2000, and their references).

Table 1. Biosphere richness and its systematic structure. Table contents follow Varga (1996) and sources therein. The total number of species existing today is estimated to range from a few million up to 120 million. The average estimated number is about 12 million. Only a fraction of these are so far named, and much fewer studied. See web addresses: <http://www.wri.org>, www.unep.org and www.iucn.org.

| Organismal type | Estimated number of species x1000 | | | % identified |
|-----------------|-----------------------------------|---------------|--------------|--------------|
| | Identified | Upper | Average | |
| Viruses | 5 | 500 | 500 | 1 |
| Bacteria | 4 | 3000 | 400 | 1 |
| Fungi | 70 | 1500 | 1000 | 7 |
| Plankton | 40 | 200 | 100 | 40 |
| Algae | 40 | 10000 | 200 | 20 |
| Other plants | 250 | 500 | 300 | 83 |
| Vertebrates | 45 | 50 | 50 | 90 |
| Flatworms | 15 | 1000 | 500 | 3 |
| Molluscs | 70 | 180 | 200 | 35 |
| Crustaceans | 40 | 150 | 150 | 26 |
| Arachnids | 75 | 1000 | 750 | 10 |
| Insects | 950 | 100000 | 8000 | 11 |
| Total | 1604 | 118080 | 12150 | 13 |

structure as the manner in which organism types are sorted.

3) *Cause and effect.* The identity of the causal factors is diagnosed from their sorting effects. The purpose of biodiversity analysis should in fact be, at one level, the isolation of diversity components in three categories: *main*, *joint*, and *interaction effects*. As a corollary to this, it is important to recognise that the perception of cause/effect relations is fraught by scale dependence (Schneider 1994, Orlóci 2000, O'Neill 2001), which is responsible for *context*. Therefore, biodiversity analysis is best to be performed over ranges of scale.

A further point along this line of reasoning regards the inherently convoluted nature of richness and structure. Because of this, richness and structure can stand as distinct things only in the abstract. They can materialise only as a single dynamic duplet inseparable in natural space or time. We see the analysis of this duplet as a problem in the additive partitioning of measures defined on them, such as *entropy* and *information*.

What are the objectives of biodiversity analysis in general? Wilson's (2000) list on this is reproduced in Appendix A. Where does the present paper have contacts with Wilson's objectives? These are across the categories where general principles and conceptual tools are emphasised. A preview of the present paper's contents should help at this point. The main text begins with an account of data sources, diversity functions, and models for the quan-

titative isolation of biodiversity effects in relation to specific sorting factors. Numerical examples follow, leading to considerations of diversity, complexity, and process stability. Separate sections are devoted to the topic of prediction. Issues and facts about biodiversity, and some technical details about the methods are collected in separate appendices.

2. Data sources, measuring scales, partition model

Biodiversity being a dynamic community property, time series data are ideal for its analysis. The data sources include *permanent plots*, *sediment cores*, and *transects*. The latter is in conjunction of the manoeuvre known as *space-for-time substitution*. We present concrete examples of the first and second, but for more details about the third we refer readers to Wildi and Schütz (2000).

What ever the nature of the basic observation, biodiversity analysis as presented in this paper requires *categorical data* in the manner of Kullback (1959). The frequency distribution in Table 1 is an example. This simple case involves two *richness components* (species identity, type identity) and several *structural features*. The latter are related to the manner in which the frequencies are distributed among the 12 groups, and to the state of the distribution in comparison with some standard arrangement. Structures of this kind are measurable in any one of several ways:

Table 2. Results of diversity analysis performed with the “Average” column of Table 1. Symbols: H_0 – entropy of order zero, H_1 - entropy of order one, I_1 – information (divergence) of order one. Entropy and information functions are discussed in the main text and in Appendix B. See also Orlóci (1991b, 2000). * The units are *bits*. Conversion to natural units: *nats* = *bits* / $\log_2 e$.

| Diversity component | Specifications | Entropy and information* | | |
|---------------------|-------------------------------------|--------------------------|---------|-----------------------|
| | | % of total | Maximum | Observed over maximum |
| Richness | Species ($H_0 = \log_2 12150000$) | 23.54 | 77 | – |
| | Organism type ($H_0 = \log_2 12$) | 3.58 | 12 | – |
| Structure | Disorder (H_1) | 1.98 | 6 | 3.58 |
| | Divergence ($I_1/12150000$) | 1.60 | 5 | 0.22 |
| Total | | 30.70 | 100 | |

1) *Disorder*. Rényi’s (1961) *generalised entropy of order alpha* (see Appendix B) is ideal to measure this. It should be mentioned that disorder is maximal when the frequency distribution is completely flat. Kulback (1959) uses the term “equidistribution” to characterise such a case, while others use terms such as “even”, “most dispersed”, or “most contiguous”. Interestingly, minimal disorder (maximal contagion) occurs when all but one of the cells of the frequency distribution are represented by a single observation. This case is important to set bounds about the observed level of diversity.

2) *Complexity*. There are many ways to define complexity.³ We find particularly useful for our purposes Kolmogorov’s definition (see Anand and Orlóci 1996, 2000). This makes the measured level of complexity conditional on the code length $L = \Delta + H_1$, or in other words the level of the difficulty in an object’s description. Since H_1 is disorder related, the Δ term captures that portion of complexity that is not disorder related. As expected, Δ is zero when the distribution is most dispersed, and maximal, when the distribution is least dispersed. Other measures of complexity may target the *shape* of objects in other than coding theoretical term. This is so when a frequency distribution’s *skewness* and *kurtosis* is measured, or a graph’s *fractal dimension* is determined in the manner of Mandelbrot (1967, 1972).

3) *Divergence*. We use Rényi’s *generalised information of order alpha* for this. Two distributions are involved. One is the observed and the other a standard from which the divergence is measured.

More details are found on these in Appendix B.

3 Design (Dawkins 1986), organisation (Fosberg 1965), shape (Mandelbrot 1967, 1971), or coding related structure (Anand 2000, Anand and Orlóci 1996, 2000, Orlóci 2000).

From a pragmatic point of view, the central dilemma in the statistical analysis of biodiversity is in the model design based on which the effect of specified causal factors can be measured statistically. The model at best should accomplish the task in a perfectly additive manner. The following examples clarify this point.

3. A case of taxonomic diversity

We analysed the average estimates in Table 1 and present the results in Table 2. The analysis of such a case may strike the reader as a trivial undertaking. The results, nevertheless, bring up some interesting points:

1) Taxonomic systems are never absolute. They come about and undergo change in the wake of the evolving view of what should constitute a taxon. We refer back to comments above, regarding different taxonomic systems. The taxonomic criterion in Table 1 is common inheritance.

2) Each value in Table 2 is a “point estimate” specific to diversity of order one. When the order variable is allowed to range free, a curve is generated. The table below takes values from the curve in Figure 1:

| | | | | |
|-------|-------|-------|----------|----------|
| H_0 | H_1 | H_2 | H_{10} | H_{20} |
| 3.58 | 1.98 | 0.80 | 0.66 | 0.63 |

Note the rapid decline initially and then the levelling off with increasing order.

3) Also note the two bounding lines (maximum, minimum) in Figure 1. The lower one corresponds to the hypothetical most contagious distribution. No point exists below this line at the given number of cells (12) and distribution total (12,150,000). The upper bound is straight

at 3.58 bits, the maximum entropy that could ever be attained at the given number of cells, independently from the actual distribution total or entropy order.

4) Note the additive relationship of maximum entropy (3.5849625 bits), disorder based entropy (1.9772667 bits), and information divergence (1.6076958 bits). Clearly, the divergence measured is the entropy deficit, the “equivocation entropy” of Abramson (1963), in the distribution with respect to maximum entropy.

5) Single point diversity is usually taken as entropy of order one (Shannon’s entropy) or order two (a function of Simpson’s index). Entropy of order one is a necessary choice when additive partitions are sought. The choice may follow a different rule where no partitions are intended. For example, one may select a point estimate for general comparison farther out in the right tail, say at H_{10} , to enhance the comparability of different cases.

4. A case of tangible structure

The example to be considered involves two idealised forest stands (Figure 2). The two stands differ in the layering of the tree canopy. The simplest description of such a stand structure is in species presence-absence terms:

| | |
|---------------------------|------------------------|
| 4-species in one stratum: | 4-species in 3 strata: |
| [1 1 1 1] | [1 1 1 1] |
| | [1 1 1 1] |
| | [1 1 1 1] |

The corresponding H_I quantities are:
 Richness (species) = $\log_2 4 = 2$ bits = $\log_2 4 = 2$ bits
 (strata) = $\log_2 1 = 0$ bits = $\log_2 3 = 1.58$ bits
 Within strata = $\log_2 4 = 2$ bits = $3 \log_2 4 = 6$ bits
 Total diversity = 4 bits = 9.58 bits

Clearly, succession from a single stratum to three strata

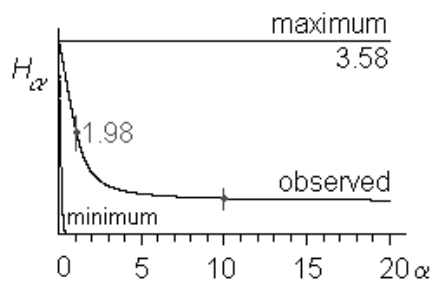


Figure 1. Entropy curve of the average column in Table 1. The curve is marked at H_I and H_{10} . Upper (maximum) and lower bounds (minimum) are shown. The upper bound is at $\log_2 12$. The lower bound approaches zero at about $\alpha=0.5$. See the explanations in the text.

has increased entropy two folds plus 1.58 bits. The 1.58 bits is the unique consequence of the process by which the stand becomes structurally more complex.

