THE ROBUSTNESS OF PHYLOGENETIC DIVERSITY INDICES

KERRY MANSON

School of Mathematics and Statistics
University of Canterbury, Christchurch, New Zealand

Abstract. Phylogenetic diversity indices provide a formal way to apportion evolutionary heritage amongst extant species. In this short note, we investigate some questions posed in a recent paper (Fischer et al., 2022). In that paper, it is shown that under certain extinction scenarios, the ranking of the surviving species by their Fair Proportion index scores may be the reverse of their ranking beforehand. Here, we provide a necessary condition for such reversals to occur on phylogenetic trees whose edge lengths obey the ultrametric constraint. Secondly, we show that while a direct analogue of their reversal result does not hold when using the Equal-Splits (ES) diversity index, nonetheless just two extinctions can lead to a complete ES-ranking reversal on caterpillar trees.

Keywords: Biodiversity conservation, Fair Proportion index, Equal Splits index, phylogenetic diversity, species prioritization

1. Introduction

A recent paper (Fischer et al., 2022) assesses the robustness of the Fair Proportion (FP) index on phylogenetic trees. Here, we discuss the extension of their results in two contexts: the introduction of an ultrametric constraint on edge lengths, and using the Equal-Splits (ES) index in place of FP. These directions were suggested by Fischer et al. as useful extensions of their results.

The Fair Proportion index assigns to each species an index score, which provides a measure of that species' share of the overall diversity contained in a phylogenetic tree. These scores are used to suggest priorities for biodiversity conservation efforts (for example, see Isaac et al., 2007; Bordewich et al., 2008; Jetz et al., 2014; Forest et al., 2018). Extinctions lead to a recalculation of index scores on the surviving subtree. Conservation programmes often employ large amounts of scarce resources. Hence it is useful to know if and when extinction events could lead to recalculations which markedly change the order of these priorities.

Informally, a diversity index can be considered 'robust' provided that extinctions do not cause large rearrangements of the ranking of species' index scores. Fischer et al. (2022) showed that, for the FP index, the changes can be quite pronounced following certain sets of extinction events, and furthermore, "for each phylogenetic tree, there are edge lengths such that the extinction of one leaf per cherry completely reverses the ranking" (Fischer et al., 2022, p. 2). We note that Fischer et al. place no constraint on the size of edge lengths required to obtain such a reversal. The examples contained in the original paper, and the constructive method appearing in the proof of their Theorem 2 (Fischer et al., 2022, Supp. Mat. pp. 2-15), tend to place the leaves at quite varied distances from the root vertex. This leads to natural questions about whether a similar result can be obtained when edge lengths obey an ultrametric constraint. In particular:

E-mail address: kerry.manson@pg.canterbury.ac.nz.
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> "if we restrict the analysis to ultrametric trees where all leaves have the same distance to the root, what are the worst-case scenarios in this setting?"

(Fischer et al., 2022, p. 5). By "worst-case" these authors refer to a combination of edge lengths and extinctions which re-orders the FP index score ranking as much as possible. Here we outline some necessary conditions for a complete reversal of FP index scores in the ultrametric context. Then we present examples of binary ultrametric phylogenetic trees for which the FP index score rankings are reversible. This answers the question above by showing that the "worst-case scenario" on an ultrametric phylogenetic tree is as 'bad' as possible.

Additionally, we briefly investigate the robustness of the ES index. We illustrate that this index is not always reversible under the same extinctions that reverse FP index scores, and provide examples of reversals caused by the extinction of just two species.

2. Preliminaries

Let X be a non-empty set of taxa (e.g. species), with $|X| = n$. A *rooted binary phylogenetic X-tree* is a rooted tree $T = (V, E)$, where X is the set of leaves, and all edges are directed away from a distinguished root vertex ρ, and every non-leaf, non-root vertex has in-degree 1 and out-degree 2. All edges drawn in this paper will be directed down the page.

For any edge $e \in E(T)$, we write $x \in c_T(e)$ if $x \in X$ and the unique path from ρ to x includes e. That is, $c_T(e)$ is the set (*cluster*) of leaves descended from the terminal vertex of e. For $v \in V(T)$, we also write $x \in c_T(v)$ if $x \in X$ and the unique path from ρ to x includes v. If the (directed) edge (u, v) appears in a phylogenetic tree T, we say that u is the *parent* of v. If two distinct leaves x_1 and x_2 in X have the same parent vertex, then we call $\{x_1, x_2\}$ a *cherry*, and a rooted binary phylogenetic tree with exactly one cherry is called a *caterpillar* tree.

