

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: 4959

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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 developmental biology (Delsuc et al., 2018; Laubichler & Maienschein,
50 2009), conservation biology (Felsenstein, 1985; Webb, 2000), historical biogeography
51 (Posadas, Crisci, & Katinas, 2006), and species diversification (Magallon & Sanderson, 2001;
52 Morlon, 2014).

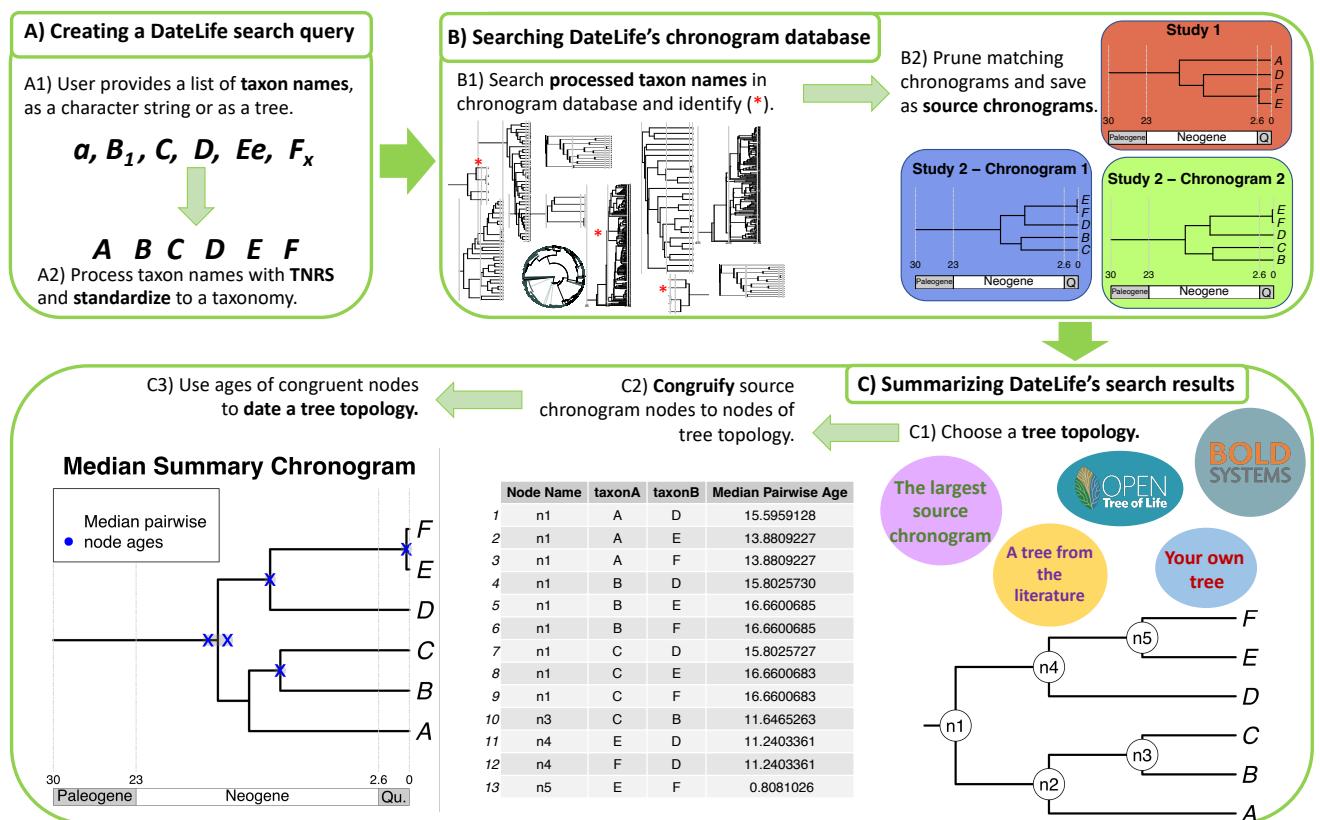
53 Building a chronogram is not an easy task. It requires obtaining and curating data to
54 construct a phylogeny, selecting and placing appropriate calibrations on the phylogeny using
55 independent age data points from the fossil record or other dated events, and inferring the
56 full dated tree; it 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. 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 current
 70 stable version – v0.6.6, is available from The Comprehensive R Archive Network (CRAN)
 71 repository (Sanchez-Reyes et al., 2022), and relies on functionalities from various biological
 72 R packages: `ape` (Paradis, Claude, & Strimmer, 2004), `bold` (Chamberlain, 2018), `geiger`
 73 (Pennell et al., 2014), `paleotree` (Bapst, 2012), `phyloch` (Heibl, 2008), `phylocomr` (Ooms &
 74 Chamberlain, 2018), `phytools` (Revell, 2012), `rotl` (Michonneau, Brown, & Winter, 2016),
 75 and `taxize` (Chamberlain, 2018; Chamberlain & Szöcs, 2013). Figure 1 provides a graphical
 76 summary of the three main steps of the DateLife workflow: creating a search query,
 77 searching a database, and 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, 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 <https://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
87 lengths, 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 standard taxonomy of choice, and adds them to the input string. Taxonomies currently
94 supported by DateLife are Open Tree of Life (OpenTree) unified Taxonomy (OTT, Rees &
95 Cranston, 2017), the National Center of Biotechnology Information (NCBI) taxonomic
96 database (Schoch et al., 2020), the Global Biodiversity Information Facility (GBIF)
97 taxonomic backbone (GBIF Secretariat, 2022), and the Interim Register of Marine and
98 Nonmarine Genera (IRMNG) database (Rees et al., 2017). If the flag is inactive, DateLife
99 excludes any taxon names above the species level from the search query.

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

107 The processed input taxon names are saved as an R object of a newly defined class,

108 `datelifeQuery`, that is used in the following steps. This object contains the standardized

109 names, the corresponding OTT identification numbers, and the topology of the input tree if

110 any was provided.

111 **Searching a chronogram database**

112 At the time of writing of this manuscript (Jun 22, 2022), DateLife's chronogram

113 database latest version consist of 253 chronograms published in 187 different studies. It is

114 curated from OpenTree's phylogenetic database, the Phylesystem, which constitutes an open

115 source of expert and peer-reviewed phylogenetic knowledge with rich metadata (McTavish et

116 al., 2015), which allows automatic and reproducible assembly of our chronogram database.

117 Datelife's chronogram database is navigable as an R data object within the `datelife` R

118 package.

119 A unique feature of the Phylesystem is that any user can add new published,

120 state-of-the-art chronograms any time, through their curator application

121 (<https://tree.opentreeoflife.org/curator>). As chronograms are added to Phylesystem, they are

122 incorporated into the chronogram database of the `datelife` package. The updated database

123 is assigned a new version number, followed by a package release on CRAN. `datelife`'s

124 chronogram database is updated as new chronogram data is added to Phylesystem, at a

125 minimum of once a month and a maximum of every 6 months. Users can also implement

126 functions from the `datelife` R package to trigger an update of the local chronogram

127 database, to incorporate any new chronograms to the user's DateLife analysis before an

128 official database update is released on CRAN.

129 A DateLife search is implemented by matching processed taxon names provided by the

130 user to tip labels in the chronogram database. Chronograms with at least two matching

131 taxon names on their tip labels are identified and pruned down to preserve only the matched

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

139 **Summarizing search results**

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

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

153 ***Choosing a topology.***— DateLife requires a tree topology to summarize age data
154 upon. We recommend that users provide as input a tree topology from the literature, or one
155 of their own making. If no topology is provided, DateLife automatically extracts one from
156 the OpenTree synthetic tree, a phylogeny 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 combine topologies from source chronograms into a single summary (or supertree) topology, the DateLife workflow 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). 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. If source chronograms do not form a grove, the supertree reconstruction will fail.