5. A case of regional floristic diversity

The geographic location of this example is Heilongjiang in China. As one would expect, many vegetation zones are involved. Li (1993) describes these in detail. X. S. He’s code (Orlóci and He 1996) was used to sort Li’s 646 species (see Table 3) among functional types (5), flora elements (3), and climax types (3). Some revisions were implemented by L.O. The basic records have the format:

| | |
|-------------------------------|----------------------------------|
| 1 Abies holophylla 131 | 4 Acanthopanax sessiliflorus 231 |
| 2 Abies nephrolepis 111 | ... |
| 3 Acanthopanax senticosus 221 | 646 Zigadenus sibiricus 323 |

The digits following a species name identify the states of the sorting criteria. Diversity partitions for the design in Table 3 are given in Tables 4 and 5. The partition functions are listed in Appendix B. Some of the functions are graphed over the range of 10 ranks in Figure 3.

An obvious benefit to be drawn from Table 4 is the quantitative ranking of the sorting criteria. It should be noted that the conditional terms weigh the criteria according to entropy not shared, in other words the independently exercised effect of the sorting factors: functional type (1.718) > climax type (0.913) > flora element (1.185). The difference of the marginal entropy and conditional entropy ranks a criterion according to what it shares with the other criteria: functional type (0.233) > climax type (0.230) > flora element (0.198).

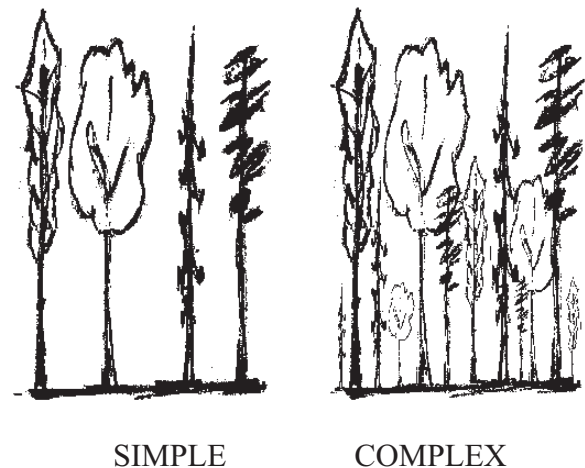


Figure 2. Sketches of idealised stands. The complex stand evolved from the simple by regeneration under the main canopy. See the explanations in the text.

Table 3. Three-way sorting of 646 species from the Heilongjiang flora in China. The data source is Li (1993, Orłóci and He 1996). The three consecutive tables represent layers in a cubic distribution whose principal dimensions correspond to sorting criteria. See further specifications in the text and in the caption of Partition-set 1, Appendix C.

| Functional type within climax type <i>i</i> | Flora element <i>j</i> | | | |
|--|------------------------|-------------------------|---------|------------------|
| | <i>Climax type k</i> | Boreal & sub- alpine | Montane | Forest steppe |
| <i>1 Climatic climax</i> | | | | |
| 1 Trees | | 4 | 5 | 8 |
| 2 Shrubs | | 10 | 58 | 18 |
| 3 Geophytes | | 9 | 79 | 2 |
| 4 Other herbs | | 11 | 131 | 11 |
| 5 Chamaephytes | | 7 | 10 | 2 |
| <i>2 Edaphic climax</i> | | | | |
| 1 | | 1 | 1 | 0 |
| 2 | | 1 | 17 | 8 |
| 3 | | 1 | 58 | 2 |
| 4 | | 1 | 22 | 3 |
| 5 | | 3 | 0 | 0 |
| <i>3 Serial</i> | | | | |
| 1 | | 0 | 0 | 1 |
| 2 | | 3 | 5 | 7 |
| 3 | | 0 | 16 | 13 |
| 4 | | 2 | 46 | 39 |
| 5 | | 7 | 18 | 5 |

Table 4. Typical diversity partitions for the sorting model adapted in Table 3. Partitions accord with the equations in Partition-set 1. See complete set in Table 5 and Partition-set 2. The percentages in the table are relative to total diversity. Since the marginal quantities carry shared effects, percentages are not shown.

| Sources of diversity | Entropy or information of order one | | Proportion relative to possible maximum value |
|------------------------------|--|-----|---|
| | bits | % | |
| Inheritance ($\log_2 646$) | 9.335 | 69 | |
| <i>Sorting criteria</i> | | | |
| <i>Marginal</i> | | | |
| Functional type $H(A)$ | 1.951 | | |
| Flora element $H(B)$ | 1.111 | | |
| Climax type $H(C)$ | 1.415 | | |
| Total | 4.477 | | |
| <i>Conditional</i> | | | |
| Functional type $H(A B,C)$ | 1.718 | 13 | /1.951 = 0.88 |
| Flora element $H(B A,C)$ | 0.913 | 7 | /1.111 = 0.82 |
| Climax type $H(C B,A)$ | 1.185 | 8 | /1.415 = 0.84 |
| Total conditional | 3.816 | 28 | /4.477 = 0.85 |
| Interaction $H(A;B;C)$ | 0.303 | 2 | /4.174 = 0.07 |
| Mutual $H(ABC)$ | 0.054 | 1 | /1.111 = 0.05 |
| Joint $H(A,B,C)$ | 4.174 | 31 | /13.509 = 0.31 |
| Total diversity | 13.509 | 100 | 1.00 |

Table 5. Numerical values of diversity partitions, corresponding to the design in Table 3 and functions listed in Partition-set 2. Taking order in the range from 0 to 5 in unit steps is an arbitrary choice. A broader range is covered in very small steps in Figure 3. All values are given in bits. Combinations of terms are additive in the manner of the Venn diagram (Figure 11). *

| Order (alpha) | 0 | 1 | 2 | 3 | 4 | 5 |
|---------------------|-----------|----------|----------|----------|----------|----------|
| Diversity component | Diversity | | | | | |
| 1 H(A): | 2.321928 | 1.951334 | 1.766663 | 1.662564 | 1.593843 | 1.544130 |
| 2 H(B): | 1.584962 | 1.110980 | 0.828246 | 0.693303 | 0.626091 | 0.588599 |
| 3 H(C): | 1.584962 | 1.415377 | 1.265123 | 1.152364 | 1.074673 | 1.022084 |
| 4 H(A B): | 2.321928 | 1.877857 | 1.694064 | 1.598457 | 1.539693 | 1.499559 |
| 5 H(A C): | 2.321928 | 1.845936 | 1.625515 | 1.499634 | 1.418283 | 1.361917 |
| 6 H(B A): | 1.584962 | 1.037503 | 0.78910 | 0.681844 | 0.626761 | 0.594251 |
| 7 H(B C): | 1.584962 | 1.040948 | 0.77370 | 0.668455 | 0.620685 | 0.594390 |
| 8 H(C A): | 1.584962 | 1.309978 | 1.149723 | 1.058772 | 1.002526 | 0.964616 |
| 9 H(C B): | 1.584962 | 1.345344 | 1.156861 | 1.033503 | 0.957242 | 0.908998 |
| 10 H(A,B,C): | 5.491853 | 4.174310 | 3.513039 | 3.169640 | 2.967968 | 2.836009 |
| 11 H(A,B): | 3.906890 | 2.988838 | 2.468848 | 2.232938 | 2.109470 | 2.034227 |
| 12 H(A,C): | 3.906890 | 3.261312 | 2.943977 | 2.752562 | 2.624777 | 2.532658 |
| 13 H(B,C): | 3.169925 | 2.456325 | 1.992373 | 1.725911 | 1.575209 | 1.485472 |
| 14 H(A,B C): | 3.906890 | 2.758933 | 2.233248 | 2.000912 | 1.876410 | 1.798813 |
| 15 H(A,C B): | 3.906890 | 3.063329 | 2.703030 | 2.487700 | 2.349276 | 2.254983 |
| 16 H(B,C A): | 3.169925 | 2.222975 | 1.802900 | 1.590475 | 1.473856 | 1.403401 |
| 17 H(A B,C): | 2.321928 | 1.717985 | 1.503585 | 1.384099 | 1.308268 | 1.256840 |
| 18 H(B A,C): | 1.584962 | 0.912997 | 0.706719 | 0.631069 | 0.594037 | 0.572196 |
| 19 H(C A,B): | 1.584962 | 1.185472 | 0.990882 | 0.889081 | 0.831966 | 0.796753 |
| 20 I(A,B;C): | 0 | 0.303381 | 0.538290 | 0.772290 | 0.995880 | 1.194012 |
| 21 I(A;B): | 0 | 0.073477 | 0.162661 | 0.286843 | 0.454314 | 0.641772 |
| 22 I(A;C): | 0 | 0.105398 | 0.201458 | 0.292610 | 0.379968 | 0.462217 |
| 23 I(B;C): | 0 | 0.070032 | 0.148533 | 0.237017 | 0.333079 | 0.429795 |
| 24 I(A;B C): | 0 | 0.127950 | 0.296893 | 0.581209 | 0.880787 | 1.131498 |
| 25 I(A;C B): | 0 | 0.159872 | 0.28799 | 0.425537 | 0.576731 | 0.727719 |
| 26 I(B;C A): | 0 | 0.124505 | 0.251787 | 0.409520 | 0.572753 | 0.710942 |
| 27 I(A;B,C): | 0 | 0.233349 | 0.473069 | 0.794898 | 1.157766 | 1.470527 |
| 28 I(B;A,C): | 0 | 0.197982 | 0.383913 | 0.664029 | 1.088284 | 1.528958 |
| 29 I(C;A,B): | 0 | 0.229904 | 0.410925 | 0.580382 | 0.732187 | 0.859159 |
| 30 I(mutual): | 0 | 0.054473 | 0.106132 | 0.181595 | 0.299537 | 0.469501 |

* A note to the inquisitive reader: the effect of computer rounding errors in the arithmetic requires the proof of additivity to be developed in terms of symbolic algebra, according to the logic in the Venn diagram, rather than on a purely numerical basis.

