

1 **Retaining the double dimension of species diversity: Application of partially**
2 **ordered set theory and Hasse diagrams**

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16 The measurement of species diversity has been a central task of community ecology from the mid
17 20th century onward. The conventional method of designing a diversity index is to combine values
18 for species richness and assemblage evenness into a single composite score. The literature abounds
19 with such indices. Each index weights richness and evenness in a different fashion. The
20 conventional approach has repeatedly been criticized since there is an infinite number of potential
21 indices which have a minimum value when S (species richness) = 1 and a maximum value when S
22 = N (number of individuals). We argue that partial order theory is a sound mathematical fundament
23 and demonstrate that it is an attractive alternative for comparing and ranking biological diversity
24 without the necessity of combining values for species richness and evenness into an ambiguous
25 diversity index. The general principle of partial ordering is simple: one particular assemblage is

26 regarded as more diverse than another when both its species richness and its evenness are higher.
27 Assemblages are not comparable with each other when one has a higher value for species richness
28 and a lower value for evenness. Hasse diagrams can graphically represent partially ordered
29 communities. Linear extensions and rank-frequency distributions reveal the potential of partial
30 order theory as a means to support decisions when assemblage ranking is desired.

31 **Introduction**

32

33 A crucial task of community ecology since the mid 20th century has been the measurement of
34 species diversity. Literally, dozens of diversity indices abound in the literature (Magurran 2004)
35 each with different characteristics, for example the Simpson index, the Shannon index and the Hill
36 series of diversity indices. In their classical form¹, these indices map two central attributes of
37 species assemblages into a single index, the number of species present (species richness) and the
38 evenness of the assemblage (the relative proportions of the constituent species). Since different
39 diversity indices weight richness and evenness differently, they can lead to different rankings when
40 comparing a number of assemblages. Although, at first sight, species diversity might appear a
41 simple and straightforward concept, it admittedly lacks a well-defined theoretical foundation;
42 diversity has not a single, unequivocal definition but is only implicitly defined by the respective
43 index which is applied.

44

45 Widely-used textbooks on ecology normally introduce the subject of species diversity by presenting
46 intuitive examples, as in Begon et al. (2006, p. 471, italics ours): "Consider a community of 10
47 species with equal numbers in each, and a second community, again consisting of 10 species, but
48 with more than 50% of the individuals belonging to the most common species and less than 5% in
49 each of the other nine. Each community has the same species richness, but the first, with a more
50 'equitable' distribution of abundances, *is clearly more diverse* than the second. Richness and
51 equitability combine to determine community diversity." Likewise, in the popular textbook on
52 diversity and its measurement by Magurran (2004, p. 9), one finds little more than the promulgation
53 that, "A diversity index is a single statistic that incorporates information on richness and evenness.
54 [...] The weighting placed on one component relative to the other can have significant influence on
55 the value of the diversity recorded." Although textbooks are not the final authority on scientific

¹ We do not consider indices of functional or phylogenetical diversity in this paper.

56 thinking, they are the portal for the next generation of ecologists and their failure to explain in
57 theory why species richness and patterns of relative abundance should be boiled down to a single
58 index (Brüggemann and Fromm 2001) is perplexing. In the opinion of Lamshead et al. (1983), “to
59 suggest that diversity is lower with a reduced number of species or that diversity is higher if the
60 species abundances are more evenly distributed is to give an indication of how a measure of
61 diversity should behave and not to define diversity itself.”

62

63 Almost 40 years ago, Hurlbert (1971) declared diversity to be a non-concept. Referring to the
64 widely-used Shannon index as an example, he stated that “it has not been shown that information
65 theoretic indices have any greater biological relevance than do the *infinite number of other potential*
66 *indices* which have a minimum value when $S = 1$ and a maximum value when $S = N$ ” (italics ours).
67 Indeed, present-day ecologists continue to develop indices as if this were the solution to the
68 conceptual deficiencies (e.g., Gorelick 2006, Grunewald and Schubert 2006, Campos and Isaza
69 2009). The complexity of the methodological approaches is steadily increasing and the numbers of
70 indices has soared such that some papers set out to explore the diversity of diversity indices rather
71 than diversity itself (e.g., Ricotta 2007). Articles comparing the performance of different indices in
72 different contexts continue to flourish today (e.g., Lamb et al. 2009, Beck and Schwanghart 2010).
73 However, an ecological concept is different from diversity as a statistical index, no matter how
74 complex and elaborate the latter might be defined (Pielou 1980, Sugihara 1982). This leads to the
75 question whether the methodological development since Hurlbert (1971) has been paralleled by
76 conceptual progress or not. Some advocate that diversity values are merely numbers whose
77 relevance to ecological problems must be judged on the basis of observed correlations with other
78 environmental variables (e.g., Molinari 1989). Although one might argue that Hurlbert's (1971)
79 critique of the ambiguous definition of diversity is now outdated, discussion about the meaning of
80 diversity has been kept alive by ecologists and philosophers of science (e.g., Gutmann and Janisch

81 2001, Ricotta 2005, Jost 2006).

