AXIOMATIC PHYLOGENETICS

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Abstract. We use the language of quivers to formulate a mathematical framework for phylogenetics.

1. Introduction

Mathematical methods are commonly used in biology which, in some cases, leads to new mathematical theories, see [DHKMS], [ERSS], [Gr], [Re], [SS], [Ti]. In this paper we study certain mathematical ideas suggested by evolutionary biology. Biological evolution is described in wikipedia as the “change in the heritable characteristics of biological populations over successive generations”. Evolution creates a sequence of generations of species, each generation arising from the previous one via natural selection and/or genetic drift. Every species produces descendants in the next generation. The branching diagram showing the evolutionary relationships between species is called the evolutionary tree. This tree has a distinguished vertex - a root - as all life on Earth is believed to share a common ancestor known as the last universal common ancestor (LUCA). Phylogenetics studies the evolutionary tree and aims to recover it from the current generation of living organisms. For a review of phylogenetic analysis, see [YR]; for mathematical aspects of phylogenetics, see [SS], [DHKMS].

We introduce here a mathematical formalism for evolution emphasizing its phylogenetic aspects. While it remains to be seen whether this formalism may be of use in theoretical biology, it does suggest new mathematical concepts. Our main idea is to consider not only the historical evolution but all possible evolutions of primitive beings into complex organisms. To this end we use the language of quivers (directed graphs). We introduce analogues of many key notions of phylogenetics in the setting of quivers. This includes analogues of the notions of species, parents/children, LUCAs, evolutions, generations, etc. We show that under appropriate assumptions on the quiver, it gives rise to an evolutionary tree. We give examples of quivers satisfying these assumptions.

This work was partially supported by the NSF grant DMS-1664358.

2. Quivers and evolutions

2.1. Quivers. A quiver $O$ is formed by a class of vertices and a collection of sets $\{O(A,B)\}_{A,B}$ where $A, B$ run over the vertices of $O$. The elements of the set $O(A,B)$ are called edges from $A$ to $B$ and are represented by arrows $A \to B$ or

2010 Mathematics Subject Classification. 18A10, 54E99, 92D15.
B ← A. (We allow $A = B$, i.e., the quiver $O$ may have loops). To indicate that $A$ is a vertex of $O$ we write $A \in O$. A biologically minded reader may replace the word vertex with “species”. An arrow $B \leftarrow A$ is understood in the sense that $B$ is a “parent” of $A$.

2.2. Evolutions. An evolutionary chain or, shorter, an evolution of length $m \geq 0$ in a quiver $O$ is a sequence
\begin{equation}
A_0 \leftarrow A_1 \leftarrow A_2 \leftarrow \cdots \leftarrow A_m
\end{equation}
where $A_0, A_1, \ldots, A_m \in O$ and the arrows are edges of $O$. We call $A_0$ the initial vertex and $A_m$ the terminal vertex of the evolution.

For $A, B \in O$, we write $A \leq B$ and say that $A$ is an ancestor of $B$ and $B$ is a descendant of $A$ if there is an evolution in $O$ leading from $A$ to $B$, i.e., starting at $A$ and terminating at $B$.

Lemma 2.1. The relation $\leq$ is reflexive and transitive.

Proof. The reflexivity of $\leq$ means that $A \leq A$ for any $A \in O$. In other words, every $A \in O$ is both its own ancestor and its own descendant. This is obtained using the evolution of $A$ to itself of length 0. The transitivity of $\leq$ means that if $A \leq B$ and $B \leq C$, then $A \leq C$ for any $A, B, C \in O$. This is obtained by concatenating an evolution from $A$ to $B$ with an evolution from $B$ to $C$. □

2.3. Isotypy. We say that vertices $A, B$ of a quiver $O$ are isotypic and write $A \sim B$ if both $A \leq B$ and $B \leq A$, i.e., if $A, B$ are descendants of each other. The vertices $A, B$ are isotypic iff there is a circle formed by arrows and traversing both $A$ and $B$:
\[A \leftarrow \cdots \leftarrow B \leftarrow \cdots \leftarrow A.\]

The relation $\sim$ is an equivalence relation: every vertex is isotypic to itself (the reflexivity); if $A \sim B$, then $B \sim A$ for any $A, B \in O$ (the symmetry); if $A \sim B \sim C$, then $A \sim C$ for any $A, B, C \in O$ (the transitivity). The first two properties follow from the definitions. The transitivity holds because if $A \sim B \sim C$, then $A \leq B \leq C$ and $C \leq B \leq A$. Therefore $A \leq C$ and $C \leq A$, i.e., $A \sim C$.

The next lemma shows that isotypic vertices are equivalent from the evolutionary viewpoint and may be considered as inessential variations of each other.

Lemma 2.2. For any $A, B \in O$ the following five conditions are equivalent:

(i) $A$ and $B$ are isotypic;
(ii) $A$ is both an ancestor and a descendant of $B$;
(iii) $B$ is both an ancestor and a descendant of $A$;
(iv) $A$ and $B$ have the same ancestors;
(v) $A$ and $B$ have the same descendants.

Proof. The equivalences $(i) \iff (ii) \iff (iii)$ follow directly from the definitions. If $A \sim B$ and $X$ is an ancestor of $A$, then $X \leq A \leq B$. So, $X \leq B$, i.e., $X$ is an ancestor of $B$. Similarly, all ancestors of $B$ are ancestors of $A$. Thus, $(i) \implies (iv)$. Conversely, if $(iv)$ holds, then $A$ being its own ancestor must be an ancestor of $B$, i.e., $A \leq B$. Analogously, $B \leq A$. Thus, $(iv) \implies (i)$ and so $(i) \iff (iv)$. The equivalence $(i) \iff (v)$ is checked similarly. □
Note that all vertices appearing in an evolution between isotypic vertices are isotypic: For any evolution \((2.2.1)\) between isotypic vertices \(A_0, A_m\), we have \(A_0 \sim A_k\) for \(k = 0, 1, \ldots, m\). Indeed, the existence of the evolution \((2.2.1)\) implies that \(A_0 \leq A_k \leq A_m\). Since \(A_0, A_m\) are isotypic, \(A_m \leq A_0\). Therefore \(A_k \leq A_0\). Thus, \(A_k \sim A_0\).

2.4. Hereditary and anti-hereditary properties. A property, say, \(P\) of vertices of a quiver is hereditary if for any vertex having \(P\), all its descendants also have \(P\). Similarly, the property \(P\) is anti-hereditary if for any vertex having \(P\), all its ancestors also have \(P\). If the property \(P\) is hereditary or anti-hereditary, then it is isotypy invariant, i.e., all vertices isotypic to a vertex having \(P\) also have \(P\). If a property is hereditary, then its negation is anti-hereditary and vice versa.

2.5. Examples. 1. Let \(SET\) be the quiver formed by finite non-empty sets as vertices and maps between sets as edges. An evolutionary chain of length \(m \geq 0\) in \(SET\) is a sequence of finite non-empty sets \(A_0, A_1, ..., A_m\) and maps \(\{A_k \to A_{k-1}\}_{k=1}^m\). The elements of \(A_k\) can be viewed as the species of the \(k\)-th generation while the map \(A_k \to A_{k-1}\) carries each species to its parent. Such evolutions reflect asexual reproduction: each species has a single parent. (Reproduction involving two parents may be formalized by taking as edges between sets \(A, B\) the maps \(B \to A \times A\).) For any \(A, B \in SET\), a map carrying \(B\) to a single element of \(A\) yields a length 1 evolution \(A \leftarrow B\). Thus, \(A \leq B\). Consequently, all vertices of \(SET\) are isotypic.

2. Let \(S\) be the quiver formed by finite non-empty sets as vertices and surjective maps between sets as edges. It is clear that \(A \leq B\) for \(A, B \in S\) if and only if \(\text{card}(A) \leq \text{card}(B)\) where \(\text{card}\) is the number of elements of a set. Therefore, \(A \sim B\) if and only if \(\text{card}(A) = \text{card}(B)\).

3. Primitivity and the height

3.1. Primitive vertices. The role of LUCAs in evolutionary biology will be played here by so-called primitive vertices. We call a vertex \(A\) of a quiver \(O\) primitive if all ancestors of \(A\) also are descendants of \(A\). Thus, \(A \in O\) is primitive if \(B \leq A \implies A \leq B\) for all \(B \in O\). It is clear from our definitions that a vertex \(A\) is primitive iff all its ancestors are isotypic to \(A\).

A quiver may have no primitive vertices. If it has primitive vertices, then they may be non-isotypic to each other. At the same time, all vertices isotypic to a primitive vertex are primitive, as is clear from the following lemma.

Lemma 3.1. All ancestors of a primitive vertex are primitive.

