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# A mathematical description of fossilisation

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**Keywords:** Fossils, Taphonomy, Decay, Diagenesis, Palaeontology, Price Equation

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## 1. Summary

1  
1  
1 Fossils constitute an inestimable archive of past life on Earth. However, the stochastic processes, driving decay  
2 and fossilisation and overwhelmingly distorting this archive, are challenging to interpret. Consequently,  
3 concepts of exceptional or poor preservation are often subjective or arbitrarily defined. Here, we offer an  
4 alternative way to think about fossilisation. We propose a mathematical description of decay and fossilisation  
5 relying on the change in the relative frequency and characteristics of biogenic objects (e.g., atoms, functional  
6 groups, molecules, body parts, organisms) within an organism–fossil system. This description partitions  
7 taphonomic changes into three categories: gain, loss, and alteration of state. Although the changes undergone  
8 by organisms through decay, preservation and alteration are varying a lot for different organisms under  
9 different conditions, we provide a unified formalism which can be applied directly in the comparison of  
10 different assemblages, experiments, and fossils. Our expression is closely related to George R. Price’s famous  
11 equation for the change of evolutionary traits and can be adapted to the study of palaeontological systems and  
12 many others.

## 1. Introduction

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2 Taphonomy, a sub-discipline of palaeontology, archaeology, and forensic science, is the study of the  
3 degradation of living matter in natural environments and, ultimately, its translation from the biosphere into  
4 the geosphere [1]. To identify and characterize extinct life forms from the rock record, taphonomists  
5 investigate the post-mortem, pre- and post-depositional processes whereby organisms are modified by their  
6 physico-chemical environment (e.g., microbial activity, diagenetic alteration, and metamorphism; see [2]).

7 Evidently, the original composition of the organism also plays a fundamental role in its taphonomic  
8 trajectory in a given setting. The composition of the biological organic material buried in sediment depends on  
9 the stability, resistance, and solubility of its constituents and upon the extent of biological and chemical attack  
10 [3]. The remaining fraction, if not rapidly incorporated into the sediment, will undergo various condensation  
11 reactions forming new polymeric material, like the formation of melanoidin-like compounds via the Maillard  
12 reaction [4-6], although the global contribution of such compounds to the final sedimentary organic mix has  
13 been questioned [7]. Survival of labile material can be observed, notably by association with more resistant  
14 molecule acting as “shelter” (e.g., lipids; [8]) but the preservation of pristine or lightly altered organic  
15 precursors in a fossil remains an exception. Therefore, the survival of biomolecules could not be solely  
16 explained by strong preservation potentials and selective preservation pathways [2, 3, 9].

17 Considering all this, an exceptional morphological preservation cannot be automatically synonymous of  
18 exceptional molecular preservation. For example, the exceptional state of preservation observed for many  
19 Ediacaran fossils is considered the result of microbially mediated mineral formation resulting in detailed cast  
20 of the organism (the “death mask” model; [10, 11]) but do not directly preserve original organic material (with  
21 notable exceptions; see [12]). As a results, defining “exceptional” preservation within Konservat-Lagerstätten  
22 may be subjective, depending on the chosen point of view.

23 However, whatever the biological and environmental settings, fossilisation (and to wider extent, quality of  
24 preservation) can be abstracted as a change occurring between two systems: an organism and its decayed – or  
25 its fossil – counterpart. Insights from taphonomy and decay experiments [2,3, 13-17] and molecular  
26 investigation of fossil [e.g., 6-8, 18-22], show that post-mortem processes acting on any organisms or biological  
27 remains can be broken down into three broad categories of change: (i) gain of features (deposition of new  
28 material, including molecular and mineral), (ii) loss of features (e.g., disappearance of body parts or molecular

29 components), and (iii) modification of the state of the features (decay and alteration). From this perspective,  
 30 fossilisation can have a general, mathematical definition.

31 Building on this thought, we derive here a general mathematical expression, showing similarity with the  
 32 Price Equation for evolutionary biology, that allow the description of the taphonomic process in term of  
 33 changes in frequency and characteristic of a set of objects. By describing how the value of a chosen character  
 34 can change between an organism and its fossil, this expression offers a quantifiable partition of post-mortem  
 35 dynamics.

36

### 37 3. Mathematical framework

38

#### 39 3.1 Definitions

40

41 Consider two multicomponent entities  $Q$  and  $Q'$ . Let  $q_i$  be the relative frequency of the  $i$ th object in  $Q$  and  $q'_i$   
 42 the relative frequency (here after designated as frequency) of the  $i$ th object in  $Q'$ . For our narrative,  $Q$  and  $Q'$   
 43 may represent the source organism and its fossil, respectively. The objects are any unit of interest within these  
 44 entities, for example atoms, functional groups, molecules, tissues, or body parts. Alternatively,  $Q$  and  $Q'$  can  
 45 represent a living population and its fossil counterpart.