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

Once a topology is chosen, DateLife applies the congruification method (Eastman, Harmon, & Tank, 2013) to find nodes belonging to the same clade across source chronograms, and extract the corresponding node ages from the patristic distance matrices stored as `datelifeResult`. By definition, the matrices store total distance (time from tip to tip), hence, node ages correspond to half the values stored in the patristic distance matrices. This assumes that the terminal taxa are coeval and occur at the present. A table of

183 congruified node ages that can be used as calibrations for a dating analysis is stored as a
184 `congruifiedCalibrations` object.

185 For each congruent node, the pairwise distances that traverse that node are
186 summarized into a single summary matrix using classic summary statistics (i.e., mean,
187 median, minimum and maximum ages), and the Supermatrix Distance Method (SDM;
188 Criscuolo, Berry, Douzery, & Gascuel, 2006), which deforms patristic distance matrices by
189 minimizing variance and then averaging them. These single summary taxon pair age
190 matrices (Summarized calibrations) can be applied as calibrations to date a tree topology,
191 using different dating methods currently supported within DateLife: MrBayes (Huelsenbeck
192 & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), PATHd8 (Britton, Anderson, Jacquet,
193 Lundqvist, & Bremer, 2007), BLADJ (Webb, Ackerly, & Kembel, 2008; Webb & Donoghue,
194 2005), and treePL (Smith & O'Meara, 2012).

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

205 Alternative phylogenetic dating options supported in DateLife (MrBayes, PATHD8,
206 TreePL) incorporate branch length information from the input topology in combination with
207 the calibrations. PATHd8 is a non-clock, rate-smoothing method (Britton et al., 2007) to
208 date trees. treePL (Smith & O'Meara, 2012), is a semi-parametric, rate-smoothing,

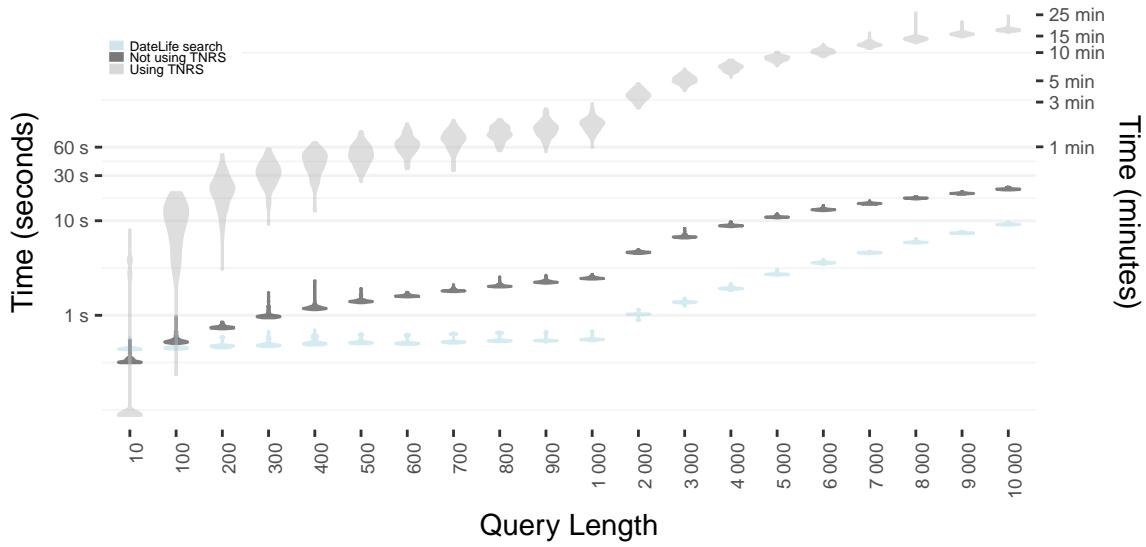
209 penalized likelihood dating method (Sanderson, 2002). The MrBayes (Huelsenbeck &
210 Ronquist, 2001; Ronquist & Huelsenbeck, 2003) approach in DateLife uses the calibrations as
211 priors on node ages.

212 ***Visualizing results.***— Finally, users can save all source and summary chronograms in
213 formats that permit reuse and reanalyses (newick and R “phylo” format), as well as visualize
214 and compare results graphically, or construct their own graphs using DateLife’s chronogram
215 plot generation functions available from the R package `datelifeplot` (Sanchez-Reyes &
216 O’Meara, 2022).

217

Benchmark

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



227

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

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

242 **Case studies**

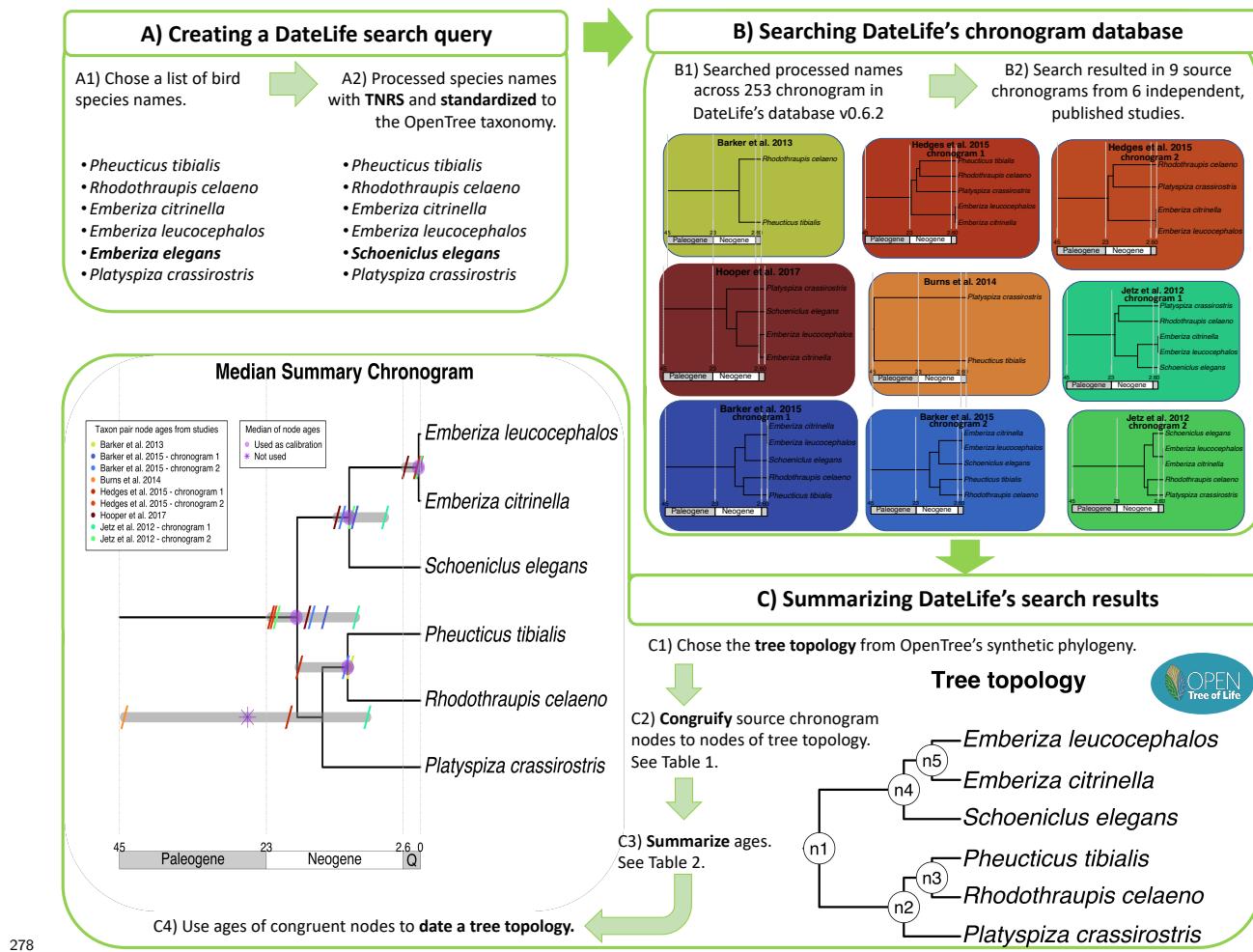
243 We illustrate the DateLife workflow using a family within the Passeriform birds
244 encompassing the true finches, Fringillidae, as case study. On a small example, we analysed 6
245 bird species, and results from each step of the workflow are shown in Fig. 3. As a second
246 example, we analysed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