Proof. Let \(A\) be a primitive vertex of a quiver \(O\) and let \(B \in O\) be an ancestor of \(A\). If \(C\) is an ancestor of \(B\), then \(C \leq B \leq A\) and by transitivity, \(C \leq A\). Since \(A\) is primitive, we must have \(A \leq C\). Since \(B \leq A\), the transitivity yields \(B \leq C\). Thus, \(C \leq B \implies B \leq C\), i.e., \(B\) is primitive. \(\square\)
3.2. **The height.** By a *full evolution* for a vertex $X \in \mathcal{O}$ we mean an evolutionary chain in $\mathcal{O}$ which starts at a primitive vertex and terminates at $X$. We view such an evolution as an evolutionary history of $X$. A full evolution for $X$ does not necessarily exist, and if it exists, it is not necessarily unique.

We define the *height* $h(X)$ of $X \in \mathcal{O}$ to be the smallest integer $h \geq 0$ such that there is a full evolution for $X$ of length $h$. The height measures the evolutionary complexity of $X$, i.e., the number of steps needed to evolve from a primitive vertex to $X$. If there are no full evolutions for $X$, then we set $h(X) = \infty$.

It is clear that a vertex $X \in \mathcal{O}$ has a finite height if and only if $X$ has a primitive ancestor. Concatenating evolutionary chains we conclude that the property of a vertex to have finite height is hereditary. Note also that $h(X) = 0$ if and only if $X$ is primitive, and $h(X) = 1$ if and only if $X$ is not primitive but there is an edge from $X$ to a primitive vertex.

A full evolution for a vertex $X \in \mathcal{O}$ is said to be *short* if its length is the smallest among all full evolutions for $X$. Such an evolution exists if and only if $h(X) < \infty$ and its length is equal to $h(X)$.

**Lemma 3.2.** Let $\alpha = (A_0 \leftarrow \cdots \leftarrow A_m)$ be a full evolution for a vertex $A_m \in \mathcal{O}$. Then $h(A_k) \leq k$ for all $k = 0, 1, \ldots, m$. If $\alpha$ is short, then $h(A_k) = k$ for all $k$.

**Proof.** For $k = 0, 1, \ldots, m$, let $\alpha_k = (A_0 \leftarrow \cdots \leftarrow A_k)$ be the initial segment of $\alpha$ of length $k$ and let $\alpha^k = (A_k \leftarrow \cdots \leftarrow A_m)$ be the terminal segment of $\alpha$ of length $m - k$. Since $\alpha$ is a full evolution, $A_0$ is a primitive vertex and so $\alpha_k$ is a full evolution for $A_k$. Thus, $h(A_k) \leq k$. If there is a full evolution for $A_k$ of length $< k$ then concatenating it with $\alpha^k$ we obtain a full evolution for $A_m$ of length $< k + (m - k) = m$. Therefore, if $\alpha$ is short, then so is $\alpha_k$ and $h(A_k) = k$. \(\square\)

Lemma 3.2 implies that any vertex of finite height $m \geq 1$ has ancestors of heights $0, 1, \ldots, m - 1$.

3.3. **Examples.** 1. All vertices of the quiver $\mathcal{S}\mathcal{E}\mathcal{T}$ from Example 2.5.1 are primitive and have zero height. Consider next the quiver $\mathcal{S}$ from Example 2.5.2. A finite non-empty set $X \in \mathcal{S}$ is primitive if and only if $\operatorname{card}(X) = 1$. Every $X \in \mathcal{S}$ is the terminal vertex of a full evolution: if $\operatorname{card}(X) = 1$, then this is the length 0 evolution $(X)$; if $\operatorname{card}(X) \geq 2$, then this is the length 1 evolution $A \leftarrow X$ where $A$ is a 1-point set and the arrow stands for the only map from $X$ to $A$. Thus, $h(X) = 0$ if $\operatorname{card}(X) = 1$ and $h(X) = 1$ otherwise.

2. Let $\Gamma$ be a rooted tree, i.e., a connected graph without cycles and with a distinguished vertex $*$ (the root). We direct all edges of $\Gamma$ as follows: if an edge of $\Gamma$ connects vertices $A, B$ and there is a path from $*$ to $A$ missing $B$, then this edge is directed from $B$ to $A$. This turns $\Gamma$ into a quiver. It is easy to check that: different vertices of $\Gamma$ cannot be isotypic; the vertex $*$ is the only primitive vertex of $\Gamma$; every vertex $X \in \Gamma$ is the terminal vertex of a unique full evolution formed by the vertices and edges of the shortest path from $*$ to $X$, this full evolution is short.
3. Consider the quiver with three vertices $A, B, C$ and three edges leading from $B$ to $A$, from $B$ to $C$, and from $C$ to $B$. Then $A \preceq B \sim C$ and $h(A) = 0$, $h(B) = 1$, $h(C) = 2$. Thus, isotypic vertices may have different heights.

4. The quiver with vertices $\{A_k\}_{k \in \mathbb{Z}}$ and arrows $\{A_k \leftarrow A_{k+1}\}_{k \in \mathbb{Z}}$ has no primitive vertices and $h(A_k) = \infty$ for all $k$.

### 4. Universal evolutions and phylogenetic vertices

We introduce so-called universal evolutions and phylogenetic vertices.

#### 4.1. Universal evolutions

Given two evolutionary chains

$$\alpha = (A_0 \leftarrow \cdots \leftarrow A_m) \quad \text{and} \quad \beta = (B_0 \leftarrow \cdots \leftarrow B_n)$$

in a quiver $O$, we say that $\alpha$ embeds in $\beta$ if $m \leq n$ and there are integers

$$0 \leq r_0 < r_1 < \cdots < r_m \leq n$$

such that $A_k \sim B_{r_k}$ for $k = 0, 1, \ldots, m$. For $m = n$, this condition amounts to $A_k \sim B_k$ for all $k$. In this case we say that the evolutions $\alpha, \beta$ are isotypic.

A universal evolution for a vertex $X \in O$ is a full evolution for $X$ which embeds in all full evolutions for $X$. Thus, the vertices of a universal evolution for $X$ must appear (in the same order) in any full evolution for $X$, at least up to isotypy. A universal evolution for $X$ is necessarily short. So, its length is equal to $h(X)$. A universal evolution for $X$ may exist only if $h(X) < \infty$.

Clearly, any two universal evolutions for a vertex $X \in O$ are isotypic. Any evolution isotypic to a universal evolution is itself universal. We view a universal evolution for $X$ as a complete evolutionary history of $X$.

#### 4.2. Phylogenetic vertices

A vertex $X \in O$ is phylogenetic if there is a universal evolution for $X$ in $O$. For example, for a primitive $X$, the length zero evolution $(X)$ is universal. Thus, all primitive vertices are phylogenetic.

We state several properties of phylogenetic vertices.

**Theorem 4.1.** Let $X \in O$ be a phylogenetic vertex. Then:

(i) $X$ has a primitive ancestor;

(ii) all primitive ancestors of $X$ are isotypic to each other;

(iii) all short full evolutions for $X$ are universal;

(iv) all vertices appearing in a universal evolution for $X$ are phylogenetic.

**Proof.** Pick a universal evolution $\alpha = (A_0 \leftarrow \cdots \leftarrow A_m)$ for $X = A_m$. Clearly, $A_0$ is a primitive ancestor of $X$ which yields (i). To prove (ii), consider another primitive ancestor $B$ of $X$ and an evolution $\beta = (B_0 \leftarrow \cdots \leftarrow B_n)$ from $B_0 = B$ to $B_n = X$. Since $B$ is primitive, $\beta$ is full. Since $\alpha$ is universal, it embeds in $\beta$. Consequently, $A_0 \sim B_k$ for some $k \leq n$. Then $B = B_0 \leq B_k \leq A_0$. Hence $B \leq A_0$, and the primitivity of $A_0$ ensures that $B \sim A_0$. This gives (ii).

To prove (iii), consider a short full evolution $\beta = (B_0 \leftarrow \cdots \leftarrow B_m)$ for $X = B_m$. Since $\alpha$ embeds in $\beta$ and $\alpha, \beta$ have the same length, $A_k \sim B_k$ for all $k \leq m$. Therefore $\beta$ is universal.
For \( k = 0, 1, \ldots, m \), let \( \alpha_k \) and \( \alpha^k \) be the initial and terminal segments of the universal evolution \( \alpha \) as defined in the proof of Lemma 3.2. Since \( \alpha \) is a full evolution for \( A \), \( \alpha_k \) is a full evolution for \( A_k \). Any full evolution \( \gamma \) for \( A_k \) concatenated with \( \alpha^k \) yields a full evolution \( \gamma \alpha^k \) for \( A_m \). Since the evolution \( \alpha_k \alpha^k = \alpha \) is universal, it embeds in \( \gamma \alpha^k \). Therefore \( \alpha_k \) embeds in \( \gamma \). Thus, \( \alpha_k \) is a universal evolution for \( A_k \) and the vertex \( A_k \) is phylogenetic. \( \Box \)

4.3. Examples. The full evolutions in Examples 3.3.1 and 3.3.2 are universal. All vertices of the quivers in these examples are phylogenetic.