The edges of every rooted binary phylogenetic tree considered in this paper are positively weighted. Let T be a rooted binary phylogenetic X-tree, and let $\lambda : E(T) \to \mathbb{R}^{>0}$ be a function which assigns a positive real-valued length $\lambda(e)$ to each edge $e \in E(T)$. Suppose that $u, v \in V(T)$ are two vertices of T connected by a directed path from u to v (this path is unique if it exists). Then the *distance from u to v*, denoted $d(u, v)$, is the sum of the lengths of the edges in this path. If λ is such that for any two distinct leaves x and y we have $d(\rho, x) = d(\rho, y)$, we say that λ satisfies the *ultrametric* condition.

A *diversity index* on a rooted binary phylogenetic tree T is a function that assigns a portion of the total edge length of T to each species. We consider two diversity indices in particular, the Fair Proportion (or Evolutionary Distinctiveness) index (Redding, 2003; Isaac et al., 2007) and the Equal-Splits index (Redding, 2003; Redding et al., 2014). These indices are of interest because they can be seen as partitioning the total diversity contained in a phylogenetic tree among the species. This is justified by noting that both FP and ES having the following property: for a phylogenetic X-tree T, the sum of the FP or ES values over all species in X equals the sum of all edge lengths in T (Redding, 2003).

Let $P(T; \rho, x)$ be the path from the root vertex ρ to x in T. For each leaf $x \in X$, the *Fair Proportion* (FP) index of x in T is given by

$$FP_T(x) = \sum_{e \in P(T;\rho,x)} \frac{\lambda(e)}{|c_T(e)|}.$$

As every phylogenetic tree considered in this paper is binary, we use the following particular formulation of the ES index. For each leaf $x \in X$, the (binary) *Equal-Splits* (ES) index of x in T is given

by

$$ES_T(x) = \sum_{e \in P(T;\rho,x)} \frac{\lambda(e)}{2^p},$$

where p is the number of edges between e and x in the path $P(T;\rho,x)$.

Furthermore, we use, and repeat here, the definitions of *ranking*, *strict*, and *reversible* as they appear in Fischer et al. (2022) (pp. 2,3). A *ranking* $\pi(S,f)$ for a set $S = \{s_1,\ldots,s_n\}$ based on a function $f : S \to \mathbb{R}$ is an ordered list of the elements of S such that $f(s_i) \geq f(s_j)$ if and only if s_i appears before s_j in π. A ranking $\pi(S,f)$ is called *strict* if none of the values in S are equal. A ranking π_T is called *reversible* if there is a subset X' of X whose removal from T leads to an induced subtree $\tilde{T}$ whose corresponding ranking $\pi_{\tilde{T}} = \pi(X \backslash X', FP_{\tilde{T}})$ ranks the species in the opposite order to π_T.

3. Robustness of Fair Proportion under the ultrametric constraint

We note that the ranking $\pi(X, FP_T)$ on an ultrametric rooted phylogenetic X-tree T cannot be strict, as both leaves from any cherry have equal FP scores. With this in mind, we impose some further conditions which are not explicitly addressed by the above definitions.

Whenever $\pi_T(x_i) < \pi_T(x_j)$, we require $\pi_{\tilde{T}}(x_i) > \pi_{\tilde{T}}(x_j)$ for $\pi_{\tilde{T}}$ to be considered to be in the opposite order to π_T. That is, it is not enough for $\pi_{\tilde{T}}(x_i) = \pi_{\tilde{T}}(x_j)$. Moreover, to eliminate trivial reversals, for a ranking $\pi_{\tilde{T}}$ to be considered to be in the opposite order to π_T, we require $\pi_T(x_i) < \pi_T(x_j)$ and $\pi_{\tilde{T}}(x_i) > \pi_{\tilde{T}}(x_j)$ for at least one pair of distinct leaves x_i, x_j.

Figure 1a illustrates such a reversal caused by the extinction of the single leaf x from the tree T_1. Before the extinction of x, it was the case that $FP_{T_1}(v) = 4 > \frac{23}{6} = FP_{T_1}(y)$. The extinction of x does not change the FP index score of v or w, but the FP index score of y and z increase to 4.5. We now outline some necessary conditions for the reversibility of FP index scores in the ultrametric context.

Proposition 1. *Let T be a rooted binary phylogenetic X-tree whose edge lengths satisfy the ultrametric condition, and let π_T be the ranking of FP index scores for T. Suppose $x \in X$ is a leaf vertex contained in no cherry of T. Let $c_T(v) = \{x\} \dot{\cup} A$, where v is the parent vertex of x and A contains at least two distinct leaves of T.*

Then, there exist ultrametric edge lengths and a set of extinction events for which the ranking π_T is reversible only if, whenever x survives, the entire set A has become extinct.

