

¹ 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 and 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, 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;

⁴³ Congruification; Supertree; Calibrations; Secondary calibrations

⁴⁴ Word count: 5386

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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 comparative analysis (Freckleton, Harvey, & Pagel, 2002; Harvey, Pagel, &
50 others, 1991), developmental biology (Delsuc et al., 2018; Laubichler & Maienschein, 2009),
51 conservation and ecology (Felsenstein, 1985; Webb, 2000), historical biogeography (Posadas,
52 Crisci, & Katinas, 2006), and species diversification (Magallon & Sanderson, 2001; Morlon,
53 2014).

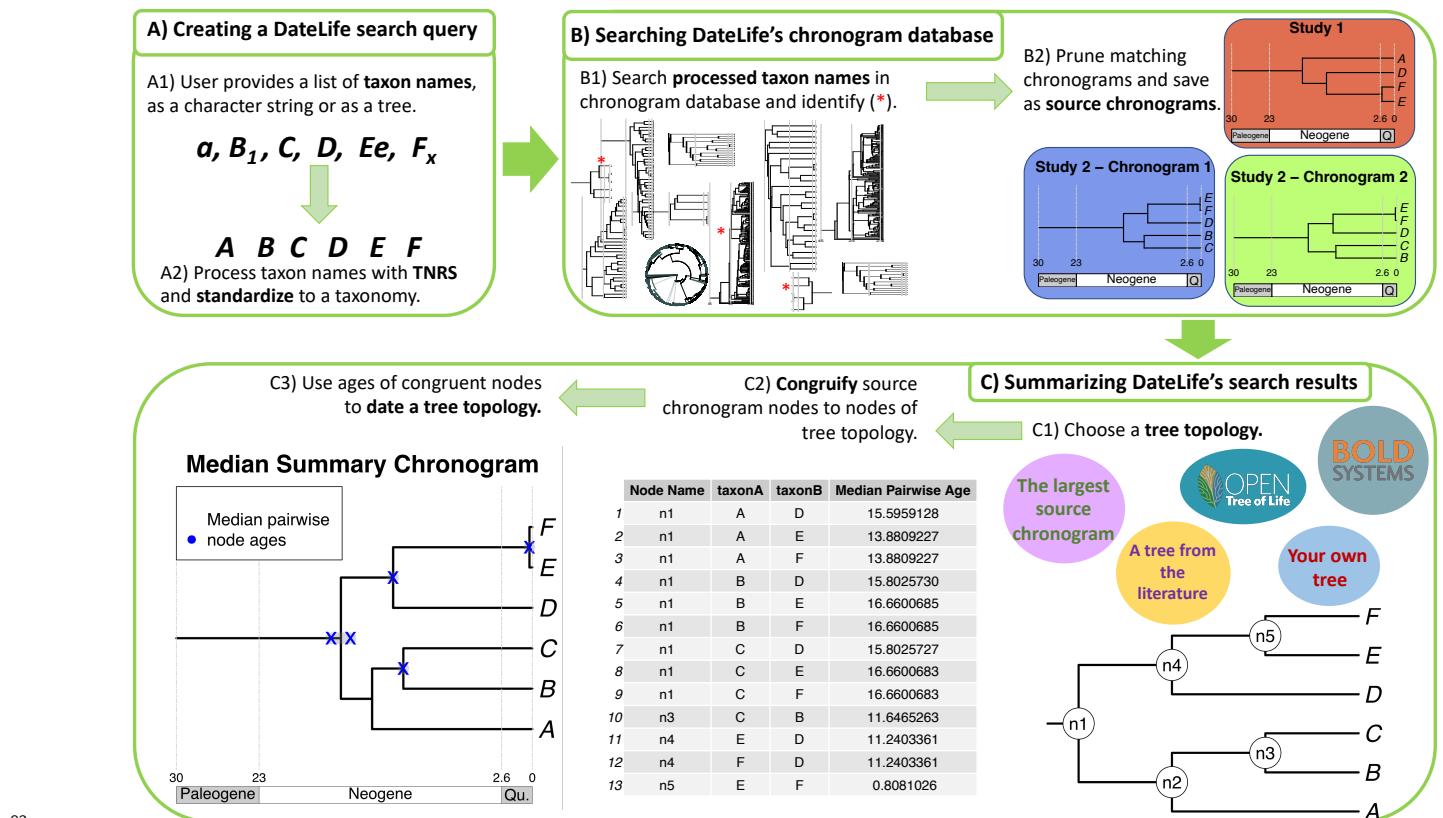
54 Building a chronogram is not an easy task. It requires obtaining and curating data to
55 construct a phylogeny, selecting and placing appropriate calibrations on the phylogeny using
56 independent age data points from the fossil record or other dated events, and inferring the
57 full dated tree; it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

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

70

Description

71 DateLife's core software application consists of the R package `datelife`. Its current
 72 stable version – v0.6.6, is available from the Comprehensive R Archive Network (CRAN)
 73 repository (Sanchez-Reyes et al., 2022), and relies on functionalities from various biological
 74 R packages: `ape` (Paradis, Claude, & Strimmer, 2004), `bold` (Chamberlain, 2018), `geiger`
 75 (Pennell et al., 2014), `paleotree` (Bapst, 2012), `phyloch` (Heibl, 2008), `phylocomr` (Ooms &
 76 Chamberlain, 2018), `phytools` (Revell, 2012), `rotl` (Michonneau, Brown, & Winter, 2016),
 77 and `taxize` (Chamberlain, 2018; Chamberlain & Szöcs, 2013). Figure 1 provides a graphical
 78 summary of the three main steps of the DateLife workflow: creating a search query,
 79 searching a database, and summarizing results from the search.



83

80 FIGURE 1. Main DateLife workflow. Analyses can be performed via DateLife's interactive website
 81 at www.datelife.org, or using the `datelife` R package. Details on the R functions used to perform
 82 the analyses are available from `datelife`'s R package vignettes at <https://phylotastic.org/datelife>.

84 Creating a search query

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

91 DateLife processes input scientific names using a Taxonomic Name Resolution Service
92 (TNRS), which increases the probability of correctly finding the queried taxon names in the
93 chronogram database. TNRS detects, corrects and standardizes name misspellings and typos,
94 variant spellings and authorities, and nomenclatural synonyms to a single taxonomic
95 standard (Boyle et al., 2013). TNRS also allows to correctly choose between homonyms, by
96 considering other taxa provided as input to infer the taxonomic context of the homonym.

