Easy identification of generalized common nested intervals

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Abstract. In this paper we explain how to easily compute gene clusters formalized by generalized nested common intervals between a set of \(K\) genomes represented as \(K\) permutations. A \(b\)-nested common interval \(I\) of size \(|I|\) is either an interval of size 1 or contains at least another \(b\)-nested common interval of size at least \(|I| - b\). When \(b = 1\), this corresponds to the original notion of nested interval. We exhibit a simple algorithm to output all \(b\)-nested common intervals between \(K\) permutations in \(O(Kn + nocc)\) time, where \(nocc\) is the total number of such intervals. We eventually explain how to count all \(b\)-nested intervals in \(O(Kn)\) time.

1 Introduction

Comparative genomics is nowadays a classical field in computational biology, and one of its typical problems is to cluster sets of orthologous genes that have virtually the same function in several genomes. A very strong paradigm is that groups of genes which remain “close” during evolution work together. Thus, a widely used approach to obtain interesting clusters is to try to cluster genes or other biological units (for instance unique contigs of protein domains) according to their common proximity on several genomes. For this goal, many different cluster models have been proposed, like common intervals [13], conserved intervals [3], \(\pi\)-patterns [10], gene teams [2], domain teams [11], approximate common intervals [1] and so on, considering different chromosome models (permutations, signed permutations, sequences, graphs) or different distance models (accepting gaps, distance modeled as weighted graphs, etc).

Among all those models, the first which appeared, but which is still one of the most used in practice, is the concept of common interval on sequences represented by permutations. A set of genes form a common interval of \(K\) genomes if it appears as a segment on the \(K\) unsigned permutations that represent the genomes. The orders inside the segments might be totally different.

Recently, nested common intervals were introduced in [7] based on real data observation [8]. Hoberman and Durand [7] pointed that the nestedness assumption can strengthen the significance of detected clusters since it reduces the probability of observing them randomly. An \(O(n^2)\) time algorithm to compute
all nested common intervals between 2 permutations has been presented in [5] while between K permutations a recent $O(Kn + nocc)$ algorithm is proposed in [12], where nocc is the number of solutions.

In this paper, we introduce a generalization of nested common intervals, called $b$-nested common intervals (where $b$ is a positive integer), which allows for a less constraint containment between the intervals in the family. From a biological point of view, this is equivalent to both modeling clusters with a larger variability in gene content and gene order, and to allowing algorithms to deal with annotation errors. Given a set $P$ of $K$ permutations on $n$ elements representing genomes with no duplication, our simple algorithm for finding all $b$-nested common intervals of $P$ runs in $O(Kn + nocc)$-time and needs $O(n)$ additional space, where nocc is the number of solutions. In this way, our algorithm performs as well as the algorithm in [12] for the particular case of 1-nested common intervals of $K$ permutations, and proposes an efficient approach for the new classes of $b$-nested common intervals.

Moreover, a modification of our approach allows us to count the number of $b$-nested common intervals of $K$ permutations in $O(Kn)$ time.

The paper is organized as follows. In Section 2 we present the main definitions, and precisely state the problem to solve. In Section 3 we recall the data structure called a PQ-tree which allows to store the common intervals using $O(n)$ space. Sections 4 and 5 respectively present the main results and the algorithm. Section 6 explains how to linearly count the $b$-nested common intervals. Section 7 is the conclusion.

2 Generalities

A permutation $P$ on $n$ elements is a complete linear order on the set of integers $\{1,2,\ldots,n\}$. We denote $Id_n$ the identity permutation $(1,2,\ldots,n)$. An interval of a permutation $P = (p_1,p_2,\ldots,p_n)$ is a set of consecutive elements of the permutation $P$. An interval of a permutation will be denoted by giving its first and last positions, such as $[i,j]$. An interval $[i,j] = \{i,i+1,\ldots,j\}$ of the identity permutation will be simply denoted by $(i..j)$.

Definition 1. Let $P = \{P_1,P_2,\ldots,P_K\}$ be a set of $K$ permutations on $n$ elements. A common interval of $P$ is a set of integers that is an interval in each permutation of $P$.