249 **A small example**

250 **Creating a search query.** We chose 6 bird species within the Passeriformes. The sample
251 includes two species of cardinals: the black-thighed grosbeak – *Pheucticus tibialis* and the
252 crimson-collared grosbeak – *Rhodothraupis celaeno*; three species of buntings: the
253 yellowhammer – *Emberiza citrinella*, the pine bunting – *Emberiza leucocephalos* and the
254 yellow-throated bunting – *Emberiza elegans*; and one species of tanager, the vegetarian finch –
255 *Platyspiza crassirostris*. Processing of input names found that *Emberiza elegans* is synonym
256 for *Schoeniclus elegans* in the default reference taxonomy (OTT v3.3, June 1, 2021). For a
257 detailed discussion on the state of the synonym, refer to Avibase (Avibase, 2022; Lepage,
258 2004; Lepage, Vaidya, & Guralnick, 2014). Discovering this synonym allowed assigning five
259 age data points for the parent node of *Emberiza elegans*, shown as *Schoeniclus elegans* in
260 figure 3A, which would not have had any data otherwise.

261 **Searching the database.** DateLife used the processed input names to search the local
262 chronogram database and found 9 matching chronograms in 6 different studies (Fig. 3B).
263 Three studies matched five input names (Barker, Burns, Klicka, Lanyon, & Lovette, 2015;
264 Hedges, Marin, Suleski, Paymer, & Kumar, 2015; Jetz, Thomas, Joy, Hartmann, & Mooers,
265 2012), one study matched four input names (Hooper & Price, 2017) and two studies matched
266 two input names (Barker, Burns, Klicka, Lanyon, & Lovette, 2013; Burns et al., 2014). No
267 studies matched all input names. Together, source chronograms provide 28 unique age data
268 points, covering all nodes on our chosen tree topology to date (Table 1).

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



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

286 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

287

288 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

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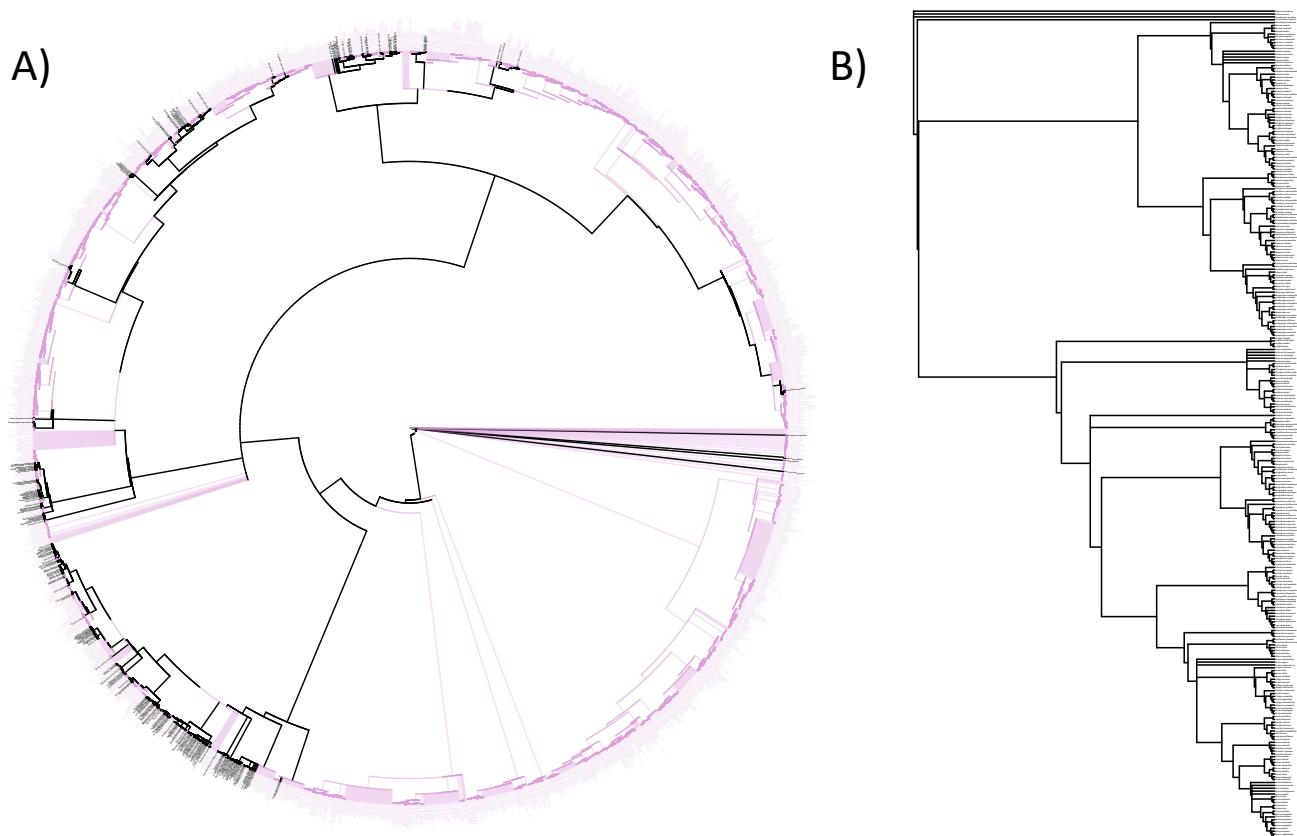
290 **An example with the family of true finches**

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

300 **Searching the database.** Next, we used the processed species names in our DateLife
301 query to identify chronograms with at least two Fringillidae species. The DateLife search
302 identified 13 chronograms containing at least two Fringillidae species, published in 9 different
303 studies (Barker et al., 2013, 2015; Burns et al., 2014; Claramunt & Cracraft, 2015; Gibb et
304 al., 2015; Hedges et al., 2015; Hooper & Price, 2017; Jetz et al., 2012; Price et al., 2014).

