

<sup>1</sup> DateLife: leveraging databases and analytical tools to reveal the dated Tree of Life

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17

## Abstract

18 Achieving a high-quality reconstruction of a phylogenetic tree with branch lengths  
19 proportional to absolute time (chronogram) is a difficult and time-consuming task. But the  
20 increased availability of fossil and molecular data, and time-efficient analytical techniques  
21 has resulted in many recent publications of large chronograms for a large number and wide  
22 diversity of organisms. Knowledge of the evolutionary time frame of organisms is key for  
23 research in the natural sciences. It also represent valuable information for education, science  
24 communication, and policy decisions. When chronograms are shared in public, open  
25 databases this wealth of expertly-curated and peer-reviewed data on evolutionary timeframe  
26 is exposed in a programmatic and reusable way, as intensive and localized efforts have  
27 improved data sharing practices, as well as incentivized open science in biology. Here we  
28 present DateLife, a service implemented as an R package and an R Shiny website application  
29 available at [www.datelife.org](http://www.datelife.org), that provides functionalities for efficient and easy finding,  
30 summary, reuse, and reanalysis of expert, peer-reviewed, public data on time frame of  
31 evolution. The main DateLife workflow constructs a chronogram for any given combination  
32 of taxon names by searching a local chronogram database constructed and curated from the  
33 Open Tree of Life Phylesystem phylogenetic database, which incorporates phylogenetic data  
34 from the TreeBASE database as well. We implement and test methods for summarizing time  
35 data from multiple source chronograms using supertree and congruification algorithms, and  
36 using age data extracted from source chronograms as secondary calibration points to add  
37 branch lengths proportional to absolute time to a tree topology. DateLife will be useful to  
38 increase awareness of the existing variation in alternative hypothesis of evolutionary time for  
39 the same organisms, and can foster exploration of the effect of alternative evolutionary  
40 timing hypotheses on the results of downstream analyses, providing a framework for a more  
41 informed interpretation of evolutionary results.

42

*Keywords:* Tree; Phylogeny; Scaling; Dating; Ages; Divergence times; Open Science;

<sup>43</sup> Congruification; Supertree; Calibrations; Secondary calibrations

<sup>44</sup> Word count: 4914

45 DateLife: leveraging databases and analytical tools to reveal the dated Tree of Life

46 **Introduction**

47 Chronograms –phylogenies with branch lengths proportional to time– provide key data  
48 on evolutionary time frame for the study of natural processes in many areas of biological  
49 research, such as developmental biology (Delsuc et al., 2018; Laubichler & Maienschein,  
50 2009), conservation biology (Felsenstein, 1985; C. Webb, 2000), historical biogeography  
51 (Posadas, Crisci, & Katinas, 2006), and species diversification (Magallon & Sanderson, 2001;  
52 Morlon, 2014).

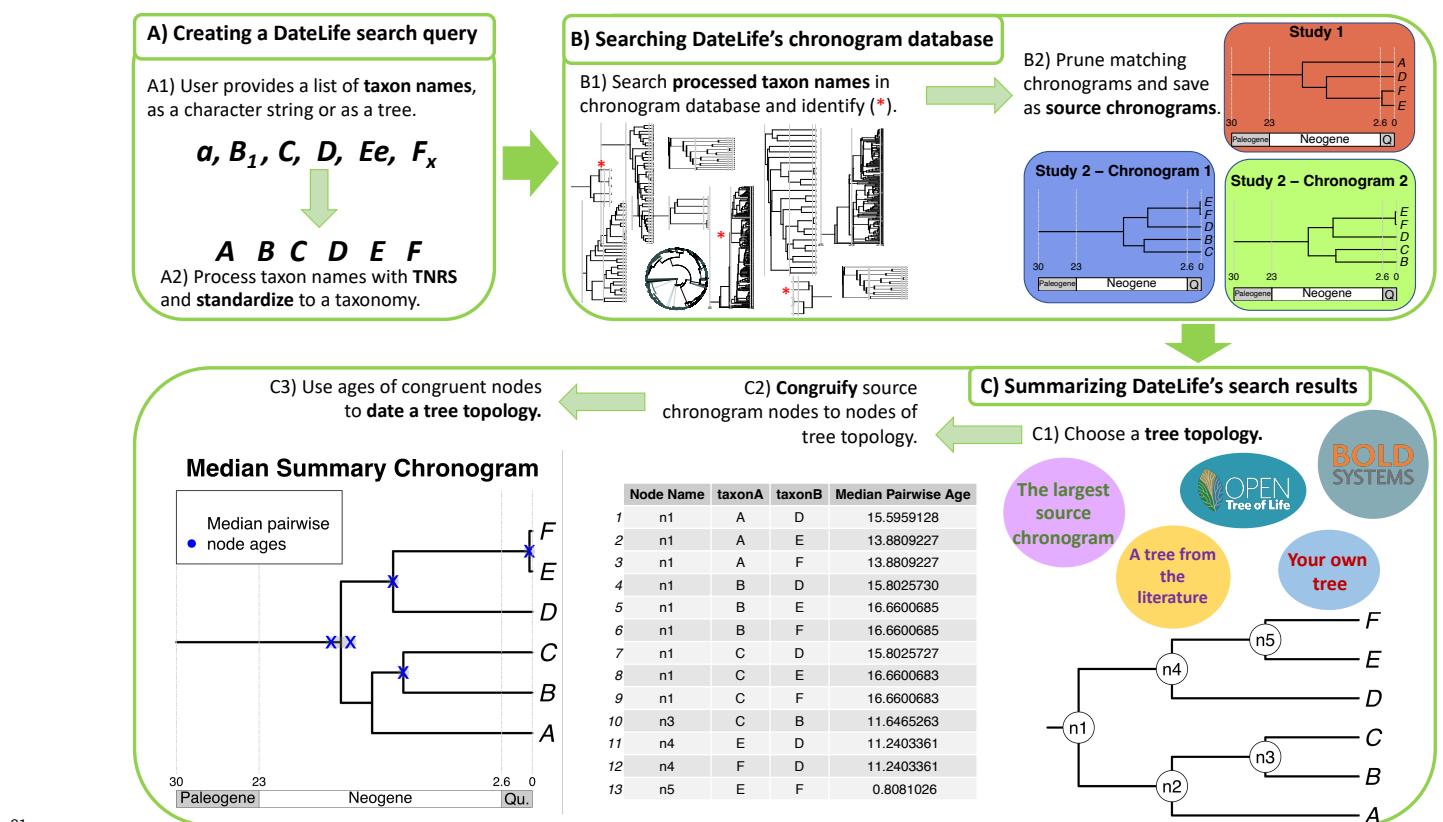
53 Building a chronogram is not an easy task. It requires obtaining and curating data to  
54 construct a phylogeny, selecting and placing appropriate calibrations on the phylogeny using  
55 independent age data points from the fossil record or other dated events, and inferring the  
56 full dated tree; it also generally requires specialized biological training, taxonomic domain  
57 knowledge, and a non-negligible amount of research time, computational resources and  
58 funding.

59 Here we present the DateLife project which has the main goal of capturing age data  
60 from published chronograms, and making these data readily accessible to the community for  
61 reuse and reanalysis, for research, teaching, and science communication and policy.  
62 DateLife’s core software application is available as an R package (Sanchez-Reyes et al., 2022),  
63 and as an online Rshiny interactive website at [www.datelife.org](http://www.datelife.org). It features key elements for  
64 scientific reproducibility, such as a versioned, open and fully public source database  
65 (McTavish et al., 2015), data stored and available in a computer readable format (Vos et al.,  
66 2012), automated and programmatic ways of accessing the data (Stoltzfus et al., 2013) and  
67 methods to summarize and compare the data.