The set $\{1,2,\ldots,n\}$ and all singletons (also called unit intervals) are always common intervals of any non-empty set of permutations. Applying the product of the inverse permutation $P_1^{-1}$ on all permutations of $P$ transforms $P_1$ into $Id_n$ while preserving common intervals. In the sequel, it is therefore assumed, for the sake of clarity, that $P_1 = Id_n$. A common interval of $P$ can thus be denoted as an interval $(i..j)$ of the identity permutation.

Definition 2. A closed family $F$ of intervals of the permutation $Id_n$ is a family that contains all singletons, the interval $(1.n)$ and that has the following prop-
erty: if \((i..k)\) and \((j..l)\) are in \(\mathcal{F}\), and \(i \leq j \leq k \leq l\), then \((i..j-1), (j..k), (k+1..l)\) and \((i..l)\) belong to \(\mathcal{F}\).

The main example of closed families of intervals is the common intervals of a set of permutations \([4]\). All what is said in this paper applies however to any closed family of intervals.

Now, \(b\)-nested common intervals are defined as follows:

**Definition 3.** Let \(\mathcal{P} := \{P_1, P_2, \ldots, P_K\}\) be a set of \(K\) permutations on \(n\) elements and let \(b\) be a positive integer. A common interval of \(\mathcal{P}\) is \(b\)-nested if either \(|I| = 1\) or \(I\) strictly contains a common interval of size at least \(|I| - b\).

We are interested in an efficient algorithm for finding all \(b\)-nested common intervals of \(\mathcal{P} := \{P_1, P_2, \ldots, P_K\}\), without redundancy. Obviously, unit intervals are, by definition, \(b\)-nested common intervals. As a consequence, from now on and without any subsequent specification, we are interested in finding \(b\)-nested common intervals of size at least 2.

### 3 PQ-tree

This section recalls the main results on the PQ-trees associated with families of intervals.

**Definition 4.** Say that an interval \((i..j)\) overlaps another interval \((k..l)\) if they intersect without inclusion, i.e. \(i < k \leq j < l\) or \(k < i \leq l < j\).

An interval \(I\) of a closed family \(\mathcal{F}\) is strong if it does not overlap any other interval of \(\mathcal{F}\), and otherwise it is weak.

Notice that \((1..n)\) and the unit intervals are always strong. The family of strong intervals of \(\mathcal{F}\) is laminar (that is, every two distinct intervals are either disjoint or included in each other) and, as \((1..n)\) belongs to the family, they form an inclusion tree that we name \(T\). Each leaf of \(T\) is labeled by a unit interval while the root is labeled by \((1..n)\). Each node \(x\) represents the strong interval, denoted \(\text{Int}(x)\), formed by the union of all leaves of the subtree it roots. We say that a node \(x\) is the parent of a weak interval \(I\) if \(\text{Int}(x)\) is the smallest strong interval containing \(I\). Two types of nodes may be defined:

- **P-nodes.** A node \(x\) is P-node if it is the parent of no weak interval. Those nodes are called round.
- **Q-nodes.** The children of a Q-node \(x\) are ordered \(y_1, y_2, \ldots, y_k\). Then \(x\) is a Q-node if for every weak interval \(I\) whose parent is \(x\), there exists \(i\) and \(j\) such that \(I = \bigcup_{z \in (i..j)} \text{Int}(y_z)\); and conversely, for each \(1 \leq i < j \leq k\), \(\bigcup_{z \in (i..j)} \text{Int}(y_z)\) is a weak interval of the family. The Q-nodes are also called square nodes.

A PQ-tree (introduced in \([6]\)) is the inclusion tree of the strong interval where each internal node \(x\) is labeled \(P\) or \(Q\). We say that a PQ-tree represents a family \(\mathcal{F}\) if

\[
\text{Int}(x) = \bigcup_{z \in \text{children}(x)} \text{Int}(y_z)
\]
every interval of $\mathcal{F}$ is either $\text{Int}(x)$ for some node $x$ of $T$ or $\bigcup_{z \in (i..j)} \text{Int}(y_z)$ for the ordered sons $y_1, y_2, ..., y_k$ of a $Q$-node
- conversely, for all nodes $x$, $\text{Int}(x) \in \mathcal{F}$ and, if $x$ is a $Q$-node with ordered sons $y_1, y_2, ..., y_k$, for each $1 \leq i \leq j \leq k$, $\bigcup_{z \in (i..j)} \text{Int}(y_z) \in \mathcal{F}$

**Theorem 1** (folklore, see for instance [9]). Given a closed family $\mathcal{F}$ of intervals, label $P$ or $Q$ may be given to each internal node of the inclusion tree on strong intervals of $\mathcal{F}$, such that the corresponding $PQ$-tree represents the family.

