

# Easy identification of generalized common and conserved nested intervals

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## Abstract

In this paper we explain how to easily compute gene clusters, formalized by classical or generalized nested common or conserved intervals, between a set of  $K$  genomes represented as  $K$  permutations. A  $b$ -nested common (resp. conserved) interval  $I$  of size  $|I|$  is either an interval of size 1 or a common (resp. conserved) interval that contains another  $b$ -nested common (resp. conserved) interval of size at least  $|I| - b$ . When  $b = 1$ , this corresponds to the classical notion of nested interval. We exhibit two simple algorithms to output all  $b$ -nested common or conserved intervals between  $K$  permutations in  $O(Kn + nocc)$  time, where  $nocc$  is the total number of such intervals. We also explain how to count all  $b$ -nested intervals in  $O(Kn)$  time. New properties of the family of conserved intervals are proposed to do so.

## 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 (see for instance Galperin and Koonin (2000), Lathe et al. (2000), Tamames (2001)). 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 in Uno and Yagiura (2000), conserved intervals in Bergeron et al. (2004),  $\pi$ -patterns in Parida (2006), gene teams in Béal et al. (2004), domain teams in Pasek et al.

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30 (2005), approximate common intervals in Amir et al. (2007) and so on, con-  
31 sidering different chromosome models (permutations, signed permutations, se-  
32 quences, graphs, etc.) or different distance models (accepting gaps, distance  
33 modeled as weighted graphs, etc.)

34 Among all those models, the first proposed, and still one of the most used in  
35 practice, is the concept of *common interval* on genomes represented by permu-  
36 tations. A set of genes form a common interval of  $K$  genomes if it appears as a  
37 segment on each of the  $K$  unsigned permutations that represent the genomes.  
38 The orders inside the segments might be totally different. The model of con-  
39 served interval is close to the model of common interval but considers signed  
40 permutations.

41 Recently, nested common intervals (easily extensible to nested conserved in-  
42 tervals) were introduced in Hoberman and Durand (2005) based on real data  
43 observation by Kurzik-Dumke and Zengerle (1996). A common interval  $I$  of size  
44  $|I|$  is nested if  $|I| = 1$  or if it contains at least one nested common interval of size  
45  $|I| - 1$ . Hoberman and Durand (2005) pointed that the nestedness assumption  
46 can strengthen the significance of detected clusters since it reduces the prob-  
47 ability of observing them randomly. An  $O(n^2)$  time algorithm to compute all  
48 nested common intervals between two permutations has been presented in Blin  
49 et al. (2010) while between  $K$  permutations a recent  $O(Kn + nocc)$  algorithm  
50 is proposed in Rusu (2013), where *nocc* is the number of solutions.

51 In this paper, we exhibit two simple algorithms to easily compute nested  
52 common and conserved intervals of  $K$  permutations from their natural tree  
53 representations. Also, with the same simplicity, we propose to deal with a gen-  
54 eralization of nested common intervals, called  $b$ -nested common intervals, and  
55 with its variant for conserved intervals (which are a signed version of common  
56 intervals), called  $b$ -nested conserved intervals. These new classes allow - as  $b$   
57 grows - for a less constraint containment between the intervals in the family.  
58 Indeed, a nested interval  $I$  must contain a nested interval of size  $|I| - 1$  or be  
59 a unit interval. A  $b$ -nested common (resp. conserved) interval must contain a  
60  $b$ -nested common (resp. conserved) interval of size at least  $|I| - b$  or be a unit  
61 interval. Nested intervals are indeed 1-nested. From a biological point of view,  
62 this is equivalent to modeling clusters with a larger variability in gene content  
63 and gene order, thus allowing algorithms to deal with annotation errors. How-  
64 ever, the study and validation of this new interval model is deferred to further  
65 applied studies. In this paper we focus on the algorithmic aspects.

66 Given a set  $\mathcal{P}$  of  $K$  permutations on  $n$  elements representing genomes with no  
67 duplicates, our simple algorithms for finding all  $b$ -nested common or conserved  
68 intervals of  $\mathcal{P}$  run in  $O(Kn + nocc)$ -time and need  $O(n)$  additional space, where  
69 *nocc* is the number of solutions. In this way, our algorithm for common intervals  
70 performs as well as the algorithm in Rusu (2013) for the case of  $K$  permutations,  
71 and proposes an efficient approach for the new classes of  $b$ -nested intervals.

72 Moreover, a slight modification of our approach allows us to count the num-  
73 ber of  $b$ -nested common or conserved intervals of  $K$  permutations in  $O(Kn)$   
74 time. Efficiently counting the number of  $b$ -nested common intervals without  
75 enumerating them is very usefull when one needs to compute similarity func-

76 tions between genomes that are expressed in terms of number of intervals. See  
77 for instance Fertin and Rusu (2011).

78 The paper is organized as follows. In Section 2 we present the main def-  
79 initions for common and conserved intervals, and precisely state the problem  
80 to solve. In Section 3 we focus on  $b$ -nested common intervals, recalling the  
81 data structure called a  $PQ$ -tree, giving a characterization of  $b$ -nested common  
82 intervals and showing how  $PQ$ -trees can be used to find all  $b$ -nested common  
83 intervals. In Section 4 we adopt a similar approach for conserved intervals, with  
84 the difference that another tree structure must be used in this case. In Section  
85 5 we eventually conclude.

## 86 2 Generalities on common and conserved inter- 87 vals

88 A *permutation*  $P$  on  $n$  elements is a complete linear order on the set of integers  
89  $\{1, 2, \dots, n\}$ . We denote  $Id_n$  the identity permutation  $(1, 2, \dots, n)$ . An *interval*  
90 of a permutation  $P = (p_1, p_2, \dots, p_n)$  is a set of consecutive elements of the  
91 permutation  $P$ . An interval of a permutation will be denoted by giving its first  
92 and last positions, such as  $[i, j]$ . Such an interval is also said *delimited* by  $p_i$  (left)  
93 and  $p_j$  (right). An interval  $[i, j] = \{i, i + 1, \dots, j\}$  of the identity permutation  
94 will be simply denoted by  $(i..j)$ .

95 **Definition 1 (Uno and Yagiura (2000))** *Let  $\mathcal{P} = \{P_1, P_2, \dots, P_K\}$  be a set*  
96 *of  $K$  permutations on  $n$  elements. A common interval of  $\mathcal{P}$  is a set of integers*  
97 *that is an interval in each permutation of  $\mathcal{P}$ .*

98 The set  $\{1, 2, \dots, n\}$  and all singletons (also called unit intervals) are com-  
99 mon intervals of any non-empty set  $\mathcal{P}$  of permutations. Moreover, one can  
100 always assume that one of the permutations, say  $P_1$ , is the identity permuta-  
101 tion  $Id_n$ . For this, it is sufficient to renumber the elements of  $P_1$  so as to obtain  
102  $Id_n$ , and then to renumber all the other permutations accordingly. Then the  
103 common intervals of  $\mathcal{P}$  are of the form  $(i..j)$  with  $1 \leq i \leq j \leq n$ .

104 Define now a *signed* permutation as a permutation  $P$  whose elements have  
105 an associated sign among  $+$  and  $-$ , making each element to be respectively  
106 *positive* or *negative*. Negative elements are denoted  $-p_i$  while positive elements  
107 are simply denoted  $p_i$ , or  $+p_i$  for emphasizing positivity. A permutation is then  
108 a signed permutation containing only positive elements.