97 DateLife implements TNRS using the Open Tree of Life (OpenTree) unified Taxonomy
98 (OTT, Open Tree Of Life et al., 2016; Rees & Cranston, 2017) as standard, storing
99 taxonomic identification numbers (OTT ids) for further processing and analysis. Other
100 taxonomies currently supported by DateLife are the National Center of Biotechnology
101 Information (NCBI) taxonomic database (Schoch et al., 2020), the Global Biodiversity
102 Information Facility (GBIF) taxonomic backbone (GBIF Secretariat, 2022), and the Interim
103 Register of Marine and Nonmarine Genera (IRMNG) database (Rees et al., 2017).

104 Besides binomial species names, DateLife accepts scientific names from any inclusive
105 taxonomic group (e.g., genus, family, tribe), as well as subspecific taxonomic variants (e.g.,
106 subspecies, variants, strains). If a taxon name belongs to an inclusive taxonomic group,
107 DateLife has two alternative behaviors defined by the “get species from taxon” flag. If the
108 flag is active, DateLife retrieves all species names within the taxonomic group from the
109 standard taxonomy of choice, and adds them to the search query. In this case, subspecific

110 variants are excluded. If the flag is inactive, DateLife excludes any taxon names above the
111 species level from the search query. Species and subspecific variant names are processed and
112 searched as provided by the user. The processed taxon names are saved as an R object of a
113 newly defined class, `datelifeQuery`, that is used in the following steps. This object contains
114 the names standardized to the taxonomy of choice, the corresponding OTT id numbers, and
115 the topology of the input tree if one was provided.

116 **Searching a chronogram database**

117 At the time of writing of this manuscript (Jun 22, 2022), DateLife's chronogram
118 database latest version consist of 253 chronograms published in 187 different studies. It is
119 curated from OpenTree's phylogenetic database, the Phylesystem, which constitutes an open
120 source of expert and peer-reviewed phylogenetic knowledge with rich metadata (McTavish et
121 al., 2015), which allows automatic and reproducible assembly of our chronogram database.
122 Datelife's chronogram database is navigable as an R data object within the `datelife` R
123 package.

124 A unique feature of the Phylesystem is that any user can add new published,
125 state-of-the-art chronograms any time, through their curator application
126 (<https://tree.opentreeoflife.org/curator>). As chronograms are added to Phylesystem, they
127 can be incorporated into the chronogram database of the `datelife` package. `datelife`'s
128 chronogram database is currently manually updated as new chronogram data is added to
129 Phylesystem. The updated database is assigned a new version number, followed by a
130 package release on CRAN. Users can also implement functions from the `datelife` R package
131 to trigger an update of the local chronogram database, to incorporate any new chronograms
132 to the user's DateLife analysis before an official database update is released on CRAN.

133 A DateLife search is implemented by matching processed taxon names provided by the
134 user to tip labels in the chronogram database. Chronograms with at least two matching

135 taxon names on their tip labels are identified and pruned down to preserve only the matched
136 taxa. These matching pruned chronograms are referred to as source chronograms. Total
137 distance (in units of millions of years) between taxon pairs within each source chronogram
138 are stored as a patristic distance matrix (Figure 1). The matrix format speeds up extraction
139 of pairwise taxon ages of any queried taxa, as opposed to searching the ancestor node of a
140 pair of taxa in a “phylo” object or newick string. Finally, the patristic matrices are
141 associated to the study citation where the original chronogram was published, and stored as
142 an R object of the newly defined class `datelifeResult`.

143 **Summarizing search results**

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

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

157 ***Choosing a topology.***— DateLife requires a tree topology to summarize age data
158 upon. We recommend that users provide a tree topology as input from the literature, or one
159 of their own making. If no topology is provided, DateLife automatically extracts one from

the OpenTree synthetic tree, a phylogeny currently encompassing 2.3 million taxa across all life, assembled from 1, 239 published phylogenetic trees and OpenTree’s unified Taxonomy, OTT (Open Tree Of Life et al., 2019). Alternatively, DateLife can combine topologies from source chronograms using a supertree approach. To do this DateLife first identifies the source chronograms that form a grove, roughly, a sufficiently overlapping set of taxa between trees, by implementing definition 2.8 for n-overlap from Ané et al. (2009). If the source chronograms do not form a grove, the supertree reconstruction will fail. In rare cases, a group of trees can have multiple groves. By default, DateLife chooses the grove with the most taxa, however, the “criterion = trees” flag allows the user to choose the grove with the most trees instead. The result is a single summary (or supertree) topology, that combines topologies from source chronograms in a grove.

Applying secondary calibrations.— Once a topology is chosen, DateLife applies the congruification method (Eastman, Harmon, & Tank, 2013) that find nodes belonging to the same clade across source chronograms, and then extracts the corresponding node ages from patristic distance matrices stored as a `datelifeResult` object. Note that by definition, these matrices store total distance (time from tip to tip), assuming that the terminal taxa are coeval and occur at the present. Hence, node ages correspond to half the values stored in the `datelifeResult` matrices. A table of congruified node ages that can be used as calibrations for a dating analysis is stored as a `congruifiedCalibrations` object.

For each congruent node, the pairwise distances that traverse that node are summarized into a single summary matrix using classic summary statistics (i.e., mean, median, minimum and maximum ages), and the Supermatrix Distance Method (SDM; Criscuolo, Berry, Douzery, & Gascuel, 2006), which deforms patristic distance matrices by minimizing variance and then averaging them. These single summary taxon pair age matrices are stored as summarized calibrations that can be used as secondary calibrations to date a tree topology - with or without initial branch lengths, using phylogenetic dating

186 methods currently supported within DateLife: BLADJ (Webb, Ackerly, & Kembel, 2008;
187 Webb & Donoghue, 2005), MrBayes (Huelsenbeck & Ronquist, 2001; Ronquist &
188 Huelsenbeck, 2003), PATHd8 (Britton, Anderson, Jacquet, Lundqvist, & Bremer, 2007), and
189 treePL (Smith & O'Meara, 2012).

190 **Dating a tree topology.**— By default, DateLife implements the Branch Length
191 Adjuster (BLADJ; Webb et al., 2008; Webb & Donoghue, 2005) algorithm to obtain a fully
192 dated topology. BLADJ is the only dating algorithm that can work with initial topologies
193 without any branch length data.

194 Alternatively, the user can chose phylogenetic dating options supported in DateLife
195 that incorporate branch length information from the input topology in combination with the
196 secondary calibrations: PATHd8 is a non-clock, rate-smoothing method (Britton et al., 2007)
197 to date trees; treePL (Smith & O'Meara, 2012), is a semi-parametric, rate-smoothing,
198 penalized likelihood dating method (Sanderson, 2002); the MrBayes (Huelsenbeck &
199 Ronquist, 2001; Ronquist & Huelsenbeck, 2003) approach in DateLife uses the calibrations as
200 priors on node ages.