82

83 A promising remedy has emerged that might circumnavigate the conceptual difficulties of
84 composite indices and keep separate the two classic dimensions of diversity, richness and evenness.
85 Accordingly, Patil and Taillie (2004) argue that there is no unique way to rank a number of objects
86 (here, assemblages) when each object is characterized by a suite of indicator values (here, richness
87 and evenness). The conventional method of combining the indicator information into a single
88 composite score implies judgments about tradeoffs or substitutability of the indicators. The authors
89 suggested that the positions of the objects in indicator space define only a partial order; and that a
90 given pair of objects may not be inherently comparable. Thus, several attempts have been made to
91 apply *poset* (partially ordered set) theory to diversity measurement (Patil and Taillie 1979, 1982,
92 Rousseau et al. 1999). Furthermore, the approach to analyzing intrinsic diversity profiles or k-
93 dominance curves (e.g. Lamshead et al. 1983, Warwick 1986, Clarke 1990, Teixeira et al. 2007) is
94 based on poset theory and dates back to an earlier paper by Patil and Taillie (1977) who determined
95 a given assemblage to be intrinsically more diverse than another without reference to indices. The
96 general principle of partial orders is simple: one assemblage is more diverse than another only when
97 its species richness and its evenness are higher; two assemblages are non-comparable when one has
98 a higher species richness but a lower evenness than the other. Instead of relying on the result of a
99 composite diversity index, we accept that different characteristics of the assemblages have a
100 different order. Nevertheless, we can compare various assemblages with respect to characteristics of
101 their richness and evenness: poset theory can handle these cases and permits a graphical
102 representation of them, for example, *via* Lorenz curves (Lorenz 1905, Rousseau et al. 1999).
103 Recently, posets have received growing attention in environmental analysis (Brüggemann and
104 Fromm 2001, Lerche et al. 2002, Brüggemann et al. 2003, Patil and Taillie 2004) since they allow
105 multi-criteria ranking. The approach has also gained interest among theoretical ecologists (e.g.

106 Gosselin, 2006, Liu et al. 2007, Gattone and Di Battista 2009). Despite its intuitive simplicity, it has
107 been only occasionally applied by ecological practitioners (e.g., Kindt et al. 2006), perhaps due to
108 the highly technical nature of the respective papers. Poset-related alternative methods to composite
109 diversity index application (intrinsic diversity profiles, k-dominance curves) continue to be greatly
110 outnumbered by classic diversity indices. Between 2005 and 2009, 30 papers applying diversity
111 profiles were published in ecologically and environmentally oriented journals monitored by the ISI
112 Web of Knowledge (<http://apps.isiknowledge.com>), while the Shannon index alone accounted for
113 115 papers in the same period.

114
115 The aim of this paper is to underpin the suitability of poset theory for measuring, representing and
116 —most of all—ranking biological diversity without the necessity of combining species richness and
117 evenness into an ambiguous diversity index. For purposes of comprehensibility, we keep
118 mathematical technicalities to a minimum in this paper. Furthermore, we apply the Hasse diagram
119 as a powerful alternative to Lorenz curves for the graphical representation of partially ordered
120 communities.

121

122 **Partial ordering and Hasse diagrams**

123

124 Both dimensions of diversity—species richness (S) and evenness (E)—can easily be compared and
125 ranked among assemblages. Species richness is simply defined by the number of species present in
126 an assemblage; its values can be determined by counting and applying species richness estimators
127 (Gotelli and Colwell 2001). Evenness is more complicated and a huge number of indices exist for
128 this measure. Rousseau et al. (1999) proposed the application of partially ordered set theory to
129 overcome this ambiguity and to base the measurement of evenness on a mathematical fundament. In
130 their approach, the cumulative proportion of species of an assemblage is plotted against the

131 cumulative proportion of abundances yielding so-called Lorenz curves (Lorenz 1905). If the curve
132 of a given assemblage lies above the curve of another, it is more even; if two curves intersect, they
133 cannot be compared, i.e., no decision can be made whether one assemblage has a higher or lower
134 evenness than the other (Fig. 1). Thus, the Lorenz curves yield a partial order and not the total
135 order. Rousseau et al. (1999) suggest dividing the reciprocal of the well-known Simpson index by
136 the number of species to obtain a measurement of evenness that respects the partial order of the
137 Lorenz curves. For a measurement of evenness, we use the index, $E = 1 / (S \sum p_i^2)$, where p_i is the
138 proportion of the i -th species in the assemblage, throughout the remainder of this paper.