Notice that, while there may be a quadratic number of intervals in $\mathcal{F}$, the $PQ$-tree is stored in $O(n)$ space, and is thus a compact representation.

**Theorem 2.** [4] The construction of the $PQ$-tree of common intervals of a set $\mathcal{P}$ of $K$ permutations may be done in $O(Kn)$ time.

Let $\mathcal{P} = \{\text{Id}_n, P_2, P_3\}$,
$P_2 = (4, 2, 3, 1, 7, 8, 9, 6, 5)$
$P_3 = (5, 6, 1, 3, 2, 4, 9, 8, 7)$
The $PQ$-tree for the set of common intervals of $\mathcal{P}$ is shown on the left.

**Fig. 1.** Example of $PQ$-tree

### 4 Properties of nested intervals

Let $T$ be the $PQ$-tree of common intervals of $\mathcal{P}$, with $\text{Id}_n \in \mathcal{P}$. Say that a common interval $I$ is a $P$-interval if it is strong and there is a $P$-node $p$ with $\text{Int}(p) = I$, and its sons are $\{x_1, ..., x_r\}$. Then we set $D(I) = \{x_1, ..., x_r\}$. $I$ is a $Q$-interval if it not a $P$-interval. Then let $p$ be the parent of $I$. There exists $i, j$ such that $I = \bigcup_{z \in (i..j)} \text{Int}(p_z)$ for the ordered sons $x_1, x_2, ..., x_r$ of $p$. Then we set $D(I) = \{x_i, ..., x_j\}$.

Recalling that $\mathcal{P}$ contains $\text{Id}_n$, we then have w.l.o.g. that the elements in $\text{Int}(x_1)$ are smaller than those in $\text{Int}(x_2)$ and so on. Recall also that, for each node $x_i$ in $D(I)$, $\text{Int}(x_i)$ is either a unit interval or a strong interval. The intervals defined below are particularly useful in the sequel.

**Definition 5.** Let $\mathcal{P} = \{P_1, P_2, ..., P_K\}$ be a set of $K$ permutations on $n$ elements and let $b$ be a positive integer. A common interval of $\mathcal{P}$ is $b$-small if its size does not exceed $b$. Otherwise, the interval is $b$-large.

Notice that all $b$-small intervals are $b$-nested, by definition and since unit intervals are $b$-nested. With the aim of identifying the particular structure of $b$-nested common intervals among all common intervals, we first prove that:
Lemma 1. Let \( I \) be a \( b \)-nested common interval with \( D(I) = \{x_1, x_2, \ldots, x_r\} \), \( r \geq 1 \). Then each of the intervals \( \text{Int}(x_i), 1 \leq i \leq r \), is either a \( b \)-small or a \( b \)-nested common interval.

Proof. Assume a contrario that some \( \text{Int}(x_i) \) is of size \( u \geq b + 1 \) and is not \( b \)-nested. Let \( I' \subseteq I \) be a \( b \)-nested common interval with the property that \( x_i \in D(I') \subseteq D(I) \) and \( D(I') \) is minimal with this property. Now, since \( I' \) is \( b \)-nested, we have that \( I' \) strictly contains \( \text{Int}(x_i) \) and thus \( |I'| > 1 \). Then \( I' \) must contain some \( b \)-nested common interval \( J \) with \( |I'| > |J| \geq |I'|-b \). Furthermore, \( J \) and \( \text{Int}(x_i) \) are disjoint since by the minimality of \( I' \) we have that \( J \) cannot contain \( \text{Int}(x_i) \). But then \( |I'| \geq |J| + |\text{Int}(x_i)| \geq |I'|-b+b+1=|I'|+1 \), a contradiction. \( \square \)

It is easy to see that:

Remark 1 Let \( I, L, J \) be common intervals such that \( J \subset L \subset I \) and \( J \) is \( b \)-nested with \( |J| \geq |I|-b \). Then \( L \) is \( b \)-nested, since \( |J| \geq |I|-b \geq |L|-b \).