201 The latter methods can assign dates using a birth-death model (all of them????), they
202 require initial branch lengths and thus require more time and expertise to run, which makes
203 BLADJ the fastest and most practical method to obtain a dated tree.

204 BLADJ fixes node ages that have calibration data, and distributes time between nodes
205 with no data evenly between calibrated nodes. This has proven effective minimizes age
206 variance in the resulting chronogram and useful for ecoogical analyses (Webb et al., 2008).
207 When there is conflict in ages between nodes with calibration data, BLADJ ignores node
208 ages that are older than the age of a parent node. BLADJ requires a root age estimate. If
209 there is no information on the age of the root in the chronogram database, users can provide
210 an estimate from the literature. If none is provided, DateLife will not return a dated

211 topology but provide a warning message along with suggestions on how the user can provide
212 an age for the root so DateLife can run.

213 **Dating a tree with branch lengths**.– Topologies obtained from OpenTree and
214 with the supertree approach described above lack branch length data. Yet, phylogenetic
215 dating using branch lengths data is the golden standard for phylogenetic dating analyses, but
216 it is costly and requires a lot of human/expert curation.

217 A fast solution implemented in DateLife is as follows. To estimate branch lengths
218 proportional to substitution rates for these topologies, DateLife currently implements a
219 simple algorithm. First, it mines the Barcode of Life Data System, BOLD (Ratnasingham &
220 Hebert, 2007) to obtain genetic markers for the input taxa. Mined genetic sequences are
221 aligned with MUSCLE (Edgar, 2004) (by default) or MAFFT (Katoh, Asimenos, & Toh,
222 2009).

223 The BOLD sequence alignment is then used to reconstruct branch lengths with the
224 accelerated transformation (ACCTRAN) parsimony algorithm, which resolves ambiguous
225 character optimization, by assigning changes along branches of the tree as close to the root as
226 possible (Agnarsson & Miller, 2008). This algorithm work rally fast and allows getting initial
227 branch lengths that ar ethen optimized using ML. Optionally, the likelihood of the tree
228 topology, the alignment and the reconstructed branch lengths given different evolutionary
229 models, is computed using functions from the `phangorn` package (Schliep, 2011).

230 Relative branch length information provides key data for phylogenetic dating,
231 especially for nodes without secondary calibrations available. Yet, topologies without branch
232 lengths can also be dated.

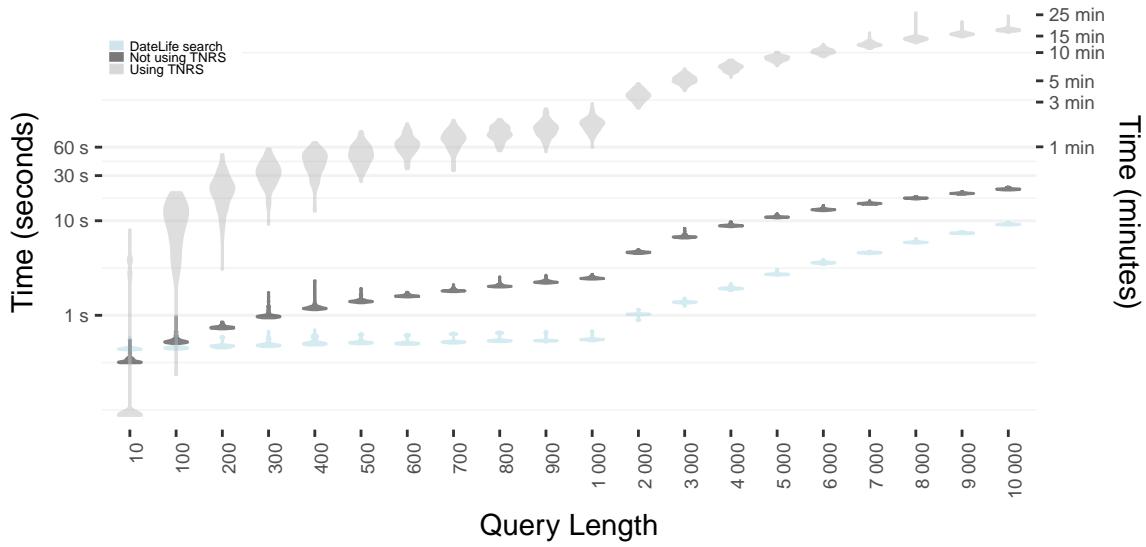
233 **Visualizing results**.– Finally, users can save all source and summary chronograms in
234 formats that permit reuse and reanalysis (such as newick and the R “phylo” format), as well
235 as visualize and compare results graphically, or construct their own graphs using DateLife’s

²³⁶ chronogram plot generation functions available from the R package **datelifeplot**
²³⁷ (Sanchez-Reyes & O'Meara, 2022).

238

Benchmark

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



248

249 FIGURE 2. *DateLife*'s benchmarking results. Computation time used to process a query and a
 250 search across *datelife*'s chronogram database, relative to number of input taxon names. For
 251 each $N = \{10, 100, 200, \dots, 1\,000, \dots, 9\,000, 10\,000\}$, we sampled N species names from
 252 the class Aves a hundred times, and then performed a *datelife* search processing the input
 253 names with Taxon Names Resolution Service (TNRS; light gray), and without processing
 254 names (dark gray). For comparison, we performed a search using an input that had been
 255 pre-processed with TNRS (light blue).

256 `datelife`'s code performance was evaluated with a set of unit tests designed and
257 implemented with the R package `testthat` (R Core Team, 2018) that were run both locally
258 with the `devtools` package (R Core Team, 2018), and on a public server using the continuous
259 integration tool of GitHub actions (<https://docs.github.com/en/actions>). At present, unit
260 tests cover more than 40% of `datelife`'s code (<https://codecov.io/gh/phylotastic/datelife>).
261 Unit testing helps identify potential issues as code is updated or, more critically, as services
262 code relies upon may change.