109 **Definition 2 (Bergeron and Stoye (2006))** *Let  $\mathcal{P} = \{P_1, P_2, \dots, P_K\}$  be*  
110 *a set of signed permutations over  $\{1, 2, \dots, n\}$ , with first element  $+1$  and last*  
111 *element  $+n$ , for each  $k \in \{1, 2, \dots, K\}$ . Assume  $P_1 = Id_n$ . A conserved interval*  
112 *of  $\mathcal{P}$  is either a unit interval or a common interval (a..c) of  $\mathcal{P}$  (ignoring the*  
113 *signs) which is delimited, in each  $P_k$ , either by  $a$  (left) and  $c$  (right), or by  $-c$*   
114 *(left) and  $-a$  (right).*

115 **Remark 1** *In the subsequent, we assume that  $\mathcal{P} = \{P_1, P_2, \dots, P_K\}$  with*  
 116  *$P_1 = Id_n$ . Moreover, when we deal with conserved intervals, the permutations*  
 117 *are assumed to satisfy the hypothesis in Definition 2.*

118 Now, we are ready to introduce the new classes of intervals.

119 **Definition 3** *Let  $\mathcal{P} = \{P_1, P_2, \dots, P_K\}$  be a set of  $K$  permutations on  $n$  ele-*  
 120 *ments and let  $b$  be a positive integer. A common (respectively conserved) interval*  
 121 *of  $\mathcal{P}$  is  $b$ -nested if either  $|I| = 1$  or  $I$  strictly contains a common (resp. con-*  
 122 *served) interval of size at least  $|I| - b$ .*

123 We are interested in efficient algorithms for finding and counting all  $b$ -nested  
 124 common (resp. conserved) intervals of  $\mathcal{P} = \{P_1, P_2, \dots, P_K\}$ , without redun-  
 125 dancy. Obviously, unit intervals are, by definition,  $b$ -nested common (resp. con-  
 126 served) intervals. As a consequence, from now on and without any subsequent  
 127 specification, we focus on finding  $b$ -nested common (resp. conserved) intervals  
 128 of size at least 2. The following notions will be very useful in the subsequent.

129 **Definition 4** *Let  $\mathcal{P} = \{P_1, P_2, \dots, P_K\}$  be a set of  $K$  permutations on  $n$  ele-*  
 130 *ments and let  $b$  be a positive integer. A common (resp. conserved) interval of*  
 131  *$\mathcal{P}$  is  $b$ -small if its size does not exceed  $b$ . Otherwise, the interval is  $b$ -large.*

132 Notice that all  $b$ -small intervals are  $b$ -nested, by definition and since unit  
 133 intervals are  $b$ -nested.

### 134 3 On $b$ -nested common intervals

135 This section is divided into three parts. The first one recalls a tree structure  
 136 that we associate to common intervals of permutations, the  $PQ$ -trees. The  
 137 second one discusses the properties of  $b$ -nested common intervals. Finally, we  
 138 give the algorithms for efficiently computing and counting the  $b$ -nested common  
 139 intervals.

#### 140 3.1 $PQ$ -trees and common intervals

141 **Definition 5** *Let  $\mathcal{F}$  be a family of intervals from  $Id_n$  containing the interval*  
 142  *$(1..n)$ . A  $PQ$ -tree representing the family  $\mathcal{F}$  is a tree  $T(\mathcal{F})$  satisfying:*

- 143 1. *its nodes are in bijection with a subset  $S(\mathcal{F})$  of intervals from  $\mathcal{F}$ , the root*  
 144 *corresponding to  $(1..n)$*
- 145 2. *its arcs represent all the direct (not obtained by transitivity) inclusions*  
 146 *between intervals in  $S(\mathcal{F})$*
- 147 3. *each node is labeled  $P$  ou  $Q$ , and an order is defined for the children of*  
 148 *each  $Q$ -node*

149 4. an interval  $I$  of  $Id_n$  belongs to  $\mathcal{F}$  iff either it corresponds to a node, or there  
 150 exists a unique  $Q$ -node  $z$  such that  $I$  is the union of intervals corresponding  
 151 to successive children of  $z$ , according to the order defined for  $z$ .

152 Note that the size of the tree is in  $O(|S(\mathcal{F})|)$ , thus allowing to drastically  
 153 reduce the memory space needed to store all the intervals in  $\mathcal{F}$ . When labels  $P$   
 154 and  $Q$  are forgotten, the tree  $T(\mathcal{F})$  is called the *inclusion tree* of  $S(\mathcal{F})$ .

155 Given the  $PQ$ -tree representing a family  $\mathcal{F}$ , we denote by  $Int(x)$  the interval  
 156 from  $S(\mathcal{F})$  corresponding to a node  $x$ . We also denote, for each interval  $I$  from  
 157  $\mathcal{F}$ , by  $D(I)$  the *domain* of  $I$  defined as follows. If  $I \in S(\mathcal{F})$ , then  $D(I)$  is  
 158 the set of its children. If  $I \notin S(\mathcal{F})$ , then by condition 4. in Definition 5, let  
 159  $x_l, x_{l+1}, \dots, x_r$  be the children of the  $Q$ -node  $z$  such that  $I = \cup_{i \in (l..r)} Int(x_i)$ .  
 160 Then  $D(I) = \{x_l, x_{l+1}, \dots, x_r\}$ .

161 Fundamental results on  $PQ$ -trees involve *closed* families of intervals.

162 **Definition 6** A closed family  $\mathcal{F}$  of intervals of the permutation  $Id_n$  is a family  
 163 that contains all singletons as well as the interval  $(1..n)$ , and that in addition  
 164 has the following property: if  $(i..k)$  and  $(j..l)$ , with  $i \leq j \leq k \leq l$ , belong to  $\mathcal{F}$ ,  
 165 then  $(i..j-1)$ ,  $(j..k)$ ,  $(k+1..l)$  and  $(i..l)$  belong to  $\mathcal{F}$ .

166 The construction of a  $PQ$ -tree for a closed family of intervals relies on strong  
 167 intervals:

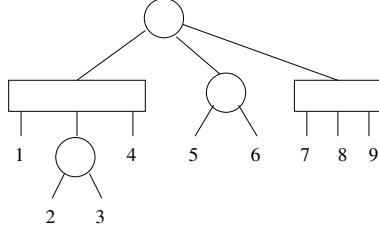
168 **Definition 7** Let  $\mathcal{F}$  be a family of closed intervals from  $Id_n$ . An interval  $(i..j)$   
 169 is said to overlap another interval  $(k..l)$  if they intersect without inclusion, i.e.  
 170  $i < k \leq j < l$  or  $k < i \leq l < j$ . An interval  $I$  of  $\mathcal{F}$  is strong if it does not  
 171 overlap any other interval of  $\mathcal{F}$ , and is weak otherwise.

172 Notice that  $(1..n)$  and the unit intervals are always strong. Also, the family  
 173 of strong intervals of  $\mathcal{F}$  is *laminar* (that is, every two distinct intervals are  
 174 either disjoint or included in each other) and, as  $(1..n)$  belongs to the family, it  
 175 is possible to define for them an inclusion tree. Then it can be shown that:

176 **Theorem 1 (Landau et al. (2005))** Given a closed family  $\mathcal{F}$  of intervals of  
 177  $Id_n$ , let  $S(\mathcal{F})$  be the set of strong intervals from  $\mathcal{F}$  and let  $T(\mathcal{F})$  be the inclusion  
 178 tree of  $S(\mathcal{F})$ . Then the  $PQ$ -tree obtained by the following rules represents the  
 179 family  $\mathcal{F}$ :

- 180 1. label with  $P$  each node  $x$  of  $T(\mathcal{F})$  such that  $\cup_{z \in D'} Int(z) \notin \mathcal{F}$  for all  
 181  $D' \subset D(Int(x))$  with  $2 \leq |D'| < |D|$ .
- 182 2. label with  $Q$  each node  $y$  of  $T(\mathcal{F})$  not labeled  $P$ , and define the order  
 183  $y_1, y_2, \dots, y_r$  of its children such that  $\max(Int(y_i)) < \min(Int(y_{i+1}))$  for  
 184 all  $i < r$ .

185 Common intervals of permutations (including those of size 1) are obviously  
 186 a closed family of intervals from  $Id_n$ , thus Theorem 1 applies. Moreover, the  
 187  $PQ$ -tree for common intervals (hereafter simply denoted  $T$ ) may be computed  
 188 in linear time:



Let  $\mathcal{P} = \{Id_9, P_2, P_3\}$ ,  
 $P_2 = (4, 2, 3, 1, 7, 8, 9, 6, 5)$   
 $P_3 = (5, 6, 1, 3, 2, 4, 9, 8, 7)$   
The  $PQ$ -tree for the set  
of common intervals of  $\mathcal{P}$   
is shown on the left.

Figure 1: Example of  $PQ$ -tree

189 **Theorem 2** *Bergeron et al. (2008)* The construction of the  $PQ$ -tree  $T$  of com-  
190 mon intervals of a set  $\mathcal{P}$  of  $K$  permutations on  $n$  elements may be done in  
191  $O(Kn)$  time.