68

## Description

69 DateLife's core software application consists of the R package `datelife`. Its latest  
 70 stable version – v0.6.4, is available from the CRAN repository (Sanchez-Reyes et al., 2022),  
 71 and relies on functionalities from various biological R packages: ape (Paradis, Claude, &  
 72 Strimmer, 2004), bold (Chamberlain et al., 2019), geiger (Pennell et al., 2014), paleotree  
 73 (Bapst, 2012), phyloch (Heibl, 2008), phylocomr (Ooms & Chamberlain, 2018), phytools  
 74 (Revell, 2012), rotl (Michonneau, Brown, & Winter, 2016), and taxize (Chamberlain & Szöcs,  
 75 2013; Chamberlain et al., 2019). Figure 1 provides a graphical summary of the three main  
 76 steps of the DateLife workflow: creating a search query, searching a database, and  
 77 summarizing results from the search.



81

78 FIGURE 1. Main DateLife workflow. Analyses can be performed via DateLife's interactive website  
 79 at [www.datelife.org](http://www.datelife.org), or using the `datelife` R package. Details on the R functions used to perform  
 80 the analyses are available from `datelife`'s R package vignettes at [phylotastic.org/datelife](http://phylotastic.org/datelife).

## 82 Creating a search query

83 DateLife starts by processing an input consisting of at least two taxon names, which  
84 can be provided as a comma separated character string or as tip labels on a tree. If the input  
85 is a tree, it can be provided as a classic newick character string (Archie et al., 1986), or as a  
86 “phylo” R object (Paradis et al., 2004). The input tree is not required to have branch lengths,  
87 and its topology is used in the summary steps described in the next section.

88 DateLife accepts scientific names that can belong to any inclusive taxonomic group  
89 (e.g., genus, family, tribe, etc.) or a binomial species name. Subspecies and variants are  
90 ignored. If an input taxon name belongs to an inclusive taxonomic group, DateLife has two  
91 alternative behaviors defined by the “get species from taxon” flag. If the flag is active,  
92 DateLife retrieves all species names within the inclusive taxonomic group (following a  
93 taxonomy of choice; current options are Open Tree of Life, NCBI, GBIF, or IRMNG  
94 taxonomies) and adds them to the input string. If the flag is inactive, DateLife excludes any  
95 taxon names above the species level from the search query.

96 DateLife processes input scientific names using a Taxonomic Name Resolution Service  
97 (TNRS), which increases the probability of correctly finding the queried taxon names in the  
98 chronogram database. TNRS detects, corrects and standardizes name misspellings and typos,  
99 variant spellings and authorities, and nomenclatural synonyms to a single taxonomic  
100 standard (Boyle et al., 2013). DateLife implements TNRS using OpenTree’s unified  
101 taxonomy as standard (Open Tree Of Life et al., 2016; Rees & Cranston, 2017), storing  
102 OpenTree’s Taxonomy identification numbers for further processing.

103 The processed input taxon names are saved as an R object of a newly defined class,  
104 `datelifeQuery`, that is used in the following steps. This object contains the standardized  
105 names, the corresponding OpenTree taxonomic id numbers, and the topology of the input  
106 tree if any was provided.

107 **Searching a chronogram database**

108 At the time of writing of this manuscript (Jun 21, 2022), DateLife's chronogram  
109 database latest version consist of 253 chronograms published in 187 different studies. It is  
110 curated from OpenTree's phylogenetic database, the Phylesystem, which constitutes an open  
111 source of expert and peer-reviewed phylogenetic knowledge with rich metadata (McTavish et  
112 al., 2015), which allows automatic and reproducible assembly of our chronogram database.  
113 Datelife's chronogram database is navigable as an R data object within the `datelife` R  
114 package.

115 A unique feature of OpenTree's Phylesystem is that the community can add new  
116 published, state-of-the-art chronograms any time through their curator application  
117 (<https://tree.opentreeoflife.org/curator>). As chronograms are added to Phylesystem, they are  
118 incorporated into an updated `datelife`'s database that is assigned a new version number,  
119 followed by a package release on CRAN. `datelife`'s chronogram database is updated as new  
120 chronogram data is added to Phylesystem, at a minimum of once a month and a maximum  
121 of every 6 months. Users can also upload and curate new chronograms to OpenTree  
122 themselves. Then, trigger an update of their local `datelife` database to incorporate the new  
123 chronograms and have them available for their current analysis.

124 A DateLife search is implemented by matching processed taxon names provided by the  
125 user to tip labels in the chronogram database. Chronograms with at least two matching  
126 taxon names on their tip labels are identified and pruned down to preserve only the matched  
127 taxa. These matching pruned chronograms are referred to as source chronograms. Total  
128 distance (in units of millions of years) between taxon pairs within each source chronogram  
129 are stored as a patristic distance matrix (Figure 1). The matrix format speeds up extraction  
130 of pairwise taxon ages of any queried taxa, as opposed to searching the ancestor node of a  
131 pair of taxa in a “phylo” object or newick string. Finally, the patristic matrices are  
132 associated to the study citation where the original chronogram was published, and stored as

133 an R object of the newly defined class `datelifeResult`.

134 **Summarizing search results**

135 Summary information is extracted from the `datelifeResult` object to inform  
136 decisions for subsequent steps in the analysis workflow. Basic summary information available  
137 to the user is:

- 138 1. The matching pruned chronograms as newick strings or “phylo” objects.
- 139 2. The ages of the root of all source chronograms. These ages can correspond to the age  
140 of the most recent common ancestor (mrca) of the user’s group of interest if the source  
141 chronograms have all taxa belonging to the group. If not, the root corresponds to the  
142 mrca of a subgroup within the group of interest.
- 143 3. Study citations where original chronograms were published.
- 144 4. A report of input taxon names matches across source chronograms.
- 145 5. The source chronogram(s) with the most input taxon names.
- 146 6. Various single summary chronograms resulting from summarizing age data, generated  
147 using the methodology described next.

148 ***Choosing a topology.***— DateLife requires a tree topology to summarize age data  
149 upon. We recommend that users provide a tree topology as input from the literature, or one  
150 of their own making. If no topology is provided, DateLife automatically obtains one from the  
151 OpenTree synthetic tree (Open Tree Of Life et al., 2019). These are known as “induced”  
152 OpenTree subtrees, which do not necessarily correspond to a monophyletic group.  
153 Alternatively, DateLife can combine topologies from source chronograms using a supertree  
154 approach. To combine topologies from source chronograms into a single summary (or  
155 supertree) topology, the DateLife workflow identifies the source chronograms that form a  
156 grove, roughly, a sufficiently overlapping set of taxa between trees, by implementing  
157 definition 2.8 for n-overlap from Ané et al. (2009). In rare cases, a group of trees can have

158 multiple groves. By default, DateLife chooses the grove with the most taxa, however, the  
159 “criterion = trees” flag allows the user to choose the grove with the most trees instead. If  
160 source chronograms do not form a grove, the supertree reconstruction will fail.

161 **Dating the topology.**— Input topologies from OpenTree or the supertree approach  
162 described above do not include branch length estimates of any kind. Optionally, to estimate  
163 branch lengths proportional to substitution rates on these topologies, DateLife can mine the  
164 Barcode of Life Data System, BOLD (Ratnasingham & Hebert, 2007) to obtain genetic  
165 markers for the input taxa. These markers are aligned with MUSCLE (Edgar, 2004) (by  
166 default) or MAFFT (Katoh, Asimenos, & Toh, 2009). This alignment can be used to  
167 estimate branch lengths on input topologies that lack branch lengths. Currently, branch  
168 length reconstruction in DateLife is performed using parsimony and the likelihood of the  
169 phylogenetic tree given a sequence alignment is computed (Schliep, 2011). While relative  
170 branch length information provides additional data for nodes without secondary date  
171 calibrations, topologies without branch lengths can also be dated.