139
140 Let us compare the abundance vectors of three communities, $A = (20, 20, 20, 20, 20)$, $B = (70, 10,$
141 $10, 10)$, and $C = (50, 30, 20)$. If we applied a traditional diversity index approach, we would readily
142 conclude that the species diversity of A is higher than that of B and C , since A contains more species
143 ($S_A = 5$) than assemblages B ($S_B = 4$) and C ($S_C = 3$), and the evenness of A ($E_A = 1$) is higher than
144 the evenness of B ($E_B = 0.48$) and C ($E_C = 0.88$). However, difficulties would arise when comparing
145 B and C , since S_B is higher than S_C , although C appears to be more evenly structured. The outcome
146 of a ranking would depend entirely on the chosen diversity index and thus usually on the decision of
147 the researcher (Solomon 1979) whose choice may be governed by personal, institutional and
148 disciplinary tradition rather than purely by reasoning. In this example, we argue against the “almost
149 irresistible human urge to combine different views [...] into a linear ordering” (Patil and Taillie
150 2004). Thus, we retain species richness and evenness as separate dimensions of diversity, and
151 accept that B and C are non-comparable and cannot be ranked. The diversity D_X of a given
152 assemblage X is said to be higher than diversity D_Y of assemblage Y only when $S_X \geq S_Y$ and $E_X \geq E_Y$,
153 i.e., the set of assemblages is interpreted as a poset. The fundamental characteristics of posets are
154 reflexivity,

155 i.e., $D_X \geq D_X$,

156 antisymmetry,

157 i.e., if $D_X \leq D_Y$ and $D_Y \leq D_X$ then $D_X = D_Y$,

158 and transitivity,

159 i.e., if $D_X > D_Y$ and $D_Y > D_Z$ then $D_X > D_Z$.

160 A compendium of different methodological aspects and applications of partial order theory is given
161 in Brüggemann and Carlsen (2006).

162

163 By way of illustration, we calculate the richness and evenness of a simulated introductory dataset in
164 Table 1. From this, we establish a complete and partial ordering and graphically represent the
165 results as Hasse diagrams. At first, we elaborate the so-called zeta matrix (Patil and Taillie 1982). It
166 is a square matrix whose rows and columns are labeled by the members of the poset (here, the
167 assemblages) and whose entries are 1 or 0. The entry is 1 if the diversity (D) of the corresponding
168 column is equal to or larger than D of the corresponding row of a given cell (Table 2). The
169 assemblage with maximal diversity—i.e., no other assemblage has an equal or higher D —can easily
170 be identified since its row contains only zeroes except for a single 1 in the diagonal position. When
171 the column of an assemblage is zero except a single 1 in the diagonal position, then the assemblage
172 has minimal diversity. In example 1, one assemblage has a maximal (Sim3) and the other minimal
173 (Sim5) diversity (Table 2A). In a Hasse diagram, the assemblages with maximal diversity are
174 represented as dots at the top of the figure while assemblages with minimal diversity appear at the
175 bottom. Assemblages that are neither maximal nor minimal are positioned intermediately, thereby
176 ensuring that, for each comparable pair of assemblages, the one with the higher diversity is located
177 higher in the graph. Pairs of comparable assemblages are connected by lines in such a way that each
178 trajectory from top to bottom of the diagram—a so-called *chain*—represents a valid ranking of
179 assemblages. From example 1, the following single chain results (Fig. 2A), $\text{Sim3} > \text{Sim2} > \text{Sim1} >$
180 $\text{Sim4} > \text{Sim5}$, thus the set of assemblages exhibits a complete linear order.