46 We take

47

$$q'_i = c_i q_i$$

48

(3.1)

49

50 With  $c$  representing the factor of the  $i$ th object by which  $q_i$  has been modified in  $q'_i$  such that  $c_i = \frac{q'_i}{q_i}$ .

51

52

$$\bar{c} = \sum q_i c_i = \sum q_i \frac{q'_i}{q_i} = \sum q'_i = 1$$

53

(3.2)

54

55 Let  $s_i$  be the state of an object in  $Q$ , and  $s'_i$  the state of an object in  $Q'$ . A state here represents the value of any  
56 characteristic of interest, for example a size, a weight, a surface, or any other variable obtained by qualitative or  
57 quantitative measurement (e.g., length of carbon chain, percentage of tissue decay, tissue hardness). We have  
58 the average (here and after understood as the expected value) value of  $s$ ,

59

60

$$\bar{s} = \sum q_i s_i$$

61

(3.3)

62 Similarly,

63

64

$$\bar{s}' = \sum q'_i s'_i$$

65

(3.4)

66 represents the average state value of the objects constituting an organism as it becomes a fossil. The change  
67 in state value of  $s_i$  in  $s'_i$ ,  $\Delta s_i$ , is:

68

69

$$\Delta s_i = s'_i - s_i$$

70

(3.5)

71 Equally,

72

$$s'_i = s_i + \Delta s_i$$

73

74 For the whole system (e.g., organism-fossil), the average change in state value for a chosen metrics,  $\Delta \bar{s}$ , can be  
75 written:

76

77

$$\Delta \bar{s} = \bar{s}' - \bar{s}$$

78

(3.6)

### 79 3.2 Derivation

80

81 With the definitions above, we can derive  $\Delta \bar{s}$  between  $Q$  and  $Q'$  as

82

83

$$\Delta \bar{s} = \bar{s}' - \bar{s}$$

84 (3.7)

$$85 = \sum q'_i s'_i - \sum q_i s_i$$

86 (3.8)

$$87 = \sum q'_i (s_i + \Delta s_i) - \sum q_i s_i$$

88 (3.9)

$$89 = \sum c_i q_i s_i + \sum c_i q_i \Delta s_i - \sum q_i s_i$$

90 (3.10)

91 For convenience we switch the order of the terms and have

$$92 \Delta \bar{s} = \sum c_i q_i s_i - \sum q_i s_i + \sum c_i q_i \Delta s_i$$

93 (3.11)

94 Multiplying the second term by  $\bar{c}$ , we can rewrite  $\Delta \bar{s}$  as

$$96 \Delta \bar{s} = \sum c_i q_i s_i - \sum q_i \bar{c} \sum q_i s_i + \sum c_i q_i \Delta s_i$$

97 (3.12)

98 Rewriting  $\Delta \bar{s}$  as a sum of expectations we obtain

$$100 \Delta \bar{s} = \mathbb{E} c_i z_i - \mathbb{E} c_i \mathbb{E} z_i + \mathbb{E} c_i \Delta s_i$$

101 (3.13)

102 By considering  $\mathbb{E} c_i z_i - \mathbb{E} c_i \mathbb{E} z_i = \mathbf{Cov}[c_i, z_i]$  we arrive at an expression in the same form than the famous Price  
103 equation for evolutionary changes [23-26].

$$104 \Delta \bar{s} = \mathbf{Cov}[c_i, s_i] + \mathbb{E} c_i \Delta s_i$$

105 (3.14)

106 In this way, the taphonomic changes can be statistically described as the change in the average value of the  
107 state of an agent. Here, the equation 3.14 represents the changes in the frequency of objects without  
108 alteration (first term) and the alteration of the states of existing objects (second term). The covariance term can  
109 also be expressed as the product of a variance and a regression coefficient [23; 27]. If this coefficient is positive  
110 (or, equivalently, if the covariance term is positive), the frequency of a specific state value is expected to rise in

111 the second entity. If this term is null, then no changes are observed in the frequency of objects between the  
 112 entities.

113 Considering the presence of new objects in  $Q'$  absent in  $Q$  (e.g., incorporation of external objects or  
 114 formation of new objects) requires a small redefinition of our system. Let us now take  $Q^*$ , such that  $Q^*$  plus  $Q'$   
 115 represents the second entity. All objects in  $Q'$  were originally in  $Q$ , whereas the objects in  $Q^*$  are the objects  
 116 that are not found originally in  $Q$ . Let  $p$  be the probability that a given object belongs to  $Q^*$  rather than  $Q'$ . We  
 117 have now

$$118 \quad \bar{s}' = p \sum q_i^* s_i^* + (1 - p) \sum q_i' s_i' \quad (3.15)$$