Proof. Let $x \in X$ be a leaf of T which is not contained in any cherry, and let v be the parent vertex of x. As x is not in a cherry, $c_T(v)$ must contain at least two distinct leaf vertices different from x, say y and z.

Then $FP_T(x)$ must be larger than $FP_T(y)$. To see this, first note that both x and y are allocated the same proportion of edge lengths along the path from the root vertex to v. As T satisfies the ultrametric condition, the length of (v,x) is the same as the length of the path between v and y. Yet while leaf x is allocated the entire length of edge (v,x), leaf y is only allocated part of the total length of the edges along the path from v to y. This is because y must share some of this total with z (from along the edges connecting the common parent of y and z to v.

Next, suppose a set of extinctions occurs that both x and y survive, and that $\tilde{T}$ is the phylogenetic tree remaining after this event. Then $FP_{\tilde{T}}(y)$ can be no larger than $FP_{\tilde{T}}(x)$, with equality holding if and only if x and y form a cherry in $\tilde{T}$. Hence x and y are not ranked in the opposite order in $\pi_{\tilde{T}}$ compared to π_T. □

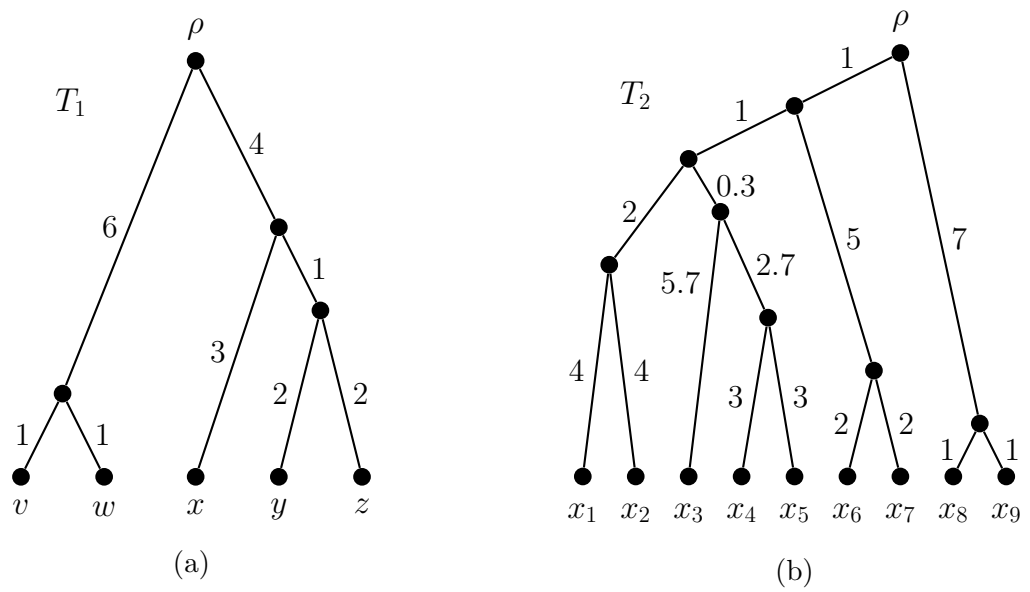

FIGURE 1. Examples of ultrametric phylogenetic trees whose FP index score rankings are reversible. Reversal occurs with the extinction of x for T_1, and the extinction of $\{x_3, x_4, x_6, x_8\}$ for T_2

Theorem 2 of Fischer et al. (2022) shows that, absent any ultrametric constraint, the extinction of one leaf per cherry is sufficient to reverse Fair Proportion index score rankings. We call such a set of concurrent extinctions a *one-per-cherry* extinction event. For ultrametric trees we have the following corollary of Proposition 1.

Corollary 2. *Let T be a rooted binary phylogenetic X-tree whose edge lengths satisfy the ultrametric condition, and let π_T be the ranking of FP index scores for T. There exist ultrametric edge lengths and a one-per-cherry extinction event for which the ranking π_T is reversible only if every leaf in X is a member of some cherry.*

Proof. Let $x \in X$ be a leaf of T which is not contained in any cherry, and let v be the parent vertex of x. As x is not in a cherry, $c_T(v)$ must contain at least two distinct leaf vertices different from x.

Choose two vertices from $c_T(v)$ which form a cherry, say y and z. Suppose that, say, y survives a one-per-cherry extinction event. Since x is not contained in any cherry of T, then x must also survive the extinction event. Therefore, by Proposition 1, the ranking π_T is not reversible. □

4. Examples of ultrametric phylogenetic X-trees with reversible rankings

We present two families of ultrametric rooted phylogenetic trees with reversible rankings. In addition, we give an example of such a tree where distinct leaves have the same FP index score only when they share a cherry. This is as close to a strict ranking as possible under the ultrametric constraint. The first family is illustrated by a representative in Fig. 2a, where $n = 12$. A similar tree can be constructed for any even number of leaves n, where the sum of the edges lengths on the unique path from the root vertex to a leaf is $n-1$. The second is the family of *balanced* phylogenetic X-trees. Balanced trees are those trees where the path from the root vertex to any leaf contains the same number of edges (Figs. 3,4).