6. Diversity, stability, complexity

Conventional wisdom holds it being true (H_0) that community stability is highest during periods of high diversity (e.g. Poore 1955). On gestalt, the graphs of Figure 4 do suggest the existence of rather close relationships, for entropy (H) and structural complexity (C) with velocity (V), a surrogate for stability.⁴ We tested the idea by probing the distribution of the correlation coefficient, computed within randomly placed windows of random lengths on the graphs, for positive and negative tenden-

cies. The result is a frequency distribution of 10000 inter-graph correlation values⁵:

| | HxV | CxV | HxC |
|------------------------|------|------|------|
| Positive correlation % | 3.7 | 63.3 | 28.4 |
| Negative correlation % | 91.2 | 19.6 | 39.3 |
| Zero % | 5.1 | 17.1 | 32.3 |

Negative correlations dominate the relationships of disorder based entropy with velocity, but the relationship of structural complexity and Velocity is overwhelmingly positive. Interestingly, the dominance of positive and negative correlations is strongly localised:

4 See explanation of terms in Appendix A.

5 Correlation coefficients were calculated after smoothing of the graphs in the manner of polynomials of order 20 (Lagoa das Patas) and 13 (Atlantic Heathland).

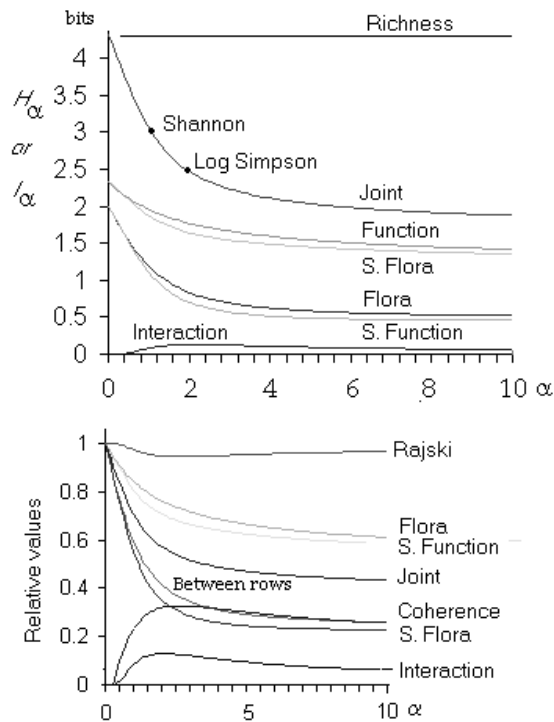


Figure 3. Graphs of selected entropy partitions for functional type and flora element based on quantities identified in Table 5. Labels “Flora”, “Function”, and “Joint” refer to sorting type. “Shared” identifies information. Note the definition of the coherence coefficient $\rho = \sqrt{(1-d^2)}$, where $d = [H(A,B) - H(A;B)] / H(A,B)$. The d quantity is known as Rajski’s metric. “S” is abbreviation for “Specific”. See text above and also in Orlóci (1991b, 2000) for details, regarding terms and algorithmic references.

| Years before present | HxV | CxV | HxC |
|----------------------|-------|-------|-------|
| 1–5000 | -0.98 | 0.22 | -0.23 |
| 5000–16500 | -0.17 | 0.36 | 0.04 |
| 16500–40000 | -0.38 | -0.04 | 0.23 |
| 40000–44500 | -0.99 | 0.36 | -0.31 |
| 1–445000 | -0.31 | 0.09 | -0.00 |

But these are results from one locality. The pattern of correlations observed may not hold for other cases. In specific periods, disturbance may counteract the ongoing process. Figure 5 presents a case in point. The observations began in 1963 after a period of severe grazing and finally burning (see Lippe et al. 1985). Rapid compositional change characterises the initial period of recovery when the process traces out a linear trajectory path (see Figure 6A). Soon after, by around 1969, occlusion develops in the form of severe reduction of bare ground (see Table 6), the process decelerates, and in turn, it enters into a period of chaotic, directionless change. It is interesting to see in this case the evolution of entropy and complexity as can be seen in terms of the correlation values. The over-

all distribution of the positive and negative correlations is as follows:

| | HxV | CxV | HxC |
|------------------------|------|------|------|
| Positive correlation % | 78.2 | 90.8 | 77.8 |
| Negative correlation % | 18.6 | 6.6 | 14.3 |
| Zero % | 3.2 | 2.6 | 7.9 |

The correlations with velocity change with the changing phase in the process:

| Years into the process | HxV | CxV | HxC |
|------------------------|------|------|------|
| 1964–69 | 0.18 | 0.59 | 0.51 |
| 1970–81 | 0.34 | 0.36 | 0.06 |
| 1964–81 | 0.53 | 0.63 | 0.67 |

During the rapidly moving linear phase, both disorder based entropy and structural complexity are dropping with process velocity. But occlusion opens a chaotic phase which disrupts relationships, and makes entropy and structural complexity oscillate in a more complex manner.

An interesting corollary to the Lagoa das Patas example is that velocity tends to decrease during global cooling, and it tends to increase during global warming. True, this is a single example. But from other cases under study it seems the same climatic effect on velocity holds globally true.

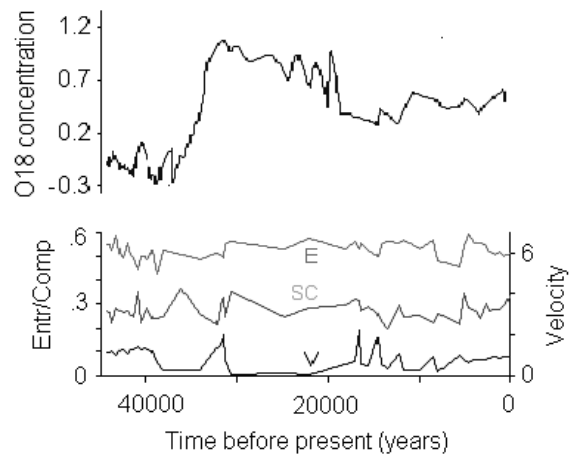


Figure 4. Long-term evolution of Rényi’s generalised entropy of order one, Anand’s structural complexity (Anand and Orlóci 1996), and process velocity (Orlóci 2000) as reflected in the records of the Lagoa das Patas paleopollen spectrum of P. E. Oliveira. Top graph shows changes in the atmospheric concentration of the isotope O^{18} , which is inversely proportional to global average temperature. Graphs are scaled for presentation. While scaling retains the relative graph amplitudes within a case, only graph shape is comparable between cases.

Table 6. The de Smidt data set from Atlantic Heathland (52°N, 6°E). Table contents after Lippe et al. (1985). Data elements are point-cover estimates. Symbols: BG - bare ground; EN - *Empetrum nigrum*; CV - *Calluna vulgaris*; ET - *Erica tetralix*; MC - *Molinia caerulea*; RA - *Rumex acetosella*; JS - *Juncus squarrosus*; CP - *Carex pilulifera*; OS - other species.

| Year | BG | EN | CV | ET | MC | CP | JS | RA | OS |
|------|------|------|------|------|-----|-----|-----|-----|-----|
| 1963 | 57.1 | 17.9 | 8.60 | 11.6 | 0.0 | 0.2 | 0.0 | 4.7 | 0.0 |
| 1964 | 44.0 | 25.0 | 13.7 | 12.2 | 0.0 | 1.1 | 0.2 | 3.9 | 0.0 |
| 1965 | 32.7 | 34.9 | 13.9 | 14.3 | 0.0 | 0.5 | 0.0 | 3.7 | 0.0 |
| 1966 | 27.5 | 36.8 | 20.0 | 14.1 | 0.1 | 0.9 | 0.2 | 0.3 | 0.1 |
| 1967 | 19.7 | 46.1 | 21.0 | 10.8 | 0.1 | 0.7 | 0.4 | 0.5 | 0.7 |
| 1968 | 10.7 | 54.2 | 22.2 | 10.6 | 0.7 | 0.6 | 0.4 | 0.0 | 0.5 |
| 1969 | 6.70 | 55.7 | 23.3 | 10.4 | 0.3 | 2.0 | 0.7 | 0.1 | 0.7 |
| 1970 | 5.80 | 61.1 | 23.7 | 6.90 | 0.2 | 1.2 | 0.7 | 0.2 | 0.3 |
| 1971 | 9.50 | 57.6 | 24.7 | 6.60 | 0.4 | 0.6 | 0.4 | 0.0 | 0.3 |
| 1972 | 8.40 | 62.1 | 23.7 | 3.60 | 0.3 | 1.2 | 0.1 | 0.0 | 0.6 |
| 1973 | 4.40 | 67.9 | 21.3 | 3.30 | 0.2 | 0.6 | 0.4 | 0.0 | 2.0 |
| 1974 | 8.50 | 58.1 | 25.8 | 4.70 | 0.6 | 1.3 | 0.7 | 0.0 | 0.4 |
| 1975 | 9.20 | 62.2 | 24.3 | 2.50 | 0.6 | 0.9 | 0.2 | 0.0 | 0.1 |
| 1976 | 9.90 | 58.2 | 24.9 | 3.70 | 0.6 | 1.1 | 0.7 | 0.0 | 1.0 |
| 1977 | 19.6 | 48.4 | 23.5 | 5.70 | 0.3 | 1.2 | 0.4 | 0.1 | 0.9 |
| 1978 | 12.1 | 58.1 | 22.7 | 4.80 | 0.4 | 0.4 | 0.0 | 0.2 | 1.3 |
| 1979 | 9.30 | 65.1 | 20.3 | 2.70 | 0.0 | 1.5 | 0.1 | 0.2 | 0.9 |
| 1980 | 7.30 | 68.2 | 21.5 | 1.20 | 0.5 | 1.0 | 0.1 | 0.1 | 0.2 |
| 1981 | 5.40 | 65.5 | 20.8 | 4.60 | 1.0 | 1.6 | 0.4 | 0.3 | 0.6 |