120 With  $\sum q_i^* s_i^*$  the expected value of  $s$  in  $Q^*$ .

121 Returning to  $\Delta \bar{s}$ , we have

$$122 \quad \Delta \bar{s} = \bar{s}' - \bar{s} \quad (3.16)$$

$$125 \quad = p \sum q_i^* s_i^* + (1 - p) \sum q_i' s_i' - \sum q_i s_i \quad (3.17)$$

$$127 \quad = p \sum q_i^* s_i^* + (1 - p) \sum q_i' s_i' - [p + (1 - p)] \sum q_i s_i \quad (3.18)$$

$$129 \quad = p \sum q_i^* s_i^* + (1 - p) \sum q_i' s_i' - p \sum q_i s_i + (1 - p) \sum q_i s_i \quad (3.19)$$

$$131 \quad = p \left( \sum q_i^* s_i^* - \sum q_i s_i \right) + (1 - p) \left( \sum q_i' s_i' - \sum q_i s_i \right) \quad (3.20)$$

133  
 134 Using the definitions above we have

$$136 \quad \Delta \bar{s} = p(\Delta \bar{s}^*) + (1 - p)(Cov[c_i, s_i] + \mathbb{E}c_i \Delta s_i) \quad (3.21)$$

138 We rearrange and develop the terms to obtain a three terms equation.

$$\Delta \bar{s} = (\mathbf{1} - \mathbf{p}) \text{Cov}[\mathbf{c}_i, \mathbf{s}_i] + (\mathbf{1} - \mathbf{p}) \mathbb{E} \mathbf{c}_i \Delta \mathbf{s}_i + \mathbf{p} (\Delta \bar{s}^*) \quad (3.22)$$

The effects of different partitions on the terms in equation 3.22 (and equation 3.14 above) are illustrated in Figure 1. Altogether, the three terms account for all possible taphonomic modifications (gain, loss and alteration of features), including the total replacement of the original material. As displayed on Figure 1A, for an ideal preservation ( $Q'$  is the exact image of  $Q$ ), all terms would vanish. This is due to the absence of alterations and additions and the preservation of each object in similar frequencies in both entities. Such a situation is not physically possible if we consider an organism as a whole. Nevertheless, it is possible that a component of interest may remain pristine or with only few alterations (Figure 1C) or that the only change may be additive (for example, the precipitation of mineral components; Figure 1D).

On the other hand, we can consider several different ways in which a fossil might be said to be poorly preserved. Most simply, poor preservation could be characterised by a low factor of retention of original objects ( $c$  tending to 0; Figure 1B). We can also describe a situation whereby all remaining objects in  $Q'$  (regardless of their preservation potential) have changed from their original value (e.g., Figure 1E). In this state of total alteration, and for all  $i$ :

$$\Delta \mathbf{s}_i = \mathbf{s}'_i - \mathbf{s}_i \neq \mathbf{0} \quad \forall i \quad (3.23)$$

Finally, if there are no common objects between the two entities, i.e., if  $p=1$  (Figure 1F), then the first two terms in eq. 3.22 vanish and

$$\bar{s}^j = \sum q_i^* s_i^* \quad (3.24)$$

is a lower bound for the retention of information in a fossil about its source organism (although in this case we do not really have a fossil at all!).

## 4. Examples

We now provide examples of using equation 3.14 and 3.22 with empirical data.

### 4.1 General examples



166 Let take an organism composed of 5 body parts: a skull, teeth, the skin, a muscle (tongue), and an internal  
 167 organ, here the brain of an imaginary *Tyrannosaurus rex* (Figure 2A). We can divide these parts into two  
 168 groups: hard-tissue (mineralised teeth and skull), for which we measured a hardness value of 2; and soft-tissue  
 169 (non-mineralised skin, muscle, brain), with a lower value of 1. Note that the choice of hardness values 1 and 2  
 170 is here made for simplicity; the value from any metrics may be chosen instead. Their respective frequencies are:

171

172 Non-mineralised ( $q_{nm}$ ): 3/5

173 Mineralised ( $q_m$ ): 2/5

174

175 We start with

$$176 \quad \bar{s} = \sum q_i s_i = q_{nm} s_{nm} + q_m s_m = \frac{3}{5} \mathbf{1} + \frac{2}{5} \mathbf{2} = \frac{7}{5}$$

177 In our first scenario (Figure 2A→2B), we have a preservation of the mineralised parts and a partial preservation  
 178 of the non-mineralised parts. The updated frequencies are:

179

180 Non-mineralised ( $q'_{nm}$ ): 1/3

181 Mineralised ( $q'_m$ ): 2/3

182

183 The  $c$  values between the two sets of frequencies are:

184

$$185 \quad c_{nm} = \frac{q'_{nm}}{q_{nm}} = \frac{1/3}{3/5} = \frac{5}{9}$$

$$186 \quad c_m = \frac{q'_m}{q_m} = \frac{2/3}{2/5} = \frac{5}{3}$$

187 The updated  $\bar{s}'$  is:

$$188 \quad \bar{s}' = \sum q'_i s'_i = q'_{nm} s'_{nm} + q'_m s'_m = \frac{1}{3} \mathbf{1} + \frac{2}{3} \mathbf{2} = \frac{5}{3}$$