5. Critical ancestors and normality

We further develop our language and, in particular, introduce the notion of a critical ancestor. In this section, \( \mathcal{O} \) is an arbitrary quiver.

5.1. The step inequality. The height of a vertex of \( \mathcal{O} \) cannot increase too quickly under evolutions. In fact, for any length 1 evolution (i.e., an edge of our quiver) \( A \leftarrow B \) we have the step inequality

\[
(5.1.1) \quad h(B) \leq h(A) + 1.
\]

More precisely, if \( h(A) < \infty \), then \( (5.1.1) \) holds and, in particular, \( h(B) < \infty \). Indeed, concatenating a full evolution for \( A \) of length \( h(A) \) with the evolution \( A \leftarrow B \) we obtain a full evolution for \( B \) of length \( h(A) + 1 \). If \( h(A) = \infty \), then the inequality \( (5.1.1) \) provides no information on \( h(B) \).

5.2. Critical ancestors. A vertex \( A \in \mathcal{O} \) is a critical ancestor of a vertex \( B \in \mathcal{O} \) if \( h(A) < \infty \) and there is an evolution \( A \leftarrow A_1 \leftarrow \cdots \leftarrow B \) of length \( \geq 1 \) such that \( h(A_1) = h(A) + 1 \). We view critical ancestors of \( B \) as gatekeepers yielding access to higher levels in evolutions from the primitives to \( B \). It follows from Lemma 3.2 that any vertex of a finite height \( m \geq 1 \) has critical ancestors of heights \( 0, 1, \ldots, m - 1 \). Primitive vertices have no critical ancestors because all ancestors of a primitive vertex are primitive and have zero height. So, the equality \( h(A_1) = h(A) + 1 \) above cannot hold.

A critical ancestor of a vertex \( B \in \mathcal{O} \) is necessarily a critical ancestor of all descendants of \( B \). Consequently, isotypic vertices have the same critical ancestors.

5.3. Normal vertices. We call a vertex \( B \in \mathcal{O} \) normal if any two critical ancestors of \( B \) of the same height are isotypic. For instance, all primitive vertices are normal simply because they have no critical ancestors.

Lemma 5.1. The normality of a vertex is anti-hereditary. Vertices isotypic to a normal vertex are normal.

Proof. If \( B \) is a descendant of \( A \), then all critical ancestors of \( A \) are critical ancestors of \( B \). Consequently, if \( B \) is normal, then so is \( A \). The second claim of the lemma follows from the first claim. \( \Box \)

Theorem 5.2. Any normal vertex of finite height is phylogenetic.
Proof. Let $X$ be a normal vertex of finite height $m$. If $m = 0$, then $X$ is primitive and therefore phylogenetic. Assume that $m \geq 1$ and pick a short full evolution $\alpha = (A_0 \leftarrow \cdots \leftarrow A_m)$ for $X = A_m$. We will prove that $\alpha$ is universal, i.e., that $\alpha$ embeds in any full evolution $\beta = (B_0 \leftarrow \cdots \leftarrow B_n)$ for $X = B_n$. Since $\beta$ starts at a vertex of zero height and terminates at a vertex of height $m$, the step inequality implies that for each $k = 0, 1, \ldots, m - 1$, there is $r \in \{0, 1, \ldots, n - 1\}$ such that $h(B_r) = k$ and $h(B_{r+1}) = k + 1$. Let $r_k$ be the smallest such $r$. Also, set $r_m = n$. Since the segment $B_0 \leftarrow \cdots \leftarrow B_{r_k}$ of $\beta$ starts from a vertex of zero height and terminates at a vertex of height $k$, the same argument as above shows that if $k > 0$, then there is an index $r < r_k$ such that $h(B_r) = k - 1$ and $h(B_{r+1}) = k$. On the other hand, $r_{k-1}$ is the smallest such index. Therefore $r_{k-1} \leq r < r_k$. Hence, $r_0 < r_1 < \cdots < r_m$. We claim that $A_k \sim B_{r_k}$ for $k = 0, 1, \ldots, m$. For $k = m$, this is obvious because $A_m = X = B_n = B_{r_m}$. For $k < m$, Lemma 3.2 and the definition of $r_k$ imply that both $A_k$ and $B_{r_k}$ are critical ancestors of $X$ of height $k$. By the normality of $X$, we have $A_k \sim B_{r_k}$. Therefore, $\alpha$ embeds in $\beta$. 

5.4. Examples. In Example 3.3.3, the vertex $A$ is primitive and has no critical ancestors. The vertex $B$ has $A, B$ as critical ancestors. This is clear from the evolutions $A \leftarrow B$ and $B \leftarrow C \leftarrow B$. The vertex $C$ is not a critical ancestor of $B$ because this quiver does not have a vertex with height $h(C) + 1 = 3$. The vertex $C$ is isotypic to $B$ and therefore has the same critical ancestors $A, B$. In this example and in Examples 3.3.1, 3.3.2, 3.3.2, all vertices are normal. The quiver in Example 3.3.4 has no normal vertices and its vertices have no critical ancestors.

6. Monotonous and phylogenetic quivers

We introduce monotonous and phylogenetic quivers.

6.1. Monotonous quivers. The height of a vertex may decrease under certain evolutions, and we view such evolutions as degenerate. We call a quiver $\mathcal{O}$ monotonous if it does not have such degenerate evolutions, i.e., if for any edge $A \rightarrow B$ in $\mathcal{O}$, we have $h(A) \geq h(B)$. This condition may be reformulated by saying that the descendants of any vertex $B \in \mathcal{O}$ have the height $\geq h(B)$. A useful consequence: in a monotonous quiver, isotypic vertices have the same height. For monotonous quivers we can invert Theorem 5.2 as follows.

Theorem 6.1. A vertex of a monotonous quiver is phylogenetic if and only if it is normal and has finite height.

Proof. In view of Theorem 5.2 it suffices to prove the “only if” part. Consider a phylogenetic vertex $X$ of a monotonous quiver and a universal evolution $\alpha = (A_0 \leftarrow \cdots \leftarrow A_m)$ for $X = A_m$ where $m = h(X) < \infty$. The evolution $\alpha$ is short, and so, by Lemma 3.2, the vertices $A_0, A_1, \ldots, A_{m-1}$ are critical ancestors of $X$ of heights respectively $0, 1, \ldots, m - 1$. To prove the normality of $X$, consider an arbitrary critical ancestor $B$ of $X$ of height $r < \infty$. By the definition of a critical ancestor, there is an evolution $\beta = (B \leftarrow B_1 \leftarrow \cdots \leftarrow X)$ with $h(B_1) = r + 1$. By
the monotonicity, all vertices in $\beta$ except $B$ have the height $\geq h(B_1) > r$. Pick any short full evolution $\gamma$ for $B$. By Lemma 5.2, all vertices in $\gamma$ except $B$ have height $< r$. Concatenating $\gamma$ with $\beta$, we obtain a full evolution $\gamma \beta$ for $X$ whose only vertex of height $r$ is $B$. Since the universal evolution $\alpha$ must embed in $\gamma \beta$, we have $A_r \sim B$. Thus, $X$ is normal. □

It is clear that in a monotonous quiver, the property of a vertex to have finite height is anti-hereditary. Combining this observation with Lemma 5.1 and Theorem 6.1, we obtain the following.

Corollary 6.2. In a monotonous quiver, the phylogeneticity of a vertex is anti-hereditary.

Theorem 6.1 and Lemma 3.2 imply the following claim.

Corollary 6.3. In a monotonous quiver, a phylogenetic vertex $X$ has precisely $h(X)$ isotypy classes of critical ancestors.

Proof. Consider universal evolutions $A_0 \leftarrow \cdots \leftarrow A_m$ and $B_0 \leftarrow \cdots \leftarrow B_m$ for isotypic phylogenetic vertices $X = A_m$, $Y = B_m$ of height $m$. For any $k = 0, 1, \ldots, m-1$, the critical ancestors $A_k$ of $X$ and $B_k$ of $Y$ have the same height $k$. Since $X \sim Y$, the vertex $B_k$ is also a critical ancestor of $X$. By Theorem 6.1, $X$ is normal and therefore $A_k \sim B_k$. Also, $A_m = X \sim Y = B_m$. □

6.2. Phylogenetic quivers. A quiver is phylogenetic if it is monotonous and all its vertices are phylogenetic. Theorem 6.1 shows that a quiver is phylogenetic if and only if it is monotonous and all its vertices are normal and have finite height.

It is easy to check that the quivers $SET$ and $S$ from Section 2.5 as well as the tree quiver $O(\Gamma)$ from Section 3.3.2 are phylogenetic. Further examples of phylogenetic quivers can be derived from various algebraic theories involving filtrations. As a specific case, we consider a quiver of finite nilpotent groups.