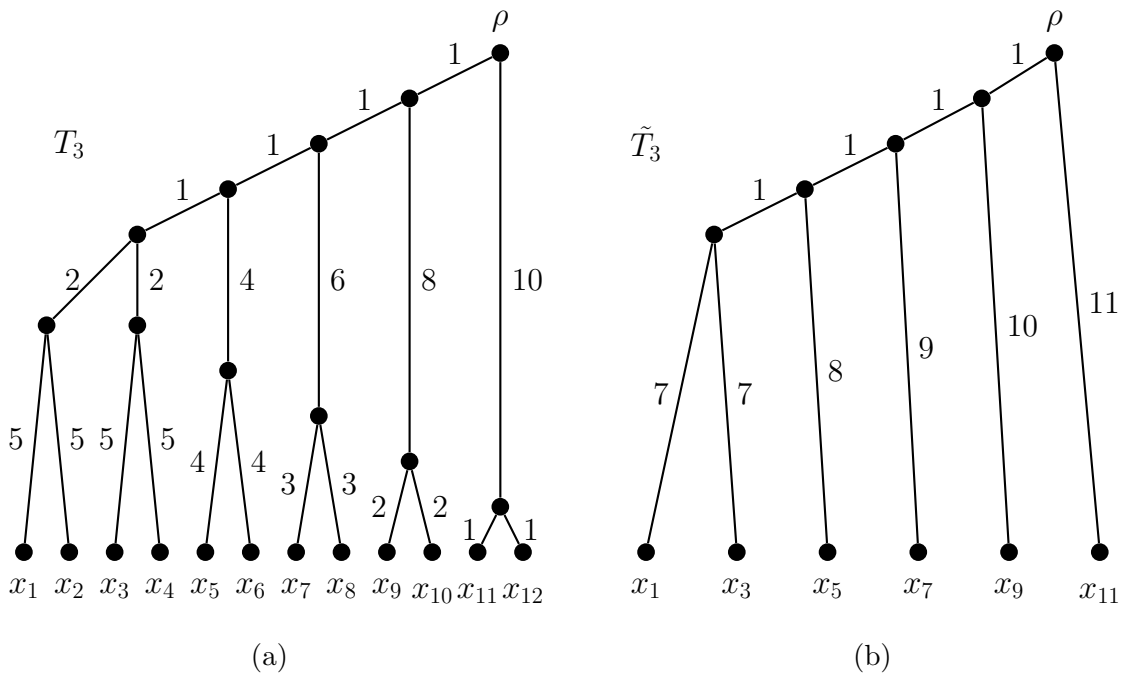

FIGURE 2. An ultrametric rooted phylogenetic tree T_3 before and after a set of extinctions that reverses both the FP and ES index score rankings for surviving species

Example 1. Let T_3 be the rooted phylogenetic tree in Fig. 2a with edge lengths as marked. The tree $\tilde{T}_3$ in Fig. 2b is obtained from T_3 after the extinction of every species with an even subscript. The Fair Proportion index scores for each surviving leaf are given in Table 1. Let π_{T_3} and $\pi_{\tilde{T}_3}$ be rankings of FP index scores for the trees T_3 and $\tilde{T}_3$ respectively. Observe that $\pi_{\tilde{T}_3}$ ranks the species in the opposite order to π_{T_3}, hence π_{T_3} is reversible. (The scores of leaves x_1 and x_3 remain equal before and after the extinctions.)

x	$FP_{T_3}(x)$	$FP_{\tilde{T}_3}(x)$	$ES_{T_3}(x)$	$ES_{\tilde{T}_3}(x)$
x_1	**6.642**	8.283	**6.469**	7.938
x_3	**6.642**	8.283	**6.469**	7.938
x_5	6.392	8.783	6.438	8.875
x_7	6.225	9.450	6.375	9.750
x_9	6.100	10.200	6.250	10.500
x_{11}	6.000	**11.000**	6.000	**11.000**

TABLE 1. Fair Proportion and Equal-Splits index values for T_3 and $\tilde{T}_3$, rounded to three decimal places. The largest value in each column appears in boldface.