181

182 In example 2, one assemblage has a maximal diversity (Sim3 – only zeroes in its row except a
183 single 1 in the diagonal) and two have minimal (Sim4, Sim5 – only zeroes in their columns except a
184 single 1 in the diagonal) (Table 2B). Those with minimal diversity cannot be compared since $S_{Sim4} >$
185 S_{Sim5} , but $E_{Sim4} < E_{Sim5}$ (Table 1), thus the set of assemblages can only be partially ordered. Sim4 and
186 Sim5 are positioned at the bottom of the Hasse diagram, and they are not connected by lines due to
187 their lack of comparability (Fig. 2B). Assemblages Sim1 and Sim2 are identical—something that
188 will rarely occur in real data; thus, they are plotted at the same level in the graph and are connected
189 by a horizontal line. The Hasse diagram of example 2 contains four chains:

190 $Sim3 > Sim2 > Sim4$

191 $Sim3 > Sim2 = Sim1 > Sim5$

192 $Sim3 > Sim1 > Sim5$

193 and

194 $Sim3 > Sim1 = Sim2 > Sim4$

195 which can be simplified to

196 $Sim3 > Sim1, Sim2 > Sim4$

197 and

198 $Sim3 > Sim1, Sim2 > Sim5$ (Fig. 2C).

199

200 The Hasse diagrams for these introductory examples can easily be sketched. For Hasse diagrams
201 that are more complicated, Patil and Taillie (1982) provided a recipe of matrix operations to
202 generate them from their corresponding zeta matrices. Computer programs for generation of Hasse
203 diagrams are available (see software overview in Brüggemann et al. 2008, Sargin and Ünlü 2010).

204 The open-source program PyHasse can be downloaded from

205 <http://www.zalf.de/en/forschung/institute/lisa/forschung/methodik/samt/Pages/Download.aspx>.

206

207 Table 3 presents simulated data of nine assemblages with different species richness as a third
208 example. Three assemblages each have $S = 10, 5$ or 2 , respectively, and the levels of evenness
209 differ. In this hypothetical example there is no need to weight richness or evenness as done
210 explicitly or implicitly by any composite diversity index; thus assigning equal importance to
211 richness and evenness with the application of partial ordering is an objective way to evaluate and
212 rank the diversity of these assemblages. The corresponding zeta matrix (Table 4) shows that there is
213 a single maximal element (Sim1), as well as three minimal elements (Sim3, Sim6, Sim9 – only
214 zeroes in their columns except a single 1 in the diagonal). The Hasse diagram of the poset contains
215 four chains (Fig. 2D):

216 $\text{Sim1} > \text{Sim2} > \text{Sim3}$

217 $\text{Sim1} > \text{Sim2} > \text{Sim6}$

218 $\text{Sim1} > \text{Sim4} > \text{Sim5} > \text{Sim6}$

219 and

220 $\text{Sim1} > \text{Sim4} > \text{Sim7} > \text{Sim8} > \text{Sim9}$

221 yielding 19 pairs of assemblages that can be compared (e.g., Sim1-Sim4, Sim2-Sim6, Sim7-Sim9).

222 The remaining 17 pairs of assemblages cannot be compared, for example, Sim2-Sim4, Sim3-Sim5
223 or Sim6-Sim8.

224

225 As an example for the application of partial ordering to real data, we analyze data of five stream
226 fish assemblages (Ross et al. 1987); used also by Magurran (1988) in her famous book on species
227 diversity and its measurement (see Appendix A for full data on species and abundance). The
228 application of two of the most common diversity indices, the Shannon-Index H' and Fisher's α , to
229 these data yield a contradictory ranking of assemblages:

230 $\text{Ross3} > \text{Ross1} > \text{Ross2} > \text{Ross5} > \text{Ross4} (H')$

231 and

232 $Ross4 > Ross1 > Ross3 > Ross5 > Ross2 (\alpha)$.

233 Species richness ranges from 18 to 24, and sample size ranges between 785 and 4504 individuals.

234 The differences in observed S between sites thus might be due to a sampling effect since the more

235 individuals are sampled in an assemblage the larger the number of registered species will be. In

236 such a case, it is advisable to standardize species richness by rarefaction (Gotelli and Colwell 2001)

237 prior to partial ordering. We applied the R package `vegan` (Oksanen et al. 2008; R Development

238 Core Team 2009) using the function `rarefy` and all sites were standardized to a sample size of

239 785 individuals. Evenness was calculated on the basis of the rarefied community data, since S

240 appears in the denominator of the evenness index which was suggested by Rousseau et al. (1999)

241 (for standardized species richness and evenness, see Table 5). (The order of the sites according to

242 evenness was not altered by the rarefaction.)