(Similar phylogenetic quivers can be formed from finite solvable groups and from nilpotent/solvable finite-dimensional Lie algebras.) Recall the lower central series $G_0 \supset G_1 \supset \cdots$ of a group $G$: by definition, $G_0 = G$ and for $n \geq 0$, the group $G_{n+1} \subset G_n$ is generated by the commutators $xyx^{-1}y^{-1}$ with $x \in G_n$ and $y \in G$. The group $G$ is nilpotent if $G_n = \{1\}$ for some $n \geq 0$, and the smallest such $n$ is denoted $n(G)$. Let $\mathcal{N}$ be the quiver formed by finite nilpotent groups and group epimorphisms $f : G \to H$ such that $n(G) \geq 1$ and $\text{Ker}(f) \subset G_{n(G)-1}$. It is easy to check that: groups in $\mathcal{N}$ are isotypic if and only if they are isomorphic; a group in $\mathcal{N}$ is primitive as a vertex if and only if it is trivial; for any $G \in \mathcal{N}$, the sequence of quotient groups and projections

$$
\{e\} = G/G_0 \leftarrow G/G_1 \leftarrow \cdots \leftarrow G/G_{n(G)} = G
$$

is a universal evolution for $G$. The quiver $\mathcal{N}$ is phylogenetic.
6.3. **Remark.** Any monotonous quiver $\mathcal{O}$ determines a quiver $\mathcal{O}'$ consisting of all phylogenetic vertices of $\mathcal{O}$ and all edges between them in $\mathcal{O}$. It is easy to show using Corollary 6.2 that the quiver $\mathcal{O}'$ is phylogenetic.

7. **THE EVOLUTIONARY SEQUENCE AND THE EVOLUTIONARY FOREST**

7.1. **The evolutionary sequence.** Here we restrict ourselves to so-called small quivers. We call a quiver small if the isotypy classes of its vertices form a set. This condition is satisfied in all our examples.

Consider a small phylogenetic quiver $\mathcal{O}$ and let $\tilde{\mathcal{O}}$ be the set of isotypy classes of vertices of $\mathcal{O}$. Each vertex $A \in \mathcal{O}$ represents an element $[A]$ of $\tilde{\mathcal{O}}$. Two vertices $A, B \in \mathcal{O}$ represent the same element of $\tilde{\mathcal{O}}$ if and only if $A \sim B$. The relation $\leq$ in the class of vertices of $\mathcal{O}$ induces a relation $\leq$ in $\tilde{\mathcal{O}}$: for $a, b \in \tilde{\mathcal{O}}$, we set $a \leq b$ if $A \leq B$ for some (and then for all) $A, B \in \mathcal{O}$ representing respectively $a$ and $b$. The relation $\leq$ in $\tilde{\mathcal{O}}$ is a partial order, i.e., it is reflexive, transitive, and antisymmetric (if $a \leq b$ and $b \leq a$, then $a = b$). Clearly, $\tilde{\mathcal{O}} = \bigcup_{m \geq 0} \mathcal{O}_m$ where $\mathcal{O}_m$ is the set of isotypy classes of vertices of $\mathcal{O}$ of height $m$. In particular, $\mathcal{O}_0$ is the set of isotypy classes of primitive vertices of $\mathcal{O}$.

For each $m \geq 1$, we define the *parental map*

$$p = p_m : \mathcal{O}_m \rightarrow \mathcal{O}_{m-1}$$

as follows. For any $A \in \mathcal{O}$ of height $m \geq 1$, consider a universal evolution $A_0 \leftarrow \cdots \leftarrow A_{m-1} \leftarrow A_m = A$ and set $p([A]) = [A_{m-1}]$. By Corollary 6.4 this yields a well-defined map (7.1.1). The resulting sequence of sets and maps

$$\mathcal{O}_0 \leftarrow p \mathcal{O}_1 \leftarrow p \mathcal{O}_2 \leftarrow p \mathcal{O}_3 \leftarrow \cdots$$

is called the *evolutionary sequence* of $\mathcal{O}$.

**Theorem 7.1.** Let $a \in \mathcal{O}_m$ and $b \in \mathcal{O}_n$ with $m, n \geq 0$. Then:

(i) $a \leq b$ if and only if $m \leq n$ and $a \leq p^{n-m}(b) \in \mathcal{O}_m$;

(ii) For $m \geq n = 0$, we have $a \leq b \iff a = b$;

(iii) For $m = n \geq 1$, if $a \leq b$, then $p(a) = p(b) \in \mathcal{O}_{m-1}$;

(iv) For $m = n - 1$, the equality $a = p(b)$ holds if and only if there is an edge $B \rightarrow A$ in $\mathcal{O}$ such that $A, B \in \mathcal{O}$ represent respectively the isotypy classes $a, b$.

Theorem 7.1 is proved below. Note that by Claim (i), the partial order in $\tilde{\mathcal{O}}$ is fully determined by its restrictions to the sets $\{\mathcal{O}_m\}_m$ and the parental maps.

7.2. **Proof of Theorem 7.1** We begin with a lemma.

**Lemma 7.2.** Let $\alpha = (A_0 \leftarrow \cdots \leftarrow A_m)$ and $\beta = (B_0 \leftarrow \cdots \leftarrow B_n)$ be universal evolutions for vertices $A_m, B_n$ in a monotonous quiver such that $A_m \leq B_n$. If $m = n$, then $A_{m-1} \sim B_{n-1}$. If $m < n$, then $A_m \leq B_{n-1}$.

**Proof.** By Lemma 3.2, $h(A_k) = k$ for all $k \leq m$ and $h(B_l) = l$ for all $l \leq n$. Since $A_m \leq B_n$, there is an evolution $\gamma$ from $A_m$ to $B_n$, and then $\alpha \gamma$ is an evolution from $A_0$ to $B_n$. Since $\beta$ is universal, it embeds in $\alpha \gamma$. So, $B_{n-1}$ is isotypic to a vertex in $\alpha \gamma$ of the same height $n - 1$ (here we use the monotonicity of the
quiver). Clearly, all vertices in $\gamma$ have height $\geq h(A_m) = m$. If $m = n$, then the only vertex of height $n - 1 = m - 1$ in $\alpha\gamma$ is $A_{m-1}$. Thus, $A_{m-1} \sim B_{n-1}$. If $m < n$, then all vertices in $A$ other than $A_m$ have height $m \leq n - 1$. In this case, $B_{n-1}$ has to be isotypic to a vertex, $C$, appearing in the evolution $\gamma$, and so $A_m \leq C \leq B_{n-1}$ and $A_m \leq B_{n-1}$.

We now prove Theorem 7.1. We start with Claim (i). Suppose that $a \leq b$. By the monotonicity, $m \leq n$. If $m = n$, then $a \leq b = p^{n-m}(b)$. If $m < n$, then the second claim of Lemma 7.2 implies that $a \leq p(b)$. Iterating, we get $a \leq p^{n-m}(b)$. Conversely, suppose that $m \leq n$ and $a \leq p^{n-m}(b)$. It follows from the definitions that $p(b) \leq b$ for all $b$. Hence,

$$a \leq p^{n-m}(b) \leq p^{n-m-1}(b) \leq \cdots \leq p(b) \leq b.$$  

Claim (ii) holds because any vertex of zero height is primitive and so is isotypic to all its ancestors. Claim (iii) follows from the first claim of Lemma 7.2. We prove Claim (iv). If $p(b) = a$, then pick a representative $B \in \mathcal{O}$ of $b$ and a universal evolution $B_0 \leftarrow \cdots \leftarrow B_{n-1} \leftarrow B_n = B$. The edge $B_{n-1} \leftarrow B_n$ satisfies our conditions because $[B_{n-1}] = p(b) = a$. Conversely, suppose that there is an edge $A \leftarrow B$ in $\mathcal{O}$ such that $A, B$ represent respectively $a, b$. Concatenating a short full evolution for $A$ with the 1-edge evolution $A \leftarrow B$, we obtain a full evolution $\cdots \leftarrow A \leftarrow B$ of length $h(A) + 1 = m - 1 = n = h(B)$. This evolution is short and, by Theorem 4.1(iii), universal. Therefore $p(b) = [A] = a$.

7.3. The evolutionary forest. Any sequence of sets and maps

$$P_0 \leftarrow P_1 \leftarrow P_2 \leftarrow P_3 \leftarrow \cdots$$

determines a graph $\Gamma$: take the disjoint union $\bigcup_{m \geq 0} P_m$ as the set of vertices and connect each $a \in P_m$ with $m \geq 1$ to $P(a) \in P_{m-1}$ by an edge. This graph is a forest in the sense that all its components are trees. Clearly, every component of $\Gamma$ has a unique vertex in $P_0$. If $\text{card}(P_0) = 1$, then $\Gamma$ is a tree. In this case we define a metric $d$ in the set $\bigcup_{m \geq 0} P_m$: For any elements $a, b$ of this set, the distance $d(a, b)$ is the minimal number of edges in a path in $\Gamma$ from $a$ to $b$. Clearly, $d(a, b) = k + l$ where $k, l \geq 0$ are minimal integers such that $p^k(a) = p^l(b)$. Note that for each $m \geq 0$, the restriction of $d$ to the set $P_m$ takes only even values and is an ultrametric (the definition of an ultrametric is recalled in Section 10.1).