192 It is easy to note here that the leaves of  $T$  are the singletons. Also, the  
193 intervals  $Int(y_i)$ ,  $i = 1, 2, \dots, r$ , associated to the children of a  $Q$ -node are  
194 contiguous, i.e.  $max(Int(y_i)) + 1 = min(Int(y_{i+1}))$ . This is due to condition 4  
195 in the definition of a  $PQ$ -tree and to the assumption, that the reader must keep  
196 in mind, that  $P_1 = Id_n$  (thus all the common intervals are of the form  $(i..j)$ ).  
197 An example is given in Fig. 1.

### 198 3.2 Properties of $b$ -nested common intervals

199 Let  $\mathcal{P} = \{P_1, P_2, \dots, P_K\}$  be a set of permutations on  $n$  elements such that  
200  $P_1 = Id_n$ , and let  $T$  be the  $PQ$ -tree representing the common intervals of  $\mathcal{P}$ .  
201 Say that a common interval  $I$  is a  $P$ -interval if it is strong and there is a  $P$ -node  
202  $x$  with  $Int(x) = I$ . Otherwise,  $I$  is a  $Q$ -interval.

203 With the aim of identifying the particular structure of  $b$ -nested common  
204 intervals among all common intervals, we first prove that:

205 **Lemma 1** *Let  $I$  be a  $b$ -nested common interval with  $D(I) = \{x_1, x_2, \dots, x_r\}$ ,*  
206  *$r \geq 1$ . Then each of the intervals  $Int(x_i)$ ,  $1 \leq i \leq r$ , is either a  $b$ -small or a*  
207  *$b$ -nested common interval.*

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

216 It is easy to see that:

217 **Remark 2** Let  $I, L, J$  be common intervals such that  $J \subseteq L \subseteq I$  and  $J$  is  
218  $b$ -nested with  $|J| \geq |I| - b$ . Then  $L$  is  $b$ -nested, since  $|J| \geq |I| - b \geq |L| - b$ .

219 Now, the characterization of  $b$ -nested intervals corresponding to a  $P$ -node is  
 220 obtained as follows.

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

224 *Proof.* Since  $I$  is a  $P$ -interval, its maximal common subintervals are  $Int(x_i)$ ,  
 225  $1 \leq i \leq r$ . The " $\Leftarrow$ " part follows directly from the definition. For the " $\Rightarrow$ "  
 226 part, assume by contradiction that the affirmation does not hold. Then none  
 227 of the intervals  $Int(x_i)$ ,  $1 \leq i \leq r$ , is  $b$ -nested of size at least  $|I| - b$ , but since  
 228  $T$  is  $b$ -nested we deduce that some interval  $Int(x_i)$  exists containing a  $b$ -nested  
 229 common interval  $J$  of size at least  $|I| - b$ . But this is impossible according to  
 230 Remark 2.  $\square$

231 The structure of  $b$ -nested common intervals given by consecutive children of  
 232 a  $Q$ -node is more complex. In the next lemmas we show that at most one of the  
 233 intervals  $Int(x_i)$  composing such an interval may be  $b$ -large (see also Fig. 2).

234 **Lemma 3** *Let  $I$  be a  $Q$ -interval with  $D(I) = \{x_1, x_2, \dots, x_r\}$ . Then  $I$  is a*  
 235  *$b$ -nested common interval if and only if  $Int(x_1)$  is  $b$ -small and  $I - Int(x_1)$  is a*  
 236  *$b$ -nested common interval, or  $Int(x_r)$  is  $b$ -small and  $I - Int(x_r)$  is a  $b$ -nested*  
 237 *common interval.*

238 *Proof.* Recall that for a  $Q$ -interval  $I$ , the order  $x_1, x_2, \dots, x_r$  implies that the  
 239 equation  $\max(Int(x_i)) + 1 = \min(Int(x_{i+1}))$  holds for all  $i$  with  $1 \leq i < r$ .

240  $\Rightarrow$ : Since  $I$  is  $b$ -nested, it contains some  $b$ -nested interval  $J$  such that  $|I| >$   
 241  $|J| \geq |I| - b$ . Choose  $J$  as large as possible. Now,  $J$  cannot be strictly included  
 242 in some non  $b$ -nested  $Int(x_i)$  by Remark 2, thus  $D(J) = \{x_p, x_{p+1}, \dots, x_s\}$  with  
 243  $p \geq 1, s \leq r$ , and  $p \neq 1$  or  $s \neq r$ . Assume w.l.o.g. that  $p > 1$ . Then  $Int(x_1)$   
 244 is  $b$ -small (since  $|J| \geq |I| - b$ ) and  $I - Int(x_1)$  is  $b$ -nested by Remark 2 since it  
 245 contains  $J$  or is equal to  $J$ .

246  $\Leftarrow$ : Let  $j = 1$  or  $j = r$  according to which proposition holds. We have that  
 247  $|I - Int(x_j)| = |I| - |Int(x_j)| \geq |I| - b$  since  $|Int(x_j)| \leq b$ . Then  $I$  is  $b$ -nested.  
 248  $\square$

249 **Lemma 4** *Let  $I$  be a  $Q$ -interval with  $D(I) = \{x_1, x_2, \dots, x_r\}$  which is a  $b$ -*  
 250 *nested common interval. Then at most one of the intervals  $Int(x_i)$ ,  $1 \leq i \leq r$ ,*  
 251 *is  $b$ -large, and in this case this interval is a  $b$ -nested common interval.*

252 *Proof.* By contradiction, assume there exist  $b$ -nested common  $Q$ -intervals that  
 253 contain at least two  $b$ -large intervals of type  $Int(x_i)$ , and let  $I$  be a smallest  
 254 such interval w.r.t. inclusion. Let  $x_u$  (resp.  $x_v$ ), with  $1 \leq u, v \leq r$ , be such  
 255 that  $Int(x_u)$  (resp.  $Int(x_v)$ ) is  $b$ -large and  $u$  (resp.  $v$ ) is minimum (resp.  
 256 maximum) with this property. Then  $u = 1$  and  $v = r$ , otherwise by Lemma 3  
 257 the minimality of  $I$  is contradicted. But now Lemma 3 is contradicted, since  
 258  $Int(x_1)$  and  $Int(x_r)$  are both  $b$ -large.

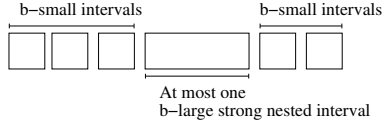


Figure 2: Structure of a  $b$ -nested  $Q$ -interval.

259 Then, at most one of the intervals  $Int(x_i)$ ,  $1 \leq i \leq r$ , is  $b$ -large. To finish  
 260 the proof, assume that  $Int(x_i)$  (for some fixed  $i$ ), is the unique  $b$ -large interval  
 261 and apply Lemma 1 to  $Int(x_i)$  to deduce that  $Int(x_i)$  is  $b$ -nested.  $\square$

262 We are able now to prove the theorem characterizing  $b$ -nested common in-  
 263 tervals.

264 **Theorem 3** *Let  $I$  be a common interval of  $\mathcal{P}$ .  $I$  is  $b$ -nested if and only if:*

- 265 (a) *either  $I$  is a  $P$ -interval and there exists  $x_h \in D(I)$  such that  $Int(x_h)$  is a*  
 266  *$b$ -nested common interval of size at least  $|I| - b$ .*
- 267 (b) *or  $I$  is a  $Q$ -interval with the property that all intervals  $Int(x_i)$  with  $x_i \in$*   
 268  *$D(I)$  are  $b$ -small, with one possible exception which is a  $b$ -large  $b$ -nested*  
 269 *interval.*

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

### 272 3.3 Computing and counting all $b$ -nested common inter- 273 vals

274 Consider Algorithm 1, which computes all  $b$ -nested common intervals. For a  
 275 node  $x_c$ , the notations  $min(c)$  and  $max(c)$  respectively indicate the minimum  
 276 and the maximum value in  $Int(x_c)$ . Figure 3 illustrates our algorithm.

277 **Theorem 4** *Algorithm 1 correctly computes all the  $b$ -nested common intervals,*  
 278 *assuming the  $PQ$ -tree is already built, in  $O(n + nocc)$  time, where  $nocc$  is the*  
 279 *number of  $b$ -nested common intervals in  $\mathcal{P}$ .*

280 *Proof.* To show the algorithm correctness, note first that all the leaves are  
 281 output in step 4, and they are  $b$ -nested common intervals. Moreover, all  $b$ -  
 282 nested common intervals corresponding to  $P$ -nodes are correctly output in step  
 283 9 according to Theorem 3(a). Next,  $Q$ -intervals corresponding to a  $Q$ -node  $x$   
 284 are generated in steps 12-22 by starting with each child  $x_c$  of  $x$ , and successively  
 285 adding right children  $x_d$  as long as condition (b) in Theorem 3 is satisfied (step  
 286 15).