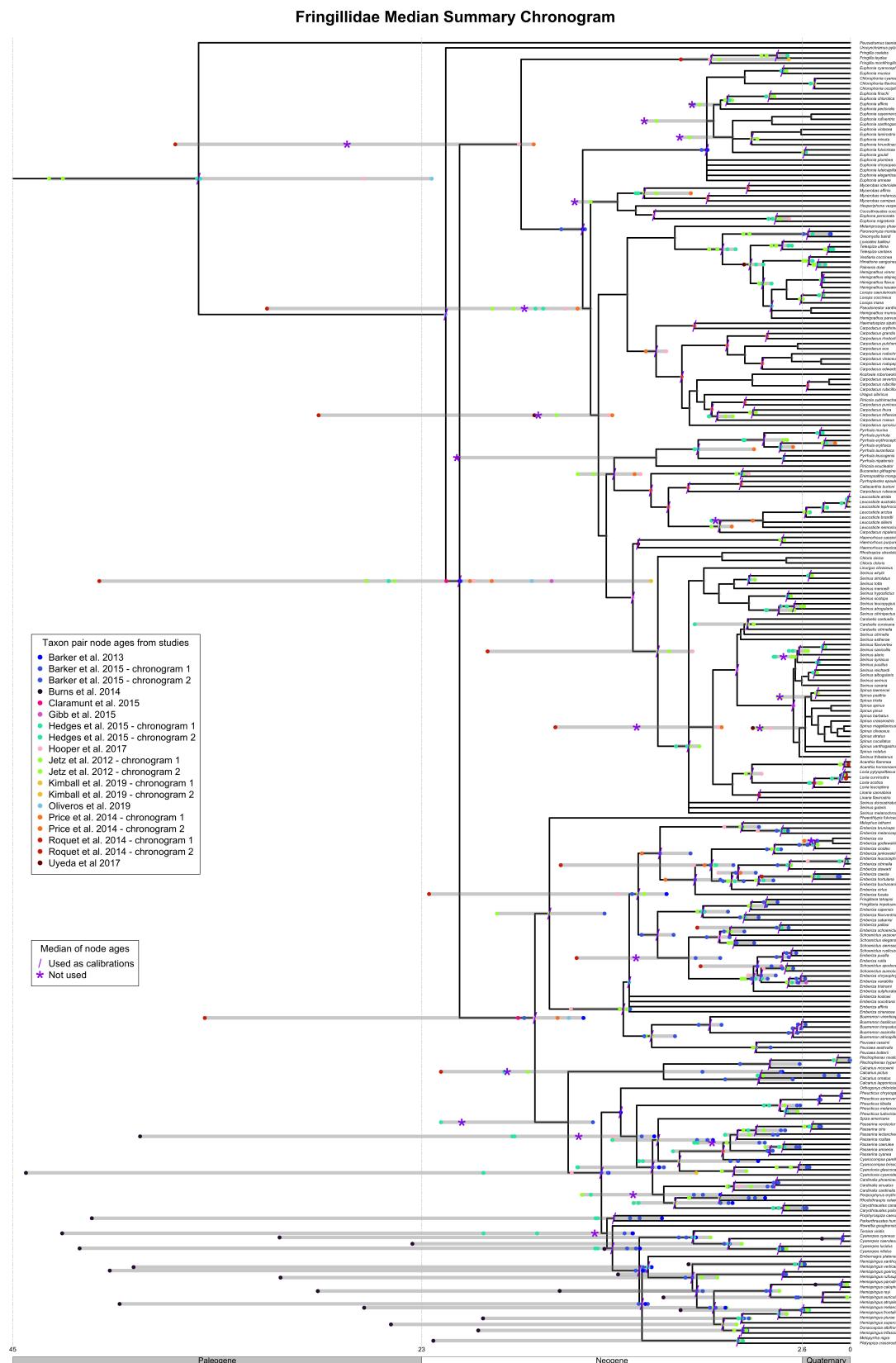
305 Once identified, DateLife pruned matching chronograms to keep Fringillidae species names
306 on tips only, and transformed these pruned chronograms to pairwise distance matrices,
307 revealing 1, 206 different age data points available for species within the Fringillidae
(Supplementray Table S1).

308 **Summarizing search results.** The final step is to congruify and summarize the age data
309 available for the Fringillidae species into single summary chronograms, using different types
310 of summary ages, median and SDM. As explained in the “Description” section, a tree
311 topology to summarize age data upon is required. By default, DateLife uses the topology
312 from OpenTree’s synthetic tree that contains the species in the search query to summarize
313 age data upon. According to OpenTree’s synthetic tree, species belonging to the family
314 Fringillidae do not form a monophyletic group (Fig. 4).



315 FIGURE 4. Tree topologies extracted from Open Tree of Life's (OpenTree) synthetic phylogenetic tree.
 316 A) Topology of 2,333 tips and 1,305 internal nodes, encompassing bird species within the family
 317 Fringillidae following the NCBI taxonomy (black), as well as all other bird species that share the same
 318 Most Recent Common Ancestor (MRCA) node in OpenTree's synthetic tree (purple). B) Subtree
 319 topology of 289 tips and 253 internal nodes, resulting from pruning species that do not belong to the
 320 family Fringillidae according to the NCBI taxonomy (purple branches in topology A). Bird species
 321 within the Fringillidae are paraphyletic (Alström et al. 2014, Barker, Cibois, Schikler, Feinstein, &
 322 Cracraft 2004, Barker et al. 2013, Barker 2014, Barker et al. 2015, Beresford, Barker, Ryan, &
 323 Crowe 2005, Bryson Jr et al. 2014, Burleigh, Kimball, & Braun 2015, Burns et al. 2014, Chaves,
 324 Hidalgo, & Klicka 2013, Claramunt & Cracraft 2015, Gibb et al. 2015, Hackett et al. 2008, Jetz et al.
 325 2012, Johansson, Fjeldså, & Bowi 200, Kimball et al. 2019, Klicka et al. 2014, Lamichhaney et al.
 326 2015, Lerner, Meyer, James, Hofreiter, & Fleischer 2011, Lovette et al. 2010, Moyle et al. 2016,
 327 Ödeen, Håstad, & Alström 2011, Oliveros et al. 2019, Päckert et al. 2012, Parchman, Benkman, &
 328 Mezquida 2007, Powell et al. 2014, Price et al. 2014, Pulgarín-R, Smith, Bryson Jr, Spellman, &
 329 Klicka 2013, Selvatti, Gonzaga, & Moraes Russo 2015, Tietze, Päckert, Martens, Lehmann, & Sun
 330 2013, Treplin et al. 2008, Zuccon, Prŷs-Jones, Rasmussen, & Ericson 2012).