Applying these constructions to the evolutionary sequence (7.1.2), we obtain a forest called the evolutionary forest of the quiver $\mathcal{O}$. If $\text{card}(\mathcal{O}_0) = 1$, i.e., if all primitive vertices of $\mathcal{O}$ are isotypic, then we also obtain a metric in the set $\mathcal{O}$ of isotypy classes of vertices of $\mathcal{O}$.

7.4. Examples. The evolutionary forest of the quiver $\mathcal{SET}$ is a single point. The evolutionary forest of the quiver $\mathcal{S}$ from Example 2.5.2 is a wedge of a countable number of segments. The evolutionary forest of the tree quiver $\Gamma$ from Example 3.3.2 can be identified with $\Gamma$. 
8. **E-sequences and Reconstruction**

8.1. **E-sequences.** Axiomatizing the properties of the evolutionary sequences, we define so-called E-sequences. An E-sequence consists of partially ordered sets \((P_m, \leq)_{m \geq 0}\) and maps \((p = p_m : P_m \to P_{m-1})_{m \geq 1}\) such that the partial order in \(P_0\) is trivial and for any \(a, b \in P_m\) with \(m \geq 1\), if \(a \leq b\), then \(p(a) = p(b)\). We will sometimes use the strict partial order \(<\) in \(P_m\) defined by \(a < b\) if \(a \leq b\) and \(a \neq b\).

Two E-sequences \(P, P'\) are isomorphic if there are bijections \(\{f_m : P_m \to P'_m\}_{m \geq 0}\) such that for all \(m \geq 1\), we have \(p'f_m = f_{m-1}p : P_m \to P'_{m-1}\) and \(f_m\) is order-preserving in the sense that \(a \leq b \iff f_m(a) \leq f_m(b)\) for any \(a, b \in P_m\).

By Theorem 7.1 the evolutionary sequence of a small phylogenetic quiver is an E-sequence. We show now that all E-sequences arise in this way.

**Theorem 8.1.** Every E-sequence is isomorphic to the evolutionary sequence of a small phylogenetic quiver.

*Proof. Given an E-sequence \(P\), we define a quiver \(O\) as follows. The vertices of \(O\) are the elements of the set \(\Pi_{m \geq 0} P_m\). For all \(a, b \in P_m\) with \(m \geq 0\), there is a single edge \(a \to b\) if \(b < a\) and a single edge \(a \to p(a) \in P_{m-1}\) if \(m \geq 1\). We claim that the quiver \(O\) is phylogenetic. A typical evolutionary chain in \(O\) starts at some \(a_0 \in P_m\) with \(m \geq 0\) and consecutively takes bigger and bigger elements \(a_0 < a_1 < \cdots\) of \(P_m\). At some step, one either stops at \(a_i \in P_m\) or proceeds to the higher level by taking for \(a_i + 1\) any element of the set \(p^{-1}(a_i) \subset P_{m+1}\) (if this set is non-void). Then the whole process is repeated starting at \(a_{i+1}\), etc. (One has to stop eventually.) The antisymmetry of the partial order implies that an evolution in \(O\) of non-zero length cannot start and end at the same vertex. Consequently, isotypic vertices of \(O\) must coincide so that \(O\) is small and \(\tilde{O} = \Pi_{m \geq 0} P_m\). The primitive vertices of \(O\) are the elements of \(P_0\) (here we use that the partial order in \(P_0\) is trivial). All full evolutions for any \(a \in P_m\) with \(m \geq 1\) start at \(p^m(a) \in P_0\) and include the vertices \(\{p^k(a)\}_{k=1}^m\). Therefore the full evolution

\[
p^m(a) \leftarrow p^{m-1}(a) \leftarrow \cdots \leftarrow p(a) \leftarrow a
\]

is universal for \(a\). As a consequence, \(h(a) = m\) and \(O_m = P_m\). Therefore the quiver \(O\) is monotonous and all its vertices are phylogenetic. It is clear that the evolutionary sequence of \(O\) is isomorphic to \(P\). \qed

8.2. **Reconstruction.** The main objective of phylogenetics is to recover the evolutionary tree from the current generation of species. We briefly discuss reconstruction in our context. The reconstruction aims to recover the initial segment

\[
(8.2.1) \quad P_0 \leftarrow^p P_1 \leftarrow^p \cdots \leftarrow^p P_N
\]

of an E-sequence from the set \(P_N\), eventually endowed with additional data. For simplicity, we assume here that \(\text{card}(P_0) = 1\) and all the maps \(p\) are surjective. One well-known approach to reconstruction uses the ultrametric \(\rho\) in \(P_N\) defined by letting the distance \(\rho(a, b)\) between any \(a, b \in P_N\) to be the minimal integer \(k \geq 0\) such that \(p^k(a) = p^k(b)\). (Note that \(\rho(a, b) = \frac{1}{2}d(a, b)\) where \(d\) is the metric defined in Section 7.3.) The sets and maps (8.2.1) can be fully recovered from
the ultrametric space \((P_N, \rho)\). Namely, for \(s = 0, 1, \ldots, N\), the elements of \(P_s\) can be identified with balls in \(P_N\) or radius \(N - s\); for \(s \geq 1\), the map \(p : P_s \to P_{s - 1}\) carries a ball \(B \subset P_N\) or radius \(N - s\) to the unique ball of radius \(N - s + 1\) in \(P_N\) containing \(B\). Next, we encode in terms of \(P_N\) the given strict partial order \(<\) in \(P_1, \ldots, P_N\). This partial order induces a binary relation \(\prec\) in \(P_N\) by the rule \(a \prec b\) if \(a \neq b\) and \(p^{k - 1}(a) < p^{k - 1}(b)\) for \(k = \rho(a, b) \geq 1\). Conversely, the strict partial order \(<\) in \(P_1, \ldots, P_N\) can be fully recovered from \(\prec\) and \(\rho\): two balls \(B, B' \subset P_N\) of the same radius \(r\) satisfy \(B < B'\) if and only if \(a \prec b\) and \(\rho(a, b) = r + 1\) for some (and then for all) \(a \in B, b \in B'\). In particular, for \(r = 0\), two points \(a, b \in P_N\) satisfy \(a \prec b\) if and only if \(a \prec b\) and \(\rho(a, b) = 1\).

8.3. Remark. So far we have studied evolutions in a static world in which all vertices (species) coexist together. To relate to the real world, we briefly discuss the timeline. One way to involve time is to accept the following three principles:

(i) (the moment zero) all primitive vertices come to existence at the same moment of time, the moment zero;

(ii) (the molecular clock) the time needed for an accomplishment of an evolutionary chain is equal to a constant coefficient \(C\) times the length of the chain;

(iii) (the least wait) every non-primitive vertex comes to existence at the earliest possibility, i.e., at the end of a short full evolution.

These principles ensure that each vertex \(X\) of a phylogenetic quiver \(\mathcal{O}\) evolves in the moment of time \(C \cdot h(X)\). The sequence (7.1.2) is then the sequence of generations: each set \(\mathcal{O}_m\) with \(m \geq 0\) is the generation of vertices that have evolved at the moment of time \(Cm\).

The principles (i) and (ii) above can be generalized by agreeing that (i)' each primitive vertex comes to existence at a certain moment of time (not necessarily the same) and (ii)' each edge carries a positive length and the length of any evolution is the sum of the lengths of the constituent edges.

8.4. Remark. A binary relation \(\prec\) in an ultrametric space \((X, \rho)\) arises as in Section 5.2 from the initial segment of length \(N \geq 1\) of an \(E\)-sequence iff

(i) the ultrametric \(\rho\) takes values in the set \(\{0, 1, \ldots, N\}\);

(ii) \(a \prec b \implies b \not\prec a\) for all \(a, b \in X\) (in particular, \(a \not\prec a\) for all \(a \in X\));

(iii) for any distinct \(a, b, c \in X\),

- if \(a \prec b\) and \(\rho(a, c) \prec \rho(a, b)\), then \(c \prec b\);
- if \(a \prec b\) and \(\rho(b, c) \prec \rho(a, b)\), then \(a \prec c\);
- if \(a \prec b \prec c\) and \(\rho(a, b) = \rho(a, c) = \rho(b, c)\), then \(a \prec c\).

9. Clades in phylogenetic quivers

9.1. Clades. Any vertex \(A\) of a quiver \(\mathcal{O}\) determines a quiver \(\mathcal{O}_A\) formed by all descendants of \(A\) and all edges between them in \(\mathcal{O}\). Following the standard taxonomic terminology, we call \(\mathcal{O}_A\) the clade of \(A\). Clearly, \(A \in \mathcal{O}_A\). We state a few properties of \(\mathcal{O}_A\).