287 Let us analyze now the running time. The  $PQ$ -tree has size  $O(n)$ , and the  
 288 traversal considers every node  $x$  exactly once. Working once on the children of  
 289 each node takes  $O(n)$ . The test in line 8 considers every child of a  $P$ -node one  
 290 more time, so that the  $O(n)$  time is ensured when the  $Q$ -interval generation is  
 291 left apart. Now, during the generation of the  $Q$ -intervals, a node  $x_d$  that belongs



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

**Output:** All  $b$ -nested common intervals of  $\mathcal{P}$

```

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  $Int(x)$  as  $b$ -nested
5   else
6     let  $x_1, x_2, \dots, x_p$  be the children of  $x$ 
7     if  $x$  is a  $P$ -node then
8       if  $\exists i$  such that  $Int(x_i)$  is  $b$ -nested and  $|Int(x_i)| \geq |Int(x)| - b$ 
9         then
10          output  $Int(x)$  as  $b$ -nested
11        endif
12      else
13        for  $c \leftarrow 1$  to  $p$  do
14           $large \leftarrow 0$  // number of  $b$ -large intervals already included
15           $d \leftarrow c$  // considers all children starting with  $x_c$ 
16          while  $d \leq p$  and ( $|Int(x_d)| \leq b$  or  $Int(x_d)$  is  $b$ -nested) and
17             $large \leq 1$  do
18              if  $|Int(x_d)| > b$  then  $large \leftarrow large + 1$  endif
19              if  $c < d$  and  $large \leq 1$  then
20                output  $(min(c)..max(d))$  as  $b$ -nested
21              endif
22               $d \leftarrow d + 1$ 
23            endwhile
24          endfor
25        endif
26      endif
27    endfor

```

**Algorithm 1:** The  $b$ -NestedCommonSearch algorithm

292 to no  $b$ -nested common interval is uselessly included in some interval candidate  
293 at most once by left initial positions for the scan (beginning line 12), which is in  
294 total bounded by  $n$  since there exists a linear number of initial positions in the  
295 PQ-tree. At each iteration of the loop line 15, a unique distinct  $b$ -nested interval  
296 is output, or  $c = d$  (that happens once for each node since  $d$  is incremented at  
297 each iteration), or  $large = 2$  (that also happens once for each node since it ends  
298 the loop). The total number of iterations is thus  $O(n + nocc)$ , each iteration  
299 taking  $O(1)$ . The overall running time is thus in  $O(n + nocc)$ , where  $nocc$  is the  
300 total number of  $b$ -nested common intervals.  $\square$

301 The previous approach can be modified to count the  $b$ -nested common in-  
302 tervals instead of enumerating them, by simply analyzing more precisely the  
303 structure of the  $Q$ -nodes. The goal is to count the  $b$ -nested common intervals in

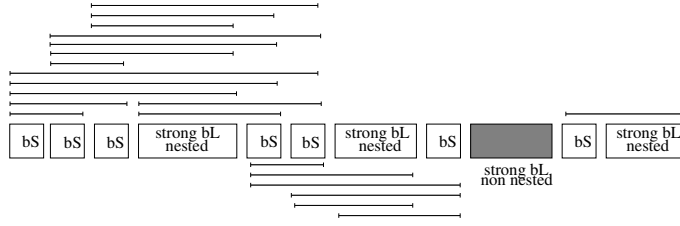


Figure 3: Computing all  $b$ -nested intervals of a  $Q$ -interval, where  $bS$  (resp.  $bL$ ) means  $b$ -small (resp.  $b$ -large). The algorithm considers all positions from left to right and expands the  $b$ -nested interval while it is possible.

304 a time proportional to the number of children instead of the number of  $b$ -nested  
 305 common intervals. To perform the count, we assume that the traversal is post-  
 306 order, that it marks each vertex as  $b$ -nested or not, and that it computes the  
 307 cardinality of each  $Int(x_i)$ .

308  **$P$ -nodes.** Obviously, a  $P$ -node (including the leaves) counts for 1 if the  
 309 associated interval is  $b$ -nested, and for 0 otherwise.

310  **$Q$ -nodes.** To make the computation for a  $Q$ -node with children  $\{x_1, x_2, \dots,$   
 311  $x_p\}$ , the algorithm looks for the  $b$ -large  $b$ -nested intervals  $Int(x_d)$  and counts

- 312 1) the  $b$ -nested common intervals containing each  $Int(x_d)$ , and  
 313 2) the  $b$ -nested common intervals generated by maximal sets of consecutive  
 314  $b$ -small common intervals  $Int(x_i)$ . To this end, the vertices  $x_i$  are considered  
 315 from left to right in order to identify both the  $b$ -large  $b$ -nested common intervals  
 316  $Int(x_d)$ , and the maximal sets of consecutive  $b$ -small common intervals  $Int(x_i)$ .  
 317 Then:

To solve 1), each encountered  $b$ -large  $b$ -nested interval  $Int(x_d)$  has the following treatment. We count the number of consecutive  $b$ -small nodes  $x_i$  on its right (resp. left), denoted by  $r(d)$  (resp.  $l(d)$ ). Then we compute the number of  $b$ -nested common intervals which contain child  $x_d$  as

$$l(d) * (r(d) + 1) + r(d).$$

To solve 2), for each maximal set of consecutive  $b$ -small common intervals  $Int(x_i)$ , assuming it has size  $h$ , we count

$$h * (h - 1) / 2.$$

318 One may easily decide whether the interval corresponding to the  $Q$ -node  
 319 itself is  $b$ -nested or not, and compute its size.

320 All these operations may be performed in  $O(k)$  time, where  $k$  is the number  
 321 of sons of the  $Q$ -node.

322 **Example.** On the example in Fig. 3, we count (from left to right): (a)  
 323 for the first  $b$ -large strong child to the left:  $3 * (2 + 1) + 2 = 11$   $b$ -nested  
 324 common intervals; (b) for the  $b$ -large second strong child:  $2 * (1 + 1) + 1 = 5$   
 325  $b$ -nested common intervals; (c) for the last  $b$ -large strong child:  $1 * (0 + 1) = 1$   
 326  $b$ -nested common intervals. We sum up to obtain 17  $b$ -nested common intervals

327 containing one  $b$ -large  $b$ -nested interval  $Int(x_i)$ . Now we add the nested intervals  
 328 generated between the  $b$ -large intervals:  $3 + 1 = 4$ . Altogether, the  $Q$ -node of  
 329 Figure 3 generates 21  $b$ -nested intervals.

330 **Complexity** The time complexity of the counting procedure is obviously  
 331  $O(n)$ , the size of the underlying  $PQ$ -tree. The time needed to get the  $PQ$ -tree  
 332 itself given  $K$  permutations is however  $O(Kn)$ , as indicated before.

## 333 4 On $b$ -nested conserved intervals

334 As stated before, we assume the set  $\mathcal{P}$  of permutations has the properties re-  
 335 quired in Definition 2. As conserved intervals are common intervals, one may  
 336 be tempted to follow the same approach using  $PQ$ -trees. Unfortunately, the  
 337 inclusion tree of strong conserved intervals does not define a  $PQ$ -tree represent-  
 338 ing the family of conserved intervals, due to the fact that a conserved interval  
 339 cannot be written as a disjoint union of strong conserved intervals. The result-  
 340 ing *ordered tree* has been used in the literature Bergeron et al. (2004), but its  
 341 underlying properties have not been clearly stated. We do it here, before using  
 342 these properties.