243

244 Two assemblages have maximal ($Ross1, Ross3$) diversity and three minimal ($Ross2, Ross4, Ross5$)

245 (Table 6). No assemblages are in the intermediate position, and the Hasse diagram consists of only

246 two layers (Fig. 2E). Four pairs of assemblages can be compared: $Ross1$ has higher diversity than

247 $Ross2, Ross4$ and $Ross5$, and $Ross3$ has higher diversity than $Ross2$. The remaining six pairs

248 ($Ross1-Ross3, Ross2-Ross4, Ross2-Ross5, Ross3-Ross4, Ross3-Ross5, Ross4-Ross5$) cannot be

249 compared.

250

251 Patil and Taillie (1979) and Rousseau et al. (1999) proposed using modified Lorenz curves—the

252 well-known “diversity profiles” or “k-dominance curves”—for assemblage comparison. These

253 curves retain all information on species numbers and relative abundance structure of the compared

254 assemblages, but have the drawback of becoming quite confusing once the number of assemblages

255 becomes moderately high. Clarke (1990) proposed a logistic transformation of the y axis which has

256 a linearising effect on k-dominance curves without altering their cumulative structure. Although this
257 may facilitate visual discrimination, Hasse diagrams are much clearer and can be more easily
258 interpreted.

259

260 **Linear extensions and the rank-frequency distribution**

261

262 Although we should accept the fact that assemblages may not be comparable, it is sometimes
263 desirable to rank assemblages linearly, for example, to prioritize conservation efforts. For these
264 purposes, it is necessary to rank the members of a poset by considering all possible linear rankings
265 —called *linear extensions* in poset theory terminology—that are consistent with its partial order
266 (Patil and Taillie 2004). Non-comparable pairs of assemblages, X and Y , may take on any
267 relationship, i.e., $X > Y$ and $Y > X$. For example, the linear extension

$$268 \quad \text{Ross1} > \text{Ross3} > \text{Ross2} > \text{Ross4} > \text{Ross5}$$

269 respects the relationships $\text{Ross1} > \text{Ross2}$, $\text{Ross1} > \text{Ross4}$, $\text{Ross1} > \text{Ross5}$ and $\text{Ross3} > \text{Ross2}$
270 defined by the partial order (Fig. 2E) and further assumes $\text{Ross1} > \text{Ross3}$, $\text{Ross2} > \text{Ross4}$ and Ross2
271 $> \text{Ross5}$. There are 18 possible rankings consistent with the partial order for the stream fish data
272 which can easily be visualized as branches of a tree with linear extensions (Fig. 3). Each
273 assemblage appears with a certain frequency on a given rank. For example, in 12 of the linear
274 extensions, the assemblage Ross1 appears on the first rank, and in six linear extensions on the
275 second rank. Table 7 sums up rank frequency information for all assemblages; according to rank
276 frequency the fish stream data can be linearly ranked as

$$277 \quad \text{Ross1} > \text{Ross3} > \text{Ross4} = \text{Ross5} > \text{Ross2}.$$

278 As a control, row and column sums of frequencies must equal the number of linear extensions.

279 As clear as this method seems to be, its implementation is limited to comparisons of ≤ 15

280 assemblages. Brüggemann et al. (2004) proposed an alternative approximation of linear extensions.

281

282 **Conclusions**

283

284 Poset theory appears to be a powerful alternative to the common approach of composite diversity
285 indices. Richness and evenness are retained separately and are evaluated on a firm mathematical
286 basis (Patil and Taillie 2004, Pavan and Todeschini 2008) without the necessity of arbitrary or
287 controversial judgments about how to weight them. At the same time, a poset is a straightforward
288 and easy to comprehend concept which can be used without necessarily referring to its
289 mathematical background. Hasse diagrams visualize partial orders in a comprehensible way and can
290 be easily interpreted if the number of assemblages is not too high. Linear extensions and rank-
291 frequency distributions show the potential of posets as decision-supporting tools when assemblage
292 ranking is desirable, for example, to identify trends in diversity change or to prioritize restoration,
293 conservation or other management measures.

294

295 Poset theory is a well established field of mathematics and its numerous tools available to the
296 ecologists await detection, evaluation and application. In this paper, for example, we concentrated
297 on the classic approach of regarding species richness and evenness as core elements in estimating
298 diversity. However, we do not favor restricting the measurement of diversity to just two numbers. It
299 would be interesting in future work to extend partial order theory to the diversity profile of Hill
300 numbers (Hill 1973) as a characterization of community. Since the 1990s, the necessity of including
301 phylogenetic relationships into measures of diversity became recognized (Vane-Wright et al. 1991)
302 and has given rise to a voluminous body of literature (e.g. Moreno et al. 2009, Ricotta et al. 2009).
303 The discussion on how diversity determines ecosystem function and services have raised interest in
304 functional diversity (e.g. Petchey and Gaston 2002, Naeem and Wright 2003). Particularly in these
305 contexts, we maintain that poset theory could prove its potential for multi- criteria ranking strategies

306 (Patil and Taillie 2004).