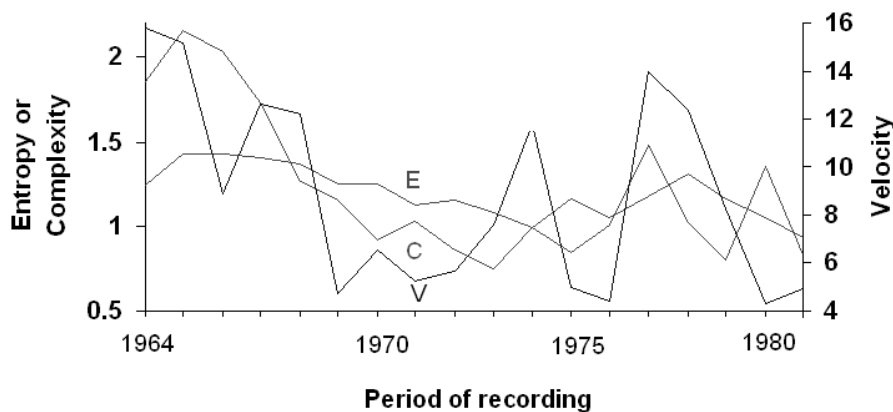


Figure 5. Evolution of compositional diversity (entropy of order one, E) and structural complexity (C, Anand and Orlóci 1996) in relation to process velocity (compositional change in unit time, V on same scale as E) in Atlantic Heathland site. See the explanations in the text and the data in Table 6. Significant events: 1964 – emergence from period of heavy grazing and fire, 1968 – severe reduction of bare ground; 1976-1977 – draught.

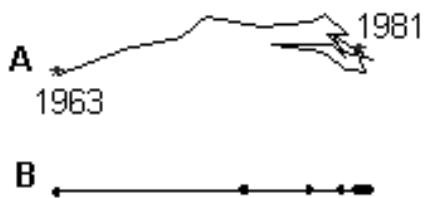


Figure 6. Eigenprojections of the process trajectory (Graph A) and fitted Markov chain (Graph B) in Atlantic Heathland. Graph A recovers 98% of the original distance configuration. See the explanations in the text, and data in Table 6.

7. Prediction

We can bring the technical difficulties of diversity prediction into focus by considering high-order polynomials, sinusoid functions, Markov chain, and a general analogue model. All of these assume something more or less about the type of process that leads into the future. Typically, the process constants are determined in post-diction and extrapolation is the basis of prediction.

Model 1: high-order polynomial, sinusoid curve

Figure 7 is our example. It displays curves fitted to the entropy graph in Figure 5. The irregular curve is a Fourier polynomial of order 16. At this order, the fit is extremely precise. But is it the type on which a prediction should be based? Not really. The problem with polynomials is that they cannot be used reliably outside the data range. To see this, it is sufficient to consider the case of the same type of polynomial fitted to the same entropy graph shortened just by one time step. The predicted entropy for 1980 becomes 2.14 bits. This is a point far exceeding the 1980 level in the original curve (1.34 bits), and far above the observed value (1.55 bits).

The sinusoid curve is the second residual obtained in the third step of the decomposition of the entropy graph. The decomposition is such that the sum of all stepwise sinusoid curves recreates exactly the observed entropy graph.⁶ The decomposition statistics (up to the 5th residual) are as follows:

| | | | | | | |
|----------------------------------|-----|-----|-----|-----|-----|-----|
| Residual # | 0 | 1 | 2 | 3 | 4 | 5 |
| Wave frequency: | 1 | 2 | 3 | 4 | 5 | 1 |
| Wave amplitude: | .19 | .15 | .13 | .08 | .04 | .04 |
| % of total entropy accounted for | 45 | 24 | 18 | 6 | 2 | 2 |
| Cumulative %: | 45 | 69 | 87 | 93 | 95 | 97 |

The numbers indicate rapid decline in wave amplitude and in the amount of entropy in the residuals. Choice of the 2nd residual serves a purely cosmetic purpose, namely the assurance to have a reasonable number of entropy waves covered. In any case, the sinusoid curve is too regular and as such it should not be expected to be a reliable descriptor of the natural diversity process.

Model 2: Markov chain

The logic is completely different. Stated in abbreviated terms, the predicted diversity at the m^{th} step into the future is the diversity in the community whose composi-

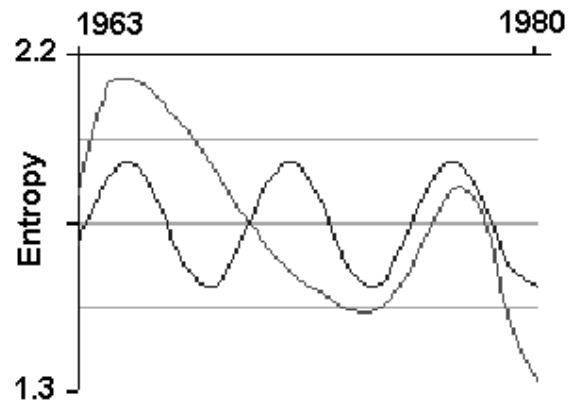


Figure 7. Fourier polynomial of order 16 and the sinusoid curve fitted to the entropy graph of Figure 5. See the explanations in the text.

tion is specified by M_m , the m^{th} term in the Markov chain $M_1 = X_0 P, M_2 = M_1 P, M_3 = M_2 P, \dots$ ⁷ In this, X_0 is the quantitative description of the initial state (perhaps the last paleopollen relevé on record), and P is the transition probability matrix determined from the previous paleopollen relevés.⁸ An element p_{hi} of P is the proportion of cases in which a taxon h is expected to be replaced by taxon i in the next step of the process as consequence of pure chance. The example below uses the Atlantic Heathland data set (Table 6) and the method of Orłóci et al. (1993) to determine the transition probabilities. The Eigenmapping of the fitted Markov chain is given as Figure 6B.

Starting with $X_{1980} = [7.3 \ 68.2 \ 21.5 \ 1.2 \ .5 \ 1 \ 1 \ .1 \ .2]$ as the null state (Table 6), the Markov community state one step into the future is $M_{1981} = X_{1980} P = [6.890 \ 67.71 \ 21.535 \ 1.827 \ 0.535 \ 1.108 \ 0.855 \ 0.129 \ 0.405]$. The predicted Markov community state 10 steps into the future is $M_{1990} = M_{1989} P = [5.815 \ 65.493 \ 21.958 \ 4.1160 \ 0.646$

6 It should be clear that the descriptors of a sinusoid curve (wave frequency, amplitude, phase angle, phase shift) will change depending on the period length. It is to be noted also that while the idea of “best fit” is operational with sinusoid curves, it is absolutely not so with polynomials. There can be a unique wave frequency at which the sinusoid fit to the observations is best, but there is no uniqueness in the same sense with polynomials whose precision of fit is expected to increase by simply increasing the polynomial’s order. The technique and theory for polynomial fitting and sinusoid decomposition are described elsewhere (Fox and Parker 1968, Rayner 1971, He and Orłóci 1998, and references therein).

7 Note that backtracking is analytically possible by postdiction of the kind $M_i = M_{i+1} P^{-1}$. But it will work only if the stable state has not been reached (stability of the numerical values which depends on the computers accuracy is implied). Note also that the case of Markovity used involves discrete states. The Markov chain may appear an inappropriate model, if one considers that syndynamics is a continuous process. Whatever the case, we have no choice. The process can only be recorded in discrete steps, usually on an annual, seasonal, or multi-annual basis.

8 Regarding the determination of transition probabilities from survey type data, the reader is referred to a method devised by Orłóci, Anand, and He (1983). Waggoner and Stephens (1970), Horn (1981), Usher (1981), Lippe et al. (1985), van Hulst (1992), Wagner and Wildi (1997), Balzter (2000), Horváth and Csontos (1992), and Wootton (2001) present thoughts and describe examples relating to ecological applications of the Markov chain. Feller (1957) is the premier reference on Markov chain theory for the statistically-minded ecologist.

1.426 0.510 0.164 0.868]. The corresponding predictions are:

| $H_{1,1980}$ | $H_{1,1981}$ | $H_{1,1990}$ |
|--------------|--------------|--------------|
| 1.4049 bits | 1.4451 bits | 1.555 bits |

How good is the prediction? This is entirely dependent on the transition probabilities resistance to random and directed change. In other words, process stability is important, in the sense that proportionalities are retained. But both environmental and compositional changes are chance driven. Because of this, at least in good part, predictions based on the stationary Markov chain are unlikely to satisfy high expectations.

Model 3: analogues

A prediction could go like this:

- 1) Determine probabilistic linkages between environmental types and community types in the region under observation.
- 2) Use as a prediction the diversity in the existing community type with strongest linkage to the environmental type most likely to materialise in the same site at a future point in time.

A prediction of community composition on such a basis is called “analogue prediction”. Plant geographers and ecologists use analogue prediction regularly, albeit not always in a formal manner. We refer to Orłóci (1978), Box (1981), Aszalós and Horváth (1998), and Kűchler (1974, 1990) for typical examples.

It is clear from the logic that analogue predictions involve the assumption that biological laws (adaptation, plasticity, etc.) interplay with chance effects and the result is determinism, weak or strong, never vanished. Thus, prediction is a game with stochastics (Orłóci 2001a), and as such, the tenets of statistical prediction and scale constraints apply.