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

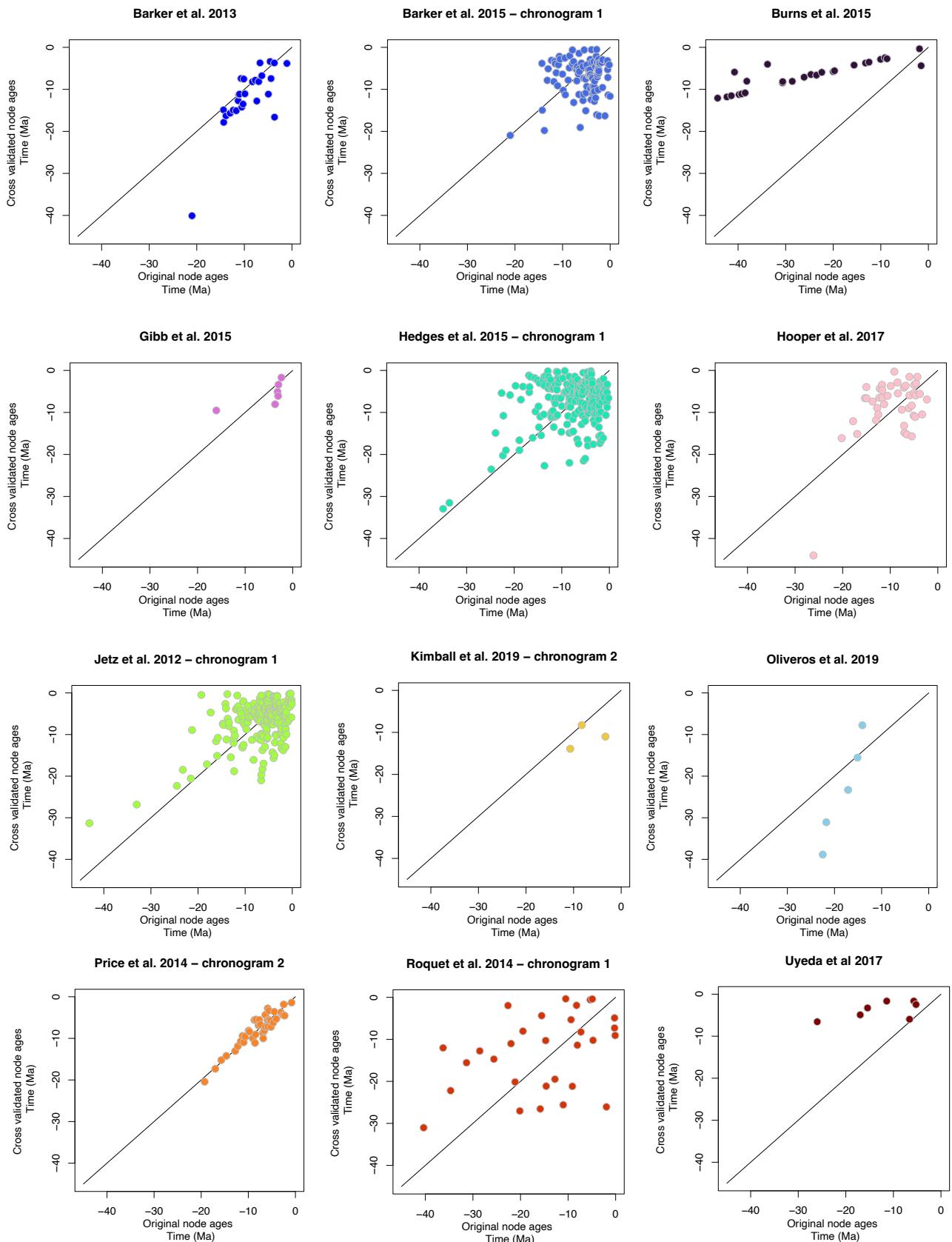


337 FIGURE 5. *Fringillidae median summary chronogram generated with DateLife*. It has 289 tips and
 338 253 nodes, from which 212 have age data from at least one published chronogram. These nodes have
 339 age data points from 19 different chronograms from 13 different studies (colored circles), which were

343

Cross-validation test

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



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

357

Discussion

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

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

372 **Age variation in source chronograms**

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

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

391 **Primary vs Secondary calibrations.** While most chronograms in DateLife’s database
392 are constructed using primary calibrations (molecular substitution rates or ages obtained
393 from the fossil record or geological events), DateLife summarizes chronograms using
394 secondary calibrations (ages coming from other chronograms). Graur and Martin (2004)
395 cautioned on the increased error and uncertainty in estimated ages when using secondary
396 calibrations in dating analyses. Schenk (2016) showed that, in simulations, divergence times
397 inferred using secondary calibrations are significantly younger than those inferred with
398 primary calibrations, when obtained with Bayesian inference methods, and when priors are
399 implemented in similar ways in both analyses. Accordingly, the scientific community seems
400 to have more confidence in chronograms obtained from a single analysis, using fossil data as
401 primary sources of calibrations (Schenk, 2016), and using fossils that have been widely
402 discussed and curated as calibrations to date other trees, making sure that all data reflect a
403 coherent evolutionary history (Sauquet, 2013), as for example done by Antonelli et al.
404 (2017). There have been attempts to create fossil calibration databases (Ksepka et al., 2015),
405 though these still have room to grow.

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

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

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

423 Sumarizing chronograms

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

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

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

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

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

452 Effects on downstream analyses

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

456 In ecology and conservation biology, incorporating at least some data on lineage divergence
457 times represents a relevant improvement for testing alternative hypothesis using phylogenetic
458 distance (Webb et al., 2008). Hence, DateLife's workflow features different ways of
459 estimating node ages in the absence of calibrations and branch length information for certain
460 taxa. “Making up” branch lengths is a common practice in scientific publications: Jetz et al.
461 (2012), created a chronogram of all 9, 993 bird species, where 67% had molecular data and

462 the rest was simulated; Rabosky et al. (2018) created a chronogram of 31, 536 ray-finned
463 fishes, of which only 37% had molecular data; Smith and Brown (2018) constructed a
464 chronogram of 353, 185 seed plants where only 23% had molecular data.

465 Notably, risks come with this practice. Taken to the extreme, one could make a fully
466 resolved, calibrated tree of all modern and extinct taxa using a single taxonomy and a single
467 calibration, using polytomy resolution and branch estimation methods. There has yet to be
468 a thorough analysis of what can go wrong when one extends inferences beyond the data in
469 this way, so we urge caution; we also urge readers to follow the example of the large tree
470 papers cited above, by carefully considering the statistical assumptions being made, and
471 assessing the consistency of the results with prior work.

472 Conclusions

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

481 The DateLife project allows for easy and fast summary of public and state-of-the-art data on
482 time of lineage divergence. It provides a straightforward way to get an informed idea on the
483 state of knowledge of the time frame of evolution of different regions of the tree of life, and
484 allows identification of regions that require more research, or that have conflicting
485 information. It is available as an R package, and as a web-based R shiny application at
486 www.datelife.org Both summary and newly generated trees are useful to evaluate
487 evolutionary hypotheses in different areas of research. The DateLife project helps with

488 awareness of the existing variation in expert time of divergence data, and will foster
489 exploration of the effect of alternative divergence time hypothesis on the results of analyses,
490 nurturing a culture of more cautious interpretation of evolutionary results.

491 **Availability**

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

502 **Supplementary Material**

503 Code used to generate all versions of this manuscript, the biological examples, as well as the
504 benchmark of functionalities are available at `datelifeMS1`, `datelife_examples`, and
505 `datelife_benchmark` repositories in LLSR's GitHub account.

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510

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523

References

- 524 Alström, P., Hooper, D. M., Liu, Y., Olsson, U., Mohan, D., Gelang, M., ... Price, T. D.
525 (2014). Discovery of a relict lineage and monotypic family of passerine birds. *Biology
Letters*, 10(3), 20131067.
- 526
- 527 Ané, C., Eulenstein, O., Piaggio-Talice, R., & Sanderson, M. J. (2009). Groves of
528 phylogenetic trees. *Annals of Combinatorics*, 13(2), 139–167.
- 529 Antonelli, A., Hettling, H., Condamine, F. L., Vos, K., Nilsson, R. H., Sanderson, M. J., ...
530 Vos, R. A. (2017). Toward a self-updating platform for estimating rates of speciation
531 and migration, ages, and relationships of Taxa. *Systematic Biology*, 66(2), 153–166.
532 <https://doi.org/10.1093/sysbio/syw066>
- 533 Archie, J., Day, W. H., Felsenstein, J., Maddison, W., Meacham, C., Rohlf, F. J., &
534 Swofford, D. (1986). The Newick tree format. Retrieved from
535 {<https://evolution.genetics.washington.edu/phylip/newicktree.html>}
- 536 Avibase. (2022). Yellow-throated Bunting. *Avibase - the World Bird Database*, (Online
537 Resource). Retrieved from
538 {<https://avibase.bsc-eoc.org/species.jsp?lang=EN&avibaseid=82D1EE0049D8D927>}
- 539 Bapst, D. W. (2012). Paleotree: An R package for paleontological and phylogenetic analyses
540 of evolution. *Methods in Ecology and Evolution*, 3(5), 803–807.
541 <https://doi.org/10.1111/j.2041-210X.2012.00223.x>
- 542 Barba-Montoya, J., Reis, M. dos, Schneider, H., Donoghue, P. C., & Yang, Z. (2018).
543 Constraining uncertainty in the timescale of angiosperm evolution and the veracity of
544 a cretaceous terrestrial revolution. *New Phytologist*, 218(2), 819–834.
- 545 Barker, F. K. (2014). Mitogenomic data resolve basal relationships among passeriform and
546 passeridan birds. *Molecular Phylogenetics and Evolution*, 79, 313–324.
- 547 Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2013). Going to
548 extremes: Contrasting rates of diversification in a recent radiation of new world
549 passerine birds. *Systematic Biology*, 62(2), 298–320.