307

308

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311

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458 **Table 1.** Simulated data for two introductory examples of complete and partial ordering.

459

| Assemblage | Example 1 (complete ordering) | | Example 2 (partial ordering) | |
|------------|-------------------------------------|----------|------------------------------------|----------|
| | <i>S</i> | <i>E</i> | <i>S</i> | <i>E</i> |
| Sim1 | 18 | 0.48 | 18 | 0.65 |
| Sim2 | 19 | 0.60 | 18 | 0.65 |
| Sim3 | 21 | 0.67 | 20 | 0.71 |
| Sim4 | 16 | 0.45 | 17 | 0.49 |
| Sim5 | 12 | 0.43 | 16 | 0.57 |

460

461

462 **Table 2.** Zeta matrices for the simulated data from Table 1.

463 Example 1

| | Sim1 | Sim2 | Sim3 | Sim4 | Sim5 |
|------|------|------|------|------|------|
| Sim1 | 1 | 1 | 1 | 0 | 0 |
| Sim2 | 0 | 1 | 1 | 0 | 0 |
| Sim3 | 0 | 0 | 1 | 0 | 0 |
| Sim4 | 1 | 1 | 1 | 1 | 0 |
| Sim5 | 1 | 1 | 1 | 1 | 1 |

464

465 Example 2

| | Sim1 | Sim2 | Sim3 | Sim4 | Sim5 |
|------|------|------|------|------|------|
| Sim1 | 1 | 1 | 1 | 0 | 0 |
| Sim2 | 1 | 1 | 1 | 0 | 0 |
| Sim3 | 0 | 0 | 1 | 0 | 0 |
| Sim4 | 0 | 1 | 1 | 1 | 0 |
| Sim5 | 0 | 0 | 1 | 0 | 1 |

466

467 **Table 3.** Simulated assemblage data for the third introductory example.

468

| Species | Assemblages | | | | | | | | |
|----------|-------------|-------|-------|-------|-------|-------|-------|-------|-------|
| | Sim 1 | Sim 2 | Sim 3 | Sim 4 | Sim 5 | Sim 6 | Sim 7 | Sim 8 | Sim 9 |
| 1 | 10 | 55 | 91 | 20 | 60 | 92 | 50 | 75 | 95 |
| 2 | 10 | 5 | 1 | 20 | 10 | 2 | 50 | 25 | 5 |
| 3 | 10 | 5 | 1 | 20 | 10 | 2 | - | - | - |
| 4 | 10 | 5 | 1 | 20 | 10 | 2 | - | - | - |
| 5 | 10 | 5 | 1 | 20 | 10 | 2 | - | - | - |
| 6 | 10 | 5 | 1 | - | - | - | - | - | - |
| 7 | 10 | 5 | 1 | - | - | - | - | - | - |
| 8 | 10 | 5 | 1 | - | - | - | - | - | - |
| 9 | 10 | 5 | 1 | - | - | - | - | - | - |
| 10 | 10 | 5 | 1 | - | - | - | - | - | - |
| <i>S</i> | 10 | 10 | 10 | 5 | 5 | 5 | 2 | 2 | 2 |
| <i>E</i> | 1 | 0.31 | 0.12 | 1 | 0.5 | 0.24 | 1 | 0.8 | 0.55 |

469

470

471

472 **Table 4.** Zeta matrix for the simulated data from Table 3.

473

| | Sim 1 | Sim 2 | Sim 3 | Sim 4 | Sim 5 | Sim 6 | Sim 7 | Sim 8 | Sim 9 |
|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Sim1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Sim2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Sim3 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Sim4 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Sim5 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| Sim6 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| Sim7 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| Sim8 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| Sim9 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 |

474

475 **Table 5.** Species richness and evenness of five stream fish assemblages (Ross et al. 1987). See
 476 Appendix A for complete data on species and abundance. Since sample size was different among
 477 assemblages ranging from $N = 785$ to 4504, we standardized species richness to the smallest sample
 478 size by rarefaction (Hurlbert 1971). Evenness was calculated on base of the rarefied community
 479 matrix.