Lemma 9.1. The primitive vertices of \(\mathcal{O}_A\) are all the vertices of \(\mathcal{O}\) isotypic to \(A\). In particular, \(A\) is a primitive vertex of \(\mathcal{O}_A\).
Proof. If $B \in \mathcal{O}_A$ is primitive in $\mathcal{O}_A$, then the relation $A \leq B$ implies that $B \leq A$, i.e., that $A, B$ are isotypic in $\mathcal{O}$. Conversely, if $B \in \mathcal{O}$ is isotypic to $A$, then $B \in \mathcal{O}_A$ and for any $C \in \mathcal{O}_A$, we have $B \leq A \leq C$ so that $B \leq C$. Thus, $B$ is primitive as a vertex of $\mathcal{O}_A$. \hfill \Box

**Lemma 9.2.** All vertices of $\mathcal{O}_A$ have finite height in $\mathcal{O}_A$.

**Proof.** Since $A$ is primitive in $\mathcal{O}_A$ and all vertices of $\mathcal{O}_A$ are terminal vertices of evolutions starting at $A$, all vertices of $\mathcal{O}_A$ have final height. \hfill \Box

The heights of vertices in the quivers $\mathcal{O}$ and $\mathcal{O}_A$ will be denoted respectively by $h$ and $h_A$. The following theorem estimates $h_A$ via $h$ for monotonous $\mathcal{O}$.

**Theorem 9.3.** If $A$ is a vertex of finite height in a monotonous quiver $\mathcal{O}$, then for all $B \in \mathcal{O}_A$ we have $\infty > h(B) \geq h(A)$ and $h_A(B) \geq h(B) - h(A)$.

**Proof.** The inequalities $\infty > h(B) \geq h(A)$ follow from the definitions of Section 9.2 and the monotonicity of $\mathcal{O}$. By Lemmas 9.1 and 9.2, there is a short full evolution, $\beta$, in $\mathcal{O}_A$ starting at a vertex $C \in \mathcal{O}$ isotypic to $A$ and terminating at $B$. We have $h(C) = h(A) < \infty$ so that there is a short full evolution, $\gamma$, for $C$ in $\mathcal{O}$. Then $\gamma \beta$ is a full evolution for $B$ in $\mathcal{O}$ of length $h(C) + h_A(B) = h(A) + h_A(B)$. Therefore $h(A) + h_A(B) \geq h(B)$ and $h_A(B) \geq h(B) - h(A)$. \hfill \Box

9.2. **Regular vertices.** We call a vertex $A$ of a quiver $\mathcal{O}$ regular if for any $B \in \mathcal{O}_A$ with $h(A) = h(B)$, there is an edge $A \leftarrow B$ in $\mathcal{O}$. This condition is a very weak form of a composition law in $\mathcal{O}$: it may be rephrased by saying that if there is a finite chain of edges $A \leftarrow \cdots \leftarrow B$ in $\mathcal{O}$ and $h(A) = h(B)$, then there is an edge $A \leftarrow B$ in $\mathcal{O}$. The reader may check that in our examples of phylogenetic quivers all vertices are regular.

We now state the main result of this section.

**Theorem 9.4.** The clade of any regular vertex of a small phylogenetic quiver is a small phylogenetic quiver.

The proof of this theorem occupies the rest of the section.

9.3. **Lemmas.** Consider a vertex $A$ of a small phylogenetic quiver $\mathcal{O}$ and a vertex $B \in \mathcal{O}_A$. Set $m = h(A) \geq 0$ and $n = h(B)$. By Theorem 9.3, we have $n \geq m$ and $h_A(B) \geq n - m$. Recall the isotypy classes $[A] \in \mathcal{O}_m$, $[B] \in \mathcal{O}_n$, and the iterated parental map $p^{n-m} : \mathcal{O}_n \to \mathcal{O}_m$.

**Lemma 9.5.** If $p^{n-m}([B]) = [A]$, then $B$ is a phylogenetic vertex of $\mathcal{O}_A$ and $h_A(B) = n - m$.

**Proof.** Suppose first that $n = m$. Then the condition $p^{n-m}([B]) = [A]$ means that $B \sim A$. Then $B$ is primitive in $\mathcal{O}_A$ by Lemma 9.1. Therefore $h_A(B) = 0 = n - m$ and $B$ is phylogenetic in $\mathcal{O}_A$. Suppose now that $n > m$. Pick universal evolutions $\alpha$ for $A$ and $\beta = (B_0 \leftarrow \cdots \leftarrow B_n = B)$ for $B$ in $\mathcal{O}$. The condition $p^{n-m}([B]) = [A]$ implies that $B_n \sim A$. Then the terminal segment $\beta^n = (B_m \leftarrow \cdots \leftarrow B_n)$ of $\beta$ is a full evolution in $\mathcal{O}_A$ for $B$ of length $n - m$. For any evolution $\gamma$ from $A$ to $B$ in $\mathcal{O}$, the universal evolution $\beta$ must embed in $\alpha \gamma$. 

Theorem 7.1(iii) implies that \( B \) in \( O_A \). So, \( B \) is a phylogenetic vertex of \( O_A \) and \( h_A(B) = n - m \).

Lemma 9.6. If \( p^{n-m}([B]) \neq [A] \) and \( A \) is regular, then \( B \) is a phylogenetic vertex of \( O_A \) and \( h_A(B) = n - m + 1 \).

Proof. Suppose first that \( n = m \). Then the condition \( p^{n-m}([B]) \neq [A] \) means that \( A \) and \( B \) are not isotypic in \( O \). By Lemma 9.1 \( B \) is not a primitive vertex of \( O_A \) and so \( h_A(B) \geq 1 \). Since \( B \in O_A \), there is an evolution from \( A \) to \( B \) in \( O \) of non-zero length. The regularity of \( A \) and the assumption \( h(B) = n = m = h(A) \) imply that there is an edge \( A \leftarrow B \) in \( O \). This edge yields a universal evolution for \( B \) in \( O_A \) of length 1. Thus, \( B \) is a phylogenetic vertex of \( O_A \) and \( h_A(B) = 1 = n - m + 1 \).

Suppose now that \( n > m \). Pick a universal evolution \( \beta = (B_0 \leftarrow \cdots \leftarrow B_n) \) for \( B = B_n \) in \( O \) and an arbitrary evolution \( \gamma = (A_0 \leftarrow \cdots \leftarrow A_k) \) from \( A = A_0 \) to \( B = A_k \) in \( O \) (for some \( k \geq 0 \)). The same argument as in the proof of the previous lemma shows that the terminal segment \( \beta^m = (B_m \leftarrow \cdots \leftarrow B_n) \) of \( \beta \) embeds in \( \gamma \). In particular, \( B_m \sim A_i \) for some \( i \). So \( A \leq A_i \leq B_m \) and \( B_m \in O_A \). The condition \( p^{n-m}([B]) \neq [A] \) implies that \( B_m \) and \( A = A_0 \) are not isotypic, i.e., \( i \neq 0 \). Therefore there is an evolution from \( A = A_0 \) to \( B_m \sim A_i \) in \( O \) of length \( \geq i \neq 0 \). The regularity of \( A \) and the equalities \( h(B_m) = m = h(A) \) imply that there is an edge \( A \leftarrow B_m \) in \( O \). Concatenating this edge with \( \beta^m \), we obtain an evolution \( \beta^m \) from \( A \) to \( B = B_n \) of length \( n - m + 1 \). By the above, \( \beta^m \) embeds in \( \gamma \). Therefore, \( \beta^m \) is a universal evolution for \( B \in O_A \), \( B \) is phylogenetic in \( O_A \), and \( h_A(B) = n - m + 1 \).

9.4. Proof of Theorem 9.4. Let \( A \) be a regular vertex of a phylogenetic quiver \( O \). Since \( O \) is small, so is the clade \( O_A \) of \( A \). In view of Lemmas 9.5 and 9.6 we need only to prove that \( O_A \) is monotous, i.e., that \( h_A(B) \leq h_A(C) \) for any \( B, C \in O_A \) such that there is an edge \( B \leftarrow C \) in \( O \). Set \( m = h(A), n = h(B) \) and \( k = h(C) \). By the monotonicity of \( O \) and the definition of the height,

\[
m \leq n \leq k \leq n + 1.
\]

We distinguish three cases.

Case \( m = n = k \). If \( A \sim B \), then \( h_A(B) = 0 \leq h_A(C) \). If \( A \sim C \), then \( A \leq B \leq C \leq A \) so that \( A \sim B \) and we proceed as above. If neither \( B \) nor \( C \) are isotypic to \( A \), then Lemma 9.6 applies to \( B, C \) and gives \( h_A(B) = 1 = h_A(C) \).

Case \( m < n \). Since there is an edge \( B \leftarrow C \) in \( O \) and \( h(B) = n = k = h(C) \), Theorem 7.1(iii) implies that \( p([B]) = p([C]) \). Therefore \( p^{n-m}([B]) = p^{n-m}([C]) \).