Now, the characterization of \( b \)-nested intervals corresponding to a \( P \)-node is obtained as follows.

Lemma 2. Let \( I \) be a \( P \)-interval with \( D(I) = \{x_1, x_2, \ldots, x_r\} \). Then \( I \) is a \( b \)-nested common interval if and only if there is some \( i, 1 \leq i \leq r \), such that \( \text{Int}(x_i) \) is a \( b \)-nested common interval of size at least \( |I|-b \).

Proof. Since \( I \) is a \( P \)-interval, its maximal common subintervals are \( \text{Int}(x_i), 1 \leq i \leq r \). The ”\( \Rightarrow \)" part follows directly from the definition. For the ”\( \Leftarrow \)" part, assume by contradiction that the affirmation does not hold. Then none of the intervals \( \text{Int}(x_i), 1 \leq i \leq r \), is \( b \)-nested of size at least \( |I|-b \), but the definition implies that some interval \( \text{Int}(x_i) \) exists containing a \( b \)-nested common interval \( J \) of size at least \( |I|-b \). But this is impossible according to Remark 1. \( \square \)

The structure of \( b \)-nested intervals given by consecutive children of a \( Q \)-node is more complex. In the next lemmas we show that at most one of the intervals \( \text{Int}(x_i) \) composing such an interval may be \( b \)-large.

Lemma 3. Let \( I \) be a \( Q \)-interval with \( D(I) = \{x_1, x_2, \ldots, x_r\} \). Then \( I \) is a \( b \)-nested common interval if and only if \( \text{Int}(x_1) \) is \( b \)-small and \( I - \text{Int}(x_1) \) is a \( b \)-nested common interval, or \( \text{Int}(x_r) \) is \( b \)-small and \( I - \text{Int}(x_r) \) is a \( b \)-nested common interval.

Proof. Recall that for a \( Q \)-interval \( I \), the order \( x_1, x_2, \ldots, x_r \) implies that \( x_1 \) (resp. \( x_r \)) contains the smallest (resp. largest) elements in \( I \).

\( \Rightarrow \): Since \( I \) is \( b \)-nested, it contains some \( b \)-nested interval \( J \) such that \( |J| > |I|-b \). Now, \( J \) cannot be strictly included in some non \( b \)-nested \( \text{Int}(x_i) \) by Remark 1. Thus \( D(J) = \{x_p, x_{p+1}, \ldots, x_s\} \) with \( p \geq 1, s \leq r \), and \( p \neq 1 \) or \( s \neq r \). Assume w.l.o.g. that \( p > 1 \). Then \( \text{Int}(x_1) \) is \( b \)-small (since \( |J| \geq |I|-b \)) and \( I - \text{Int}(x_j) \) is \( b \)-nested by Remark 1 since it contains \( J \) or is equal to \( J \).

\( \Leftarrow \): Let \( j = 1 \) or \( j = r \) according to which proposition holds. We have that \( |I - \text{Int}(x_j)| = |I| - |\text{Int}(x_j)| \geq |I|-b \) since \( |\text{Int}(x_j)| \leq b \). Then \( I \) is \( b \)-nested. \( \square \)
Lemma 4. Let $I$ be a $Q$-interval with $D(I) = \{x_1, x_2, \ldots, x_r\}$ which is a b-nested common interval. Then at most one of the intervals $Int(x_i)$, $1 \leq i \leq r$ is b-large, and in this case this interval is a b-nested common interval.