### 343 4.1 Structure of conserved intervals

344 We start by an easy property about intersection of conserved intervals:

345 **Lemma 5** *Let  $I = (u..v)$  and  $J = (c..d)$  be two conserved intervals of  $\mathcal{P}$  with*  
 346  *$u < c \leq v < d$ . Then the intervals  $(u..c)$ ,  $(c..v)$ ,  $(v..d)$  and  $(u..d)$  are conserved*  
 347 *intervals.*

348 *Proof.* As an element  $x$  from  $I$  fulfills  $u \leq x \leq v$  and an element  $y$  from  $J$  fulfills  
 349  $c \leq y \leq d$  then an element  $z$  from  $I \setminus J$  fulfills  $u \leq z < c$ . These elements are  
 350 exactly those between  $u$  and  $c$  and  $(u..c)$  is thus a conserved interval. Similarly,  
 351  $J \setminus I = (v..d)$ . The elements from  $I \cap J$  are all the elements not lower than  $v$  and  
 352 not larger than  $c$ , so  $(c..v)$  is a conserved interval. Finally, the elements from  
 353  $I \cup J$  are all elements greater than  $u$  and smaller than  $d$ , so  $(u..d)$  is a conserved  
 354 interval.  $\square$

355 The notions of strong/weak intervals and of a frontier are essential in our  
 356 study.

357 **Definition 8** *A conserved interval  $I$  of  $\mathcal{P}$  is strong if it has cardinality at least*  
 358 *two, and does not overlap other conserved intervals. Otherwise, it is weak.*

359 Notice that unit conserved intervals are not strong.

360 **Definition 9** *Let  $I = (a..c)$  be a conserved interval. A set  $\{f_1, \dots, f_k\}$  of*  
 361 *elements satisfying  $a = f_1 < f_2 < \dots < f_k = c$  is a set of frontiers of  $I$  if*  
 362  *$(f_i..f_j)$  is a conserved interval, for all  $i, j$  with  $1 \leq i < j \leq k$ . An element of  $I$*   
 363 *is a frontier of  $I$  if it occurs in at least one set of frontiers of  $I$ .*

364 The two following properties are easy ones:

365 **Lemma 6** *Let  $I = (a..c)$  be a conserved interval and  $F$  be a set of frontiers of*  
 366  *$I$ . The elements of  $F$  are either all positive or all negative.*

367 *Proof.* By the definition of a conserved interval, its two endpoints have the same  
 368 sign. By the definition of a set on frontiers, any two frontiers are the extremities  
 369 of some conserved interval.  $\square$

370 **Lemma 7** *Let  $I = (a..c)$  be a conserved interval, and let  $F = \{f_1, \dots, f_k\}$  and*  
 371  *$F' = \{f'_1, \dots, f'_l\}$  be two sets of frontiers of  $I$ . Then  $F \cup F'$  is also a set of*  
 372 *frontiers of  $I$ .*

373 *Proof.* We show that any interval between two elements of  $F \cup F'$  is conserved.  
 374 Let  $f_i \in F$  and  $f'_j \in F'$ , and suppose that  $f_i < f'_j$ . If  $f_i = a$ , then we have  
 375  $(f_i..f'_j) = (f'_1..f'_j)$  and we are done. If  $f'_j = c$ , then  $(f_i..f'_j) = (f_i..f_k)$  and we are  
 376 also done. If  $f_i \neq a$  and  $f'_j \neq c$ , then Lemma 5 allows to conclude. The same  
 377 proof holds if  $f_i > f'_j$ .  $\square$

378 Let now  $T$  be the inclusion tree of strong intervals from  $\mathcal{P}$ , in which every  
 379 node  $x$  corresponds to a strong interval denoted  $Int(x)$ , and node  $x$  is the  
 380 parent of node  $y$  iff  $Int(x)$  is the smallest strong conserved interval strictly  
 381 containing  $Int(y)$ . Then  $T$  contains two types of nodes: those corresponding to  
 382 strong conserved intervals with no internal frontier, and those corresponding to  
 383 strong conserved intervals with at least one internal frontier. We will show that  
 384 weak conserved intervals are the conserved strict subintervals of the latter ones,  
 385 defined by two frontiers. Overall, we have a structure working pretty much as  
 386 a  $PQ$ -tree, but which cannot be mapped to a  $PQ$ -tree. This is proved in the  
 387 next theorem.

388 Given a conserved interval, denote by  $Container(I)$  the smallest strong con-  
 389 served interval such that  $I \subseteq J$ .

390 **Theorem 5** *Each conserved interval  $I$  of  $\mathcal{P}$  admits a unique maximal (w.r.t.*  
 391 *inclusion) set of frontiers denoted  $F_I$ . Moreover, each conserved interval  $I$  of*  
 392  *$\mathcal{P}$  satisfies one of the following properties:*

- 393 1.  $I$  is strong
- 394 2.  $I$  is weak and there exists a unique strong conserved interval  $J$  of  $\mathcal{P}$ , and  
 395 two frontiers  $f_i, f_j \in F_J$  with  $f_i < f_j$ , such that  $I = (f_i..f_j)$ . Moreover  
 396  $F_I = F_J \cap I$  and  $J = Container(I)$ .

397 *Proof.* Let us first prove the uniqueness of the maximal set of frontiers. By  
 398 contradiction, assume two distinct maximal sets of frontiers  $F = \{f_1, \dots, f_k\}$   
 399 and  $F' = \{f'_1, \dots, f'_l\}$  exist for a conserved interval  $I$ . Using Lemma 7, we  
 400 deduce that  $F \cup F'$  is a larger set of frontiers of  $I$ , a contradiction.

401 Let us now prove that if  $I$  is not strong, then there exists a unique strong  
 402 conserved interval  $J$ , and two frontiers  $f_i, f_j \in F_J$  with  $f_i < f_j$ , such that  
 403  $I = (f_i..f_j)$ .

404 *Existence of  $J$ .* Let  $I_1 = I = (a_0..a_1)$  be a weak conserved interval of  $\mathcal{P}$ .  
405 Then there is another interval  $I_2$  overlapping it, either on its left (i.e.  $I_2 =$   
406  $(a_2..x_2)$  with  $a_2 < a_0 \leq x_2 < a_1$ ) or on its right (i.e.  $I_2 = (x_2..a_2)$  with  
407  $a_0 < x_2 \leq a_1 < a_2$ ). According to Lemma 5,  $J_2 = I_1 \cup I_2$  is a conserved  
408 interval, and  $F_2 = \{a_0, a_1, a_2, x_2\}$  is a set of frontiers for  $J_2$  (not necessarily all  
409 distinct). If  $J_2$  is not strong then it is overlapped by another interval  $I_3$ . We  
410 build an increasing sequence of intervals  $J_1 = I_1, J_2, \dots, J_k$ , with  $J_i$  overlapped  
411 by  $I_{i+1}$ , and  $J_{i+1} = J_i \cup I_{i+1}$ , until we find a strong conserved interval  $J_k$  (the  
412 process ends since (1.. $n$ ) is strong). Each time Lemma 5 ensures that  $J_{i+1}$  is  
413 a conserved interval, and  $F_{i+1} = F_i \cup \{a_{i+1}, x_{i+1}\}$  is a set of frontiers for  $J_{i+1}$   
414 (where  $a_{i+1}, x_{i+1}$  are the endpoints of  $I_{i+1}$ ). But then  $F_k$  is a subset of the  
415 maximal set of frontiers  $F_{J_k}$  of  $J_k$  and the two frontiers of  $J_k$  defining  $I_1$  are  
416  $a_0, a_1$ , since  $\{a_0, a_1\} \subseteq F_2 \subseteq F_3 \subseteq \dots \subseteq F_k \subseteq F_{J_k}$ .

417 *Uniqueness of  $J$ .* Assume a contrario that two strong intervals  $J_1$  and  $J_2$   
418 exist with  $F_{J_1} = \{f_1, \dots, f_p\}$ ,  $F_{J_2} = \{f'_1, \dots, f'_r\}$  and such that  $I = (f_i..f_j) =$   
419  $(f'_k..f'_l)$  with  $1 \leq i < j \leq p$  and  $1 \leq k < l \leq r$ . Then, clearly,  $f_i = f'_k$  and  
420 this is the left endpoint of  $I$ , whereas  $f_j = f'_l$  and this is the right endpoint  
421 of  $I$ . Since  $J_1$  and  $J_2$  are both strong, they cannot overlap. Assume then  
422 w.l.o.g. that  $J_1$  is strictly included in  $J_2$ , and more precisely that  $f_p \neq f'_r$  (then  
423  $f_p < f'_r$  due to inclusion). Now,  $(f'_k..f'_r)$  overlaps  $J_1$  (which is forbidden) unless  
424  $i = 1$ , in which case we have  $f_1 = f_i = f'_k$  and this is the left endpoint of  $I$ .  
425 Now, since  $I$  is strictly included in  $J$ , we deduce  $j < p$  and  $(f'_l..f'_r)$  overlaps  
426  $J_1$ . This contradiction proves the uniqueness of the strong interval  $J$  satisfying  
427 condition 2.