172 Once a topology is chosen, DateLife applies the congruification method (Eastman,  
173 Harmon, & Tank, 2013) to find nodes belonging to the same clade across source  
174 chronograms, and extract the corresponding node ages from the patristic distance matrices  
175 stored as `datelifeResult`. By definition, the matrices store total distance (time from tip to  
176 tip), hence, node ages correspond to half the values stored in the patristic distance matrices.  
177 This assumes that the terminal taxa are coeval and occur at the present. A table of  
178 congruified node ages that can be used as calibrations for a dating analysis is stored as a  
179 `congruifiedCalibrations` object.

180 For each congruent node, the pairwise distances that traverse that node are  
181 summarized into a single summary matrix using classic summary statistics (i.e., mean,  
182 median, minimum and maximum ages), and the Supermatrix Distance Method [SDM;  
183 Criscuolo, Berry, Douzery, and Gascuel (2006)], which deforms patristic distance matrices by

184 minimizing variance and then averaging them. These single summary taxon pair age  
185 matrices (Summarized calibrations) can be applied as calibrations to date a tree topology,  
186 using different dating methods currently supported within DateLife: MrBayes (Huelsenbeck  
187 & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), PATHd8 (Britton, Anderson, Jacquet,  
188 Lundqvist, & Bremer, 2007), BLADJ (Campbell O. Webb, Ackerly, & Kembel, 2008;  
189 Campbell O. Webb & Donoghue, 2005), and treePL (Stephen A. Smith & O'Meara, 2012).

190 By default, DateLife implements the Branch Length Adjuster (BLADJ) algorithm to  
191 obtain a fully dated topology. BLADJ fixes node ages that have calibration data, and  
192 distributes time between nodes with no data evenly between nodes with calibration data.  
193 This minimizes age variance in the resulting chronogram (Campbell O. Webb et al., 2008).  
194 BLADJ does not use branch lengths even when they are present in the input tree or  
195 summarizing topology. When there is conflict in ages between nodes with calibration data,  
196 BLADJ ignores node ages that are older than the age of a parent node. BLADJ requires a  
197 root age estimate. If there is no information on the age of the root in the chronogram  
198 database, users can provide an estimate from the literature. If none is provided, DateLife  
199 assigns an arbitrary age to the root as 10% older than the oldest age available within the  
200 group.

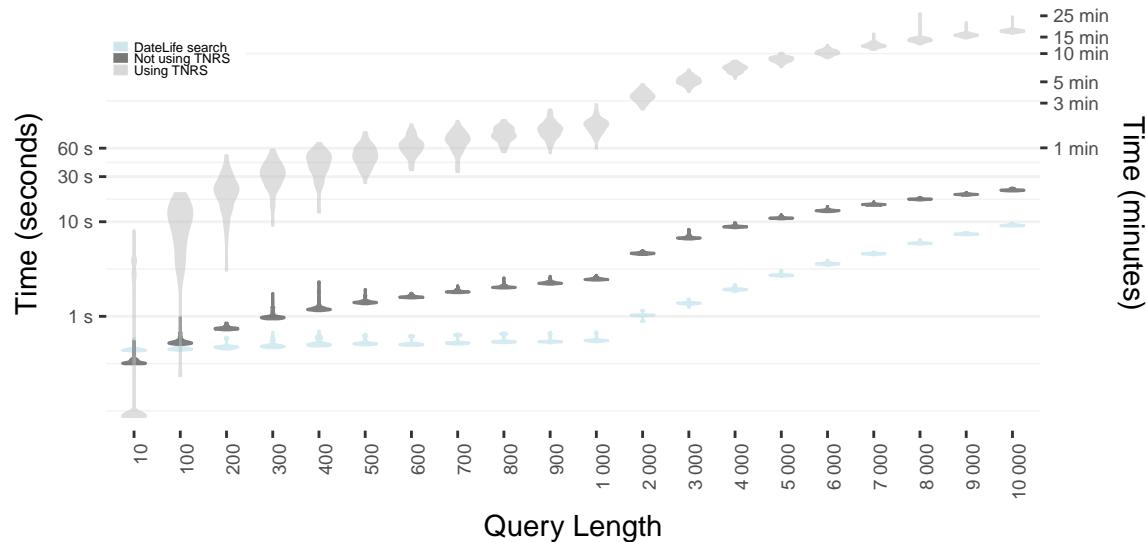
201 Alternative options supported in DateLife (MrBayes, PATHD8, TreePL) incorporate  
202 branch length information from the input topology in combination with the calibrations.  
203 PATHd8 is a non-clock, rate-smoothing method (Britton et al., 2007) to date trees. treePL  
204 (Stephen A. Smith & O'Meara, 2012), is a semi-parametric, rate-smoothing, penalized  
205 likelihood dating method (Michael J. Sanderson, 2002). The MrBayes (Huelsenbeck &  
206 Ronquist, 2001; Ronquist & Huelsenbeck, 2003) approach in datelife uses the calibrations as  
207 priors on node ages.

208 **Visualizing results.**— Finally, users can save all source and summary chronograms in  
209 formats that permit reuse and reanalyses (newick and R “phylo” format), as well as visualize

and compare results graphically, or construct their own graphs using `datelife`'s chronogram plot generation functions available from the R package `datelifeplot` (Sanchez-Reyes & O'Meara, 2022).

## Benchmark

`datelife`'s code speed was tested on an Apple iMac with one 3.4 GHz Intel Core i5 processor. We registered variation in computing time of query processing and search through the database relative to number of queried taxon names. Query processing time increases roughly linearly with number of input taxon names, and increases considerably if Taxonomic Name Resolution Service (TNRS) is activated. Up to ten thousand names can be processed and searched in less than 30 minutes with the most time consuming settings. Once names have been processed as described in methods, a name search through the chronogram database can be performed in less than a minute, even with a very large number of taxon names (Fig. 2).



223

FIGURE 2. DateLife's benchmarking results. Computation time used to process a query and a search across `datelife`'s chronogram database, relative to number of input taxon names.

226 *Caption continues.*

227 *Figure caption continued.* For each  $N = \{10, 100, 200, \dots, 1\ 000, \dots, 9\ 000, 10\ 000\}$ , we  
228 sampled  $N$  species names from the class Aves a hundred times, and then performed a datelife  
229 search processing the input names with Taxon Names Resolution Service (TNRS; light gray),  
230 and without processing names (dark gray). For comparison, we performed a search using an  
231 input that had been pre-processed with TNRS (light blue).

232 `datelife`'s code performance was evaluated with a set of unit tests designed and  
233 implemented with the R package `testthat` (R Core Team, 2018) that were run both locally  
234 with the `devtools` package (R Core Team, 2018), and on a public server –via GitHub, using  
235 the continuous integration tool Travis CI (<https://travis-ci.org>). At present, unit tests cover  
236 more than 40% of `datelife`'s code (<https://codecov.io/gh/phylotastic/datelife>). Unit  
237 testing helps identify potential issues as code is updated or, more critically, as services code  
238 relies upon may change.

239

## Case studies

240 We illustrate the DateLife workflow using a family within the Passeriform birds  
241 encompassing the true finches, Fringillidae, as case study. The first example analyses 6 bird  
242 species and shows all steps of the workflow. The second example is an analysis of 289 species  
243 in the family Fringillidae that are included in the NCBI taxonomy.