8. Concluding remarks

The paper outlines a view of biodiversity analysis that is wide in scope and analytically complex. The breadth of the topics notwithstanding, the paper has not been intended to be monographic. We do not supply a detailed review and evaluation of the broader literature. Those objectives have been pre-empted many times over, since R. K. Peet’s comprehensive paper (1974) and E. C. Pielou’s book (1975), most recently by the authors of the *Encyclopaedia of Biodiversity*. It is true, as one of our critiques observed, that some terms frequent in ecological parlance (such as alpha, beta, and gamma diversity) are left out.

Our reason for that is straightforward: formulations that we described apply to diversity, period — with whatever local qualifications.

It should be clear from what has been presented that there is much more to the analytical problem than the calculation of some index, say entropy of order one or two. It is, however, important to note that in our case the analysis starts with some well-taught out proposition that fixes the identity of the sorting factors and allow meaningful diversity partitions. It should also be noted that we expect the same data set, when probed for diversity structures at different scales, to yield different results. This is not an aberration.

After identification of the sorting factors and meaningful diversity partitions, the analysis becomes a simple three-step procedure at each time point in each site:

- 1) Total diversity is computed, followed by additive partitions specific to the sorting factors and their interactions.
- 2) A given factor’s importance is measured by how much of the total diversity can be loaded onto it. To avoid obtaining spurious interpretations, tests are performed to verify statistical significance.
- 3) The analyses at the time points are linked into an analytical chain to create an image of the process trajectory across sites.

The results suggest interesting facts about diversity, stability, and complexity:

- 1) The importance of the sorting factors is measurable. But the importance measured is comparable only between models that use similar scales.
- 2) Overall, diversity partitions lend themselves readily to interpretation in ecological terms. There are, of course, exceptions. Yet, it remains a meritorious undertaking to compute a complete set of partitions. The computational time is not a problem under automation, and the results give precision to the description of the community’s diversity state. This enhances the reliability of comparisons made with other cases somewhere else at the same time or in the same place at other points in time.
- 3) Diversity, complexity, and stability are linked in our scheme:
 - a) Total complexity cannot exceed maximum disorder based diversity ($\ln s$). When disorder-based diversity (entropy) is maximal, structural complexity is zero.
 - b) It appears reasonable to propose that in the wake of a major disturbance, the velocity of composition change in-

creases in the community, but disorder-based entropy and structural complexity may or may not do the same.

c) It is intuitive that if something is changing rapidly, it is less stable than if it changed slowly under similar conditions. By this criterion, increased velocity of compositional change implies decreased community stability. The correlation criterion suggests that under the same conditions, disorder based entropy and structural complexity behave as opposites. It must be understood that we are not referring to absolute threshold behaviour, only to tendencies, and as the examples indicated, the tendencies may change in different phases of the process.

4) Regarding the techniques of diversity prediction, it is quite fair to say that prediction by analogues is preferred under a broad range of conditions over the other techniques that we examined.

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APPENDICES

by L. Orlóci

A. Biodiversity issues, global warming prospects

I believe biodiversity is a unifying concept in ecology, and the biodiversity problem is defining the global eco-

logical agenda. I mention in support of this, the dual role that biodiversity is known to play, simultaneously a cause and an effect, in the functioning of the global ecosystem, and the sensitive dependence of the functioning of the global ecosystem on biodiversity, and biodiversity on disturbance.⁹ The magnitude of the biodiversity problem can be gauged based on the following facts:

1) The entire genetic, functional, association, and interaction domain of the biota is involved.

2) Species extinctions are very high (Wilson 1992, p. 280; Ehrlich and Ehrlich 1981). Based on Wilson's calculations, the annual species extinction rate is in the range of one thousand to 10 thousand species per one million. This is to be compared to the historical background extinction rate estimated to be one species per million. This is based on fossil records and the implications of the MacArthur-Wilson species-area equation.

3) The number of species named by science is probably only a small portion of the total number in most organismal groups (see Table 1). The number actually studied in detail for biological, economic, medicinal, or ecological significance, is probably much smaller.

Thomas Berry (1990) narrates the general issues involved and suggests radical solutions. The *Encyclopaedia of Biodiversity* (Levin 2001) takes stock of the accumulated knowledge. Based on the foregoing, a broad array of objectives is expected to be addressed by biodiversity studies. Wilson's (2001, p. XXV) list covers the field:

1) Carrying the systematics and biogeography of the world fauna and flora toward completion.

2) Mapping the hot spots where conservation will save most biodiversity.

3) Orienting studies to save threatened species.

4) Advancing ecosystem studies and biogeography to create the needed principles of community assembly and maintenance.

5) Acquiring the knowledge of resource use, economics, and polity to advance conservation programs based on sustainability.

6) Enriching the ethic of global conservation.

The multilingual reader will find many interesting details on different aspects elsewhere, but none probably more elaborating on the design aspects than the Hungar-

9 See more facts and sources reviewed in Levin (1997) and in the *Encyclopaedia of Biodiversity* (Levin 2001).

Table 7. Local thermal flux rates after Orlóci (1994). Rates are based on premises different from the large physico-mathematical circulation models, and can be applied with very little cost to the user. Find the technique described in the 1994 paper's pre-publication manuscript downloadable from <http://mywebpage.netscape.com/lorloci/koa> at link "Warming" or <http://ecoqua.ecologia.ufrgs.br/> at link "Archives" then link "Ipe" then "Warming". Life zone boundary shifts are based on the data of Delcourt and Delcourt (1987) for sites along roughly longitude 85° W in North America. The Mauna Kea vegetation records follow Krajina (1963). Data in rows 3, 4 are from Walter et al. (1975), except in the last two cells which are from Krajina (1963). Note: thermal flux rates are specific to sites and not transferable to others. Abbreviations: AMP – annual mean precipitation; AMT – annual mean temperature; TFR – local thermal flux rate; TR - local temperature rise; EAMT - expected annual mean temperature under the Manabe et al. (1990) scenario, i.e., 3.6 °C global warming on a 100 year basis (2.5 °C temperature rise in 70 years).

| Vegetation | Arctic Tundra | Boreal | Mixed Conifer-Northern Hardwood | Cool Temperate Deciduous | Warm Temperate Evergreen | Tropical Alpine (3,300m) | Tropical Subalpine (2,000m) |
|--------------------|--------------------|------------------|---------------------------------|--------------------------|--------------------------|--------------------------|-----------------------------|
| 1 Climatic station | Port Harrison, Qu. | Timmins, Ontario | Stratford, Ontario | Nashville, Tennessee | Mobil, Alabama* | Mauna Kea, Hawaii | |
| 2 N.latitude | 58° 26' | 48°31' | 43°22' | 36° 10' | 31° 42' | 19°49' | 19° 49' |
| 3 AMP mm | 372 | 711 | 773 | 1,144 | 1,439 | 510 | 1020 |
| 4 AMT °C | -7.5 | 1.3 | 8.3 | 15.6 | 19.8 | 0 | 4.4 |
| 5 TFR | 4.9 | 3.7 | 2.8 | 2.1 | 1.5** | 1.8 | 1.8 |
| 6 TR | 17.6 | 13.3 | 10.1 | 7.6 | 5.4 | 6.5 | 6.5 |
| 7 EAMT | 10.1 | 14.6 | 18.4 | 23.2 | 25.2 | 6.5 | 10.9 |

* Not a climatic limit. ** Extrapolation according to $TFR = -2.57538 + 0.12749X$ where X is the decimal equivalent of locality's N latitude. Coefficient of determination is 0.97. Mauna Kea site not included in the calculations.

ian Natural Sciences Museum's "Handbooks of the National Biodiversity Monitoring System".¹⁰

Environmental deterioration is expected to reach new heights within decades should global warming occur at the rate predicted by IPCC¹¹. I quote from their report: "The globally averaged surface temperature is projected to increase by 1.4 to 5.8°C over the period 1990 to 2100." The IPCC range is equivalent to global average climate warming at 1.3 to 5.3 Celsius degrees on a 100-year basis.¹² What could be the effect of such level of warming? A good estimate is based on historic evidence, particularly from the knowledge of what has taken place during 8 millennia ending with the Hypsothermal about 6 thousand years ago. It was by that time that the global vegetation had attained its modern composition and geographic pattern. It is significant that the IPCC rates are 22 to 93 times greater than the average historic rate for the period mentioned. It is also significant that the actual local tem-

perature is likely to increase at a rate higher than the global average, depending on geographic location. Orlóci's (1994) numbers on this are reproduced in Table 7. Clearly, steep amplification should be expected across latitudes. For example, on longitude 85 °W, roughly the track of the Delcourt and Delcourt (1987) transect, temperature increase can be 5 times the global average at latitude 58°, 4 times at latitude 48°, 3 times at latitude 43°, and 2 times at latitude 36°. I can make some interesting points about the climatic effect on the vegetation in historic terms based on Figure 8. This figure pictures the temporal dynamics of Lucy Braun's Eastern Deciduous Forest (Braun 1950; area D in Figure 9) from its inception 14 thousand years ago. It is clear that climate warming at a less than 0.1° rate per 100 years is sufficient to force the rise of a major vegetation formation and its expansion over many degrees of latitude at an average velocity of about 0.15° latitudes per 100 years. Obviously, the 0.15° rate is one that

10 The *Handbook* is being published in 10 volumes under the general editorship of F. Horváth, Z. Korsós, E. Kovács Láng and I. Matskási, with participation of a multidisciplinary team of 17 subject editors and scores of authors. The reader is directed for a call to arms, as it were, that laid foundations of the *Handbook*, to Fekete (1994).