263 **Case studies**

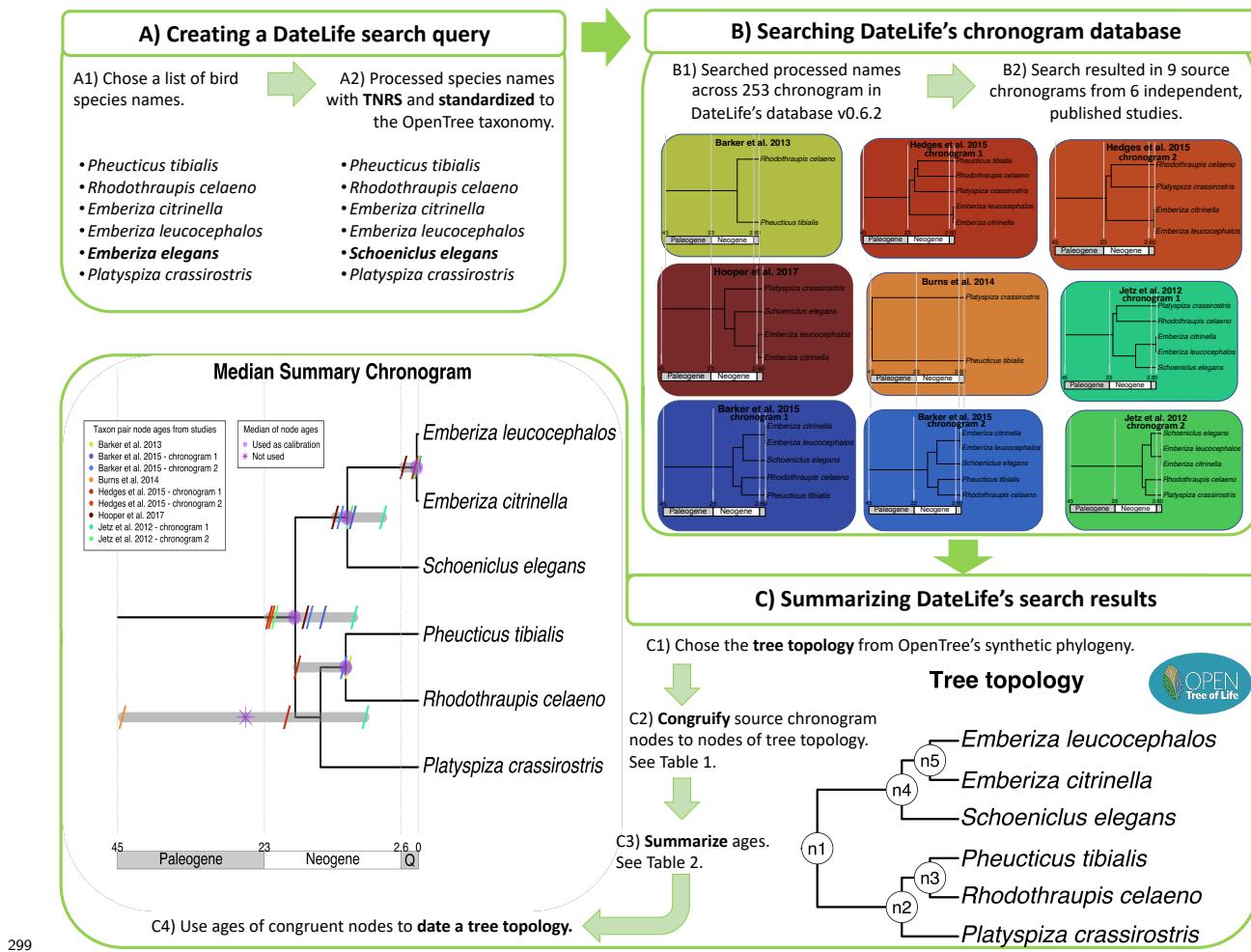
264 We illustrate the DateLife workflow using a family within the Passeriform birds
265 encompassing the true finches, Fringillidae, as case study. On a small example, we analysed 6
266 bird species, and results from each step of the workflow are shown in Fig. 3. As a second
267 example, we analysed 289 bird species in the family Fringillidae that are included in the
268 NCBI taxonomy. The resulting summary chronogram is shown in Fig. 5, and results from
269 previous steps of the workflow are available as Supplementary Figures.

270 **A small example**

271 **Creating a search query.** We chose 6 bird species within the Passeriformes. The sample
272 includes two species of cardinals: the black-thighed grosbeak – *Pheucticus tibialis* and the
273 crimson-collared grosbeak – *Rhodothraupis celaeno*; three species of buntings: the
274 yellowhammer – *Emberiza citrinella*, the pine bunting – *Emberiza leucocephalos* and the
275 yellow-throated bunting – *Emberiza elegans*; and one species of tanager, the vegetarian finch –
276 *Platyspiza crassirostris*. Processing of input names found that *Emberiza elegans* is synonym
277 for *Schoeniclus elegans* in the default reference taxonomy (OTT v3.3, June 1, 2021). For a
278 detailed discussion on the state of the synonym, refer to Avibase (Avibase, 2022; Lepage,
279 2004; Lepage, Vaidya, & Guralnick, 2014). Discovering this synonym allowed assigning five
280 age data points for the parent node of *Emberiza elegans*, shown as *Schoeniclus elegans* in
281 figure 3A, which would not have had any data otherwise.

282 **Searching the database.** DateLife used the processed input names to search the local
283 chronogram database and found 9 matching chronograms in 6 different studies (Fig. 3B).
284 Three studies matched five input names (Barker, Burns, Klicka, Lanyon, & Lovette, 2015;
285 Hedges, Marin, Suleski, Paymer, & Kumar, 2015; Jetz, Thomas, Joy, Hartmann, & Mooers,
286 2012), one study matched four input names (Hooper & Price, 2017) and two studies matched
287 two input names (Barker, Burns, Klicka, Lanyon, & Lovette, 2013; Burns et al., 2014). No
288 studies matched all input names. Together, source chronograms provide 28 unique age data
289 points, covering all nodes on our chosen tree topology to date (Table 1).

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



299

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

307 TABLE 1. Ages of congruified nodes. See Figure 3, step C2.

	Node Name	taxon A	taxon B	Node Age	Study chronogram
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

308

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

Node Name	Min Age	Q1	Median Age	Mean Age	Q3	Max Age	Variance	SD
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

310

311 **An example with the family of true finches**

312 **Creating a query.** To obtain ages for all species within the family of true finches,
313 Fringillidae, we ran a DateLife query using the “get species from taxon” flag, which gets all
314 recognized species names within a named group from a taxonomy of choice. Following the
315 NCBI taxonomy, our DateLife query has 289 Fringillidae species names. This
316 taxon-constrained approach implies that the full DateLife analysis will be performed using a
317 tree topology and ages available for species names from a given taxonomic group, which do
318 not necessarily correspond to a monophyletic group. Users can change this behaviour by
319 providing all species names corresponding to a monophyletic group as input for a DateLife
320 search, or a monophyletic tree to construct a DateLife summary.