428 Let us prove that  $F_I = F_J \cap I$ . Suppose by contradiction that  $F_I$  contains a  
429 frontier  $f$  not in  $F_J$ . Recall that  $I = (a_0..a_1)$  and  $a_0, a_1$  belong to  $F_J$ . Now, for  
430 each  $f_l \in F_J$  with  $f_l < f$ , we have that  $(f_l..f)$  is a conserved interval either by  
431 Lemma 5 applied to  $(a_0..f)$  and  $(f_l..f_l)$  (when  $f_l \geq a_0$ ) or since it is the union of  
432 the two conserved intervals  $(f_l..a_0)$  and  $(a_0..f)$  (when  $f_l < a_0$ ). Symmetrically,  
433  $(f..f_l)$  is also a conserved interval when  $f_l \in F_J$ ,  $f_l > f$ . But then  $F_J \cup \{f\}$  is  
434 a set of frontiers of  $J$  larger than  $F_J$ , which contradicts the maximality of  $F_J$ .

435 Eventually, let us prove that  $J = \text{Container}(I)$ . Assume that  $F = \{f_1, f_2, \dots,$   
436  $f_k\}$ , that  $I = (f_i..f_j)$  and that, by contradiction, there is a smallest strong  
437 conserved interval  $J' = (a..c)$  which contains  $I$ . Then  $J' \subsetneq J$  since otherwise  $J$   
438 and  $J'$  would overlap. W.l.o.g. assume that  $f_j \neq c$ . Then  $(f_i..f_k)$  overlaps  $J'$ ,  
439 and this contradicts the assumption that  $J'$  is strong.  $\square$

440 We only need three more results before dealing with  $b$ -nested conserved intervals.  
441

442 **Lemma 8** *Let  $I$  and  $J$  be two conserved intervals. If there exists a frontier*  
443  *$f \in F_I \cap F_J$ , then  $\text{Container}(I) = \text{Container}(J)$ .*

444 *Proof.* Since both  $\text{Container}(I)$  and  $\text{Container}(J)$  are strong, and since they  
445 share a common element, one contains the other. Now, suppose w.l.o.g. that  
446  $\text{Container}(I) \subseteq \text{Container}(J)$ . By contradiction, assume that  $\text{Container}(I) \subsetneq$   
447  $\text{Container}(J)$  and let  $\text{Container}(J) = (a..c)$ . Since  $f \in F_J$  and that by Theorem

448 5 we have  $F_J = F_{(a..c)} \cap J$ , we deduce that  $f \in F_{(a..c)}$  and thus  $(a..f)$  and  $(f..c)$   
449 are conserved intervals. Now, one of them necessarily overlaps  $\text{Container}(I)$ ,  
450 since at least one of  $a, c$  is not an endpoint of  $\text{Container}(I)$ . But this is impos-  
451 sible. Therefore  $\text{Container}(I) = \text{Container}(J)$ .  $\square$

452 **Lemma 9** *Let  $I$  be a (weak or strong) conserved interval with frontier set  $F_I =$   
453  $\{f_1, \dots, f_k\}$  and let  $(a..c) \subseteq I$  be a conserved interval. Then exactly one of the  
454 following cases occurs for the interval  $(a..c)$ :*

- 455 1. *either there exists  $l$  such that  $f_l \in (a..c)$ , and then there exist  $i$  and  $j$  such  
456 that  $(a..c) = (f_i..f_j)$ .*
- 457 2. *or  $(a..c)$  contains no frontier of  $F_I$ , and then there exists  $i$  such that  
458  $f_i < a \leq c < f_{i+1}$ .*

459 *Proof.* Obviously, the two cases cannot hold simultaneously. Moreover, in case  
460 2., the deduction is obvious.

461 Let us focus now on the case 1. Let  $(a..c)$  contain some frontier  $f_l \in F_I$ .  
462 Consider now the two intervals  $(f_1..f_l)$  and  $(f_l..f_k)$ . Then either (i)  $(a..c) =$   
463  $(f_1..f_k) = I$ , or (ii)  $(a..c) = (f_l..f_l)$ , or (iii)  $l = 1$  or  $l = k$ , or (iv)  $(a..c)$  overlaps  
464  $(f_1..f_l)$  or  $(f_l..f_k)$ . The two first cases are trivial, let us consider the two last  
465 cases.

466 In case (iii) assume w.l.o.g. that  $l = 1$  (the case  $l = k$  is symmetric). Then  
467  $a = f_1$  since  $(a..c) \subseteq I$ . Since  $(a..c)$  contains the elements of  $I$  that are smaller  
468 or equal to  $c$ , then  $(c..f_k)$  is a conserved interval. Thus  $\{f_1, c, f_k\}$  is a frontier  
469 set of  $I$ . If  $c \notin F_I$  then according to Lemma 7 we have that  $\{f_1, c, f_k\} \cup F_I$  is  
470 a frontier-set of  $I$  contradicting the maximality of  $F_I$ . We deduce that there  
471 exists  $j$  such that  $c = f_j$ . Now we are done, since  $(a..c) = (f_1..f_j)$ .

472 In case (iv),  $(a..c)$  is necessarily weak since it overlaps another conserved  
473 interval. W.l.o.g. we assume that  $(f_1..f_l)$  overlaps  $(a..c)$ . Let us first prove that  
474  $f_l$  is also a frontier of  $(a..c)$ . Indeed, assume *a contrario* that  $f_l \notin F_{(a..c)}$ , and  
475 denote  $F_{(a..c)} = \{f_1^*, \dots, f_p^*\}$ . With  $h \in \{1, 2, \dots, p\}$ , we have either  $f_h^* < f_l$   
476 and by Lemma 5 for  $(f_1..f_l)$  and  $(f_h^*..c)$  we deduce that  $(f_h^*..f_l)$  is conserved,  
477 or  $f_l < f_h^*$  and then Lemma 5 for  $(a..f_h^*)$  and  $(f_l..c)$  we deduce that  $(f_l..f_h^*)$  is  
478 conserved. Then  $F_{(a..c)} \cup \{f_l\}$  is a set of frontiers of  $(a..c)$ , which contradicts the  
479 maximality of  $F_{(a..c)}$ . Now, by Lemma 8 for  $\text{Container}((a..c))$  (whose frontier set  
480 contains  $f_l$  by Theorem 5) and  $\text{Container}(I)$  we deduce that  $\text{Container}((a..c)) =$   
481  $\text{Container}(I)$ . Thus using Theorem 5, we conclude that  $(a..c) = (f'_i..f'_j)$  for some  
482  $f'_i, f'_j \in F_{\text{Container}(I)}$ . But since  $(a..c) \subseteq I$  and  $F_I = F_{\text{Container}(I)} \cap I$ , we are  
483 done.  $\square$

484 The following theorem ensures that in the inclusion tree  $T$  of the strong con-  
485 served intervals of  $\mathcal{P}$ , weak intervals are exactly the intervals extending between  
486 two frontiers of a strong interval. Moreover, each weak interval is uniquely rep-  
487 resented in such a way. In addition, the computation of the tree and of all the  
488 frontier sets is linear.

489 **Theorem 6** *Let  $T$  be the inclusion tree  $T$  of strong conserved intervals of a set  
490  $\mathcal{P}$  of permutations. Then:*

- 491 1. a conserved interval  $I$  of  $\mathcal{P}$  is weak if and only if there exists a strong inter-  
492 val  $J$  of  $\mathcal{P}$  and two frontiers  $f_i, f_j \in F_J$  such that  $I = (f_i..f_j)$ . Moreover,  
493 in this case  $J$  is unique.
- 494 2. for each strong conserved interval  $I$  of  $T$  with parent  $J$  in  $T$ , there is a  
495 unique conserved interval  $L(I) = (f_i..f_{i+1})$  defined by successive frontiers  
496 in  $F_J$  such that  $I \subsetneq (f_i..f_{i+1})$ .
- 497 3. the tree  $T$ , the maximal set of frontiers  $F_J$  of each strong conserved interval  
498  $J$  and the interval  $L(I)$  of each strong conserved interval  $I \neq (1..n)$  may  
499 be computed in global  $O(n)$  time and  $O(n)$  space.