Then either \( p^{n-m}([B]) = [A] \) and Lemma 9.5 gives

\[
h_A(B) = n - m = k - m = h_A(C)
\]
or \( p^{n-m}([B]) \neq [A] \) and Lemma 9.5 gives

\[
h_A(B) = n - m + 1 = k - m + 1 = h_A(C).
\]
Case $k = n + 1$. Concatenating a universal evolution for $B$ in $O$ with the edge $B \leftarrow C$ we obtain a short full evolution for $C$ in $O$. The latter evolution is universal and so $p([C]) = [B]$. Therefore $p^{n-m}([B]) = p^{n-m+1}([C])$. If $p^{n-m}([B]) = [A]$, then Lemma 9.5 gives

$$h_A(B) = n - m \text{ and } h_A(C) = k - m.$$ 

If $p^{n-m}([B]) \neq [A]$, then Lemma 9.6 gives

$$h_A(B) = n - m + 1 \text{ and } h_A(C) = k - m + 1.$$ 

In both cases, $h_A(B) < h_A(C)$.

10. The quiver of finite ultrametric spaces

We form a phylogenetic quiver from finite ultrametric spaces. We first recall the definition of an ultrametric space.

10.1. Ultrametrics and contractions. A metric space is a pair $(X, d)$ consisting of a non-empty set $X$ and a map $d : X \times X \to \mathbb{R}_+ = [0, \infty)$, the metric, such that for all $x, y, z \in X$, we have $d(x, y) = d(y, x)$, $d(x, y) = 0 \iff x = y$, and

$$(10.1.1) \quad d(x, y) \leq d(x, z) + d(y, z).$$

An isometry between metric spaces is a metric-preserving bijection. A metric space $(X, d)$ is finite if $X$ is a finite set.

An ultrametric space is a metric space $(X, d)$ such that for all $x, y, z \in X$,

$$(10.1.2) \quad d(x, y) \leq \max(d(x, z), d(y, z)).$$

The map $d$ is called then an ultrametric. The condition (10.1.2) is stronger than (10.1.1); it implies that for any $x, y, z \in X$, two of the numbers $d(x, y)$, $d(x, z)$, $d(y, z)$ are equal and are greater than or equal to the third number.

For a real number $\epsilon > 0$, we call a map $f : X \to Y$ between metric spaces $X = (X, d)$ and $Y = (Y, \rho)$ an $\epsilon$-contraction if $f(X) = Y$ and

$$(10.1.3) \quad \rho(f(x), f(y)) = d(x, y) - \epsilon$$

for any distinct $x, y \in X$. Various $\epsilon$-contractions with $\epsilon \in (0, \infty)$ are collectively called contractions. Contractions are surjective but not necessarily bijective. The composition of two contractions is not necessarily a contraction.

**Theorem 10.1.** Let $U$ be the quiver whose vertices are finite ultrametric spaces and whose edges are contractions and isometries. Then:

(i) Two finite ultrametric spaces are isotypic to each other in $U$ if and only if they are isometric;

(ii) A finite ultrametric space is a primitive vertex of $U$ if and only if it consists of a single point;

(iii) The height of a finite ultrametric space $X = (X, d)$ in $U$ is equal to the number of non-zero elements in the set $d(X \times X) \subset \mathbb{R}_+$;

(iv) The quiver $U$ is phylogenetic;

(v) All vertices of $U$ are regular.
The proof of Theorem 10.1 occupies the rest of the section. We begin with notation and a lemma. For a finite metric space \( X = (X, d) \), set

\[
||X|| = \sum_{x,y \in X} d(x, y) = \sum_{x,y \in X, x \neq y} d(x, y).
\]

If \( \text{card}(X) \geq 2 \), then set

\[
|X| = \min\{d(x, y) \mid x, y \in X, x \neq y\}.
\]

**Lemma 10.2.** Let \( f : X \to Y \) be an \( \varepsilon \)-contraction between finite metric spaces \( X = (X, d) \) and \( Y = (Y, \rho) \) where \( \varepsilon > 0 \). If \( \text{card}(Y) \geq 2 \), then \( ||Y|| < ||X|| \). If \( f \) is not a bijection, then \( \text{card}(X) \geq 2 \) and \( |X| = \varepsilon \).

**Proof.** Since \( f(X) = Y \), we can pick for each \( a \in Y \) a point \( \overline{a} \in f^{-1}(a) \). Then

\[
||Y|| = \sum_{a, b \in Y, a \neq b} \rho(a, b) = \sum_{a, b \in Y, a \neq b} (d(\overline{a}, \overline{b}) - \varepsilon) < \sum_{a, b \in Y, a \neq b} d(\overline{a}, \overline{b}) \leq ||X||.
\]

If \( f \) is non-injective, then \( \text{card}(X) \geq \text{card}(Y) + 1 \geq 2 \) and \( f(a) = f(b) \) for some distinct \( a, b \in X \). Formula 10.1.3 implies that \( d(a, b) = \varepsilon \) and \( d(x, y) \geq \varepsilon \) for any distinct \( x, y \in X \). Hence, \( |X| = \varepsilon \). \( \square \)

### 10.2. Proof of Theorem 10.1

Since isometries are edges in \( \mathcal{U} \) and each edge determines a length-1 evolution, isometric ultrametric spaces are isotypic in \( \mathcal{U} \). Consequently, consider isotypic \( X, Y \in \mathcal{U} \). If \( \text{card}(X) = 1 \), then the condition \( Y \leq X \) implies that \( \text{card}(Y) = 1 \). If \( \text{card}(Y) = 1 \), then the condition \( X \leq Y \) implies that \( \text{card}(X) = 1 \). In both cases, \( X \) is isometric to \( Y \). Suppose that \( \text{card}(X) \geq 2 \) and \( \text{card}(Y) \geq 2 \). Since \( Y \leq X \), there is an evolution \( Y \leftarrow \cdots \leftarrow X \) in \( \mathcal{U} \). By Lemma 10.2, all edges in this evolution are isometries or \( ||Y|| < ||X|| \). Similarly, the relation \( X \leq Y \) implies that either \( X, Y \) are isometric or \( ||X|| < ||Y|| \). Since we cannot have \( ||Y|| < ||X|| < ||Y|| \), the only option is that \( X \) and \( Y \) are isometric. This implies (i).

To proceed, we define certain edges in \( \mathcal{U} \). Given \( \varepsilon \in \mathbb{R} \) and a finite ultrametric space \( X = (X, d) \) having at least two points, the formula

\[
d_\varepsilon(x, y) = \begin{cases} 0 & \text{if } x = y, \\ d(x, y) - \varepsilon & \text{if } x \neq y \end{cases}
\]
defines a map \( d_\varepsilon : X \times X \to \mathbb{R} \). If \( \varepsilon < |X| \), then \( d_\varepsilon \) is an ultrametric in \( X \) and the identity map \( \text{id}_X : (X, d) \to (X, d_\varepsilon) \) is a bijective \( \varepsilon \)-contraction. For \( \varepsilon = |X| \), the map \( d^* = d_{|X|} : X \times X \to \mathbb{R} \) satisfies all requirements on an ultrametric except one: there are distinct \( x, y \in X \) with \( d^*(x, y) = 0 \). We define a relation \( \sim_{d^*} \) in \( X \) by \( x_1 \sim_{d^*} x_2 \) if \( d^*(x_1, x_2) = 0 \). It is straightforward to check that \( \sim_{d^*} \) is an equivalence relation. Let \( Y = X/\sim_{d^*} \) be the quotient set and let \( p : X \to Y \) be the projection. Then there is a unique map \( \rho : Y \times Y \to \mathbb{R} \) such that \( d^*(x, y) = \rho(p(x), p(y)) \) for all \( x, y \in X \). The map \( \rho \) is an ultrametric. We denote the ultrametric space \( (Y, \rho) \) by \( u(X) \). Clearly, the projection \( p : X \to u(X) \) is a non-injective \( |X| \)-contraction. Applying this construction recursively, we obtain an evolution in \( \mathcal{U} \)

\[
u^n(X) \leftarrow \cdots \leftarrow \nu^2(X) \leftarrow \nu(X) \leftarrow X
\]
where \( m \) is the smallest integer such that \( u^m(X) \) has only one point. Thus, \( X \) has a 1-point ancestor. We can now prove Claim (ii) of the theorem. By the definition of \( \mathcal{U} \), the only edges from a 1-point ultrametric space \( A \) to vertices of \( \mathcal{U} \) are isometries. Thus, all ancestors of \( A \) are isometric to \( A \) and \( A \) is primitive. If \( X \in \mathcal{U} \) is primitive, then \( X \) is isotypic to all its ancestors and, in particular, is isotypic to a 1-point space. By (i), \( X \) is a 1-point space. This proves (ii).