321 **Searching the database.** Next, we used the processed species names in our DateLife
322 query to identify chronograms with at least two Fringillidae species as tip taxa. The
323 DateLife search identified 19 chronograms matching this criteria, published in 13 different
324 studies (Barker et al., 2013, 2015; Burns et al., 2014; Claramunt & Cracraft, 2015; Gibb et
325 al., 2015; Hedges et al., 2015; Hooper & Price, 2017; Jetz et al., 2012; Kimball et al., 2019;
326 Oliveros et al., 2019; Price et al., 2014; Roquet, Lavergne, & Thuiller, 2014; Uyeda, Pennell,
327 Miller, Maia, & McClain, 2017). Once identified, DateLife pruned these matching
328 chronograms to remove tips that do not belong to the queried taxon names, and transformed
329 these pruned chronograms to pairwise distance matrices, revealing 1, 206 different age data
330 points available for species within the Fringillidae (Supplementray Table S1).

331 **Summarizing search results.** The final step entailed congruifying and summarizing the
332 age data available for the Fringillidae species into two single summary chronograms, using
333 two different types of summary ages, median and SDM. As explained in the “Description”
334 section, a tree topology to summarize age data upon is required. By default, to do this,
335 DateLife uses the topology from OpenTree’s synthetic tree that contains all taxa from the
336 search query. According to OpenTree’s synthetic tree, species belonging to the family
337 Fringillidae do not form a monophyletic group (Fig. 4). Hence, a topology containing only

³³⁸ the 289 species from the original query was extracted from Open Tree of Life's synthetic tree
³³⁹ v12.3 (Open Tree Of Life et al., 2019).

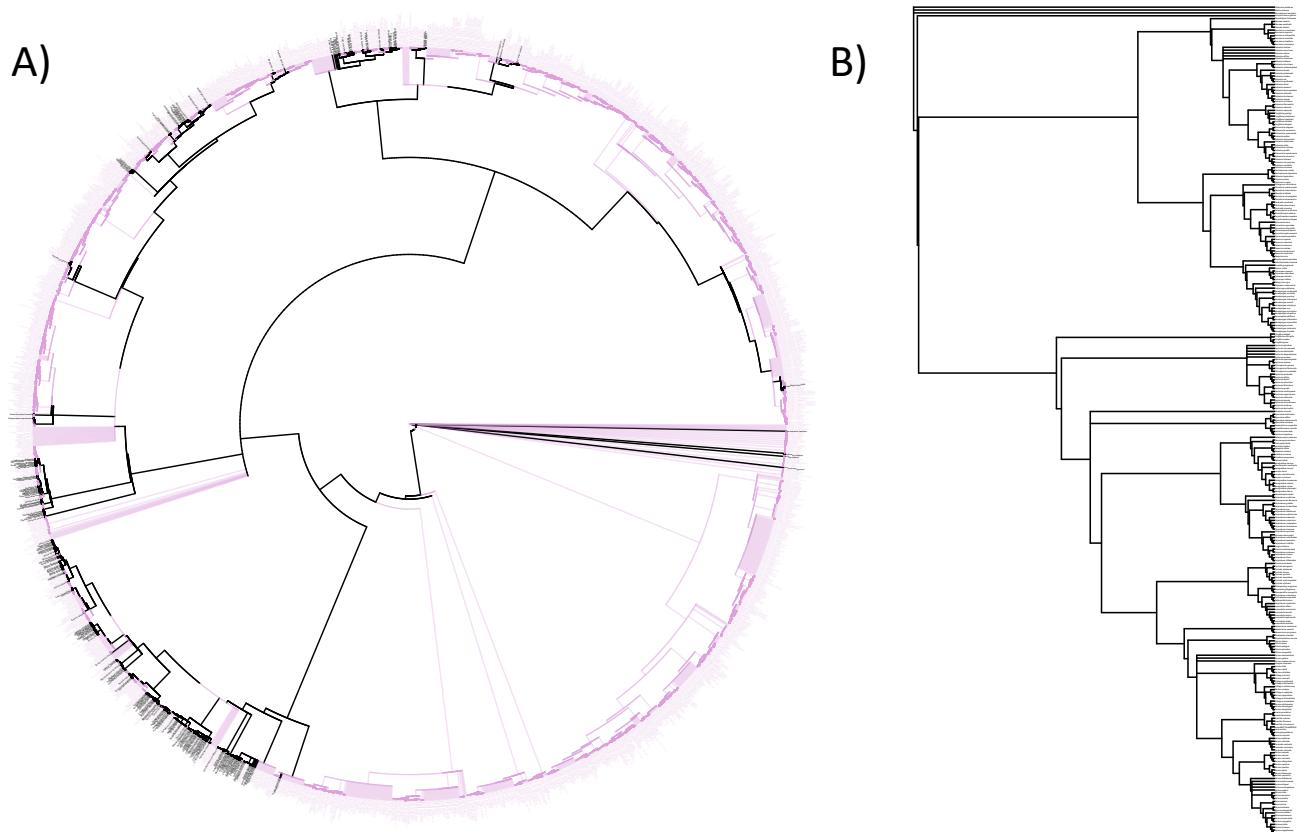
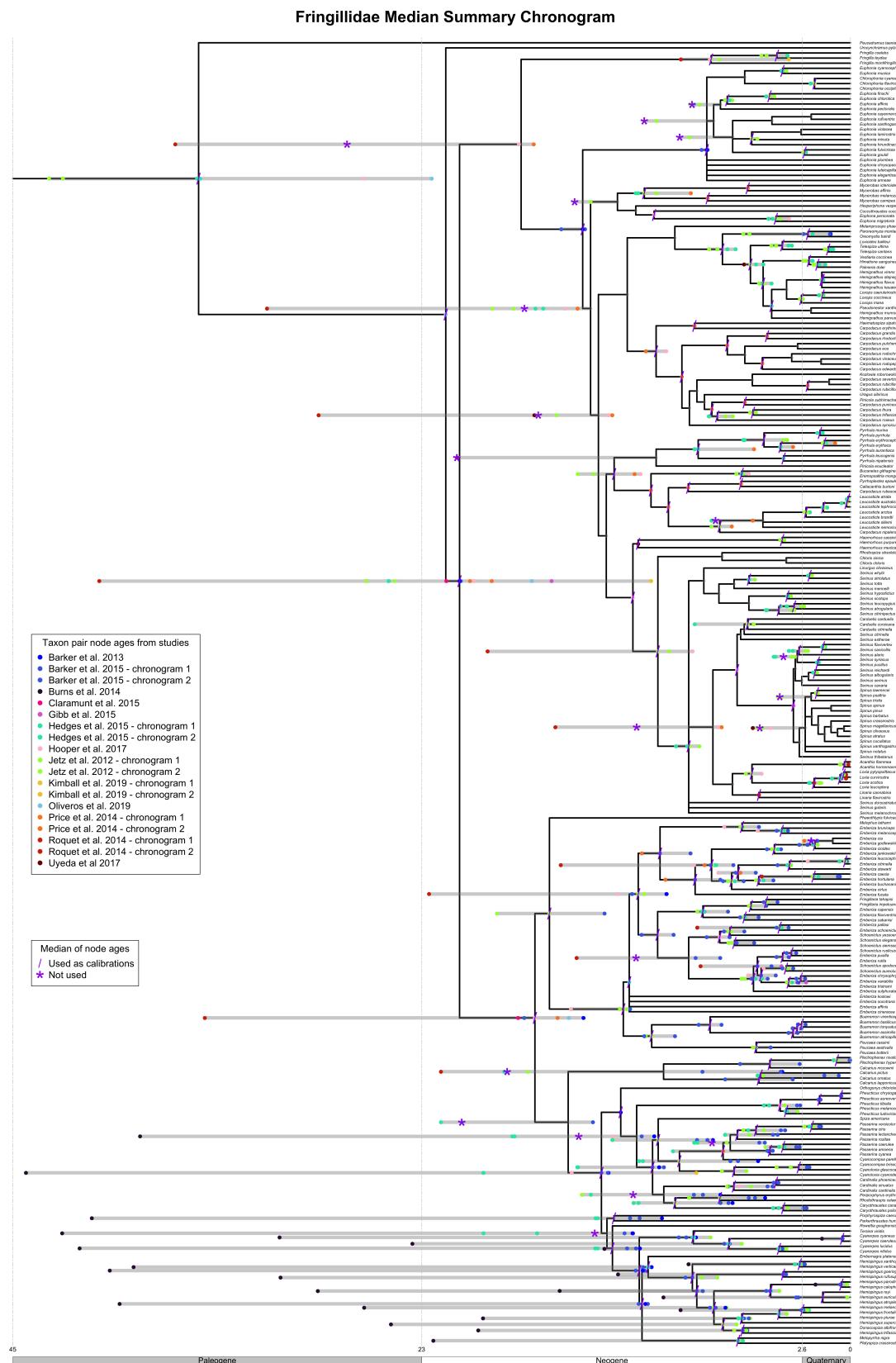