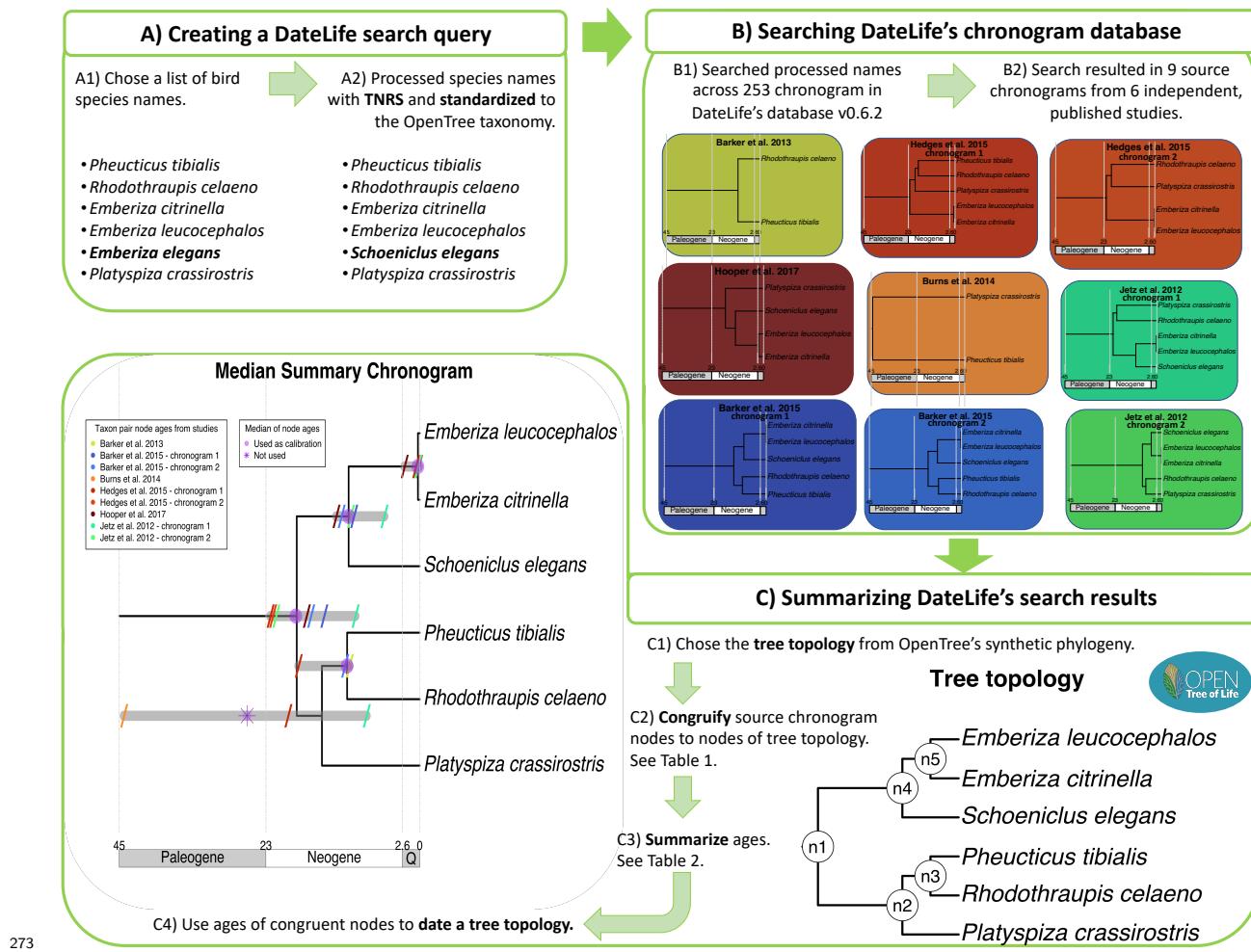
244 **A small example**

245 ***Creating a search query.***– We chose 6 bird species within the Passeriformes. The sample  
246 includes two species of cardinals: the black-thighed grosbeak – *Pheucticus tibialis* and the  
247 crimson-collared grosbeak – *Rhodothraupis celaeno*; three species of buntings: the  
248 yellowhammer – *Emberiza citrinella*, the pine bunting – *Emberiza leucocephalos* and the  
249 yellow-throated bunting – *Emberiza elegans*; and one species of tanager, the vegetarian finch –

250 *Platyspiza crassirostris*. Processing of input names found that *Emberiza elegans* is synonym  
251 for *Schoeniclus elegans* in the default reference taxonomy (Open Tree of Life Taxonomy v3.3,  
252 June 1, 2021). For a detailed discussion on the state of the synonym, refer to Avibase  
253 (Avibase, 2022; Lepage, 2004; Lepage, Vaidya, & Guralnick, 2014). Discovering this synonym  
254 allowed assigning five age data points for the parent node of *Emberiza elegans*, shown as  
255 *Schoeniclus elegans* in figure 3A, which would not have had any data otherwise.

256 **Searching the database.**- DateLife used the processed input names to search the local  
257 chronogram database and found 9 matching chronograms in 6 different studies (Fig. 3B).  
258 Three studies matched five input names (Barker, Burns, Klicka, Lanyon, & Lovette, 2015;  
259 Hedges, Marin, Suleski, Paymer, & Kumar, 2015; Jetz, Thomas, Joy, Hartmann, & Mooers,  
260 2012), one study matched four input names (Hooper & Price, 2017) and two studies matched  
261 two input names (Barker, Burns, Klicka, Lanyon, & Lovette, 2013; Burns et al., 2014). No  
262 studies matched all input names. Together, source chronograms provide 28 unique age data  
263 points, covering all nodes on our chosen tree topology to date (Table 1).

264 **Summarizing search results.**- DateLife obtained OpenTree's synthetic tree topology for  
265 these taxa (Fig. 3C), and congruified and mapped age data to nodes in this chosen topology  
266 (Table 1). The name processing step allowed including five data points for node "n4" (parent  
267 of *Schoeniclus elegans*; Fig. 3A) that would not have had any data otherwise due to name  
268 mismatch. Age summary statistics per node were calculated (Table 2) and used as  
269 calibrations to date the tree topology using the BLADJ algorithm. As expected, more  
270 inclusive nodes (e.g., node "n1") have more variance in age data than less inclusive nodes  
271 (e.g., node "n5"). Summary age data for node "n2" were excluded as final calibration  
272 because they are older than age data of the more inclusive node, "n1" (Fig. 3C4).



273

274 FIGURE 3. DateLife analysis results for a small sample of A) 6 bird species within the  
275 Passeriformes. B) Processed species names were found across 9 chronograms within 6  
276 independent studies (Barker et al. (2012), Barker et al. (2015), Burns et al. (2014), Hedges  
277 et al. (2015), Hooper and Price (2017), Jetz et al. (2012).) C) This revealed 28 source  
278 age data points for the queried species names. Summarized age data is used as secondary  
279 calibrations to date a tree topology obtained from OpenTree's synthetic tree, resulting in a  
280 summary chronogram of source ages.