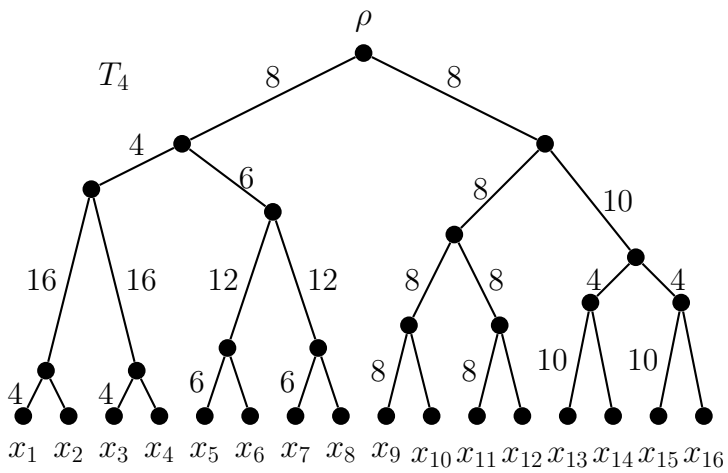

FIGURE 3. A balanced ultrametric rooted phylogenetic tree with edge lengths marked

Example 2. Let T_4 be the rooted phylogenetic tree in Fig. 3 with edge lengths as marked. The tree $\tilde{T}_4$ in Fig. 4 is obtained from T_4 after the extinction of every species with an even subscript. The Fair Proportion index scores for each surviving leaf are given in Table 2a. Let π_{T_4} and $\pi_{\tilde{T}_4}$ be rankings of FP index scores for the trees T_4 and $\tilde{T}_4$ respectively. Observe that $\pi_{\tilde{T}_4}$ ranks the species in the opposite order to π_{T_4}, hence π_{T_4} is reversible.

Example 3. Let T_2 be the rooted phylogenetic tree in Fig. 1b with edge lengths as marked. The tree $\tilde{T}_2$ in Fig. 1b is obtained from T_2 after the extinction of x_3, x_4, x_6, and x_8. The Fair Proportion index scores for each surviving leaf are given in Table 2b. Let π_{T_2} and $\pi_{\tilde{T}_2}$ be rankings of FP index scores for the trees T_2 and $\tilde{T}_2$ respectively. Observe that $\pi_{\tilde{T}_2}$ ranks the species in the opposite order to π_{T_2}, hence π_{T_2} is reversible.

x	$FP_{T_4}(x)$	$FP_{\tilde{T}_4}(x)$
x_1, x_3	14	**24**
x_5, x_7	14.5	23
x_9, x_{11}	15	22
x_{13}, x_{15}	**15.5**	21

(a)

x	$FP_{T_2}(x)$	$FP_{\tilde{T}_2}(x)$
x_1, x_2	**5.343**	5.583
x_5	4.793	6.583
x_7	4.643	7.250
x_9	4.500	**8.000**

(b)

TABLE 2. Fair Proportion index values (a) for T_4 and $\tilde{T}_4$, and (b) for T_2 and $\tilde{T}_2$. The largest value in each column appears in boldface.

4.1. **Specific edge weightings for reversibility.** Corollary 1 of Fischer et al. (2022) states that a strict and reversible ranking exists for any caterpillar tree under the Fair Proportion index. Furthermore, this reversal is caused by the extinction of the species that initially had the lowest FP index

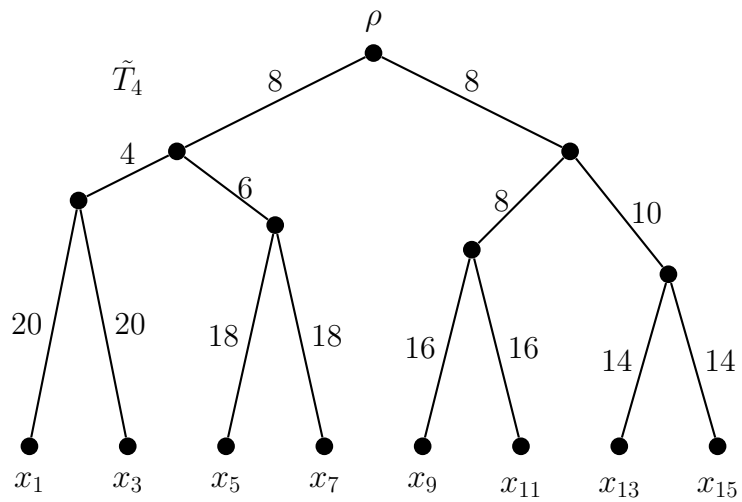

FIGURE 4. The phylogenetic tree resulting from the extinction of even-indexed species in T_4 from Fig. 3. The FP and ES index score ranking of surviving species has been reversed.

score. We now provide a specific assignment of edge lengths on caterpillar trees that exhibits this property.