500 *Proof.* Concerning affirmation 1, the " $\Rightarrow$ " part is deduced directly from Theo-  
501 rem 5, whereas the " $\Leftarrow$ " part is ensured by the definition of a set of frontiers.  
502 Again by Theorem 5, we deduce the uniqueness of  $J$ .

503 Affirmation 2 results from Lemma 9. According to affirmation 1 in this  
504 lemma,  $I$  cannot contain a frontier of  $J$ , since otherwise  $I$  would be of the form  
505  $(f_i..f_j)$ , with  $f_i, f_j \in F_J$ , and thus would not be strong. Thus, by affirmation  
506 2 in Lemma 9, we deduce the existence of  $L(I)$ , which is necessarily unique by  
507 the definition of the frontiers.

508 We focus now on affirmation 3. In Bergeron and Stoye (2006), a conserved  
509 interval is called *irreducible* if it cannot be written as the union of smaller  
510 conserved intervals. It is easy to notice that the set of irreducible intervals of  
511 size at least two is exactly composed of the intervals  $(f_i..f_{i+1})$ , where  $f_i, f_{i+1}$  are  
512 two consecutive frontiers of a strong conserved interval of  $\mathcal{P}$ . Indeed, affirmation  
513 1 shows that the only irreducible weak conserved intervals  $I = (f_i..f_j)$  are those  
514 for which  $j = i + 1$ , and obviously the only irreducible strong intervals  $I$  are  
515 those with  $|F_I| = 2$ , which are of the form  $(f_1..f_2)$ , with  $F_I = \{f_1, f_2\}$ .

516 To show affirmation 3, we notice that the number of irreducible intervals is  
517 in  $O(n)$  [Bergeron and Stoye (2006)], and that they may be computed in  $O(n)$   
518 time and space for an arbitrary number  $K$  of permutations using generators  
519 from Rusu (2012). Knowing irreducible conserved intervals, the computation  
520 of strong intervals, of their set of frontiers, as well as that of the tree is quite  
521 easy. First, one must plot on the identity permutation the  $O(n)$  irreducible  
522 intervals of size at least two, by marking the left and right endpoint of each  
523 such irreducible interval. Notice that each element  $p$  of the permutation  $Id_n$   
524 has at most two marks, the equality occurring only when  $p$  is an internal (that  
525 is, different from an endpoint) frontier of a strong interval. We assume the right  
526 mark of  $p$  (when it exists) always precedes the element  $p$  whereas the left mark  
527 (when it exists) always follows the element  $p$ , so that a left-to-right traversal of  
528  $Id_n$  allows to close the interval with right endpoint  $p$  before opening the interval  
529 with left endpoint  $p$ .

530 Replacing left and right marks with respectively (square) left and right brack-  
531 ets indexed by their corresponding element  $p$  on  $Id_n$ , we obtain an expression  $E$   
532 which has correctly nested brackets, since irreducible intervals may only overlap  
533 on one element. Moreover, if  $I$  and  $J$  are strong intervals such that  $J$  is the

534 parent of  $I$ , then  $I \subsetneq L(I) \subseteq J$  and thus these intervals are closed exactly in  
535 this order during a left-to-right traversal of the expression  $E$ . The expression  
536  $E$  then allows, during a left-to-right traversal, to discover the strong intervals  
537 according to a post-order traversal of  $T$ , which is built on the fly. A strong  
538 conserved interval  $J$  is obtained by chaining as long as possible neighboring ir-  
539 reducible intervals, i.e. such that the right bracket of an interval is followed by  
540 the endpoint  $p$  of the interval and by the left bracket of the next interval. Its  
541 frontiers are given by the endpoints of the chained irreducible intervals. Also,  
542 since  $I \subsetneq L(I)$  for all strong intervals  $I$ , it is easy to identify  $L(I)$  since it is the  
543 interval which closes immediately after  $I$  during the traversal.  $\square$

**Example.** Let  $\mathcal{P} = \{Id_9, P_2\}$ , where  $P_2 = (1, -3, -2, 4, 5, -8, -7, -6, 9)$ .  
The strong intervals are (1..9) (with frontier set  $\{1, 4, 5, 9\}$ ), (2..3) (with frontier  
set  $\{2, 3\}$ ) and (6..8) (with frontier set  $\{6, 7, 8\}$ ). To build  $T$ , we first plot the  
irreducible intervals, i.e. (1..4), (2..3), (4..5), (5..9), (6..7) and (7..8) on  $P_1$ , and  
we obtain the expression:

$$E = 1 [1 -3 [3 ]_2 - 2 ]_4 4 [4 ]_5 5 [5 -8 [8 ]_7 - 7 [7 ]_6 - 6 ]_9 9.$$

544 A left-to-right traversal of  $E$  allows to find first the interval (2..3) which is  
545 included in (1..4), and thus the node (2..3) of  $T$  is built, and a node  $x$  starting  
546 with (1..4) is created and defined as the parent of (2..3). Next, the interval (1..4)  
547 in  $x$  is continued with (4..5) (just change the interval inside the already existing  
548 node), and continued with another interval (5.. $t$ ), where  $t$  is not yet known.  
549 Still, (7..8) is discovered as a subinterval of (5.. $t$ ), and it may be continued with  
550 (6..7), thus creating together the interval (6..8) which is another child of  $x$ . Once  
551 this is done, we read 9 which indicates that  $t = 9$ . Thus  $T$  has three nodes, the  
552 root (1..9) (with frontier set  $\{1, 4, 5, 9\}$  discovered during the traversal), and its  
553 two children (2..3) (with frontier set  $\{2, 3\}$ ) and (6..8) (with frontier set  $\{6, 7, 8\}$ )  
554 discovered during the traversal).

## 555 4.2 Properties of $b$ -nested conserved intervals

556 Recall that by definition all  $b$ -small conserved intervals are  $b$ -nested conserved  
557 intervals. The characterization below of  $b$ -nested conserved intervals has some  
558 similarities with that of  $b$ -nested common intervals represented in the  $PQ$ -tree  
559 as  $Q$ -intervals (see affirmation (b) in Theorem 3).

560 Let  $J$  be a conserved interval and let  $F_J = \{f_1, f_2, \dots, f_k\}$  be its maximal  
561 set of frontiers. We say that  $J$  contains a  $b$ -gap at position  $l$  if  $(f_l..f_{l+1})$  is  
562  $(b + 1)$ -large. Furthermore, we say that a conserved interval  $(a..c)$  falls in the  
563 gap between  $f_l$  and  $f_{l+1}$  of  $J$  if  $f_l < a \leq c < f_{l+1}$  and  $\text{Container}((a..c))$  has  
564 the parent  $\text{Container}(J)$ . In other words,  $J$  is represented in  $T$  by the node  
565  $\text{Container}(J)$  and  $(a..c)$  is represented by the node  $\text{Container}((a..c))$ , in such a  
566 way that the former node is the parent of the latter one.

567 A  $b$ -gap at position  $l$  is said *good* if it contains at least one  $b$ -nested strong  
568 conserved interval  $I$  with  $|I| \geq |(f_l..f_{l+1})| - b$ , or equivalently  $|I| \geq f_{l+1} - f_l +$   
569  $1 - b$ . Then a good  $b$ -gap is a  $b$ -nested conserved interval.



570 **Theorem 7** *A conserved interval  $J$  of  $\mathcal{P}$  is  $b$ -nested if and only if it contains*  
571 *no  $b$ -gap, or if it contains exactly one good  $b$ -gap  $f_l..f_{l+1}$ .*

572 *Proof.*

573 We first prove the " $\Leftarrow$ " part. Let  $J$  be a conserved interval with maximal  
574 set of frontiers  $F_J = \{f_1, f_2, \dots, f_k\}$ . If  $J$  contains exactly one  $b$ -gap, let it be  
575 at position  $l$ . Otherwise, let us fix arbitrarily  $l = 1$ . In both cases,  $(f_l..f_{l+1})$  is a  
576 conserved  $b$ -nested interval: either because it is  $b$ -small, or because it is a good  
577  $b$ -gap. Now, for all  $j > l + 1$  in increasing order, we deduce by induction that  
578  $(f_l..f_j)$  is a conserved interval (by definition of the set of frontiers) containing  
579  $(f_l..f_{j-1})$ , and thus it is  $b$ -nested. Thus  $(f_l..f_k)$  is a conserved  $b$ -nested interval.  
580 Similarly, we deduce by induction that  $(f_u..f_k)$  is a conserved  $b$ -nested interval,  
581 for all decreasing values of  $u = l - 1, l - 2, \dots, 1$ . Thus  $J = (f_1..f_k)$  is  $b$ -nested.