	<b>Node Name</b>	<b>taxon A</b>	<b>taxon B</b>	<b>Node Age</b>	<b>Study chronogram</b>
1	n1	<i>Emberiza citrinella</i>	<i>Platyspiza crassirostris</i>	9.6509881	Jetz et al. 2012 – chronogram 1
2	n1	<i>Pheucticus tibialis</i>	<i>Schoeniclus elegans</i>	14.3336520	Barker et al. 2015 – chronogram 1
3	n1	<i>Rhodothraupis celaeno</i>	<i>Schoeniclus elegans</i>	16.2984859	Barker et al. 2015 – chronogram 2
4	n1	<i>Emberiza citrinella</i>	<i>Platyspiza crassirostris</i>	16.9499615	Hooper et al. 2017
5	n1	<i>Rhodothraupis celaeno</i>	<i>Schoeniclus elegans</i>	21.5140867	Jetz et al. 2012 – chronogram 2
6	n1	<i>Emberiza leucocephalos</i>	<i>Platyspiza crassirostris</i>	22.0000000	Hedges et al. 2015 – chronogram 2
7	n1	<i>Emberiza citrinella</i>	<i>Platyspiza crassirostris</i>	22.3757277	Hedges et al. 2015 – chronogram 1
8	n2	<i>Platyspiza crassirostris</i>	<i>Rhodothraupis celaeno</i>	7.9691925	Jetz et al. 2012 – chronogram 1
9	n2	<i>Platyspiza crassirostris</i>	<i>Rhodothraupis celaeno</i>	19.7085830	Jetz et al. 2012 – chronogram 2
10	n2	<i>Platyspiza crassirostris</i>	<i>Rhodothraupis celaeno</i>	19.7085900	Hedges et al. 2015 – chronogram 2
11	n2	<i>Platyspiza crassirostris</i>	<i>Rhodothraupis celaeno</i>	19.7128363	Hedges et al. 2015 – chronogram 1
12	n2	<i>Pheucticus tibialis</i>	<i>Platyspiza crassirostris</i>	44.2958603	Burns et al. 2014
13	n3	<i>Pheucticus tibialis</i>	<i>Rhodothraupis celaeno</i>	10.5304440	Barker et al. 2015 – chronogram 1
14	n3	<i>Pheucticus tibialis</i>	<i>Rhodothraupis celaeno</i>	10.5379092	Barker et al. 2013
15	n3	<i>Pheucticus tibialis</i>	<i>Rhodothraupis celaeno</i>	11.2095375	Barker et al. 2015 – chronogram 2
16	n3	<i>Pheucticus tibialis</i>	<i>Rhodothraupis celaeno</i>	18.1570685	Hedges et al. 2015 – chronogram 1
17	n4	<i>Emberiza citrinella</i>	<i>Schoeniclus elegans</i>	5.3238969	Jetz et al. 2012 – chronogram 1
18	n4	<i>Emberiza leucocephalos</i>	<i>Schoeniclus elegans</i>	9.8622460	Barker et al. 2015 – chronogram 1
19	n4	<i>Emberiza leucocephalos</i>	<i>Schoeniclus elegans</i>	10.3391445	Jetz et al. 2012 – chronogram 2
20	n4	<i>Emberiza leucocephalos</i>	<i>Schoeniclus elegans</i>	11.7317630	Barker et al. 2015 – chronogram 2
21	n4	<i>Emberiza citrinella</i>	<i>Schoeniclus elegans</i>	12.5133870	Hooper et al. 2017
22	n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.1407015	Jetz et al. 2012 – chronogram 1
23	n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.1516230	Hedges et al. 2015 – chronogram 2
24	n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.2011990	Barker et al. 2015 – chronogram 1
25	n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.2409300	Barker et al. 2015 – chronogram 2
26	n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.2732460	Jetz et al. 2012 – chronogram 2
27	n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.5760260	Hedges et al. 2015 – chronogram 1
28	n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	2.2898230	Hooper et al. 2017

281 TABLE 1. Ages of congruified nodes obtained from a datelife search for the Small Example  
 282 presented. See Figure 3, step C2.

<b>Node Name</b>	<b>Min Age</b>	<b>Q1</b>	<b>Median Age</b>	<b>Mean Age</b>	<b>Q3</b>	<b>Max Age</b>	<b>Variance</b>	<b>SD</b>
n1	9.6509881	15.316069	16.94996	17.5889860	21.757043	22.375728	22.2431847	4.7162681
n2	7.9691925	19.708583	19.70859	22.2790124	19.712836	44.295860	177.3279940	13.3164558
n3	10.5304440	10.536043	10.87372	12.6087398	12.946420	18.157069	13.7831237	3.7125630
n4	5.3238969	9.862246	10.33914	9.9540875	11.731763	12.513387	7.8263782	2.7975665
n5	0.1407015	0.176411	0.24093	0.5533641	0.424636	2.289823	0.6079318	0.7796998

283 TABLE 2. Summary of congruified nodes ages. See Figure 3, step C3.

<sup>284</sup> **An example with the family of true finches**

<sup>285</sup> ***Creating a query.***- To obtain ages for all species within the family of true finches,  
<sup>286</sup> Fringillidae, we ran a DateLife query using the “get species from taxon” flag, which gets all  
<sup>287</sup> recognized species names within a named group from a taxonomy of choice. Following the  
<sup>288</sup> NCBI taxonomy, our DateLife query has 289 Fringillidae species. This taxon-constrained  
<sup>289</sup> approach implies that the final results of a full DateLife analysis will be done using a tree  
<sup>290</sup> topology and ages for the species in a named group, which do not necessarily correspond to a  
<sup>291</sup> monophyletic group. Users can change this behaviour by providing a monophyletic tree as  
<sup>292</sup> input for a DateLife search, or as a tree topology for a DateLife summary.

<sup>293</sup> ***Searching the database.***- Next, we used the processed species names in our DateLife  
<sup>294</sup> query to identify chronograms with at least two Fringillidae species. The DateLife search  
<sup>295</sup> identified 13 chronograms containing at least two Fringillidae species, published in 9 different  
<sup>296</sup> studies (Barker et al., 2013, 2015; Burns et al., 2014; Claramunt & Cracraft, 2015; Gibb et  
<sup>297</sup> al., 2015; Hedges et al., 2015; Hooper & Price, 2017; Jetz et al., 2012; Price et al., 2014).  
<sup>298</sup> Once identified, DateLife pruned matching chronograms to keep Fringillidae species names  
<sup>299</sup> on tips only, and transformed these pruned chronograms to pairwise distance matrices,  
<sup>300</sup> revealing 1206 different age data points available for species within the Fringillidae  
<sup>301</sup> (supplementray table 1).

<sup>302</sup> ***Summarizing search results.***- The final step is to congruify and summarize the age data  
<sup>303</sup> available for the Fringillidae species into single summary chronograms, using different types  
<sup>304</sup> of summary ages, median and SDM. As explained in the “Description” section, a tree  
<sup>305</sup> topology to summarize age data upon is required. By default, DateLife uses as summarizing  
<sup>306</sup> topology the portion of OpenTree synthetic phylogeny that contains the species provided as  
<sup>307</sup> search query. According to this phylogeny, species belonging to the family Fringillidae do not  
<sup>308</sup> form a monophyletic group (Fig. 4).