Example 4. Consider the tree T_5 in Fig. 5a, and let $\tilde{T}_5$ be the tree obtained from T_5 after the removal of leaf x_1, and suppression of the parent vertex of x_1 and x_2 thereafter. Table 3 gives the Fair Proportion index values for the leaves in T_5 and $\tilde{T}_5$, and includes values for an example case where $n = 10$. Note that (up to a choice of x_1 or x_2) this is the unique strict ordering of FP index scores which can be reversed, although other edge length assignments are possible.

x	$FP_{T_5}(x)$	$n = 10$	$FP_{\tilde{T}_5}(x)$	$n = 10$
x_1	$1 + \frac{3}{2} + \frac{5}{3} + \frac{7}{4} + \frac{9}{5} + \cdots + \frac{2n-3}{n-1}$	15.171	extinct	—
x_2	$2 + \frac{3}{2} + \frac{5}{3} + \frac{7}{4} + \frac{9}{5} + \cdots + \frac{2n-3}{n-1}$	16.171	$\mathbf{5 + \frac{5}{2} + \frac{7}{3} + \frac{9}{4} + \ldots + \frac{2n-3}{n-2}}$	**20.718**
x_3	$4 + \frac{5}{3} + \frac{7}{4} + \frac{9}{5} + \cdots + \frac{2n-3}{n-1}$	16.671	$4 + \frac{5}{2} + \frac{7}{3} + \frac{9}{4} + \cdots + \frac{2n-3}{n-2}$	19.718
x_4	$6 + \frac{7}{4} + \frac{9}{5} + \cdots + \frac{2n-3}{n-1}$	17.004	$6 + \frac{7}{3} + \frac{9}{4} + \cdots + \frac{2n-3}{n-2}$	19.218
x_5	$8 + \frac{9}{5} + \cdots + \frac{2n-3}{n-1}$	17.254	$8 + \frac{9}{4} + \cdots + \frac{2n-3}{n-2}$	18.885
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
x_{n-1}	$2n - 4 + \frac{2n-3}{n-1}$	17.889	$2n - 4 + \frac{2n-3}{n-2}$	18.125
x_n	$\mathbf{2n - 2}$	**18.000**	$2n - 2$	18.000

TABLE 3. FP index scores for caterpillar tree T_5. The largest value in each column appears in boldface.

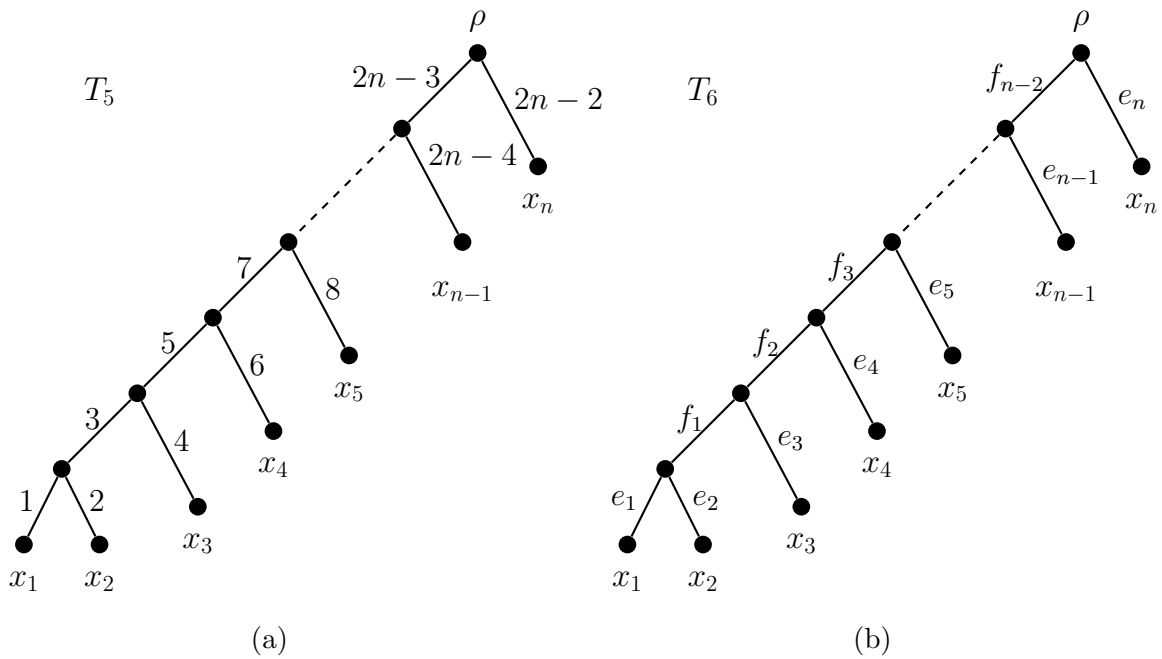

FIGURE 5. (a) A specific pattern of edge lengths that leads to a reversal of FP index score rankings following the extinction of x_1. (b) A general caterpillar tree used in Examples 6 and 7 to show that ES index score rankings can be reversed with as few as two extinctions.