480

| Assemblage | <i>S</i> | <i>E</i> |
|------------|----------|----------|
| Ross1 | 22.1 | 0.19 |
| Ross2 | 17.4 | 0.17 |
| Ross3 | 18.0 | 0.26 |
| Ross4 | 20.3 | 0.14 |
| Ross5 | 19.4 | 0.16 |

481

482

483

484 **Table 6.** Zeta matrix for five fish stream assemblages.

485

| | Ross 1 | Ross 2 | Ross 3 | Ross 4 | Ross 5 |
|-------|-----------|-----------|-----------|-----------|-----------|
| Ross1 | 1 | 0 | 0 | 0 | 0 |
| Ross2 | 1 | 1 | 1 | 0 | 0 |
| Ross3 | 0 | 0 | 1 | 0 | 0 |
| Ross4 | 1 | 0 | 0 | 1 | 0 |
| Ross5 | 1 | 0 | 0 | 0 | 1 |

486

487 **Table 7.** Rank-frequency table based on the tree of linear orderings (Fig. 3) of five fish stream
488 assemblages.

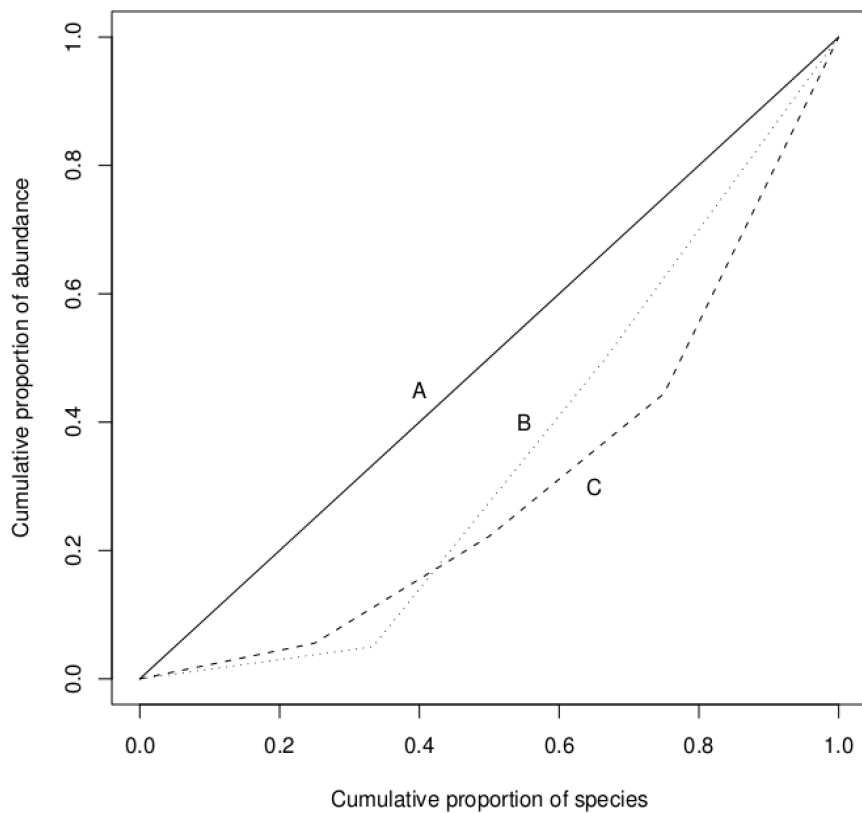
489

| Assemblage | Rank | | | | | Totals |
|------------|------|----|----|----|----|--------|
| | 1 | 2 | 3 | 4 | 5 | |
| Ross1 | 12 | 6 | 0 | 0 | 0 | 18 |
| Ross2 | 0 | 0 | 4 | 7 | 7 | 18 |
| Ross3 | 6 | 6 | 2 | 2 | 0 | 18 |
| Ross4 | 0 | 3 | 5 | 5 | 5 | 18 |
| Ross5 | 0 | 3 | 5 | 5 | 5 | 18 |
| Totals | 18 | 18 | 18 | 18 | 18 | |

490

491 **Figure 1.** Example of evenness comparison by means of Lorenz curves for three hypothetical
492 assemblages, A = (20, 20, 20, 20, 20), B = (50, 45, 5), and C = (100, 40, 30, 10). A has maximal
493 evenness; the corresponding Lorenz curve is the 45° line. The Lorenz curves of B and C lie below
494 the curve of A, thus they are less even. B and C cannot be compared since their Lorenz curves
495 intersect.