FIGURE 4. Tree topologies extracted from Open Tree of Life's (OpenTree) synthetic phylogenetic tree.
 340 A) Topology of 2,333 tips and 1,305 internal nodes, encompassing bird species within the family
 341 Fringillidae following the NCBI taxonomy (black), as well as all other bird species that share the same
 342 Most Recent Common Ancestor (MRCA) node in OpenTree's synthetic tree (purple). B) Subtree
 343 topology of 289 tips and 253 internal nodes, resulting from pruning species that do not belong to the
 344 family Fringillidae according to the NCBI taxonomy (purple branches in topology A). Bird species
 345 within the Fringillidae are paraphyletic (Alström et al. 2014, Barker, Cibois, Schikler, Feinstein, &
 346 Cracraft 2004, Barker et al. 2013, Barker 2014, Barker et al. 2015, Beresford, Barker, Ryan, &
 347 Crowe 2005, Bryson Jr et al. 2014, Burleigh, Kimball, & Braun 2015, Burns et al. 2014, Chaves,
 348 Hidalgo, & Klicka 2013, Claramunt & Cracraft 2015, Gibb et al. 2015, Hackett et al. 2008, Jetz et al.
 349 2012, Johansson, Fjeldså, & Bowi 200, Kimball et al. 2019, Klicka et al. 2014, Lamichhaney et al.
 350 2015, Lerner, Meyer, James, Hofreiter, & Fleischer 2011, Lovette et al. 2010, Moyle et al. 2016,
 351 Ödeen, Håstad, & Alström 2011, Oliveros et al. 2019, Päckert et al. 2012, Parchman, Benkman, &
 352 Mezquida 2007, Powell et al. 2014, Price et al. 2014, Pulgarín-R, Smith, Bryson Jr, Spellman, &
 353 Klicka 2013, Selvatti, Gonzaga, & Moraes Russo 2015, Tietze, Päckert, Martens, Lehmann, & Sun
 354 2013, Treplin et al. 2008, Zuccon, Prŷs-Jones, Rasmussen, & Ericson 2012).

357 Age data from source chronograms was congruified to OpenTree's topology (Fig. 4B),
358 reducing the age data set to 818 different data points (Supplementray Table S2). For each
359 congruent node, age summary statistics were calculated and used as fixed secondary
360 calibrations over the chosen tree topology, to obtain a fully dated phylogeny with the
361 program BLADJ (Fig. 5).