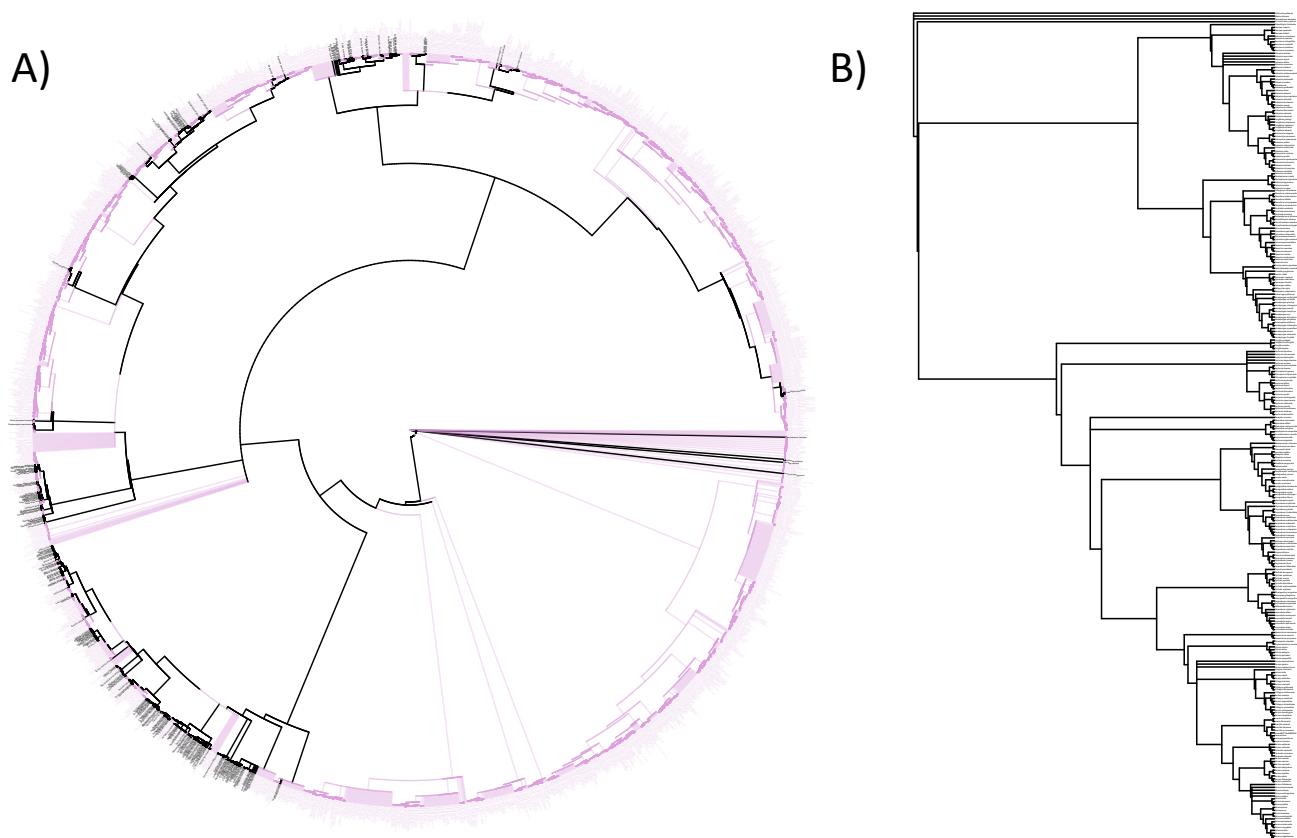
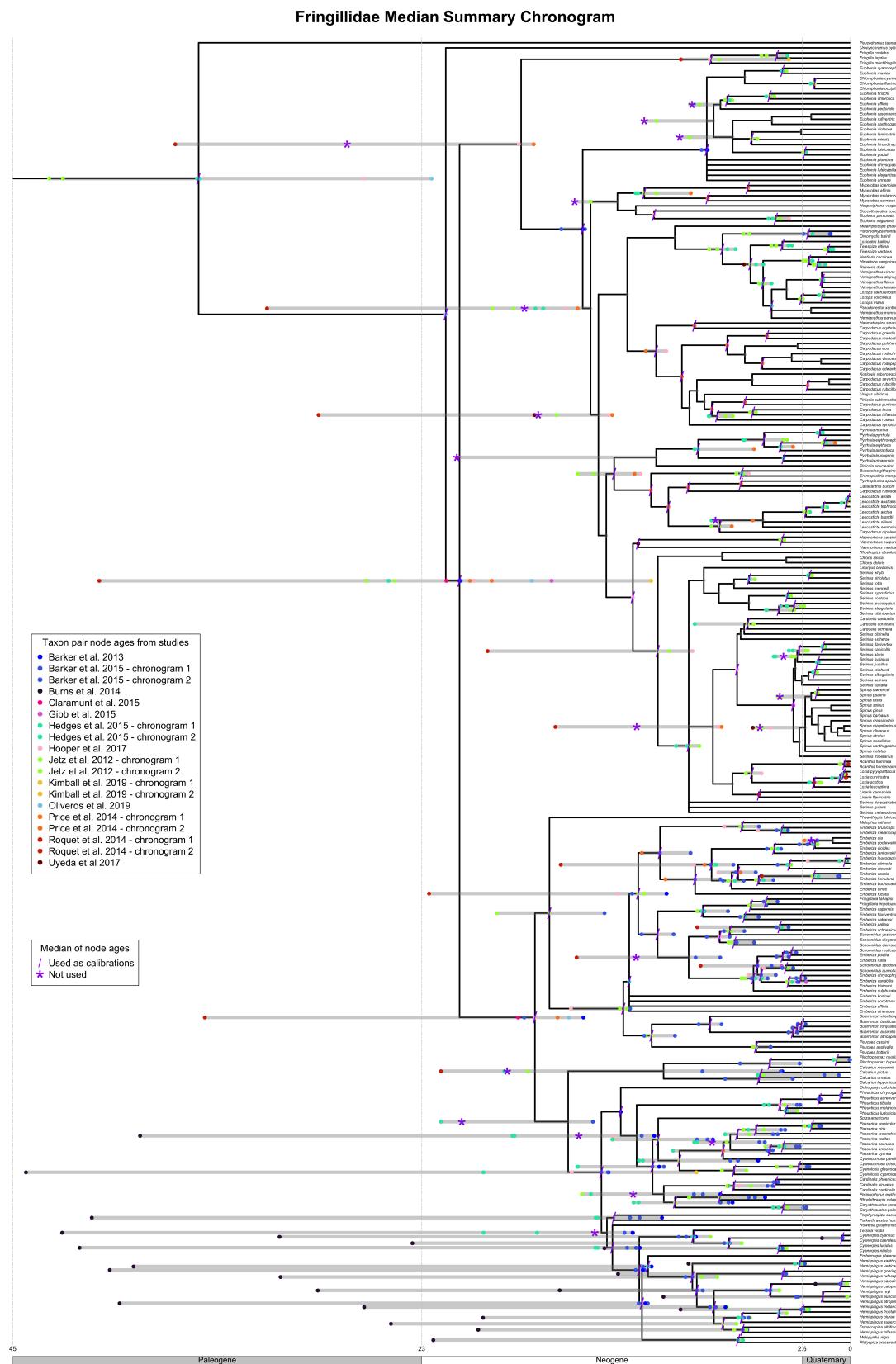


FIGURE 4. Tree topologies obtained from Open Tree of Life's (OpenTree) synthetic phylogenetic tree. A) Topology of 2,333 tips and 1,305 internal nodes, encompassing bird species within the family Fringillidae following the NCBI taxonomy (black), as well as all other bird species that share the same mrca node in OpenTree's synthetic tree (purple). B) Topology of 289 tips and 253 internal nodes, encompassing bird species within the Fringillidae only. This tree results from pruning species that are not assigned to the family Fringillidae (purple branches in topology A) but that form a monophyletic group with them. Bird species within the Fringillidae are paraphyletic (Alström et al. 2014, Barker, Cibois, Schikler, Feinstein, & Cracraft 2004, Barker et al. 2013, Barker 2014, Barker et al. 2015, Beresford, Barker, Ryan, & Crowe 2005, Bryson Jr et al. 2014, Burleigh, Kimball, & Braun 2015, Burns et al. 2014, Chaves, Hidalgo, & Klicka 2013, Claramunt & Cracraft 2015, Gibb et al. 2015, Hackett et al. 2008, Jetz et al. 2012, Johansson, Fjeldså, & Bowi 200, Kimball et al. 2019, Klicka et al. 2014, Lamichhaney et al. 2015, Lerner, Meyer, James, Hofreiter, & Fleischer 2011, Lovette et al. 2010, Moyle et al. 2016, Ödeen, Håstad, & Alström 2011, Oliveros et al. 2019, Päckert et al. 2012, Parchman, Benkman, & Mezquida 2007, Powell et al. 2014, Price et al. 2014, Pulgarín-R, Smith, Bryson Jr, Spellman, & Klicka 2013, Selvatti, Gonzaga, & Moraes Russo 2015, Tietze, Päckert, Martens, Lehmann, & Sun 2013, Treplin et al. 2008, Zuccon, Prŷs-Jones, Rasmussen, & Ericson 2012).

326 Age data from source chronograms was congruified to the chosen tree topology (OpenTree's  
327 synthetic subtree from figure 4B), reducing the age data set to 818 different data points  
328 (supplementray table 2). Age summary statistics per congruified node were calculated and  
329 used as fixed secondary calibrations over the chosen tree topology, to obtain a fully dated  
330 phylogeny with the program BLADJ (Fig. 5).



333

331 FIGURE 5. Fringillidae median summary chronogram generated with DateLife. It has 256 tips and  
 332 233 nodes, from which 212 have age data from at least one published chronogram.