189

190 Here, the state values of the body parts of our fossil are unchanged compared to the living organism ( $\mathbb{E}c_i \Delta s_i =$   
 191  $\mathbf{0}$ ). There is no new material so we may directly use equation 3.14. We have

192

$$\begin{aligned} \Delta \bar{s} &= \mathbf{Cov}[c_i, s_i] + \mathbb{E}c_i \Delta s_i \\ &= [q_{nm}(s_{nm} - \bar{s})(c_{nm} - \bar{c}) + q_m(s_m - \bar{s})(c_m - \bar{c})] + \mathbf{0} \\ &= \frac{3}{5} \left(1 - \frac{7}{5}\right) \left(\frac{5}{9} - 1\right) + \frac{2}{5} \left(2 - \frac{7}{5}\right) \left(\frac{5}{3} - 1\right) = \mathbf{0.266} \end{aligned}$$

Which is equivalent to  $\Delta \bar{s} = \bar{s}' - \bar{s} = \frac{5}{3} - \frac{7}{5} = \mathbf{0.266}$ , demonstrating the tautological nature of the Price equation [26].

This first scenario (Figure 2A→2B) illustrates how the first component of equation 3.14 and 3.22 relates to the part of the change solely due to the variation in frequencies of the objects. This variation is factored by  $c_i$  that effectively acts as a fitness function: the resistant components (here the mineralised skull and teeth) have better  $c$  factor than more labile non-mineralised skin, muscle, and organ ( $c_m=5/3 \approx 1.67$  and  $c_{nm}=5/9 \approx 0.56$ ) and are better represented in the fossil. Therefore,  $\mathbf{Cov}[c_i, s_i]$  quantifies the preservation and loss of objects during the taphonomic process solely due to the original intrinsic characteristic of the type of objects and their decay/degradation resistance. Because this covariance term includes a direct expression ( $c$ ) of the relation between the frequencies of the objects in the two entities, i.e., a growth factor, it can be considered as a selection covariance [27, 28]. Thus, this first term is a direct expression of selective preservation.

For our second scenario (Figure 2A→2C), we now consider some changes in the hardness values of our body parts in the fossil (we retain the change of frequencies from the previous scenario). The only preserved soft tissue, the skin, has been altered post-mortem and has been mineralised. Its hardness value has change from 1 to 2. The updated  $\bar{s}'$  is now:

$$\bar{s}' = \frac{1}{3} \cdot 2 + \frac{2}{3} \cdot 2 = 2$$

We now have :

$$\begin{aligned} \Delta \bar{s} &= \mathbf{Cov}[c_i, s_i] + \mathbb{E}c_i \Delta s_i \\ &= \mathbf{0.266} + \sum q_i c_i (s'_i - s_i) = \mathbf{0.266} + \sum q'_i (s'_i - s_i) \\ &= \mathbf{0.266} + \left[ \frac{1}{3} (2 - 1) + \frac{2}{3} (2 - 2) \right] = \mathbf{0.266} + \frac{1}{3} = \mathbf{0.596} \end{aligned}$$

Here, the second term,  $\mathbb{E}c_i \Delta s_i$ , describes the part of the change that is due to variation in state values (the skin hardness of 1 becoming 2 after getting mineralised). In our *T. rex* scenario, we can see that this term

220 scores  $\sim 0.33$  ( $\frac{1}{3}$ ) whereas our first term retains its score of 0.266 (no change in frequency). For simple  
 221 visualisation, we could imagine converting these two positive values as percentages of the total score, 0.596, it  
 222 means that alteration account for 55% of the observed change in hardness between the organism and the  
 223 fossil. On the other hand, the selective preservation of the mineralised hard tissues accounts for 45% of it. In  
 224 nature, such changes may have many causes, among which are microbial, chemical, and physical activities. The  
 225 second term is an expression of the modification of our object by all these processes. It is the alteration term.

226

227 To illustrate the third term of equation 3.22, we take another simple example. Let's now consider whole  
 228 organisms in a depositional environment (Figure 3A). Our living community is composed of five organisms:  
 229 three soft-bodied *Ottoia* (a priapulid worm; see [29]) and two hard-bodied trilobites. Their respective  
 230 frequencies are:

231

232 *Ottoia* ( $q_o$ ): 3/5

233 Trilobite ( $q_t$ ): 2/5

234

235 Just as with the previous examples, we can characterise the change in our system that is due to the selective  
 236 preservation of hard tissues and to alteration (e.g., soft tissues becoming mineralised). We kept the same  
 237 frequency and values than on the first examples ( $Cov[c_i, s_i] = \mathbf{0.266}$  and  $\mathbb{E}c_i\Delta s_i = \frac{1}{3}$ ), however, this time, our  
 238 fossil assemblages (Figure 3B) contains also two shell fragments transported from elsewhere and with  $s = 3$ .  
 239 The group of new objects is composed of a single type (the shells) with  $q_n^* = \mathbf{1}$ . In our fossil assemblage, the  
 240 probability of belonging to this new group is  $p = \frac{2}{5}$ . The updated  $\bar{s}'$  is :

241

$$\begin{aligned}\bar{s}' &= p \sum q_n^* s_n^* + (1-p) \sum q'_{o,t} s'_{o,t} \\ &= \frac{2}{5}(1 * 3) + \frac{3}{5}\left(\frac{1}{3} * 2 + \frac{2}{3} * 2\right) = 2.4\end{aligned}$$

243

242

244 As per equation 3.22, we now have

245

$$\begin{aligned}\Delta \bar{s} &= (\mathbf{1} - p)Cov[c_i, s_i] + (\mathbf{1} - p)\mathbb{E}c_i\Delta s_i + p(\Delta \bar{s}^*) \\ &= \frac{3}{5}\mathbf{0.266} + \frac{3}{5} * \frac{1}{3} + \frac{2}{5}\left(3 - \frac{7}{5}\right) = \mathbf{0.999}\end{aligned}$$

246

247

248 The third term,  $\Delta\bar{s}^*$ , accounts here for the change due to the appearance or migration of new objects into  
249 the system that were not present in the original entity. In our example, it represents the change induced by the  
250 transportation of external organisms to our depositional environment. In other systems, for example  
251 investigating post-mortem molecular dynamics (where molecules or functional groups are taken as objects), it  
252 would account for the part of the change resulting from *in situ* polymerisation and condensation of new  
253 material, the precipitation of minerals, and migration of material from the sediment and porewaters. It is the  
254 incorporation term.

255 With equation 3.22, we are now able to express the partition of the taphonomical change of one state.  
256 Following our last example above, we have our first, second and last term respectively scoring  $\sim 0.16$ ,  $0.2$ , and  
257  $0.64$  (weighted by the probability of new material); and a total value of  $\sim 1$ . Consequently, the change in  
258 hardness value between the extant and fossil assemblage is at 16% due to selective preservation of hard  
259 tissues, at 20% due to alteration of existing material, and at 64% due to transport of external material.

260

## 261 4.2 Specific examples

262 The previous examples can be extended to describe and partition the effect of taphonomy in various  
263 real time scenarios. For example, Zuschin and colleagues [30] interrogate the post-mortem trajectories of  
264 epibenthic communities by comparing the contribution of the organisms in a living assemblage (epifauna) with  
265 a death assemblage (benthic islands) and the sediment composition. They observe that selective preservation  
266 of mineralised organisms is the main taphonomic driver to the benthic islands but that fragile/lightly  
267 mineralised organisms are the main contribution to the sediment. The sediment fraction also contains  
268 organisms that do not contribute to the benthic islands (e.g., vagile crustaceans and sponge spicules) [30]. To  
269 study the change in composition from the living assemblage to the death assemblage and from the death  
270 assemblage to the sediment, we assigned for each category of objects in [30] (see Supplementary material) a  
271 value corresponding to their level of mineralisation (1=soft-bodied; 2=fragile; 3=well mineralised). These  
272 values are not expected to change between each transition so the second term ( $\mathbb{E}c_i\Delta s_i$ ) is null. Applying  
273 equation 3.22, we observe that the change is more important between the living and the death assemblage  
274 ( $|\Delta\bar{s}| = 0.816$ ) than between the death and the sediment assemblages ( $|\Delta\bar{s}| = 0.327$ ), as expected in [30] (Figure  
275 4). The fact that well mineralised organisms are not selectively preserved from the death to the fossil

276 assemblage (negative  $Cov[c_i, s_i]$ ) also supports the conclusion in [30]. In addition, the effect of incorporated  
277 object in the death assemblage (tubes and rocks) and in the sediment assemblages (crustaceans, sponges, and  
278 others), play only a limited role in the whole taphonomic change ( $(p(\Delta\bar{s}^*) = 0.083$  and  $-0.003$ , respectively)  
279 compared to the change in object frequencies ( $((1 - p)Cov[c_i, s_i] = 0.732$  and  $-0.324$ , respectively).