11 Intergovernmental Panel on Climate Change. 2001. Third Assessment Report. – Climate Change. <http://www.ipcc.ch>.

12 Why to use the range, why not a single value? Simply, the choice would be very arbitrary. This is because the different values are all valid predictions in the context of the model scenario that generates them. Uncertainties are involved, as can be expected, owing to the chaotic nature of the state variables, which Lorenz (1963) revealed to be such in his modelling experiment with the weather. Chaoticity carries through into modelling the climate. Another particularly unavoidable problem is the necessarily speculative manner in which some model components are treated. The handling of cloud properties, their interaction with the radiation fields, and the ways the models handle internal feedback are the cases that Mason (1990, IPCC 2001, pp. 49, 66, 67) found particularly troublesome when the reliability of a model prediction is assessed.

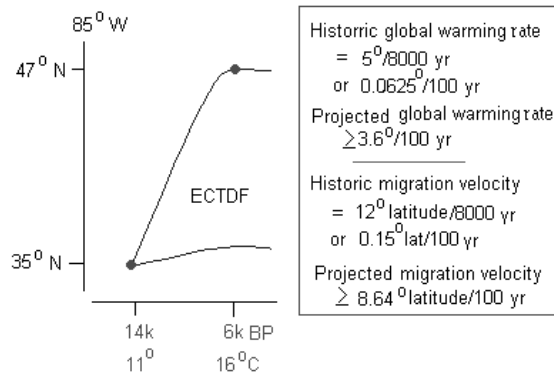


Figure 8. Migration dynamics of the Eastern Deciduous Forest in North America under global climate warming during an 8000-year period of the Late Quaternary. Curves delineate the North/South extent of the formation at given points in time. Projected migration rate accords with 3.6°C x 0.15° Lat/0.0625°. Projected warming follows Manabe at al. (1990) with rate expressed on a 100-year basis. See Table 7 and the text for explanations. The graph is based on Delcourt and Delcourt (1987, Figure 1.4, page 20) with changes.

species populations could cope with, and at which the vegetation formation could retain spatial and temporal contiguity.¹³ But, could the same species and formation cope with climate warming at the IPCC rates? My guess is that warming at even the most conservative IPCC rate would very likely deteriorate the forest environment sufficiently within the normal life span of common forest trees to cause stand-level dieback over the entire region.¹⁴

B. Measuring scales

Rényi's logarithmic expressions

Rényi (1961) generalization of entropy (H_α) and information (I_α) in order terms has the basic form of

$$H_\alpha = \frac{1}{1-\alpha} \ln \sum_{i=1}^s p_i^\alpha$$

and

$$I_\alpha = \frac{1}{\alpha-1} \ln \sum_{i=1}^s \frac{p_i^\alpha}{q_i^{\alpha-1}}$$

13 It is interesting to add that global warming and cooling cycles during the Late Quaternary had measurable effect on the vegetation of the tropics. Figure 4 portrays a case from the Amazonas of Brazil. It is obvious that over the entire 42,000-year period, diversity, complexity, and velocity respond sensitively to cycles of climate warming and cooling, without the temperature amplifying effects of latitude.

14 The reader should consult Muller-Dombois (1992 and references therein) on the dieback phenomenon.

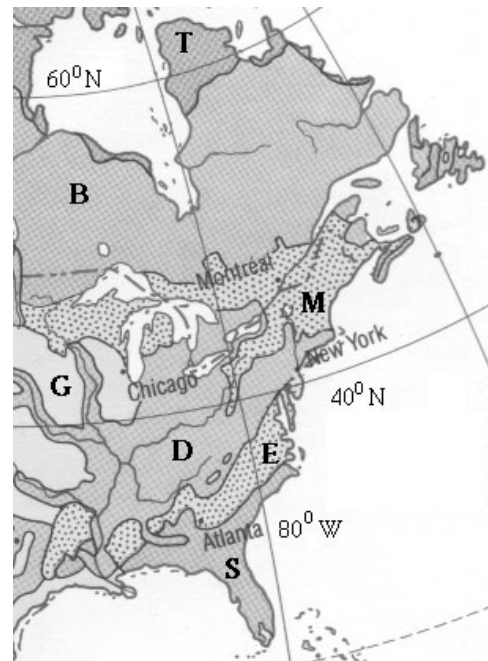


Figure 9. Vegetation map of Eastern North America. Legend: T – Tundra, B – Taiga/ Boreal Forest, M – Cool Mixed Conifer-Deciduous Forest, G – Grassland, D –Cool Temperate Deciduous Forest, E – Warm Mixed Evergreen Forest, S – Subtropical Forest. After the Rand McNally Atlas (1988) modified.

Symbols p_j and q_j are elements in two s-valued distributions, P and Q . These are identically ordered and have identical totals,

$$\sum_{i=1}^s p_i = \sum_{i=1}^s q_i$$

The terms are defined according to

$$p_i = \frac{f_i}{T} \text{ and } T = \sum_{i=1}^s f_i .$$

H_α and I_α describe curves as a function of α . The curves are descending (if not a straight line) for H_α and ascending for I_α . Both are discontinuous at $\alpha=1$, but otherwise continuous over the range from $\alpha = 0$ and up. To determine the value of entropy or information of order one, α may be set to a value close to one, say 0.9999...or the alternative expressions would have to be used,

$$H_1 = -\sum_{i=1}^s p_i \ln p_i \text{ and } I_1 = \sum_{i=1}^s p_i \ln \frac{p_i}{q_i}$$

What is the significance of α in these expressions? Alpha is a *scale variable*, and as such, it defines an infinite number of possible point measures for en-

ropy and information. Three of these had special significance for ecologists. Entropy of order zero is the upper limit. Entropy of order one is the Shannon entropy, and information of order one is one half of Kulback's (1959) minimum discrimination information statistic. Entropy of order two is a log Simpson index. Alpha is useful in other respects, such as in the detection of the region on the curve at which the diversity or information value becomes "stable". This is an advantage when comparisons are made between cases.

H_α is endowed with some interesting properties. It has maximum value equal to $\ln s$, corresponding to maximum disorder in the distribution, i.e., $p_1 = p_2 = \dots = p_s = 1/s$. The degree to which an equidistribution is approached in \mathbf{P} is measured by $E = H / \ln s$, called the "evenness" or "flatness" of \mathbf{P} . H_α has minimum value when \mathbf{P} is most contagious, i.e., when $s-1$ of the elements are equal to $1/T$ and the remaining single element is equal to $(T-s+1)/T$.

I_α is a measure of the information divergence of \mathbf{P} from distribution \mathbf{Q} as a standard. I_α has minimum value at zero when \mathbf{P} and \mathbf{Q} have element-by-element identity, and maximum value when both \mathbf{P} and \mathbf{Q} are most contagious with the $(T-s+1)/T$ quantity placed in offset positions. Kullback (1959) discusses regularity conditions, under which $2I_I$ is distributed as a Chi-squared variate with $s-1$ degrees of freedom. This property has been used to facilitate statistical tests of hypotheses about the relationship of \mathbf{P} and \mathbf{Q} . As ecological practice has it now, randomisation experiments provide a flexible alternative to finding probabilities for the test. I make reference in this regard to Edgington (1987) for underlying theory, to Pillar and Orłóci (1996) and McArdle and Anderson (2001) for contrasting ecological applications, and Orłóci (2001a) for consideration of an important dichotomy in applications of randomisation testing with theoretical consequences.

Entropy and information of order one (H_I, I_I) can be partitioned into perfectly additive components. I take advantage of this property in finding diversity partitions specific to factor effects. The models involved are very much the same in logic as in the analysis of variance and covariance.

Anand's structural complexity

The complexity measure Δ in $L = \Delta + H_I$ is of particular interest. Since Δ is a complement of disorder based entropy H_I , it has to do with order, which is *structure*. The main text and Anand and Orłóci (1996, their Figure 1) should be consulted on specific details.

Simpson's index (Simpson 1949)

This index is probability-based in the manner of

$$SI = \sum_{i=1}^s p_i^2, \text{ such that } \sum_{i=1}^s p_i = 1.$$

The symbols have similar definitions as before. As given, the index SI expresses the probability of finding a compositional duplicate of the community under the assumption that chance rules community composition. When Simpson's function is expressed in the manner of $H = -\ln SI$, Rényi's entropy of order 2 is implied. SI has minimum value at given s when an equal probability law reigns, i.e., $p_1 = p_2 = \dots = p_s = 1/s$. Considering that H reaches its maximum at the most dispersed state of the distribution, one is justified to regard SI as a measure of some compliment of disorder. Energy-focussed ecologists, like Fosberg (1965), have been tempted to use the term "negentropy" in characterisations of SI . Negentropy is a term borrowed from thermodynamics (see Prigogine 1968) where it refers to the available energy in a system. "Negentropy" is mirrored by "entropy", the energy that has been spent. Consistent with the above, SI has maximum value when "negentropy" is maximal, i.e., when \mathbf{P} is most contagious. The limits are reversed when the Simpson index is inverted in the manner of $SD = 1/SI$, which is a measure of diversity directly related to disorder. The maximum value of SD is s . The corresponding evenness quantity is $SDE = SD / s$. As a possible point of interest to some ecologists, I computed values for Simpson's index for the following distributions:

Observed $\mathbf{P} = [13/16, 1/16, 2/16]$

Most dispersed $\mathbf{P}_M = [1/3, 1/3, 1/3]$

Least dispersed $\mathbf{P}_L = [14/16, 1/16, 1/16]$

\mathbf{P}_M and \mathbf{P}_L define \mathbf{P} 's hypothetical upper and lower bounds. The numerical results are presented in Table 8. I leave the interpretation to the interested reader.