496



497 **Figure 2.** Hasse diagrams for (A), (B) and (C) two introductory examples (Table 1); (D) simulated
 498 assemblage data (Table 3); (E) five stream fish assemblages (Ross et al., 1987) (Table 5).

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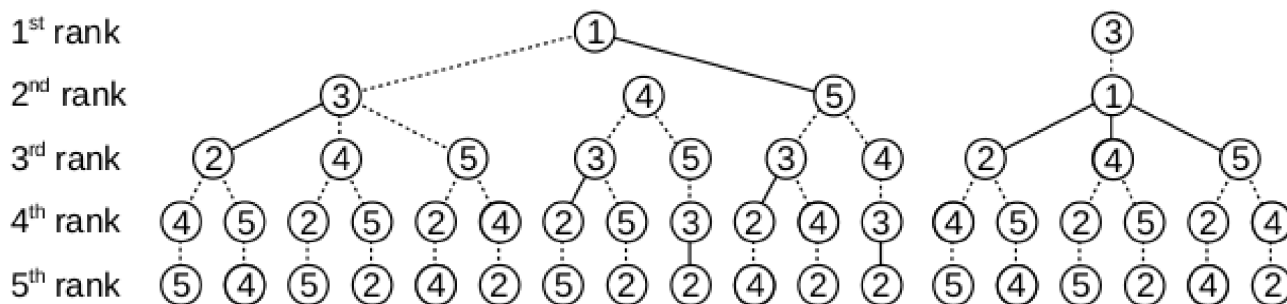
517 **Figure 3.** Tree representing all possible linear extensions of the poset of fish stream assemblages.

518 Solid lines refer to the links present in the corresponding Hasse diagram (Fig. 2E); dotted lines are

519 not implied by the partial order.

520

521



522 **Appendix A.** Stream fish data from five sections of the Black Creek, Mississippi, by Ross et al.
 523 (1987).

524

| Species | Assemblage | | | | |
|------------------------------|------------|-------|-------|-------|-------|
| | Ross1 | Ross2 | Ross3 | Ross4 | Ross5 |
| <i>Esox americanus</i> | 13 | 0 | 0 | 1 | 0 |
| <i>Ericymba buccata</i> | 3 | 56 | 2 | 9 | 83 |
| <i>Notropus volucellus</i> | 38 | 77 | 4 | 31 | 111 |
| <i>N. venustus</i> | 179 | 205 | 186 | 312 | 901 |
| <i>N. longirostris</i> | 4 | 0 | 6 | 1 | 89 |
| <i>N. texanus</i> | 749 | 330 | 39 | 122 | 100 |
| <i>N. roseipennis</i> | 1827 | 918 | 173 | 945 | 456 |
| <i>Noturus leptacanthus</i> | 56 | 56 | 7 | 67 | 51 |
| <i>Labisdethes sicculus</i> | 145 | 4 | 0 | 7 | 7 |
| <i>Fundulus olivaceus</i> | 585 | 123 | 130 | 190 | 47 |
| <i>Gambusia affinis</i> | 78 | 0 | 7 | 10 | 65 |
| <i>Aphredoderus sayanus</i> | 57 | 1 | 1 | 0 | 0 |
| <i>Micropterus salmoides</i> | 43 | 5 | 0 | 4 | 2 |
| <i>Blossoma zonatum</i> | 20 | 4 | 0 | 3 | 11 |
| <i>Lepomis macrochirus</i> | 281 | 34 | 20 | 19 | 31 |
| <i>L. punctatus</i> | 26 | 0 | 0 | 0 | 0 |
| <i>L. megalotis</i> | 104 | 33 | 25 | 36 | 39 |
| <i>L. microlophus</i> | 23 | 0 | 2 | 4 | 7 |
| <i>L. cyanellus</i> | 23 | 1 | 7 | 5 | 0 |
| <i>Ammocrypta beani</i> | 60 | 72 | 105 | 30 | 13 |
| <i>Percina sciera</i> | 7 | 11 | 7 | 15 | 22 |
| <i>Ethostoma swaini</i> | 140 | 54 | 24 | 12 | 4 |
| <i>E. zonale</i> | 4 | 38 | 0 | 51 | 14 |
| <i>E. stigmaeum</i> | 39 | 52 | 40 | 46 | 24 |
| <i>N</i> | 4504 | 2074 | 785 | 945 | 2077 |
| <i>S</i> | 24 | 19 | 18 | 22 | 20 |

525