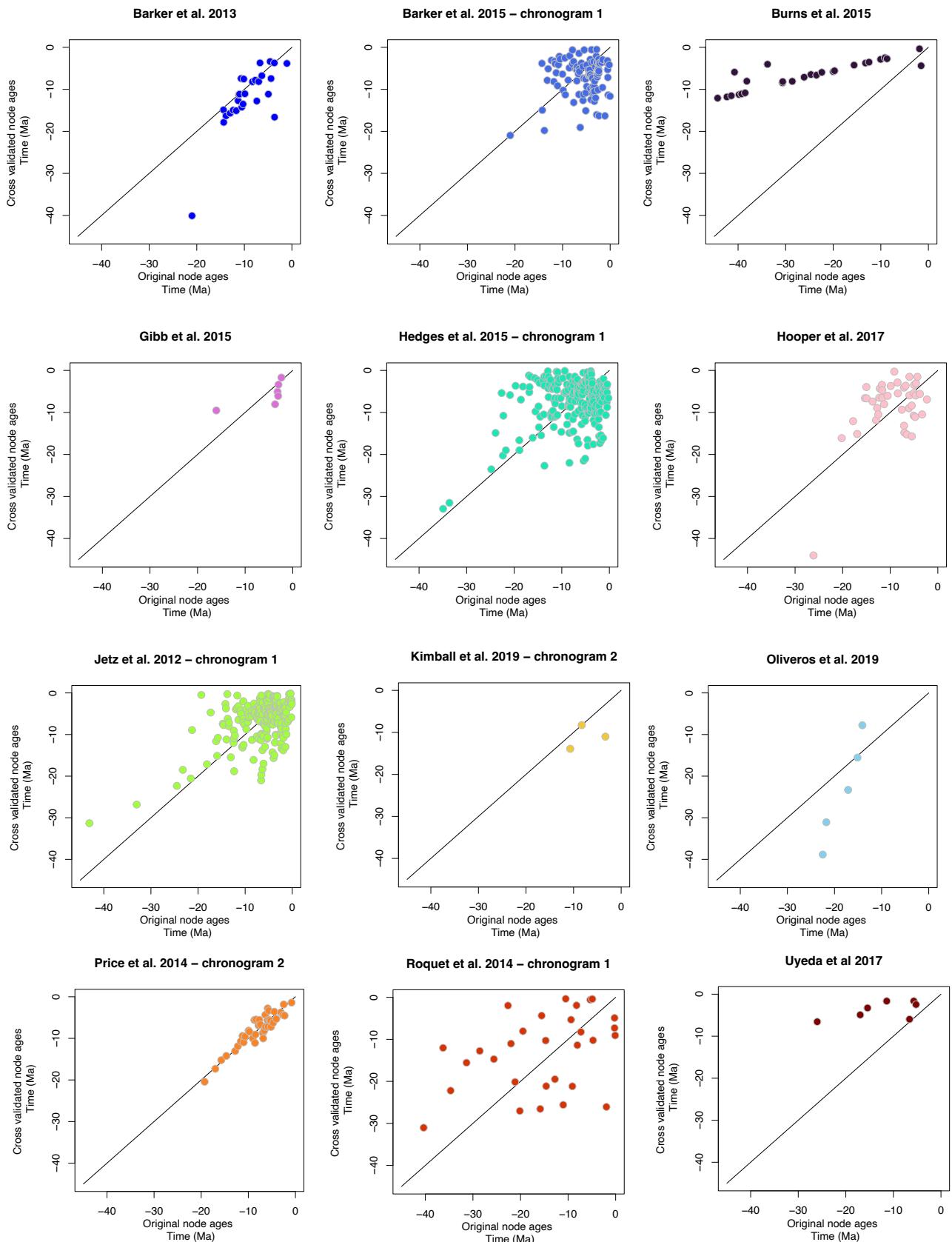


362 FIGURE 5. *Fringillidae* median summary chronogram generated with DateLife. It has 289 tips and
 363 253 nodes, from which 212 have age data from at least one published chronogram. These nodes have
 364 age data points from 19 different chronograms from 13 different studies (colored circles), which were

368

Cross-validation test

369 We performed a cross validation analysis of the DateLife workflow using the Fringillidae
370 chronograms. We used the individual tree topologies from each of the 19 source chronograms
371 from 13 studies as inputs, treating their node ages as unknown. We then estimated dates for
372 these topologies using the node ages from the chronograms from the other studies as
373 calibrations and smoothing using BLADJ. We found that node ages from original study, and
374 ages estimated using all other age data available are correlated (Fig. 6). For five studies,
375 Datelife tended to underestimate ages for topologically deeper nodes (those with many
376 descendant taxa, aka “closer to the root”) relative to the original estimate, and overestimate
377 ages for nodes closer to the tips. Accordingly, root ages are generally older in the original
378 study than estimated using cross-validated ages (Supplementary Fig. S1).



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

382

Discussion

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

388 A total of 99,474 unique terminal taxa are represented in DateLife’s database. Incorporation
389 of more chronograms into the database will continue to improve DateLife’s services. One
390 option to increase the number of chronograms in the DateLife database is the Dryad data
391 repository. Methods to automatically mine chronograms from Dryad could be designed and
392 implemented. However, Dryad’s metadata system has no information to automatically detect
393 branch length units, and those would still need to be determined manually by a human
394 curator. We would like to emphasize on the importance of sharing chronogram data,
395 including systematically curated metadata, into open repositories, such as OpenTree’s
396 Phylesystem (McTavish et al., 2015) for the benefit of the scientific community as a whole.

397 **Age variation in source chronograms**

398 Conflict in estimated ages among alternative studies is common in the literature. See, for
399 example, the robust ongoing debate about crown group age of angiosperms (Barba-Montoya,
400 Reis, Schneider, Donoghue, & Yang, 2018; Magallón, Gómez-Acevedo, Sánchez-Reyes, &
401 Hernández-Hernández, 2015; Ramshaw et al., 1972; Sanderson & Doyle, 2001; Sauquet,
402 Ramírez-Barahona, & Magallón, 2021). Source chronograms available for the same
403 organisms have potentially been estimated implementing calibrations very differently. For
404 example, the chronograms from Burns et al. (2014) were inferred using molecular
405 substitution rate estimates across birds (Weir & Schluter, 2008), and have much older age
406 estimates for the same nodes than chronograms that were inferred using fossils as
407 calibrations (Figs. 5, 6; Supplementary Figs. S1, S5).

408 Different calibration implementations might also imply fundamentally distinct evolutionary
409 hypotheses (Antonelli et al., 2017). For example, two independent researchers working on
410 the same clade should both carefully select and justify their choices of fossil calibration
411 placement. Yet, if one researcher concludes that a fossil should calibrate the ingroup of a
412 clade, while another researcher concludes that the same fossil should calibrate the outgroup
413 of the clade, the resulting age estimates will differ, as the placement of calibrations as stem
414 or crown group has been proven to significantly affect time of lineage divergence estimates
415 (Sauquet, 2013).

416 **Primary vs Secondary calibrations.** While most chronograms in DateLife’s database
417 are constructed using primary calibrations (molecular substitution rates or ages obtained
418 from the fossil record or geological events), DateLife summarizes chronograms using
419 secondary calibrations (ages coming from other chronograms). Graur and Martin (2004)
420 cautioned on the increased error and uncertainty in estimated ages when using secondary
421 calibrations in dating analyses. Schenk (2016) showed that, in simulations, divergence times
422 inferred using secondary calibrations are significantly younger than those inferred with
423 primary calibrations, when obtained with Bayesian inference methods, and when priors are
424 implemented in similar ways in both analyses. Accordingly, the scientific community seems
425 to have more confidence in chronograms obtained from a single analysis, using fossil data as
426 primary sources of calibrations (Schenk, 2016), and using fossils that have been widely
427 discussed and curated as calibrations to date other trees, making sure that all data reflect a
428 coherent evolutionary history (Sauquet, 2013), as for example done by Antonelli et al.
429 (2017). There have been attempts to create fossil calibration databases (Ksepka et al., 2015),
430 though these still have room to grow.