The metric connection

A typical example in the use of the Euclidean metric for diversity measurement is the McIntosh diversity index (McIntosh 1967). The Simpson index is this kind when given as SI , which happens to be a squared Euclidean distance. Another information theoretical metric, Rajski's (1961), is not Euclidean (Orłóci 1978). Additive partitioning can be performed directly on Euclidean metrics in the manner of an analysis of variance, or such as in the method of sums of squares partitioning used in Edwards and Cavalli-Sforza (1965, Pillar and Orłóci 1996, Legendre and Anderson 1999, and McArdle and Anderson 2001). The numbers may not add up in the case of non-

Table 8. Values of the Simpson index computed for distribution [13/16, 1/16, 2/16]. See earlier sections for the explanation of symbols.

| | P | P_M | P_L |
|-------------------------------------|-------|-------|-------|
| $SI = \frac{1}{\sum_{j=1}^s p_j^2}$ | 0.506 | 0.333 | 0.629 |
| $SD = \frac{1}{SI}$ | 1.975 | 3.000 | 1.588 |
| $SDE = \frac{SD}{s}$ | 0.658 | 1.000 | 0.529 |
| $H_2 = -\ln \sum_{j=1}^s p_j^2$ | 0.680 | 1.098 | 0.462 |
| $E = \frac{H_2}{\ln s}$ | 0.619 | 1.000 | 0.421 |

Euclidean metrics. On these, I refer for complementary materials presented by others (Peet 1974, Pielou 1975, Patil and Taillie 1979, Rao 1982, Juhász-Nagy and Podani 1983, Magurran 1988, Orlóci 1978,1991a, Tóthmérész 1997,1998a,b, and Levin 2001).

Fractal dimension

This is a descriptor of “shape” complexity. I applied fractal dimension to describe complexity in the trajectory of the entropy process. An entropy trajectory is two-dimensional in the ordinary sense. But its dimension in Mandelbrot’s (1967, 1972) can be a fractal. The “fractal dimension”, symbol D , is related to the power law, linking graph length $L(r)$ with scale unit r , in the manner of $L(r) \sim r^{1-D}$. The exponent $1-D$ is negative if $L(r)$ increases as r decreases, which is the case if the shape is not smooth. By contrast, for smooth shape, D tends to 1 as r is tending to zero. Taking logarithms, $\log L(r) = (1-D) \log r$, and performing linear regression analysis, D is approximated by the regression coefficient, symbol b , in the manner of $D=1-b$. D has value in the range from 1 (smooth curve) to 2 (total randomness such as in the Brownian trajectory of a molecule). The reader is referred to Mandelbrot (1967, 1972, also Schroeder 1991) for details on theory, and to

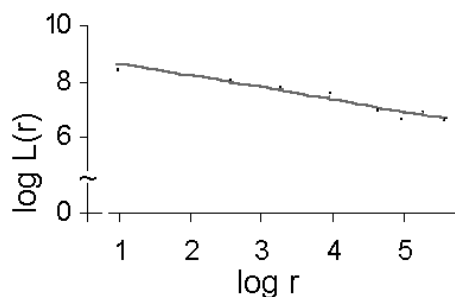


Figure 10. Regression line fitted to $\log L(r)$, the length of the entropy graph for Lagoa das Patas (Figure 4) at step size r , as a function of $\log r$. The regression coefficient b (slope of line) is -0.42 .

Palmer (1988, 1992), Kenkel and Walker (1993), Scheuring (1993), and Walker and Kenkel (1998) for details on ecological applications. The D value of the Lagoa das Patas entropy graph (Figure 4) is around 1.4, suggesting a rather simple process shape. The following example illustrates the arithmetic:

- 1) Step through the diversity graph at different calliper settings and record the following:

| | | | | | | | | |
|----------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|
| Calliper setting (r) mm | 2 | 6 | 10 | 16 | 24 | 32 | 40 | 48 |
| Number of steps | 163 | 47 | 24 | 13 | 5 | 3 | 3 | 2 |
| Approximate length* $L(r)$ mm | 326 | 282 | 240 | 208 | 120 | 96 | 120 | 96 |
| $\log r$ bits | 1 | 2.6 | 3.3 | 4 | 4.6 | 5 | 5.3 | 5.6 |
| $\log L(r)$ bits | 8.4 | 8.1 | 7.9 | 7.7 | 6.9 | 6.6 | 6.9 | 6.6 |

*Note: the graphs as published are smaller than the graphs on which the lengths were measured.

- 2) Perform linear regression analysis on $\log L(r)$ as a function of $\log r$ to obtain an equation as in Figure 10.
- 3) Calculate fractal dimension in the manner of $D=1-b = 1.42$.

C. Partition-sets

Partition-set 1. Functional forms of entropy of order one. Symbols are defined to correspond to the design in Table 3. The equations in the partition set correspond to segments, or sums of segments, in a Venn diagram (Figure 11). The following conventions apply: i - functional type, j - flora element, k - climax type: a, b, c - number of states in sorting criteria i, j, k ; f_{ijk} - an element in the three dimensional distribution, corresponding to Table 3; $f_{i..}, f_{.j.}, f_{..k}$ - principle marginal totals; $f_{ij.}, f_{i.k}, f_{.jk}$ pair-wise joint marginal totals. Examples from Table 5: $a=5, b=3, c=3, f_{123}=0, f_{12.}=6, f_{1..}=20, f_{...}=646$.

$$\begin{aligned}
 H(A) &= - \sum_{i=1}^a p_i \ln p_i; \quad p_i = \frac{f_{i..}}{f_{...}} \\
 H(B) &= - \sum_{j=1}^b p_j \ln p_j; \quad p_j = \frac{f_{.j.}}{f_{...}} \\
 H(C) &= - \sum_{k=1}^c p_k \ln p_k; \quad p_k = \frac{f_{..k}}{f_{...}} \\
 H(A|B,C) &= - \frac{1}{f_{...}} \sum_{j=1}^b \sum_{k=1}^c f_{.jk} \sum_{i=1}^a p_{i|jk} \ln p_{i|jk}; \quad p_{i|jk} = \frac{f_{ijk}}{f_{.jk}} \\
 H(B|A,C) &= - \frac{1}{f_{...}} \sum_{i=1}^a \sum_{k=1}^c f_{i.k} \sum_{j=1}^b p_{j|ik} \ln p_{j|ik}; \quad p_{j|ik} = \frac{f_{ijk}}{f_{i.k}} \\
 H(C|A,B) &= - \frac{1}{f_{...}} \sum_{i=1}^a \sum_{j=1}^b f_{ij.} \sum_{k=1}^c p_{k|ij} \ln p_{k|ij}; \quad p_{k|ij} = \frac{f_{ijk}}{f_{ij.}} \\
 I(A;B;C) &= \sum_{i=1}^a \sum_{j=1}^b \sum_{k=1}^c p_{ijk} \ln \frac{p_{ijk}}{q_{ijk}^{\alpha-1}}; \quad p_{ijk} = \frac{f_{ijk}}{f_{...}}, \quad q_{ijk} = \frac{f_{i..} f_{.j.} f_{..k}}{f_{...}^3} \\
 H(A,B,C) &= - \sum_{i=1}^a \sum_{j=1}^b \sum_{k=1}^c p_{ijk} \ln p_{ijk}; \quad p_{ijk} = \frac{f_{ijk}}{f_{...}} \\
 I(ABC) &= \sum_{i=1}^a \sum_{j=1}^b \sum_{k=1}^c p_{ijk} \ln \frac{p_{ijk}}{q_{ijk}}; \quad p_{ijk} = \frac{f_{ijk}}{f_{...}}, \quad q_{ijk} = \frac{f_{ij.} f_{i.k} f_{.jk}}{f_{i..} f_{.j.} f_{..k}}
 \end{aligned}$$

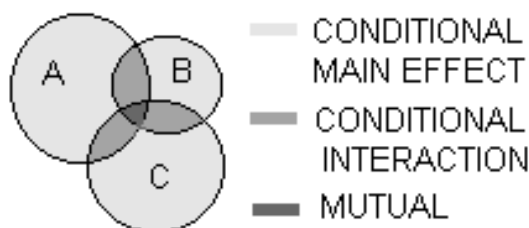


Figure 11. Venn diagram of three-way sorting. Circles represent sorting criteria. The area of circles or circle segments corresponds to diversity terms in the partition sets of Appendix B. Conditional main effects (specifics) $H(A|B,C)$, $H(B|A,C)$, $H(C|A,B)$, $I(A;B|C)$, $I(A;C|B)$, $I(B;C|A)$, conditional interactions $I(A;B|C)$, $I(A;C|B)$, $I(B;C|A)$, and the mutual portion of total diversity $I(ABC)$ are shown. Other terms in Partition-set 2 represent specific sums of area segments in the Venn diagram. On this basis, additive sequences can be identified among the terms in Table 5.

Specific entropy and information quantities have special designations in P. Juhász-Nagy’s scheme (see Juhász-Nagy and Podani 1983, Podani, Czárán and Bartha 1993, Tóthmérész 1997, 1998a,b and references therein). Some examples:

- a) **Local distinctiveness (LD).** This is proportional to the sum of areas A, B, C, but entropy of order one has to be expressed in the manner of Brillouin’s total information (Brillouin 1962) for the numbers to add up. Using my symbols and the case in Figure 2, $LD = f_{...} (H(A) + H(B) + H(C))$.
- b) **Local valence.** This is a Brillouin type multiple of entropy of order one, defined for a marginal distribution when the basic data set contains presence/absence scores.
- c) **Florula diversity (FD).** The term “florula” identifies a subset of species of the sample. When species are taken in pairs, albeit they may be taken in higher numbers, calculus permitting, in a set of s species, the maximum number of florulas is $s!/[2(s-2)!]$. The frequency of the distinct combinations in the sample of relevés is the basis on which FD is defined as a Brillouin type multiple of entropy of order one.
- d) **Mosaic or b diversity.** The idea appears to be shared with Whittaker (1960). It was introduced to handle diversity on the level of mosaics or patches. Tóthmérész (1998) reviews the concept and also the different measuring functions. At least one of these, Routledge’s (1977), is defined in entropy terms and is suitable for additive partitions.