280 Changes in composition during taphonomy can also be tracked within a single organism. Wilson and  
281 Butterfield [31] investigate the changes in molecular composition of a polychaete, *Nereis virens*, buried for 4  
282 months in various environmental conditions (artificial sea water, kaolinite, calcite, quartz, and montmorillonite),  
283 to test the effects of sediment mineralogy on preservation potential. Their results show that the fossilisation  
284 potential of tissues depends on the interplay of the organic composition and the early diagenetic conditions,  
285 more than on alleged recalcitrance. We assigned a value to each of the studied molecular types based on their  
286 alleged recalcitrance [3] (Water soluble proteins=1; Recalcitrant proteins=2; Carbohydrates=3; Chitin=4;  
287 Lipids=5). For this example, we consider these values to be stable during decay ( $\mathbb{E}c_i\Delta s_i = \mathbf{0}$ ). Similarly, there is  
288 no incorporation of new component ( $\Delta\bar{s}^* = \mathbf{0}$ ). Using equation 3.14, we calculate a larger departure from the  
289 original composition of *N. virens* (as defined in [32]) in kaolinite ( $|\Delta\bar{s}|=0.957$ ), quartz (0.513), and  
290 montmorillonite than in calcite (0.067) and artificial sea water (ASW; 0.137). However, the negative covariance  
291 shows that molecules with high preservation potentials (lipids and structural carbohydrates) are selected  
292 against in ASW, kaolinite and calcite ( $Cov[c_i, s_i] = -0.137$ ;  $-0.957$ ; and  $-0.067$ , respectively; Figure 5), supporting  
293 Wilson and Butterfield [31] results.

294 Distortions of the original composition, or appearance, between an organism and its fossil can lead to  
295 an erroneous interpretation of its nature. For example, Sansom and colleagues [33] observed that, after decay,  
296 specimens of cyclostomes (lamprey and hagfish) appear morphologically more primitive (plesiomorphic). They  
297 also compared various fossils to the decayed specimens to clarify their putative taxonomic affinities. We group  
298 the studied characters in [33] by their taxonomic levels and assigned each group a value corresponding to  
299 their mean synapomorphic ranks (see supplementary file in [33]). The higher the value, the more plesiomorphic  
300 the taxonomic rank. Using equation 3.22, we observe that plesiomorphic characters seems to be selected  
301 against in decayed lamprey (negative  $Cov[c_i, s_i] = -0.086$ ) compared to decayed hagfish ( $Cov[c_i, s_i] = 0.111$ )  
302 (Figure 6). For both specimens, the selection term is also less contributing to the change than the alteration  
303 term ( $\mathbb{E}c_i\Delta s_i = 2.070$  for the lamprey and  $\mathbb{E}c_i\Delta s_i = 0.491$  for the hagfish). Here, both terms account for the  
304 effects of decay on the organism but the higher values for the alteration term indicate that the observed

305 plesiomorphic appearance is due more to the change in value for the groups of characters being preserved  
306 than to simple selective preservation of synapomorphic characters. When compared to non-decayed lamprey,  
307 fossil specimens of *Haikouichthys*, *Mayamyzon* and *Hardistiella* also present higher alteration than selection  
308 ( $\mathbb{E}c_i\Delta s_i=1.066, 1.323$  and  $3.128$  against  $Cov[c_i, s_i]= 0.245, -0.335,$  and  $0.410$ , respectively) (Figure 6), although  
309 selective preservation seemed to have more contributed to their present plesiomorphic appearance (note that  
310 only the preserved characters were considered here, see figure 2 in [33]). Finally, fossil *Hardistiella* presents less  
311 difference with lamprey than with hagfish ( $|\Delta\bar{s}|= 3.538$  and  $9.323$ , respectively), as showed by Sansom and  
312 colleagues [33] (Figure 6).

313

## 314 5. Discussion

315

316 It is now well understood that selective preservation cannot solely accounts for the survival of organic material  
317 through geological ages [2, 9, 34]. This implies that taphonomic change is partitioned. In the present work, we  
318 mathematically decompose this change into 3 terms accounting for each aspect of decay and fossilisation. The  
319 resulting equation (equation 3.22) is an elaboration of the Price equation [23-28] with a third term accounting  
320 for the incorporation of new material (e.g., migration from the sediment, neoformation of mineral, transport).  
321 Indeed, the original expression of the Price equation is limited to changes occurring between descendant and  
322 their respective ancestors [27].

323 Kerr and Godfrey-Smith [35] and Fox and Kerr [36] derived an equation resembling 3.22 above, that  
324 they applied for the expression of total change in ecosystem function. Their expression is built upon the  
325 connectiveness of the objects between the two studied sites and considers the effect of loss and migration of  
326 species. The expression from Kerr and Godfrey-Smith [35] and Fox and Kerr [36], along with equation 3.22  
327 above, can extend the use made of the Price equation in evolutionary palaeontology [37, 38] to the study of  
328 extinction events and speciation dynamics where the extra term can account for the appearance of new  
329 species. In a similar way, the present expression 3.22 extends it to the study of fossil assemblages and  
330 depositional environments, providing insight into the bias of preservation due to the organisms themselves  
331 (e.g., presence of hard resistant mineral parts or not); the environmental conditions of the site; or the transport

332 of external organisms to the depositional site, as demonstrated above (first example in section 4.2, Figure 4).  
333 The same object placed to decay in variable settings may provide widely different outcome [13, 31], illustrating  
334 the important role of substrate and mineral interactions in taphonomy. Understanding these roles is crucial to  
335 determine and reduce biases, especially in settings of high diagenetic alteration and low fossil abundance (e.g.,  
336 the Precambrian) [13]. As shown by the second example in section 4.2 above (Figure 5), equations 3.14. and  
337 3.22 provide a way to quantified differences in depositional and preservation conditions that is directly  
338 comparable between settings, providing a unifying mathematical way to characterise biases in the fossils  
339 record.