- 550 Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2015). New insights
551 into new world biogeography: An integrated view from the phylogeny of blackbirds,
552 cardinals, sparrows, tanagers, warblers, and allies. *The Auk: Ornithological Advances*,
553 132(2), 333–348.
- 554 Barker, F. K., Cibois, A., Schikler, P., Feinstein, J., & Cracraft, J. (2004). Phylogeny and
555 diversification of the largest avian radiation. *Proceedings of the National Academy of
556 Sciences*, 101(30), 11040–11045.
- 557 Beresford, P., Barker, F., Ryan, P., & Crowe, T. (2005). African endemics span the tree of
558 songbirds (passeri): Molecular systematics of several evolutionary “enigmas”.
559 *Proceedings of the Royal Society B: Biological Sciences*, 272(1565), 849–858.
- 560 Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J. A., Mozzherin, D., Rees, T., ... Enquist,
561 B. J. (2013). The taxonomic name resolution service: An online tool for automated
562 standardization of plant names. *BMC Bioinformatics*, 14(1).
563 <https://doi.org/10.1186/1471-2105-14-16>
- 564 Britton, T., Anderson, C. L., Jacquet, D., Lundqvist, S., & Bremer, K. (2007). Estimating
565 Divergence Times in Large Phylogenetic Trees. *Systematic Biology*, 56(788777878),
566 741–752. <https://doi.org/10.1080/10635150701613783>
- 567 Bryson Jr, R. W., Chaves, J., Smith, B. T., Miller, M. J., Winker, K., Pérez-Emán, J. L., &
568 Klicka, J. (2014). Diversification across the new world within the ‘blue’cardinalids
569 (aves: Cardinalidae). *Journal of Biogeography*, 41(3), 587–599.
- 570 Burleigh, J. G., Kimball, R. T., & Braun, E. L. (2015). Building the avian tree of life using a
571 large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution*, 84, 53–63.
- 572 Burns, K. J., Shultz, A. J., Title, P. O., Mason, N. A., Barker, F. K., Klicka, J., ... Lovette,
573 I. J. (2014). Phylogenetics and diversification of tanagers (passeriformes:
574 Thraupidae), the largest radiation of neotropical songbirds. *Molecular Phylogenetics
575 and Evolution*, 75, 41–77.
- 576 Chamberlain, S. (2018). *bold: Interface to Bold Systems API*. Retrieved from

- 577 <https://CRAN.R-project.org/package=bold>
- 578 Chamberlain, S. A., & Szöcs, E. (2013). taxize : taxonomic search and retrieval in R [version
579 2; referees: 3 approved]. *F1000Research*, 2(191), 1–29.
580 <https://doi.org/10.12688/f1000research.2-191.v2>
- 581 Chaves, J. A., Hidalgo, J. R., & Klicka, J. (2013). Biogeography and evolutionary history of
582 the neotropical genus *Saltator* (aves: Thraupini). *Journal of Biogeography*, 40(11),
583 2180–2190.
- 584 Claramunt, S., & Cracraft, J. (2015). A new time tree reveals earth history's imprint on the
585 evolution of modern birds. *Science Advances*, 1(11), e1501005.
- 586 Criscuolo, A., Berry, V., Douzery, E. J., & Gascuel, O. (2006). SDM: A fast distance-based
587 approach for (super)tree building in phylogenomics. *Systematic Biology*, 55(5),
588 740–755. <https://doi.org/10.1080/10635150600969872>
- 589 Delsuc, F., Philippe, H., Tsagkogeorga, G., Simion, P., Tilak, M.-K., Turon, X., ... Douzery,
590 E. J. (2018). A phylogenomic framework and timescale for comparative studies of
591 tunicates. *BMC Biology*, 16(1), 1–14.
- 592 Eastman, J. M., Harmon, L. J., & Tank, D. C. (2013). Congruification: Support for time
593 scaling large phylogenetic trees. *Methods in Ecology and Evolution*, 4(7), 688–691.
594 <https://doi.org/10.1111/2041-210X.12051>
- 595 Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high
596 throughput. *Nucleic Acids Research*, 32(5), 1792–1797.
- 597 Felsenstein, J. (1985). Phylogenies and the Comparative Method. *The American Naturalist*,
598 125(1), 1–15. Retrieved from <http://www.jstor.org/stable/2461605>
- 599 GBIF Secretariat. (2022). GBIF Backbone Taxonomy. *Checklist dataset*, (Online Resource
600 accessed via GBIF.org). Retrieved from {<https://doi.org/10.15468/39omei> }
- 601 Gibb, G. C., England, R., Hartig, G., McLenachan, P. A., Taylor Smith, B. L., McComish,
602 B. J., ... Penny, D. (2015). New Zealand passerines help clarify the diversification of
603 major songbird lineages during the oligocene. *Genome Biology and Evolution*, 7(11),

- 604 2983–2995.
- 605 Graur, D., & Martin, W. (2004). Reading the entrails of chickens: Molecular timescales of
606 evolution and the illusion of precision. *TRENDS in Genetics*, 20(2), 80–86.
- 607 Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C., Braun, E. L., Braun, M. J., ...
608 others. (2008). A phylogenomic study of birds reveals their evolutionary history.
609 *Science*, 320(5884), 1763–1768.
- 610 Hedges, S. B., Marin, J., Suleski, M., Paymer, M., & Kumar, S. (2015). Tree of life reveals
611 clock-like speciation and diversification. *Molecular Biology and Evolution*, 32(4),
612 835–845. <https://doi.org/10.1093/molbev/msv037>
- 613 Heibl, C. (2008). *PHYLOCH: R language tree plotting tools and interfaces to diverse*
614 *phylogenetic software packages*. Retrieved from
615 <http://www.christophheibl.de/Rpackages.html>
- 616 Hooper, D. M., & Price, T. D. (2017). Chromosomal inversion differences correlate with
617 range overlap in passerine birds. *Nature Ecology & Evolution*, 1(10), 1526.
- 618 Huelsenbeck, J. P., & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic
619 trees. *Bioinformatics*, 17(8), 754–755.
620 <https://doi.org/10.1093/bioinformatics/17.8.754>
- 621 Jetz, W., Thomas, G., Joy, J. J., Hartmann, K., & Mooers, A. (2012). The global diversity
622 of birds in space and time. *Nature*, 491(7424), 444–448.
623 <https://doi.org/10.1038/nature11631>
- 624 Johansson, U. S., Fjeldså, J., & Bowie, R. C. (2008). Phylogenetic relationships within
625 passerida (aves: Passeriformes): A review and a new molecular phylogeny based on
626 three nuclear intron markers. *Molecular Phylogenetics and Evolution*, 48(3), 858–876.
- 627 Katoh, K., Asimenos, G., & Toh, H. (2009). Multiple alignment of dna sequences with mafft.
628 In *Bioinformatics for dna sequence analysis* (pp. 39–64). Springer.
- 629 Kimball, R. T., Oliveros, C. H., Wang, N., White, N. D., Barker, F. K., Field, D. J., ...
630 others. (2019). A phylogenomic supertree of birds. *Diversity*, 11(7), 109.