582 Now let us prove the " $\Rightarrow$ " part, by proving (a) that an conserved interval  
583 with two  $b$ -gaps or more is not  $b$ -nested, and (b) that if a  $b$ -nested conserved  
584 interval contains one  $b$ -gap then this  $b$ -gap is good.

585 **Proof of (a).** Assume by contradiction that  $J$  with  $F_J = \{f_1, f_2, \dots, f_k\}$  is  
586 conserved  $b$ -nested and contains two  $b$ -gaps at initial positions  $l$  and  $r$  ( $l < r$ ).  
587 The  $b$ -nestedness of  $J$  implies the existence of a  $b$ -nested conserved interval  
588  $J' \subsetneq J$  such that  $|J'| \geq |J| - b$ . Now,  $|J' \cap (f_l..f_{l+1})| \geq 2$ , otherwise  $J'$   
589 misses at least  $b + 1$  elements from  $(f_l..f_{l+1})$  (which is  $(b + 1)$ -large) and thus  
590  $|J'| \leq |J| - (b + 1)$ , a contradiction. Similarly,  $|J' \cap (f_r..f_{r+1})| \geq 2$ . We deduce  
591 that  $J'$  contains both  $f_{l+1}$  and  $f_r$ , as well as at least one additional element  
592 on the left of  $f_{l+1}$  and one additional element on the right of  $f_r$ . By Lemma 9  
593 with  $I = J$  and  $(a..c) = J'$  we have that  $J' = (f_u..f_v)$  with  $u \leq l$  and  $r + 1 \leq v$ .  
594 Thus the existence of the  $b$ -nested interval  $J$  containing the two  $b$ -gaps implies  
595 the existence of a smaller  $b$ -nested interval  $J'$  still containing the two  $b$ -gaps.

596 Now assume a maximal size series  $J_0 = J, J_1 = J', \dots$  of  $b$ -nested conserved  
597 intervals has been built similarly, each interval being strictly included in the  
598 previous one, all containing the two  $b$ -gaps. Such a series ends with  $(f_l..f_{r+1})$ ,  
599 since otherwise (if the last interval is larger) it is possible to construct a smaller  
600  $b$ -nested interval included in the last interval and containing  $(f_l..f_{r+1})$ . Thus  
601  $(f_l..f_{r+1})$  is  $b$ -nested. But this is not possible, as it cannot strictly contain  
602 another  $b$ -nested common interval of size at least  $(|f_l..f_{r+1}|) - b$ . As before,  
603 such an interval needs to contain the two gaps, and it is therefore not strictly  
604 included in  $(f_l..f_{r+1})$ .

605 **Proof of (b).** Assume now that  $J$  with  $F_J = \{f_1, f_2, \dots, f_k\}$  is conserved  $b$ -  
606 nested and has a unique  $b$ -gap situated at position  $l$ . As before,  $J$  must contain  
607 a  $b$ -nested conserved interval  $J'$  with  $|J'| > |J| - b$  and then  $|J' \cap (f_l..f_{l+1})| \geq 2$   
608 implying by Lemma 9 that  $J'$  must contain  $(f_l..f_{l+1})$ . The smallest interval  
609 obtained following the same reasoning is then  $(f_l..f_{l+1})$  itself, which must be  
610  $b$ -nested. As this interval has no internal frontiers (otherwise  $F_J$  would not be  
611 maximal), any  $b$ -nested common interval  $I = (a..c)$  of size at least  $f_{l+1} - f_l + 1 - b$   
612 it contains satisfies  $f_l < a < c < f_{l+1}$ . If  $I$  is strong then we are done, otherwise  
613  $\text{Container}(I)$  is strong and has all the required properties.  $\square$

614 **4.3 Computing and counting all  $b$ -nested conserved inter-**  
615 **vals**

616 Theorem 6 allows to count and to enumerate efficiently all  $b$ -nested conserved  
617 intervals. The computation may be performed, as was the case for common  
618 intervals, in a single post-order traversal of the inclusion tree  $T$ , focusing on  
619 each strong conserved interval  $I$  of  $\mathcal{P}$ . First compute the  $b$ -gaps of  $I$ . Mark  $I$   
620 as  $b$ -nested if it contains no  $b$ -gap or one  $b$ -gap  $(f_l..f_{l+1})$ , with  $f_l, f_{l+1} \in F_I$ ,  
621 that is a good one. The latter verification assumes that during the treatment of  
622 each child  $I'$  of  $I$ , if  $I'$  is detected as  $b$ -nested, then  $L(I')$  (which is an interval  
623  $(f_j..f_{j+1})$  with  $f_j, f_{j+1} \in F_I$ ) is marked as good if and only if  $L(I')$  is a  $b$ -gap  
624 and  $|I'| \geq |L(I')| - b$  (otherwise,  $L(I')$  is not marked at all). Now, if  $I$  is  $b$ -nested  
625 and  $I \neq (1..n)$ , the same type of mark is performed on  $L(I)$  if the conditions  
626 are fulfilled.

627 Then, applying Algorithm 2 on each strong conserved interval  $I$  allows to  
628 enumerate all the  $b$ -nested conserved intervals generated by the frontiers of  $I$ ,  
629 according to Theorem 6. Affirmation 1 in Theorem 6 ensures that each interval  
630 is output exactly once. The running time of Algorithm 2 is clearly linear in the  
631 number of intervals output plus the numbers of children of  $I$ , yielding a global  
632  $O(n + nocc)$  time.

**Input:** A strong conserved interval  $I$ , its frontier set  $F_I$ , the children of  $I$   
in  $T$  marked as nested or not

**Output:** The conserved  $b$ -nested intervals generated by the frontiers of  $I$   
and strictly included in  $I$

```

1 for  $i$  from 1 to  $|F_I|$  do
2    $j \leftarrow i + 1$ 
3   goodgaps  $\leftarrow 0$  // counts the good  $b$ -gaps between  $f_i$  and  $f_j$ 
4   stop  $\leftarrow false$ 
5   repeat
6     if  $f_j - f_{j-1} > b + 1$  then
7       // Found a  $b$ -gap at  $j$ 
8       if  $(f_j, f_{j+1})$  is a good gap and goodgaps = 0 then
9         goodgaps  $\leftarrow 1$ 
10      else
11        stop  $\leftarrow true$ 
12      endif
13    endif
14    if not stop then output  $(f_i..f_j)$  end if // notice  $(f_1..f_{|F_I|})$  is not
        output
15     $j \leftarrow j + 1$ 
16  until stop and  $(j = |F_I| + 1$  or  $(i = 1$  and  $j = |F_i|))$ 
17 endfor
```

**Algorithm 2:** Conserved  $b$ -nested intervals

To simply count the number of  $b$ -nested conserved intervals in  $I$ , we must

follow the same approach as for common intervals. Good and not good  $b$ -gaps are identified during a search among the intervals  $(f_i..f_{i+1})$ , where  $F_I = \{f_1, f_2, \dots, f_k\}$ . Then, for each good  $b$ -gap we compute the number  $l$  (respectively  $r$ ) of successive  $(b + 1)$ -small intervals  $(f_i..f_{i+1})$  on its left (respectively right). We count the number of  $b$ -nested conserved intervals containing the good  $b$ -gap as

$$l * (r + 1) + r.$$

Next, for each maximal set of successive  $(b + 1)$ -small intervals  $(f_i..f_{i+1})$  we add

$$h * (h - 1)/2$$

633  $b$ -nested common intervals, where  $h$  is the number of  $(b + 1)$ -small intervals in  
634 the set.

635 All these operations obviously take  $O(n)$  time and space.

## 636 5 Conclusion

637 In this paper we introduced the family of  $b$ -nested common intervals of  $K$  per-  
638 mutations, and showed that it may be computed in time proportional to its  
639 cardinality. This approach extends to any closed family of intervals that is  
640 represented by a  $PQ$ -tree. We also show that our approach can be applied  
641 to conserved intervals, whose structure and properties are close but still dif-  
642 ferent from those of common intervals. The interest of our generalization of  
643 common/conserved intervals for finding conserved clusters of genes should be  
644 attested by further experiments. Also, other applications may be devised, such  
645 as helping the identification of orthologs/paralogs or defining distances between  
646 genomes in an evolutionary approach. These are the close perspectives of our  
647 work.

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