Proof. By contradiction, assume the lemma is false, and let $I$ be a smallest w.r.t. inclusion $Q$-interval contradicting the lemma. Let $x_u$ (resp. $x_v$), with $1 \leq u, v \leq r$, be such that $Int(x_u)$ (resp. $Int(x_v)$) is b-large and $u$ (resp. $v$) is minimum (resp. maximum) with this property. Then $u = 1$ and $v = r$, otherwise by Lemma 3 the minimality of $I$ is contradicted. But now Lemma 3 is contradicted, since $Int(x_1)$ and $Int(x_r)$ are both b-large. To finish the proof, assume that $Int(x_i)$ (for some fixed $i$), is the unique b-large interval and apply Lemma 1 to $Int(x_i)$.

Figure 2 illustrates the two lemmas 3 and 4.

![Structure of a b-nested Q-interval.](image)

Fig. 2. Structure of a b-nested Q-interval.

We are able now to prove the theorem characterizing b-nested common intervals.

Theorem 3. Let $I$ be a common interval of $P$. $I$ is b-nested if and only if:

(a) either $I$ is a $P$-interval and there exists $x_h \in D(I)$ such that $Int(x_h)$ is a b-nested common interval of size at least $|I| - b$,

(b) or $I$ is a $Q$-interval with the property that all intervals $Int(x_i)$ with $x_i \in D(I)$ are b-small, with one possible exception which is a b-large b-nested interval.

Proof. Lemma 2 proves the theorem in the case where $I$ is a $P$-interval. When $I$ is a $Q$-interval, Lemma 4 proves affirmation (b). □

5 The algorithm

Algorithm 1 correctly computes all the b-nested common intervals, as shown subsequently. Moreover, it achieves the $O(n + \text{occ})$ complexity. For a node $x_c$, the notations $\min(c)$ and $\max(c)$ respectively indicate the minimum and the maximum value in $Int(x_c)$.

Algorithm correctness. All the leaves are output in step 4, and they are b-nested common intervals. Moreover, all b-nested common intervals corresponding to $P$-nodes are correctly output in step 9 according to Theorem 3(a). Next, $Q$-intervals corresponding to a $Q$-node $x$ are generated in steps 13-24 by starting with each child $x_c$ of $x$, and successively adding right children $x_d$ as long as condition (b) in Theorem 3 is satisfied (step 16).
Algorithm 1 The $b$-NestedSearch algorithm

**Input:** The PQ-tree $T = (V,E)$ of $P$ for common intervals, a positive integer $b$

**Output:** All $b$-nested common intervals of $P$.

1: Perform a post-order traversal of $T$
2: for each node $x$ of $T$ encountered during this traversal do
3: if $x$ is a leaf then
4: output $\text{Int}(x)$ as $b$-nested
5: else
6: let $x_1, x_2, \ldots, x_p$ be the children of $x$
7: if $x$ is a $P$-node then
8: if $\exists i$ such that $\text{Int}(x_i)$ is $b$-nested and $|\text{Int}(x_i)| \geq |\text{Int}(x)| - b$ then
9: output $\text{Int}(x)$ as $b$-nested
10: end if
11: else
12: $c \leftarrow 1$ // $c$ is the first child defining the interval to be output
13: while $c \leq p$ do // $c$ is the first child defining the interval to be output
14: $d \leftarrow c$ // considers all children starting with $x_c$
15: while $d \leq p$ and $(|\text{Int}(x_d)| \leq b$ or $\text{Int}(x_d)$ is $b$-nested) and $\text{large} \leq 1$ do
16: if $|\text{Int}(x_d)| > b$ then $\text{large} \leftarrow \text{large} + 1$ end if
17: if $c < d$ and $\text{large} \leq 1$ then
18: output $(\min(c), \max(d))$ as $b$-nested
19: end if
20: $d \leftarrow d + 1$
21: end while
22: $c \leftarrow c + 1$
23: end while
24: end if
25: end if
26: end if
27: end for