340 As for the Price equation, equation 3.22 is not a mechanistic model and cannot directly predict the  
341 changes between the two entities but is instead an abstract, mathematically constrained, expression of these  
342 changes (see [28]). Because of this universalistic nature (effectively simply describing the changes between  
343 entities A and B); the Price equation has been adapted for many fields outside evolutionary biology (e.g., [39-  
344 44]). The present expression 3.22, applied to the study of taphonomic change, offers a framework to describe  
345 and partition degradation both in natural and in experimental conditions (when both the starting conditions  
346 and the derived state are known or can be estimated) with which measurements from any metrics can be  
347 incorporated. For example, work from Gibson and colleagues [17] on the experimental decay of sea anemones  
348 relied on artificially (although carefully selected) binned decay stages (4 stages associated with 0-25%; 25-50%,  
349 50-75% and 75-100% loss of the feature). Using the formalism presented here, these stages can be redefined  
350 as continuous variables. Each of their four characters of interest (anterior region, body tissue, outer dermal and  
351 gut) can be associated to a state value, for example, corresponding to the remaining percentage of the feature  
352 compared to the original state. This allows an illustration of the loss of feature over time, just as Gibson and  
353 colleagues have demonstrated, but with one major difference. Because it only relied on the frequency of  
354 objects and on their state value, it is possible to apply it on widely morphologically diverging organisms under  
355 the same experimental conditions (for example a shrimp and a sea anemone). For a selected metric, the  
356 present expression would then offer a description of their respective changes that is directly comparable, in  
357 addition to provide an insight on the respective decay dynamics of each organism.

358 In some situation, the loss of features during diagenesis follows a consistent sequence even across  
359 various environmental conditions, resulting in a morphological regression to the ancestral state [33, 45, 46].  
360 This "stem-ward slippage" has been observed in cephalochordate and cyclostomes [33, 45] whereas other

361 organisms may show no evidence for such patterns of degradation [13]. If morphological characters, labelled  
362 as plesiomorphic or apomorphic, were to be assigned a value according to a characteristic of interest, equation  
363 3.14 or 3.22 could partition the effect of stem-ward slippage between the selective preservation of  
364 plesiomorphic characters (accounted by the first term of 3.14 and 3.22) and the alteration of the character  
365 values during decay. More interestingly perhaps, we could assign to each character a value corresponding to  
366 its degree of ancestry (e.g., the synapomorphic rank in [33]), providing an average plesiomorphic score for one  
367 organism. The evolution of this score can be tracked along decay in experimental setting using equation 3.14  
368 or 3.22, effectively recording the stem-ward slippage (section 4.2; Figure 6). If their degrees of ancestry are  
369 hierarchically comparable, the use of the present formalism permits direct comparison between organisms  
370 from different phylogenetic origin and can clarify some unclear taxonomic affinities, as with *Hardistiella* above  
371 (see [33]).

372 The present formalism also constitutes an interesting new chemometric tool for molecular palaeobiology.  
373 Equation 3.22 is directly applicable to vibrational spectroscopy data, for example infrared spectroscopy.  
374 Infrared spectroscopy, notably Fourier transform (FTIR) identifies chemical bonds in a sample by detecting their  
375 vibrational modes, yielding information about their molecular composition and structure in the form of an  
376 absorption (or reflectance) spectrum. The technique has been applied for degradation experiments of  
377 organism (e.g., [47, 48]) or for the thermal degradation of chemical and molecular compounds (e.g., [5, 18]). By  
378 considering each band of interest in this spectrum as an "object" and its measured parameters (e.g., peak  
379 intensity, width, position) as the possible state values, we can track the evolution of the signal partition (the  
380 part due to appearance and disappearance of absorption bands and the part due to the changes in band  
381 parameter values) during degradation of a sample in a simple and consistent manner and compare this  
382 partition for each parameter. The evolution of the spectrum of a decaying organism may be very different for  
383 different organisms decaying under different conditions, but our formalism allows all the data to be unified in  
384 a common expression for the extent of taphonomic change.

385 The present work, by mathematically describing and partitioning the effect of post-mortem changes,  
386 constitutes a widely extendable approach for the study of taphonomical dynamics and the characterisation of  
387 taphonomical systems (taphonometrics), with promising possible future applications in palaeoenvironmental,  
388 archaeological, or forensic sciences.