- 631 Klicka, J., Barker, F. K., Burns, K. J., Lanyon, S. M., Lovette, I. J., Chaves, J. A., & Bryson
632 Jr, R. W. (2014). A comprehensive multilocus assessment of sparrow (aves:
633 Passerellidae) relationships. *Molecular Phylogenetics and Evolution*, 77, 177–182.
- 634 Ksepka, D. T., Parham, J. F., Allman, J. F., Benton, M. J., Carrano, M. T., Cranston, K.
635 A., . . . others. (2015). The fossil calibration database—a new resource for divergence
636 dating. *Systematic Biology*, 64(5), 853–859.
- 637 Lamichhaney, S., Berglund, J., Almén, M. S., Maqbool, K., Grabherr, M., Martinez-Barrio,
638 A., . . . others. (2015). Evolution of darwin’s finches and their beaks revealed by
639 genome sequencing. *Nature*, 518(7539), 371–375.
- 640 Laubichler, M. D., & Maienschein, J. (2009). *Form and function in developmental evolution*.
641 Cambridge University Press.
- 642 Lepage, D. (2004). *Avibase: The world bird database*. Bird Studies Canada.
- 643 Lepage, D., Vaidya, G., & Guralnick, R. (2014). Avibase—a database system for managing
644 and organizing taxonomic concepts. *ZooKeys*, (420), 117.
- 645 Lerner, H. R., Meyer, M., James, H. F., Hofreiter, M., & Fleischer, R. C. (2011). Multilocus
646 resolution of phylogeny and timescale in the extant adaptive radiation of hawaiian
647 honeycreepers. *Current Biology*, 21(21), 1838–1844.
- 648 Lovette, I. J., Pérez-Emán, J. L., Sullivan, J. P., Banks, R. C., Fiorentino, I.,
649 Córdoba-Córdoba, S., . . . others. (2010). A comprehensive multilocus phylogeny for
650 the wood-warblers and a revised classification of the parulidae (aves). *Molecular
651 Phylogenetics and Evolution*, 57(2), 753–770.
- 652 Magallon, S., & Sanderson, M. (2001). Absolute diversification rates in angiosperm clades.
653 *Evolution*, 55(9), 1762–1780.
- 654 Magallón, S. (2010). Using fossils to break long branches in molecular dating: A comparison
655 of relaxed clocks applied to the origin of angiosperms. *Systematic Biology*, 59(4),
656 384–399.
- 657 Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L., & Hernández-Hernández, T. (2015).

658 A metacalibrated time-tree documents the early rise of flowering plant phylogenetic
659 diversity. *New Phytologist*, 207(2), 437–453.

660 McTavish, E. J., Hinchliff, C. E., Allman, J. F., Brown, J. W., Cranston, K. A., Holder, M.
661 T., ... Smith, S. (2015). Phylesystem: A git-based data store for community-curated
662 phylogenetic estimates. *Bioinformatics*, 31(17), 2794–2800.

663 Michonneau, F., Brown, J. W., & Winter, D. J. (2016). rotl: an R package to interact with
664 the Open Tree of Life data. *Methods in Ecology and Evolution*, 7(12), 1476–1481.
665 <https://doi.org/10.1111/2041-210X.12593>

666 Morlon, H. (2014). Phylogenetic approaches for studying diversification. *Ecology Letters*,
667 17(4), 508–525. <https://doi.org/10.1111/ele.12251>

668 Moyle, R. G., Oliveros, C. H., Andersen, M. J., Hosner, P. A., Benz, B. W., Manthey, J. D.,
669 ... Faircloth, B. C. (2016). Tectonic collision and uplift of Wallacea triggered the
670 global songbird radiation. *Nature Communications*, 7(1), 1–7.

671 Oliveros, C. H., Field, D. J., Ksepka, D. T., Barker, F. K., Aleixo, A., Andersen, M. J., ...
672 others. (2019). Earth history and the passerine superradiation. *Proceedings of the
673 National Academy of Sciences*, 116(16), 7916–7925.

674 Ooms, J., & Chamberlain, S. (2018). *Phylocomr: Interface to 'phylocom'*. Retrieved from
675 <https://CRAN.R-project.org/package=phylocomr>

676 Open Tree Of Life, Redelings, B., Cranston, K. A., Allman, J., Holder, M. T., & McTavish,
677 E. J. (2016). Open Tree of Life APIs v3.0. *Open Tree of Life Project*, (Online
678 Resources). Retrieved from
679 {[https://github.com/OpenTreeOfLife/germinator/wiki/Open-Tree-of-Life-Web-
APIs](https://github.com/OpenTreeOfLife/germinator/wiki/Open-Tree-of-Life-Web-
680 APIs)}

681 Open Tree Of Life, Redelings, B., Sánchez Reyes, L. L., Cranston, K. A., Allman, J., Holder,
682 M. T., & McTavish, E. J. (2019). Open tree of life synthetic tree v12.3. *Zenodo*.
683 Retrieved from <https://doi.org/10.5281/zenodo.3937742>

684 Ödeen, A., Håstad, O., & Alström, P. (2011). Evolution of ultraviolet vision in the largest

- 685 avian radiation-the passerines. *BMC Evolutionary Biology*, 11(1), 1–8.
- 686 Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and
687 evolution in R language. *Bioinformatics*, 20(2), 289–290.
- 688 Parchman, T. L., Benkman, C. W., & Mezquida, E. T. (2007). Coevolution between
689 hispaniolan crossbills and pine: Does more time allow for greater phenotypic
690 escalation at lower latitude? *Evolution*, 61(9), 2142–2153.
- 691 Päckert, M., Martens, J., Sun, Y.-H., Severinghaus, L. L., Nazarenko, A. A., Ting, J., ...
692 Tietze, D. T. (2012). Horizontal and elevational phylogeographic patterns of
693 himalayan and southeast asian forest passerines (aves: Passeriformes). *Journal of
694 Biogeography*, 39(3), 556–573.
- 695 Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G.,
696 ... Harmon, L. J. (2014). Geiger v2. 0: An expanded suite of methods for fitting
697 macroevolutionary models to phylogenetic trees. *Bioinformatics*, 30(15), 2216–2218.
- 698 Posadas, P., Crisci, J. V., & Katinas, L. (2006). Historical biogeography: A review of its
699 basic concepts and critical issues. *Journal of Arid Environments*, 66(3), 389–403.
- 700 Powell, A. F., Barker, F. K., Lanyon, S. M., Burns, K. J., Klicka, J., & Lovette, I. J. (2014).
701 A comprehensive species-level molecular phylogeny of the new world blackbirds
702 (icteridae). *Molecular Phylogenetics and Evolution*, 71, 94–112.
- 703 Price, T. D., Hooper, D. M., Buchanan, C. D., Johansson, U. S., Tietze, D. T., Alström, P.,
704 ... others. (2014). Niche filling slows the diversification of himalayan songbirds.
705 *Nature*, 509(7499), 222.
- 706 Pulgarín-R, P. C., Smith, B. T., Bryson Jr, R. W., Spellman, G. M., & Klicka, J. (2013).
707 Multilocus phylogeny and biogeography of the new world pheucticus grosbeaks (aves:
708 Cardinalidae). *Molecular Phylogenetics and Evolution*, 69(3), 1222–1227.
- 709 Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., ... others.
710 (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*,
711 559(7714), 392.