Partition-set 2. Generalised entropy and information functions for which quantities are shown in Table 5. Sym-

bols are consistent with their definition in the caption of Partition-set 1.

- 1) $H(A) = \frac{1}{1-\alpha} \ln \sum_{i=1}^a p_i^\alpha; p_i = \frac{f_{i..}}{f_{...}}$
- 2) $H(B) = \frac{1}{1-\alpha} \ln \sum_{j=1}^b p_j^\alpha; p_j = \frac{f_{.j.}}{f_{...}}$
- 3) $H(C) = \frac{1}{1-\alpha} \ln \sum_{k=1}^c p_k^\alpha; p_k = \frac{f_{..k}}{f_{...}}$
- 4) $H(A|B) = \frac{1}{(1-\alpha)f_{...}} \sum_{j=1}^b f_{.j.} \ln \sum_{i=1}^a p_{i|j}^\alpha; p_{i|j} = \frac{f_{ij.}}{f_{.j.}}$
- 5) $H(A|C) = \frac{1}{(1-\alpha)f_{...}} \sum_{k=1}^c f_{..k} \ln \sum_{i=1}^a p_{i|k}^\alpha; p_{i|k} = \frac{f_{i.k}}{f_{..k}}$
- 6) $H(B|A) = \frac{1}{(1-\alpha)f_{...}} \sum_{i=1}^a f_{i..} \ln \sum_{j=1}^b p_{j|i}^\alpha; p_{j|i} = \frac{f_{ij.}}{f_{i..}}$
- 7) $H(B|C) = \frac{1}{(1-\alpha)f_{...}} \sum_{k=1}^c f_{..k} \ln \sum_{j=1}^b p_{j|k}^\alpha; p_{j|k} = \frac{f_{.jk}}{f_{..k}}$
- 8) $H(C|A) = \frac{1}{(1-\alpha)f_{...}} \sum_{i=1}^a f_{i..} \ln \sum_{k=1}^c p_{k|i}^\alpha; p_{k|i} = \frac{f_{i.k}}{f_{i..}}$
- 9) $H(C|B) = \frac{1}{(1-\alpha)f_{...}} \sum_{j=1}^b f_{.j.} \ln \sum_{k=1}^c p_{k|j}^\alpha; p_{k|j} = \frac{f_{.jk}}{f_{.j.}}$
- 10) $H(A,B,C) = \frac{1}{1-\alpha} \ln \sum_{i=1}^a \sum_{j=1}^b \sum_{k=1}^c p_{ijk}^\alpha; p_{ijk} = \frac{f_{ijk}}{f_{...}}$
- 11) $H(A,B) = \frac{1}{1-\alpha} \ln \sum_{i=1}^a \sum_{j=1}^b p_{ij}^\alpha; p_{ij} = \frac{f_{ij.}}{f_{...}}$
- 12) $H(A,C) = \frac{1}{1-\alpha} \ln \sum_{i=1}^a \sum_{k=1}^c p_{ik}^\alpha; p_{ik} = \frac{f_{i.k}}{f_{...}}$
- 13) $H(B,C) = \frac{1}{1-\alpha} \ln \sum_{j=1}^b \sum_{k=1}^c p_{jk}^\alpha; p_{jk} = \frac{f_{.jk}}{f_{...}}$
- 14) $H(A,B|C) = \frac{1}{(1-\alpha)f_{...}} \ln \sum_{k=1}^c f_{..k} \sum_{i=1}^a \sum_{j=1}^b p_{ij|k}^\alpha; p_{ij|k} = \frac{f_{ijk}}{f_{..k}}$
- 15) $H(A,C|B) = \frac{1}{(1-\alpha)f_{...}} \ln \sum_{j=1}^b f_{.j.} \sum_{i=1}^a \sum_{k=1}^c p_{ik|j}^\alpha; p_{ik|j} = \frac{f_{ijk}}{f_{.j.}}$
- 16) $H(B,C|A) = \frac{1}{(1-\alpha)f_{...}} \ln \sum_{i=1}^a f_{i..} \sum_{j=1}^b \sum_{k=1}^c p_{jk|i}^\alpha; p_{jk|i} = \frac{f_{ijk}}{f_{i..}}$
- 17) $H(A|B,C) = \frac{1}{(1-\alpha)f_{...}} \ln \sum_{j=1}^b \sum_{k=1}^c f_{.jk} \sum_{i=1}^a p_{i|jk}^\alpha; p_{i|jk} = \frac{f_{ijk}}{f_{.jk}}$

- $$18) H(B|A, C) = \frac{1}{(1-\alpha)f \dots} \ln \sum_{i=1}^a \sum_{k=1}^c f_{i.k} \sum_{j=1}^b p_{jik}^\alpha; \quad p_{j|ik} = \frac{f_{ijk}}{f_{i.k}}$$
- $$19) H(C|A, B) = \frac{1}{(1-\alpha)f \dots} \ln \sum_{i=1}^a \sum_{j=1}^b f_{ij} \sum_{k=1}^c p_{k|ij}^\alpha; \quad p_{k|ij} = \frac{f_{ijk}}{f_{ij}}$$
- $$20) I(A; B; C) = \frac{1}{\alpha-1} \ln \sum_{i=1}^a \sum_{j=1}^b \sum_{k=1}^c \frac{p_{ijk}^\alpha}{q_{ijk}^{\alpha-1}}; \quad p_{ijk} = \frac{f_{ijk}}{f \dots}, \quad q_{ijk} = \frac{f_{i..} f_{.j.} f_{..k}}{f^3}$$
- $$21) I(A; B) = \frac{1}{\alpha-1} \ln \sum_{i=1}^a \sum_{j=1}^b \frac{p_{ij}^\alpha}{q_{ij}^{\alpha-1}}; \quad p_{ijk} = \frac{f_{ij}}{f \dots}, \quad q_{ijk} = \frac{f_{i..} f_{.j.}}{f^2}$$
- $$22) I(A; C) = \frac{1}{\alpha-1} \ln \sum_{i=1}^a \sum_{k=1}^c \frac{p_{ik}^\alpha}{q_{ik}^{\alpha-1}}; \quad p_{ik} = \frac{f_{ik}}{f \dots}, \quad q_{ik} = \frac{f_{i..} f_{..k}}{f^2}$$
- $$23) I(B; C) = \frac{1}{\alpha-1} \ln \sum_{j=1}^b \sum_{k=1}^c \frac{p_{jk}^\alpha}{q_{jk}^{\alpha-1}}; \quad p_{jk} = \frac{f_{jk}}{f \dots}, \quad q_{jk} = \frac{f_{.j.} f_{..k}}{f^2}$$
- $$24) I(A; B|C) = \frac{1}{(\alpha-1)f \dots} \sum_{k=1}^c f_{..k} \ln \sum_{i=1}^a \sum_{j=1}^b \frac{p_{ij|k}^\alpha}{q_{ij|k}^{\alpha-1}}; \quad p_{ij|k} = \frac{f_{ijk}}{f_{..k}}, \quad q_{ij|k} = \frac{f_{i.k} f_{.jk}}{f_{..k}^2}$$
- $$25) I(A; C|B) = \frac{1}{(\alpha-1)f \dots} \sum_{j=1}^b f_{.j.} \ln \sum_{i=1}^a \sum_{k=1}^c \frac{p_{ik|j}^\alpha}{q_{ik|j}^{\alpha-1}}; \quad p_{ik|j} = \frac{f_{ijk}}{f_{.j.}}, \quad q_{ik|j} = \frac{f_{ij.} f_{.jk}}{f_{.j.}^2}$$
- $$26) I(B; C|A) = \frac{1}{(\alpha-1)f \dots} \sum_{i=1}^a f_{i..} \ln \sum_{j=1}^b \sum_{k=1}^c \frac{p_{jki}^\alpha}{q_{jki}^{\alpha-1}}; \quad p_{jki} = \frac{f_{ijk}}{f_{i..}}, \quad q_{jki} = \frac{f_{ij.} f_{i.k}}{f_{i..}^2}$$
- $$27) I(A; \{B, C\}) = \frac{1}{\alpha-1} \ln \sum_{i=1}^a \sum_{j=1}^b \sum_{k=1}^c \frac{p_{ijk}^\alpha}{q_{ijk}^{\alpha-1}}; \quad p_{ijk} = \frac{f_{ijk}}{f \dots}, \quad q_{ijk} = \frac{f_{i..} f_{.jk}}{f^2}$$
- $$28) I(B; \{A, C\}) = \frac{1}{\alpha-1} \ln \sum_{i=1}^a \sum_{j=1}^b \sum_{k=1}^c \frac{p_{ijk}^\alpha}{q_{ijk}^{\alpha-1}}; \quad p_{ijk} = \frac{f_{ijk}}{f \dots}, \quad q_{ijk} = \frac{f_{.j.} f_{i.k}}{f^2}$$
- $$29) I(C; \{A, B\}) = \frac{1}{\alpha-1} \ln \sum_{i=1}^a \sum_{j=1}^b \sum_{k=1}^c \frac{p_{ijk}^\alpha}{q_{ijk}^{\alpha-1}}; \quad p_{ijk} = \frac{f_{ijk}}{f \dots}, \quad q_{ijk} = \frac{f_{..k} f_{ij.}}{f^2}$$
- $$30) I(ABC) = \frac{1}{\alpha-1} \ln \sum_{l=1}^a \sum_{j=1}^b \sum_{k=1}^c \frac{p_{ijk}^\alpha}{q_{ijk}^{\alpha-1}}; \quad p_{ijk} = \frac{f_{ijk}}{f \dots}, \quad q_{ijk} = \frac{f_{ij.} f_{i.k} f_{.jk}}{f_{i..} f_{.j.} f_{..k}}$$