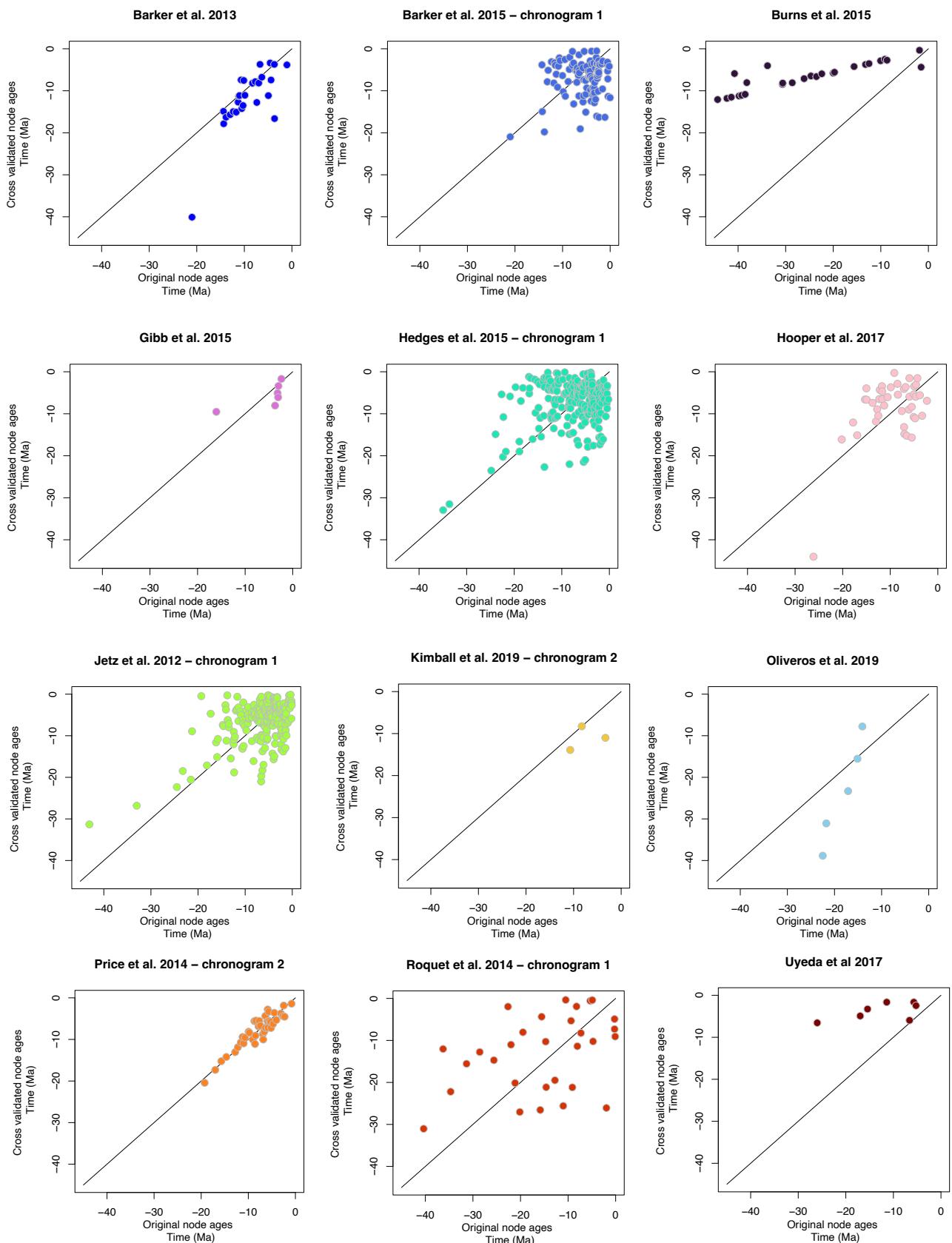
334

**Cross-validation test**

335 We performed a cross validation analysis of the DateLife workflow using the Fringillidae  
336 chronograms. We used the individual tree topologies from each of the 19 source chronograms  
337 from 13 studies as inputs, treating their node ages as unknown. We then estimated dates for  
338 these topologies using the node ages from the chronograms from the other studies as  
339 calibrations and smoothing using BLADJ.

340 We found that node ages from original study, and ages estimated using all other age data  
341 available are correlated (Fig. 6).

342 For five studies, Datelife tended to underestimate ages for topologically deeper nodes (those  
343 with many descendant taxa, aka ‘closer to the root’) relative to the original estimate, and  
344 overestimate ages for nodes closer to the tips. Accordingly, root ages are generally older in  
345 the original study than estimated using cross-validated ages (Supplementary Fig. S1).



346 FIGURE 6. Results from cross validation analysis. Each plot compares the original age estimate (x  
 axis) with the age obtained with a DateLife analysis (y axis), per node.  
 347

349

## Discussion

350 `datelife` makes state-of-the-art data on evolutionary time frame easily accessible for  
351 comparison, reuse, and reanalysis, to researchers in all areas of science and with all levels of  
352 expertise in the matter. It is an open service that does not require any expert biological  
353 knowledge from users –besides the names of the species or group they want to work with, for  
354 any of its functionality.

355 A total of 99474 unique terminal taxa are represented in `datelife`'s database. Incorporation  
356 of more chronograms into `datelife`'s database will continue to improve its services. One  
357 option to increase the number of chronograms in the DateLife database is the Dryad data  
358 repository. Methods to automatically mine chronograms from Dryad could be designed and  
359 implemented. However, Dryad's metadata system has no information to automatically detect  
360 branch length units, and those would still need to be determined manually by a human  
361 curator. We would like to emphasize on the importance of sharing chronogram data,  
362 including systematically curated metadata, into open repositories, such as OpenTree's  
363 Phylesystem (McTavish et al., 2015) for the benefit of the scientific community as a whole.

364 **Primary vs Secondary calibrations in dating analyses**

365 While most chronograms in DateLife's database are constructed using primary calibrations  
366 (molecular substitution rates or ages obtained from the fossil record or geological events),  
367 DateLife summarizes chronograms using secondary calibrations only (ages coming from other  
368 chronograms).

369 Graur and Martin (2004) cautioned on the increased error and uncertainty in estimated ages  
370 when using secondary calibrations in dating analyses. Schenk (2016) showed that, in  
371 simulations, divergence times inferred using secondary calibrations are significantly younger  
372 than those inferred with primary calibrations, when obtained with Bayesian inference  
373 methods, and when priors are implemented in similar ways in both analyses. Accordingly,  
374 the scientific community seems to have more confidence in chronograms obtained from a

375 single analysis, using fossil data as primary sources of calibrations (Schenk, 2016), and using  
376 fossils that have been widely discussed and curated as calibrations to date other trees,  
377 making sure that all data reflect a coherent evolutionary history (Sauquet, 2013), as for  
378 example done by Antonelli et al. (2017). There have been attempts to create fossil  
379 calibration databases (Ksepka et al., 2015), though these still have room to grow.

380 It seems that using several (as opposed to just a few) secondary calibrations can provide  
381 sufficient information to alleviate or even neutralize potential biases (Sauquet, 2013).

382 Certainly, further studies are required to fully understand the effect of secondary calibrations  
383 on outputs from different tree dating methods, and on downstream analyses. It is possible  
384 that secondary calibrations can be safely used with dating methods that do not require  
385 setting priors, such as penalized likelihood (Michael J. Sanderson, 2003), with methods that  
386 do not make any assumptions on the ages and fix them to a node on a tree topology, such as  
387 BLADJ (Campbell O. Webb et al., 2008; Campbell O. Webb & Donoghue, 2005), or  
388 methods that summarize age data unto a tree topology.