- 712 Ramshaw, J., Richardson, D., Meatyard, B., Brown, R., Richardson, M., Thompson, E., &
713 Boulter, D. (1972). The time of origin of the flowering plants determined by using
714 amino acid sequence data of cytochrome c. *New Phytologist*, 71(5), 773–779.
- 715 Ratnasingham, S., & Hebert, P. D. (2007). BOLD: The barcode of life data system
716 (<http://www.Barcodinglife.Org>). *Molecular Ecology Notes*, 7(3), 355–364.
- 717 R Core Team. (2018). *R: a language and environment for statistical computing*. Vienna,
718 Austria: R Foundation for Statistical Computing.
- 719 Rees, & Cranston, K. (2017). Automated assembly of a reference taxonomy for phylogenetic
720 data synthesis. *Biodiversity Data Journal*, (5).
- 721 Rees, Vandepitte, L., Decock, W., & Vanhoorne, B. (2017). IRMNG 2006–2016: 10 Years of
722 a Global Taxonomic Database. *Biodiversity Informatics*, 12.
- 723 Revell, L. J. (2012). Phytools: An r package for phylogenetic comparative biology (and other
724 things). *Methods in Ecology and Evolution*, 3, 217–223.
- 725 Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference
726 under mixed models. *Bioinformatics*, 19(12), 1572–1574.
727 <https://doi.org/10.1093/bioinformatics/btg180>
- 728 Sanchez-Reyes, L. L., & O'Meara, B. (2022). **datelifeplot**: Methods to plot chronograms
729 and outputs of the **datelife** package. *R Package Release V0.2.2*. Retrieved from
730 <https://zenodo.org/badge/latestdoi/381501451>
- 731 Sanchez-Reyes, L. L., O'Meara, B., Eastman, J., Heath, T., Wright, A., Schliep, K., ...
732 Alfaro, M. (2022). **datelife**: Scientific Data on Time of Lineage Divergence for Your
733 Taxa. *R Package Release V0.6.2*. Retrieved from
734 <https://doi.org/10.5281/zenodo.593938>
- 735 Sanderson, M. (2002). Estimating Absolute Rates of Molecular Evolution and Divergence
736 Times: A Penalized Likelihood Approach. *Molecular Biology and Evolution*, 19(1),
737 101–109. <https://doi.org/10.1093/oxfordjournals.molbev.a003974>
- 738 Sanderson, M. (2003). r8s: Inferring Absolute Rates of Molecular Evolution and Divergence

- 739 Times in the Absence of a Molecular Clock. *Bioinformatics*, 19(2), 301–302.
- 740 Sanderson, M., & Doyle, J. (2001). Sources of error and confidence intervals in estimating
741 the age of angiosperms from rbcL and 18S rDNA data. *American Journal of Botany*,
742 88(8), 1499–1516.
- 743 Sauquet, H. (2013). A practical guide to molecular dating. *Comptes Rendus Palevol*, 12(6),
744 355–367.
- 745 Sauquet, H., Ramírez-Barahona, S., & Magallón, S. (2021). *The age of flowering plants is
746 unknown*.
- 747 Schenk, J. J. (2016). Consequences of secondary calibrations on divergence time estimates.
748 *PLoS ONE*, 11(1). <https://doi.org/10.1371/journal.pone.0148228>
- 749 Schliep, K. P. (2011). Phangorn: Phylogenetic analysis in r. *Bioinformatics*, 27(4), 592–593.
- 750 Schoch, C. L., Ciufo, S., Domrachev, M., Hotton, C. L., Kannan, S., Khovanskaya, R., ...
751 others. (2020). NCBI Taxonomy: a Comprehensive Update on Curation, Resources
752 and Tools. *Database*, 2020.
- 753 Selvatti, A. P., Gonzaga, L. P., & Moraes Russo, C. A. de. (2015). A paleogene origin for
754 crown passerines and the diversification of the oscines in the new world. *Molecular
755 Phylogenetics and Evolution*, 88, 1–15.
- 756 Smith, S., & Brown, J. (2018). Constructing a broadly inclusive seed plant phylogeny.
757 *American Journal of Botany*, 105(3), 302–314.
- 758 Smith, S., & O'Meara, B. (2012). TreePL: Divergence time estimation using penalized
759 likelihood for large phylogenies. *Bioinformatics*, 28(20), 2689–2690.
760 <https://doi.org/10.1093/bioinformatics/bts492>
- 761 Stoltzfus, A., Lapp, H., Matasci, N., Deus, H., Sidlauskas, B., Zmasek, C. M., ... Jordan, G.
762 (2013). Phylotastic! Making tree-of-life knowledge accessible, reusable and convenient.
763 *BMC Bioinformatics*, 14. <https://doi.org/10.1186/1471-2105-14-158>
- 764 Tietze, D. T., Päckert, M., Martens, J., Lehmann, H., & Sun, Y.-H. (2013). Complete
765 phylogeny and historical biogeography of true rosefinches (aves: Carpodacus).

- 766 *Zoological Journal of the Linnean Society*, 169(1), 215–234.
- 767 Title, P. O., & Rabosky, D. L. (2016). Do Macrophylogenies Yield Stable Macroevolutionary
768 Inferences? An Example from Squamate Reptiles. *Systematic Biology*, syw102.
769 <https://doi.org/10.1093/sysbio/syw102>
- 770 Treplin, S., Siegert, R., Bleidorn, C., Thompson, H. S., Fotso, R., & Tiedemann, R. (2008).
771 Molecular phylogeny of songbirds (aves: Passeriformes) and the relative utility of
772 common nuclear marker loci. *Cladistics*, 24(3), 328–349.
- 773 Vos, R. A., Balhoff, J. P., Caravas, J. A., Holder, M. T., Lapp, H., Maddison, W. P., ...
774 others. (2012). NeXML: Rich, extensible, and verifiable representation of
775 comparative data and metadata. *Systematic Biology*, 61(4), 675–689.
776 <https://doi.org/10.1093/sysbio/sys025>
- 777 Webb, C. (2000). Exploring the Phylogenetic Structure of Ecological Communities : An
778 Example for Rain Forest Trees. *The American Naturalist*, 156(2), 145–155.
- 779 Webb, C., Ackerly, D., & Kembel, S. (2008). Phylocom: Software for the analysis of
780 phylogenetic community structure and trait evolution. *Bioinformatics*, 24(18),
781 2098–2100. <https://doi.org/10.1093/bioinformatics/btn358>
- 782 Webb, C., & Donoghue, M. (2005). Phylomatic: Tree assembly for applied phylogenetics.
783 *Molecular Ecology Notes*, 5(1), 181–183.
- 784 Weir, J., & Schluter, D. (2008). Calibrating the avian molecular clock. *Molecular Ecology*,
785 17(10), 2321–2328.
- 786 Zuccon, D., Prŷs-Jones, R., Rasmussen, P. C., & Ericson, P. G. (2012). The phylogenetic
787 relationships and generic limits of finches (fringillidae). *Molecular Phylogenetics and*
788 *Evolution*, 62(2), 581–596.