5. Robustness of the Equal-Splits index

We now turn to the effect of extinctions on rankings derived from the Equal-Splits (ES) index. We first note that the FP and ES indices coincide on balanced trees Wicke and Steel (2020). Hence, Example 2 provides an instance of the reversibility of the ES index. A distinct example of a reversed ES ordering is provided below.

Example 5. The ranking of leaves of T_3 is reversible when applying the ES index. Let T_3 be the rooted phylogenetic tree in Fig. 2a with edge lengths as marked. The tree $\tilde{T}_3$ in Fig. 2b is obtained from T_3 after the extinction of every species with an even subscript. The Equal-Splits index scores for each surviving leaf are given in Table 1. Let π_{T_3} and $\pi_{\tilde{T}_3}$ be rankings of ES index scores for the trees T_3 and $\tilde{T}_3$ respectively. Observe that $\pi_{\tilde{T}_3}$ ranks the species in the opposite order to π_{T_3}, hence π_{T_3} is reversible. (The scores of leaves x_1 and x_3 remain equal before and after the extinctions.)

In contrast to the FP index, a one-per-cherry extinction event is not strong enough to reverse an Equal-Splits ranking on caterpillar trees.

Proposition 3. *Let T be a rooted caterpillar tree with at least four leaves. Then the extinction of one leaf from the cherry of T is necessary, but not sufficient, to cause a strict ranking of Equal Splits index scores to reverse.*

Moreover, let $X = \{x_1, x_2, x_3, \ldots, x_n\}$ be the leaves of T, where x_n is adjacent to the root vertex, and there is a path of length two from the root vertex to x_{n-1}. Then the extinction of any strict subset of $\{x_1, x_2, x_3, \ldots, x_{n-2}\}$ cannot cause a strict ranking of Equal-Splits index scores to reverse.

Proof. Let x_1 and x_2 be the two distinct leaves which form the unique cherry of T. The paths from the root vertex to x_1 and x_2 are identical between the root and the shared parent of these leaves.

Hence, the Equal-Splits index scores of x_1 and x_2 in T differ by the difference of their pendant edge lengths (the edges incident with these leaves). The extinction of any other leaves of T does not alter this difference as the paths from the root to x_1 and x_2 are affected identically (cf. proof of Theorem 1 in Fischer et al. (2022)). Thus, for the ranking of ES index scores to reverse, it is necessary for at least one of x_1, x_2 to become extinct.

Moreover, the extinction of a leaf x_i affects the ES index score of precisely those leaves descended from the parent of x_i, and no others. The extinction of, say, x_1 will lead to an increase in the ES index score of x_2, but the ES index scores of all other vertices remain the same. If T contains at least four leaves, there are at least two leaves whose index scores are unaffected, and hence their order does not reverse.

Furthermore, suppose a strict subset of $\{x_1, x_2, x_3, \ldots, x_{n-2}\}$ becomes extinct. The ES index scores of x_{n-1} and x_n are unaffected by such an extinction, and again the ranking cannot reverse. □

Example 6. Finally, we consider the rooted caterpillar tree T_6 in Figure 5b, where $n \geq 4$. By Proposition 3, the extinction of one of x_1, x_2 is insufficient to reverse the ranking of Equal Splits index scores on T_6. However, by exhibiting specific edge lengths, we show that the concurrent extinction of one leaf from $\{x_1, x_2\}$, and one leaf from $\{x_{n-1}, x_n\}$ can be enough to effect a ranking reversal.

Let the edges of T_6 be assigned lengths by the function $\lambda : E(T_6) \to \mathbb{R}$ as follows:

- $\lambda(e_1) = \lambda(e_2) = \lambda(e_{n-1}) = 1$
- $\lambda(e_i) = 2^{i-2} + n - i - 1$, for $3 \leq i \leq n-2$
- $\lambda(e_n) = 2^{n-2} + n - 3$
- $\lambda(f_i) = 2^{n-2}$, for all $1 \leq i \leq n-2$

Then suppose that leaves x_1 and x_{n-1} become extinct, and that $\tilde{T}_6$ is the resultant phylogenetic tree. Table 4 shows the ES index scores for T_6 and $\tilde{T}_6$, illustrating the ranking reversal. In the case $n = 10$, the values for $e_1, e_2, \ldots, e_{10}$ are $1, 1, 8, 9, 12, 19, 34, 65, 1$, and 263, and $f_i = 256$ for all $1 \leq i \leq 9$. The index scores for this case also appear in Table 4.