389 Our cross validation analysis might provide some insight in this regard. When ages are  
390 estimated with secondary calibrations, nodes closer to the root do tend to be slightly younger  
391 than ages estimated with primary calibrations. However, nodes closer to the tip tend to be  
392 older when estimated using secondary calibrations with a dating method that does not make  
393 any prior assumptions on the nature of the calibrations themselves (Supplementary Figures  
394 S2-S9). The only exception to this was observed on results of the cross validation analysis of  
395 the Burns et al. (2014) chronogram, which results in much younger node ages when  
396 estimated using secondary calibrations (Supplementary figs. S1 and S4).

### 397 Variation in source chronograms

398 Conflict among alternative dating studies is common in the literature (see, for example, the  
399 robust ongoing debate about crown group age of angiosperms (Barba-Montoya, Reis,  
400 Schneider, Donoghue, & Yang, 2018; Magallón, Gómez-Acevedo, Sánchez-Reyes, &

401 Hernández-Hernández, 2015; Ramshaw et al., 1972; Michael J. Sanderson & Doyle, 2001;  
402 Sauquet, Ramírez-Barahona, & Magallón, 2021)).  
403 Source chronograms may have been estimated using different types of primary calibrations  
404 (fossil record, geologic or biogeographic events, molecular substitution rates). These  
405 differences in approach can deepen the already substantial variation in time estimates  
406 between lineages, as observed from the comparison of source chronograms in the Fringillidae  
407 example. For example, the chronograms from Burns et al. (2014) were inferred using  
408 molecular substitution rate estimates across birds (Weir & Schlüter, 2008), and have much  
409 older date estimates for the same nodes than chronograms that were inferred using fossils as  
410 primary calibrations (figs. 5, 6; supplementary figs. S1, S4).  
411 Different chronograms might also imply fundamentally distinct evolutionary hypotheses. For  
412 example, two different researchers working on the same clade could both carefully select and  
413 argue for their choices of fossil calibrations. Still, if one researcher decides a fossil will  
414 calibrate the ingroup of a clade, while another researcher uses the same one to calibrate  
415 outside the clade, the resulting age estimates will often differ substantially, as the placement  
416 of calibrations as stem or crown group is proved to deeply affect estimated times of lineage  
417 divergence (Sauquet, 2013).

#### 418 Summarizing chronograms

419 By default, DateLife currently summarizes all source chronograms that overlap with at least  
420 two species names. Users can exclude source chronograms if they have reasons to do so.  
421 Strictly speaking, a good chronogram should reflect the real time of lineage divergence  
422 accurately and precisely. To our knowledge, there are no tested measures to determine  
423 independently when a chronogram is better than another. Yet, several characteristics of the  
424 data used for dating analyses, as well as from the output chronogram itself, could be used to  
425 score the quality of source chronograms.  
426 Some measures that have been proposed are the proportion of lineage sampling and the

427 number of calibrations used Magallón et al. (2015). Some characteristics that are often cited  
428 in published studies as a measure of improved age estimates as compared to previously  
429 published estimates are: quality of alignment (missing data, GC content), lineage sampling  
430 (strategy and proportion), phylogenetic and dating inference method, number of fossils used  
431 as calibrations, support for nodes and ages, and magnitude of confidence intervals.

432 DateLife provides an opportunity to capture concordance and conflict among date estimates,  
433 which can also be used as a metric for chronogram reliability. Its open database of  
434 chronograms allows other researchers to do such analyses themselves reproducibly, and  
435 without needing permission. Though, of course, they should follow proper citation practices,  
436 especially for the source chronogram studies.

437 The exercise of summarizing age data from across multiple studies provides the opportunity  
438 to work with a more inclusive chronogram, that reflects a unified evolutionary history for a  
439 lineage, by putting together evidence from different hypotheses. The largest, and  
440 taxonomically broadest chronogram currently available from OpenTree was constructed  
441 summarizing age data from 2,274 published chronograms using NCBI's taxonomic tree as  
442 backbone (Hedges et al., 2015). A summarizing exercise may also amplify the effect of  
443 uncertainty and errors in source data, and blur parts of the evolutionary history of a lineage  
444 that might only be reflected in source chronograms and lost on the summary chronogram  
445 (Sauquet et al., 2021).

#### 446 Effects on downstream analyses

447 For downstream analyses, using alternative chronogram may deeply affect our inferences  
448 (Title & Rabosky, 2016), particularly when studying phenomena dependent on the timing of  
449 species diversification events, such as macroevolutionary processes.

450 In ecology and conservation biology, incorporating at least some data on lineage divergence  
451 times represents a relevant improvement for testing alternative hypothesis using phylogenetic  
452 distance (Campbell O. Webb et al., 2008). Hence, DateLife's workflow features different

ways of estimating node ages in the absence of calibrations and branch length information for certain taxa. “Making up” branch lengths is a common practice in scientific publications: Jetz et al. (2012), created a time-calibrated tree of all 9,993 bird species, where 67% had molecular data and the rest was simulated; Rabosky et al. (2018) created a time-calibrated tree of 31,536 ray-finned fishes, of which only 37% had molecular data; Stephen A. Smith and Brown (2018) constructed a tree of 353,185 seed plants where only 23% had molecular data. Notably, risks come with this practice. Taken to the extreme, one could make a fully resolved, calibrated tree of all modern and extinct taxa using a single taxonomy and a single calibration, using polytomy resolution and branch estimation methods. There has yet to be a thorough analysis of what can go wrong when one extends inferences beyond the data in this way, so we urge caution; we also urge readers to follow the example of the large tree papers cited above, by carefully considering the statistical assumptions being made, and assessing the consistency of the results with prior work.

## Conclusions

Knowledge of the evolutionary time frame of organisms is key to many research areas: trait evolution, species diversification, biogeography, macroecology and more. It is also crucial for education, science communication and policy, but generating chronograms is difficult, especially for those who want to use phylogenies but who are not systematists, or do not have the time to acquire and develop the necessary knowledge and skills to construct them on their own. Importantly, years of primarily public funded research have resulted in vast amounts of chronograms that are already available on scientific publications, but hidden to the public and scientific community for reuse.

The DateLife project allows for easy and fast summary of public and state-of-the-art data on time of lineage divergence. It provides a straightforward way to get an informed idea on the state of knowledge of the time frame of evolution of different regions of the tree of life, and allows identification of regions that require more research, or that have conflicting

479 information. It is available as an R package, and as a web-based R shiny application at  
480 [www.datelife.org](http://www.datelife.org) Both summary and newly generated trees are useful to evaluate  
481 evolutionary hypotheses in different areas of research. The DateLife project helps with  
482 awareness of the existing variation in expert time of divergence data, and will foster  
483 exploration of the effect of alternative divergence time hypothesis on the results of analyses,  
484 nurturing a culture of more cautious interpretation of evolutionary results.

## 485 Availability

486 The **datelife** software is free and open source and it can be used through its R shiny web  
487 application at <http://www.datelife.org>, through the **datelife** R package, and through  
488 Phylotastic's project web portal <https://phylo.cs.nmsu.edu/>. DateLife's web application is  
489 maintained using RStudio's shiny server and the shiny package open infrastructure, as well  
490 as Docker and Open Tree of Life's infrastructure ([dates.opentreeoflife.org/datelife](https://dates.opentreeoflife.org/datelife)).  
491 **datelife**'s R package stable version is available for installation from the CRAN repository  
492 (<https://cran.r-project.org/package=datelife>) using the command `install.packages(pkgs`  
493 `= "datelife")` from within R. Development versions are available from the GitHub  
494 repository (<https://github.com/phylotastic/datelife>) and can be installed using the  
495 command `devtools::install_github("phylotastic/datelife")`.

## 496 Supplementary Material

497 Code used to generate all versions of this manuscript, the biological examples, as well as the  
498 benchmark of functionalities are available at datelifeMS1, datelife\_examples, and  
499 datelife\_benchmark repositories in LLSR's GitHub account.

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504

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