431 It seems that using several (as opposed to just a few) secondary calibrations can provide
432 sufficient information to alleviate or even neutralize potential biases (Sauquet, 2013).
433 Certainly, further studies are required to fully understand the effect of secondary calibrations
434 on outputs from different tree dating methods, and on downstream analyses. It is possible

435 that secondary calibrations can be safely used with dating methods that do not require
436 setting priors, such as penalized likelihood (Sanderson, 2003), with methods that do not
437 make any assumptions on the ages and fix them to a node on a tree topology, such as
438 BLADJ (Webb et al., 2008; Webb & Donoghue, 2005), or methods that summarize age data
439 unto a tree topology.

440 Our cross validation analysis might provide some insight in this regard. When ages are
441 estimated with secondary calibrations, nodes closer to the root do tend to be slightly
442 younger than ages estimated with primary calibrations. However, nodes closer to the tip
443 tend to be older when estimated using secondary calibrations with a dating method that
444 does not make any prior assumptions on the nature of the calibrations themselves
445 (Supplementary Figures S2-S20). The only exception to this was observed on cross validation
446 results of the Burns et al. (2014) chronogram, which displays much younger node ages when
447 estimated using secondary calibrations (Supplementary Figs. S1, S5).

448 Sumarizing chronograms

449 By default, DateLife currently summarizes all source chronograms that overlap with at least
450 two species names. Users can exclude source chronograms if they have reasons to do so.
451 Strictly speaking, a good chronogram should reflect the real time of lineage divergence
452 accurately and precisely. To our knowledge, there are no tested measures to determine
453 independently when a chronogram is better than another. Yet, several characteristics of the
454 data used for dating analyses, as well as from the output chronogram itself, could be used to
455 score the quality of source chronograms.

456 Some measures that have been proposed are the proportion of lineage sampling and the
457 number of calibrations used (Magallón, 2010; Magallón et al., 2015). Some characteristics
458 that are often cited in published studies as a measure of improved age estimates as compared
459 to previously published estimates are: quality of alignment (missing data, GC content),
460 lineage sampling (strategy and proportion), phylogenetic and dating inference method,

461 number of fossils used as calibrations, support for nodes and ages, and magnitude of
462 confidence intervals.

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

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

477 Effects on downstream analyses

478 The study of phenomena dependent on the timing of species diversification events, such as
479 macroevolutionary processes, is affected by the usage of alternative chronograms that vary in
480 topology (Rabosky, 2015; Title & Rabosky, 2016).

481 On the other hand, incorporating at least some data on lineage divergence times represents a
482 relevant improvement for testing alternative hypothesis using phylogenetic distance in
483 ecological and conservation biology studies (Webb et al., 2008). Hence, DateLife's workflow
484 features different ways of generating node ages in the absence of calibration and branch
485 length information for certain taxa.

486 Adding branch lengths sampled from a birth-death model in the absence of genetic data has

487 been found to improve insight in phylogeny-based analyses.

488 is a common practice in scientific publications: Jetz et al. (2012), created a chronogram of

489 all 9, 993 bird species, where 67% had molecular data and the rest was simulated; Rabosky

490 et al. (2018) created a chronogram of 31, 536 ray-finned fishes, of which only 37% had

491 molecular data; Smith and Brown (2018) constructed a chronogram of 353, 185 seed plants

492 where only 23% had molecular data.

493 Simulating branch lengths following a birth-death species diversification model for missing

494 taxa in chronograms with non random sampling, lowers type I error (false positive,

495 incorrectly accepting the null hypothesis of a constant-rate or temporally varying rate

496 birth-death model) when analyzing changes in diversification rate using the gamma statistic

497 (Cusimano, Stadler, & Renner, 2012).

498 Thomas et al. (2013) hypothesize that results of diversification analyses will be biased

499 towards the birth-death model used to simulate branch lengths; and note that “the effects of

500 missing species placement or polytomy resolution are less clear for other phylogeny-based

501 analyses (e.g. correlates of diversification, modelling trait evolution, community

502 phylogenetics), and future work should test how the treatment of missing species influences

503 both parameter estimation and type I and II errors”

504 Notably, risks come with this practice.

505 Taken to the extreme, one could generate a fully resolved, calibrated tree of all modern and

506 extinct taxa using a single taxonomy and a single calibration, using polytomy resolution and

507 branch length simulation methods. There has yet to be a thorough analysis of what can go

508 wrong when one extends inferences beyond the data in this way, so we urge caution; we also

509 urge readers to follow the example of the large tree papers cited above, by carefully

510 considering the statistical assumptions being made, and assessing the consistency of the

511 results with prior work.

512

Conclusions

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

521 The DateLife project allows for easy and fast summary of public and state-of-the-art data on
522 time of lineage divergence. It provides a straightforward way to get an informed idea on the
523 state of knowledge of the time frame of evolution of different regions of the tree of life, and
524 allows identifying regions that require more research, or that have conflicting information. It
525 is available as an R package, and as a web-based R shiny application at www.datelife.org
526 Both summary and newly generated trees are useful to evaluate evolutionary hypotheses in
527 different areas of research. The DateLife project should improve awareness of the existing
528 variation in expert time of divergence data, and foster exploration of the effect of alternative
529 divergence time hypothesis on the results of analyses, nurturing a culture of more cautious
530 interpretation of evolutionary results.

531

Availability

532 The DateLife software is free and open source and it can be used through its R shiny web
533 application at <http://www.datelife.org>, through the **datelife** R package, and through
534 Phylotastic's project web portal <https://phylo.cs.nmsu.edu/>. DateLife's web application is
535 maintained using RStudio's shiny server and the shiny package open infrastructure, as well
536 as Docker and OpenTree's infrastructure (dates.opentreeoflife.org/datelife). **datelife**'s R
537 package stable version is available for installation from the CRAN repository

538 (<https://cran.r-project.org/package=datelife>) using the command `install.packages(pkgs`
539 `= "datelife")` from within R. Development versions are available from the GitHub
540 repository (<https://github.com/phylotastic/datelife>) and can be installed using the
541 command `devtools::install_github("phylotastic/datelife")`.

542 **Supplementary Material**

543 Supplementary material, including code, biological examples and benchmark results data
544 files and online-only appendices, can be found in the Dryad data repository
545 (<https://doi.org/10.5061/dryad.cnp5hqc6w>), as well as in the GitHub repositories used to
546 develop the reproducible manuscript (<https://doi.org/10.5281/zenodo.7435094>), the
547 biological examples (<https://doi.org/10.5281/zenodo.7435101>), and the software benchmark
548 (<https://doi.org/10.5281/zenodo.7435106>).

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