*Running time.* The PQ-tree has size $O(n)$, and the post-order traversal considers every node $x$ exactly once. Working once on the sons of each node takes $O(n)$. The test in Line 8 considers every child of a $P$-node one more time, so that the $O(n)$ time is insured when the Q-interval generation is left apart. Now, during the generation of the Q-intervals, a node $x_d$ that belongs to no $b$-nested common interval is uselessly included in some interval candidate at most once by left initial positions for the scan (beginning line 13), which is in total bounded by $n$ since there exists a linear number of initial positions in the PQ-tree. Also, an initial position $c$ might be considered one more than necessary if its right sibling is a $b$-large non $b$-nested common interval. In total however, the overhead of considering initial positions that do not lead to the outputting of at least one nested interval is also bounded by $n$. At each iteration of the loop Line 16, a unique distinct $b$-nested interval is output, or $c = d$ (that happens once for each node since $d$ is incremented at each iteration), or $\text{large} = 2$ (that also happens once for each node since it ends the loop). The total number of iterations is
thus $O(n + \text{noce})$, each iteration taking $O(1)$. The whole complexity is thus $O(n + \text{noce})$, where noce is the total number of $b$-nested intervals.

Figure 3 illustrates our algorithm.

![Diagram of nested intervals](image)

**Fig. 3.** Computing all $b$-nested intervals of a $Q$-interval, where $bS$ (resp. $bL$) means $b$-small (resp. $b$-large). The algorithm considers all positions from left to right and expands the $b$-nested interval while it is possible.

### 6 Counting all $b$-nested intervals

In some applications it can be useful to first efficiently count the number of nested intervals before deciding to enumerate them. The previous approach can be modified to count the nested intervals instead of enumerating them, by simply analyzing more precisely the structure of the $Q$-nodes. The goal is to count the nested intervals in a time proportional to the number of children instead of the number of nested intervals.

Considering $P$-node, the counting is only 1 if the $P$-node itself represents a nested interval, 0 otherwise. Since the number of leaves is known for each subtree, this takes $O(k)$ time where $k$ is the number of sons of the $P$-node.

The counting for a $Q$-node is as simple: for each $b$-large strong $b$-nested child $i$, we count the number of $b$-small node(s) to its right (resp. left), denoted by $r(i)$ (resp. $l(i)$), and then we compute the number of $b$-nested intervals which contain child $i$ as

$$l(i) \times (r(i) + 1) + r(i)$$

Once this is done, we first sum all these numbers and obtain the whole number of $b$-nested intervals which contain a $b$-large strong nested interval. In a second step, we count the number of nested intervals obtained by the concatenation of $b$-small intervals as follows: for each maximal segment of $b$-small intervals of length $l$, we add

$$l \times (l - 1)/2$$

$b$-nested intervals. We add those two numbers to get the number of $b$-nested intervals a $Q$-node contains. All these operations may be performed in $O(k)$ time, where $k$ is the number of sons of the $Q$-node.

For instance, on the example of figure 3, we count (from left to right): (a) for the first $b$-large strong child to the left: $3 \times (2 + 1) + 2 = 11$ nested intervals;
(b) for the $b$-large second strong child: $2 \ast (1 + 1) + 1 = 5$ nested intervals; (c) for the last $b$-large strong child: $1 \ast (0 + 1) = 1$ nested intervals. We sum up to 17 nested interval. Now we add the nested intervals generated by the segments of $b$-small intervals: $3 + 1 = 4$. Altogether, the $Q$-node of Figure 3 generates 21 $b$-nested intervals.

We then determine easily if the interval represented by the $Q$-node itself is $b$-nested, which is not the case in Figure 3 but it should not be counted to avoid double counting (unless it is the root).

The algorithm is thus a very easy bottom-up traversal. Count 1 for each leaf. Then go up and count for each node the number of $b$-nested intervals it generates. Also mark the node as representing a $b$-nested interval or not and compute its size. At the end, sum up all $b$-nested intervals.

**Complexity** The time complexity of the counting procedure is obviously $O(n)$, the size of the underlying $PQ$-tree. The time needed to get the $PQ$-tree itself given $K$ permutations is however $O(Kn)$ [4].

7 Conclusion

In this paper we introduced the family of $b$-nested common intervals of $K$ permutations, and showed that it may be computed in time proportional to its cardinality. Indeed this approach extends to any closed family of intervals that is represented by a $PQ$-tree (this does not apply, however, to the conserved intervals, who are represented by an ordered tree [3]). Beside its interest for finding conserved clusters of genes, that should be attested by further experimentations, other applications may be devised, such as helping the identification of orthologs/paralogs or defining distances between genomes in an evolutionary approach. These are the close perspectives of our work.

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