We verify now that every vertex \( X \in \mathcal{U} \) is phylogenetic. Let \( \alpha \) be the full evolution \([10.2.1]\) for \( X \). We claim that \( \alpha \) is universal. We must show that \( \alpha \) embeds in an arbitrary full evolution for \( X \), say,

\[
\beta = (B_0 \xleftarrow{f_0} B_1 \xleftarrow{f_2} \cdots \xleftarrow{f_{n-1}} B_{n-1} \xleftarrow{f_n} B_n = X)
\]

where \( B_0 \) is a 1-point space. Note that if for some \( k = 1, \ldots, n-1 \), the edge \( f_k : B_k \rightarrow B_{k-1} \) in \( \beta \) is an isometry, then we can delete \( B_k \) from \( \beta \) and replace \( f_k, f_{k+1} \) with their composition \( f_k f_{k+1} : B_{k+1} \rightarrow B_{k-1} \) which is a contraction or an isometry depending on whether \( f_{k+1} \) is a contraction or an isometry. This gives a shorter full evolution \( \beta' \) for \( X \) which embeds in \( \beta \). It suffices to prove that \( \alpha \) embeds in \( \beta' \). Similarly, if the edge \( f_n : B_n \rightarrow B_{n-1} \) is an isometry, then we can delete \( B_{n-1} \) from \( \beta \) and replace \( f_n, f_{n-1} \) with their composition. Thus, we can reduce ourselves to the case where all edges in \( \beta \) are contractions. In the same way, we can get rid of non-bijective contractions in \( \beta \) using the obvious fact that the composition of a non-bijective \( \epsilon \)-contraction with any \( \epsilon' \)-contraction is an \( (\epsilon + \epsilon') \)-contraction. It remains therefore to treat the case where all edges in \( \beta \) are non-bijective contractions. In particular, \( f_n : X = B_n \rightarrow B_{n-1} \) is a non-bijective \( \epsilon \)-contraction for some \( \epsilon > 0 \). By Lemma \([10.2] \), \( \epsilon = |X| \). Consequently, \( B_{n-1} \) is isometric to \( u(X) \). Proceeding by induction, we obtain that \( B_{n-k} \) is isometric to \( u^k(X) \) for all \( k \geq 1 \). Since \( m \) is the smallest integer such that \( u^m(X) \) has only one point and since \( B_0 \) is the only 1-point space in the evolution \( \beta \), we conclude that \( m = n \) and that the evolutions \( \alpha \) and \( \beta \) are isotypic. In particular, \( \alpha \) embeds in \( \beta \). This proves the universality of \( \alpha \).

To prove (iii), let \( N(X) \) be the number of non-zero elements in \( d(X \times X) \subseteq \mathbb{R}_+ \). By the above, the evolution \([10.2.1]\) is universal and so \( h(X) = m \). The values of the ultrametric in \( u(X) \) are obtained from those of \( d \) by finding the smallest non-zero value of \( d \) and subtracting it from all non-zero values of \( d \). Therefore \( N(u(X)) = N(X) - 1 \). Inductively, \( N(u^k(X)) = N(X) - k \) for \( k = 1, \ldots, m \). Since \( u^m(X) \) is a 1-point set, \( 0 = N(u^m(X)) = N(X) - m \). Thus, \( h(X) = m = N(X) \).

We now prove (iv). That \( \mathcal{U} \) is small follows from (i). As we know, all vertices of \( \mathcal{U} \) are phylogenetic. For any contraction or isometry \( X \rightarrow Y \) between finite ultrametric spaces, one easily sees that \( N(X) \geq N(Y) \). Therefore \( h(X) = N(X) \geq N(Y) = h(Y) \). Thus, \( \mathcal{U} \) is monotonous.

We leave it to the reader to check that all vertices of \( \mathcal{U} \) are regular.

11. The Quiver of Finite Metric Spaces

We form a phylogenetic quiver from finite metric spaces. We start by defining trim metric spaces and drifts following \([Tu1]\), \([Tu2]\).
11.1. **Trim metric spaces.** A metric space \((X, d)\) is trim if either \(\text{card}(X) = 1\) or for each \(x \in X\), there are distinct \(y, z \in X \setminus \{x\}\) such that
\[
d(x, y) + d(x, z) = d(y, z).
\]

The latter equality may be expressed by saying that \(x\) lies between \(y\) and \(z\). The class of finite trim metric spaces is quite narrow. In particular, there are no trim metric spaces having two or three points. A finite subset of a Euclidean space with \(\geq 2\) points and with the induced metric cannot be trim: such a subset must contain a pair of points lying at the maximal distance; these points cannot lie between other points of the subset. For examples of trim metric spaces, see [Tu1], [Tu2].

With any metric space \((X, d)\), we associate a function \(d : X \to \mathbb{R}_+\) as follows: if \(X\) has only one point, then \(d = 0\); if \(X\) has two points \(x, y\), then \(d(x) = d(y) = d(x, y)/2\); if \(X\) has three or more points, then for all \(x \in X\),
\[
d(x) = \inf_{y, z \in X \setminus \{x\}, y \neq z} \frac{d(x, y) + d(x, z) - d(y, z)}{2} \geq 0.
\]

It is easy to check that \(d(x) + d(y) \leq d(x, y)\) for any distinct \(x, y \in X\), see [Tu1]. It follows from the definitions that \(d = 0\) if and only if \((X, d)\) is trim.

11.2. **Drifts.** We call a map \(f : X \to Y\) between metric spaces \(X = (X, d)\) and \(Y = (Y, \rho)\) a drift if \(f(X) = Y\) and for any distinct \(x, y \in X\),
\[
\rho(f(x), f(y)) = d(x, y) - d(x) - d(y).
\]

A drift is surjective but not necessarily bijective. If \(X\) is trim, then all drifts \(X \to Y\) are isometries. We state a version of Theorem 10.1 for metric spaces.

**Theorem 11.1.** Let \(\mathcal{M}\) be the quiver whose vertices are finite metric spaces and whose edges are drifts and isometries. Then:

(i) Two finite metric spaces are isotypic in \(\mathcal{M}\) if and only if they are isometric;

(ii) A finite metric space is a primitive vertex of \(\mathcal{M}\) if and only if it is trim;

(iii) The quiver \(\mathcal{M}\) is phylogenetic;

(iv) All vertices of \(\mathcal{M}\) are regular.

**Proof.** Recall from Section 10.1 the isometry invariant \(||X||\) of a finite metric space \(X\). It is clear that for any edge \(f : X \to Y\) in \(\mathcal{M}\), either \(||X|| > ||Y||\) or \(f\) is an isometry. If \(X, Y \in \mathcal{M}\) are isotypic, then applying this argument to the edges in an evolution \(Y \leftarrow \cdots \leftarrow X\), we obtain that either \(||X|| > ||Y||\) or all these edges are isometries. Similarly, either \(||Y|| > ||X||\) or all edges in an evolution \(X \leftarrow \cdots \leftarrow Y\) are isometries. This implies (i).

To proceed, consider a finite metric space \(X = (X, d)\) with at least two points. The formula
\[
d^* (x, y) = \begin{cases} 
0 & \text{if } x = y, \\
 d(x, y) - d(x) - d(y) & \text{if } x \neq y
\end{cases}
\]
defines a map \(d^* : X \times X \to \mathbb{R}\) which satisfies all requirements on a metric except, possibly, one: there may be distinct \(x, y \in X\) with \(d^*(x, y) = 0\). We define an equivalence relation \(\sim_{d^*}\) in \(X\) by \(x_1 \sim_{d^*} x_2\) if \(d^*(x_1, x_2) = 0\). Let \(Y = X/\sim_{d^*}\)
be the quotient set and let \( p : X \to Y \) be the projection. Then there is a unique map \( \rho : Y \times Y \to \mathbb{R} \) such that \( d^\bullet(x, y) = \rho(p(x), p(y)) \) for all \( x, y \in X \). The map \( \rho \) is a metric in \( Y \), and we denote the metric space \((Y, \rho)\) by \( v(X)\). Clearly, the projection \( X \to v(X) \) is a drift. Applying this procedure recursively, we obtain an evolution in \( \mathcal{M} \)

\[
(11.2.2) \quad v^m(X) \leftarrow \cdots \leftarrow v^2(X) \leftarrow v(X) \leftarrow X
\]

where \( m \geq 0 \) is the smallest integer such that \( v^m(X) \) is trim. (The existence of such an \( m \) follows from the fact that if a drift \( X \to Y \) is bijective, then \( Y \) is trim, cf. [Tu1], Lemma 2.1). We conclude that each vertex of \( \mathcal{M} \) has a trim ancestor.

We can now prove Claim (ii) of the theorem. By the definition of \( \mathcal{M} \), the only edges from a trim metric space \( X \) to vertices of \( \mathcal{M} \) are isometries. Thus, all ancestors of \( X \) are isometric to \( X \), and so \( X \) is primitive. Conversely, if \( X \in \mathcal{M} \) is primitive, then \( X \) is isotypic to all its ancestors. By the above, \( X \) is isotypic to a trim metric space. By (i), \( X \) is itself a trim metric space.

As in the proof of Theorem 10.1, the evolution (11.2.2) is universal, and so all vertices of \( \mathcal{M} \) are phylogenetic. We leave it to the reader to check that \( \mathcal{M} \) is monotonous and all its vertices are regular.

\[
\square
\]

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