390 

## 6. Conclusion

391

392 Constraining the fossilisation processes is a challenging task requiring the understanding of many changing  
 393 multivariate parameters, most often specific to individual environmental settings and conditions. Here, we have  
 394 shown that the passage from an organism to a fossil could be abstracted into a change between two  
 395 collections of objects and partitioned into three terms, two of which constitute the terms of the classic  
 396 equation of George Price. The last term accounting for the presence (migration from the sediment and *in situ*  
 397 condensation) of new material within the fossil. Altogether they provide a mathematical definition of  
 398 fossilisation and taphonomy and a framework that can be applied to describe any system at a molecular,  
 399 cellular, organism or population scale. Since its first publication, the Price Equation, and its variations, has been  
 400 applied in many fields, from biology to statistical physics. It was yet to be extended to palaeontology and  
 401 taphonomy.

402

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407

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411

412 **Data Accessibility**

413 All data are available in the main text or in the supplementary material. For the purpose of open access, the  
 414 author has applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript  
 415 version arising from this submission.

416

417 **Competing Interests**

418 I have no competing interests.

419

420 

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## Figure and table captions

**Figure 1.** Partitions of taphonomical effects between an organism and its fossil counterpart. Here, shapes represent different numbered objects and shading (white, black grey) represent different state values. A to C

illustrate situations solely accounting for changes in frequencies and state values (similar to the general Price equation). Probability  $p$  of having additional objects is 0 and the term  $\Delta\bar{s}^*$  vanishes. D to F illustrate the extended Price equation presented here, accounting for the change due to the properties of the objects in the original organism plus the products of post-mortem condensation reactions and incorporation of external material. Probability  $p$  is non-zero if new objects are present and equal to 1 when the fossil no longer contains any of the original material (F).

**Figure 2.** Illustration of the Price equation formalism adapted to taphonomical systems. Here, the *T. rex* head in A is composed of three soft-tissue, non-mineralised parts (skin, internal organ and muscle) and hard-tissue, mineralised skull and teeth. A hardness value  $s$  of 1 is assigned to non-mineralised parts and of 2 otherwise. In the first fossil (B), the organ and muscle have not been preserved reducing the frequency of soft tissues compared to the living organism. Conversely, the skull and teeth have been preserved so hard tissue frequency has increased. B illustrates the covariance term of equation 1 and 2 and accounts for selective preservation. In fossil C, the frequency of original soft and hard tissues is the same than in B but, the preserved soft tissue (skin) has been altered and is now also mineralised (its hardness value has passed from 1 to 2; but it is still originally a soft tissue). This example represents the expectation term of the equations that accounts for alteration.

**Figure 3.** Illustration of the present formalism. The assemblage A is composed of three soft-bodied and two hard-bodied organisms (of hardness value 1 (yellow) and 2 (orange), respectfully) and degrades into assemblages B, composed of the same two hard-bodied fossil (value 2), one soft-bodied fossil (altered hardness value of 2) and two new fossils, transported in the assemblage from elsewhere (hardness value of 3 (green)). The state value of these new objects is accounted by the last term of equation 2, the incorporation term.

**Figure 4.** Partition of the post-mortem changes of an epibenthic community from living to death assemblage and from death to sediment assemblage. Crosses indicate the absolute total change,  $|\Delta\bar{s}|$ ; circles indicate the selection term of equation 3.22,  $(1 - p)\text{Cov}[c_i, s_i]$ , and squares indicate the incorporation term,  $p(\Delta\bar{s}^*)$ . Original data are from [30] (see Supplementary material).

**Figure 5.** Effects of sediment mineralogy on preservation potential of molecular components of the polychaete, *N. virens*. Crosses indicate the absolute total change,  $|\Delta\bar{s}|$ , and circles indicate the selection term of equation 3.14,  $\text{Cov}[c_i, s_i]$ , which is the only contributor to the taphonomic change,  $\Delta\bar{s}$ , here. ASW: artificial sea water; Kao: kaolinite; Calc: calcite; Qtz: quartz; Mont: montmorillonite. Original data are from [31, 32] (see Supplementary material).

**Figure 6.** Illustration of the post-mortem plesiomorphic drift (stem-ward slippage) in decayed (lamprey and hagfish) and fossils (*Haikouichthys*, *Mayamyzon* and *Hardistiella*) cyclostomes. *Hardistiella* (L) and *Hardistiella* (H) indicate that the fossil is compared to living lamprey and hagfish, respectively (see figure 2 in [ref]). Crosses show the absolute total change,  $|\Delta\bar{s}|$ ; circles are the selection term of equation 3.14,  $\text{Cov}[c_i, s_i]$ , and triangles indicate the alteration term,  $\mathbb{E}c_i\Delta s_i$ . Original data are from [33] (see Supplementary material).