Example 7. Alternatively, we can find edge lengths which lead to an ES ranking reversal under the concurrent extinction of x_1 and x_n. For this scenario, we adopt the convention followed in Fischer et al. (2022) that f_{n-2} is also deleted, to ensure that the root of $\tilde{T}_6$ has degree two. Let the edges of T_6 be assigned lengths by the function $\lambda : E(T_6) \to \mathbb{R}$ defined below. Note that the first two conditions are prioritised over the third if $n = 4$ or $n = 5$.

- $\lambda(e_1) = \lambda(e_n) = 1$
- $\lambda(e_{n-1}) = 2$
- $\lambda(e_i) = 1 + 2^{i-3}(3 \cdot 2^{n-i-2} - 2(n-i) + 1)$, for $3 \leq i \leq n-2$
- $\lambda(e_2) = \lambda(e_3)$, unless $n = 4$, in which case $\lambda(e_2) = 1$
- $\lambda(f_i) = 2^i$, for all $1 \leq i \leq n-2$

Table 4 shows the ES index scores for T_4 and $\tilde{T}_4$, illustrating the ranking reversal. In the case $n = 10$, the values for $e_1, e_2, \ldots, e_{10}$ are $1, 84, 84, 75, 61, 41, 17, 1, 2$, and 1. The index scores for this case also appear in Table 5.

6. Concluding Remarks

This paper has considered the Fair Proportion index scores of leaves in ultrametric rooted binary phylogenetic trees. The examples here illustrate that various extinction events can cause the ranking

x	$ES_{T_4}(x)$	$n = 10$	$ES_{\tilde{T_4}}(x)$	$n = 10$
x_2	2^{n-2}	256	$\mathbf{2^{n-1} + 1}$	**513**
x_{n-2}	$2^{n-2} + 1$	257	$2^{n-2} + 2^{n-4} + 1$	321
x_{n-3}	$2^{n-2} + 2$	258	$2^{n-2} + 2^{n-5} + 2$	290
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
x_5	$2^{n-2} + n - 6$	260	$2^{n-2} + 2^3 + n - 6$	268
x_4	$2^{n-2} + n - 5$	261	$2^{n-2} + 2^2 + n - 5$	265
x_3	$2^{n-2} + n - 4$	262	$2^{n-2} + 2^1 + n - 4$	264
x_n	$\mathbf{2^{n-2} + n - 3}$	**263**	$2^{n-2} + n - 3$	263

TABLE 4. Reversal of ES index scores for caterpillar tree T_4 under the extinction of x_1 and x_{n-1}. The largest value in each column appears in boldface.

x	$ES_{T_4}(x)$	$n = 10$	$ES_{\tilde{T_4}}(x)$	$n = 10$
x_2	$3 \cdot 2^{n-5} - n + 6$	92	$\mathbf{3 \cdot 2^{n-5} + 2}$	**98**
x_3	$3 \cdot 2^{n-5} + 2$	98	$3 \cdot 2^{n-5}$	96
x_4	$3 \cdot 2^{n-5} + 3$	99	$3 \cdot 2^{n-5} - 1$	95
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
x_{n-4}	$3 \cdot 2^{n-5} + 2^{n-7} + 1$	105	$3 \cdot 2^{n-5} - 2^{n-7} + 1$	89
x_{n-3}	$3 \cdot 2^{n-5} + 2^{n-6} + 1$	113	$3 \cdot 2^{n-5} - 2^{n-6} + 1$	81
x_{n-2}	$2^{n-3} + 1$	129	$2^{n-4} + 1$	65
x_{n-1}	$\mathbf{2^{n-3} + 2}$	**130**	2	2

TABLE 5. Reversal of ES index scores for caterpillar tree T_4 under the extinction of x_1 and x_n, where $n \geq 6$. The largest value in each column appears in boldface.

order of surviving species to reverse. In the case of small trees, such as Fig. 1a, a single extinction may be enough to reverse the order of index scores.

It may be useful for further investigation to determine the minimum number of extinctions required to cause a ranking reversal. This number will likely depend on the total number of leaves in a tree, and the number of leaves allowed to have the same FP index score despite not sharing a cherry. An understanding of these minimal extinction events could help to determine whether the converse of Prop. 1 holds.

We have also begun to investigate the robustness of the Equal-Splits index. Examples of index score ranking reversals were given in both ultrametric and non-ultrametric contexts. This illustrates that the reversal of index score rankings is not a property of FP alone.

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