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

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

18   Abstract

19   ~~Achieving a high-quality reconstruction of a phylogenetic tree~~ Chronograms

20   —phylogenies with branch lengths proportional to ~~absolute time (chronogram) is a difficult~~

21   ~~and time-consuming task. But the increased availability of fossil and molecular data , and~~

22   ~~time-efficient analytical techniques has resulted in many recent publications of large~~

23   ~~chronograms for a large number and wide diversity of organisms. Knowledge of the~~

24   ~~evolutionary time frame of organisms is key for research in the natural sciences. It also~~

25   ~~represent valuable information~~ time— represent key data on timing of evolutionary events

26   for the study of natural processes in many areas of biological research. Chronograms also

27   provide valuable information that can be used for education, science communication, and

28   conservation policy decisions. ~~When chronograms are shared in public and open databases,~~

29   ~~this wealth of expertly-curated and peer-reviewed data on evolutionary timeframe is~~

30   ~~exposed in a programatic and reusable way, as intensive and localized efforts have improved~~

31   ~~data sharing practices, as well as incentivizited open science in biology~~ Yet, achieving a

32   high-quality reconstruction of a chronogram is a difficult and resource-consuming task.

33   Here we present DateLife, a service implemented as an R package and an R Shiny ~~website~~

34   web application available at www.datelife.org, that provides ~~functionalities~~ services for

35   efficient and easy ~~finding~~discovery, summary, reuse, and reanalysis of node age data mined

36   from a curated database of expert, peer-reviewed, ~~public data on time frame of~~

37   ~~evolution~~and openly available chronograms. The main DateLife workflow ~~constructs a~~

38   ~~chronogram for any given combination of taxon names by searching a~~ starts with one or

39   more scientific taxon names provided by a user. Names are processed and standardized to

40   a unified taxonomy, allowing DateLife to run a name match across its local chronogram

41   database ~~constructed and curated from the~~ that is curated from Open Tree of

42   Life~~Phylesystem phylogenetic database, which incorporates phylogenetic data from the~~

43 ~~TreeBASE database as well. We implement and test methods for summarizing time data~~

44 ~~from multiple source chronograms using supertree and congruification algorithms, and~~

45 ~~using age data extracted from source chronogramsas secondary calibration points to add~~

46 ~~branch lengths proportional to absolute time to a tree topology. DateLife will be useful to~~

47 's phylogenetic repository, and extract all chronograms that contain at least two queried

48 taxon names, along with their metadata. Finally, node ages from matching chronograms

49 are mapped to corresponding nodes from a chosen tree topology using the congruification

50 algorithm. Congruified node ages are used as secondary calibrations to date the chosen

51 topology, with or without initial branch lengths, using different phylogenetic dating

52 methods such as BLADJ, treePL, PATHd8 and MrBayes. We performed a cross-validation

53 test to compare node ages resulting from a DateLife analysis (i.e, phylogenetic dating using

54 secondary calibrations) to those from the original chronograms (i.e, obtained with primary

55 calibrations), and found that DateLife's node age estimates are consistent with the age

56 estimates from the original chronograms, with the largest variation in ages occurring

57 around topologically deeper nodes. Results from any software for scientific analysis can

58 only be as good as the data used as input, we highlight the importance of considering the

59 results of a DateLife analysis in the context of the input chronograms. We encourage the

60 use of DateLife to help increase awareness of the existing ~~variation in alternative hypothesis~~

61 ~~of evolutionary time~~ disparities among alternative hypotheses of dates for the same

62 ~~organisms, and can foster~~ diversification events, and to support exploration of the effect of

63 alternative ~~evolutionary timing hypotheses on the results of~~ chronogram hypotheses on

64 downstream analyses, providing a framework for a more informed interpretation of

65 evolutionary results.

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

67 Congruification; Supertree; Calibrations; Secondary calibrations.

68 Word count: ~~5393~~ 6715

Chronograms –phylogenies with branch lengths proportional to time– provide key data on evolutionary time frame for the study of natural processes in many areas of biological research, such as comparative analysis (Freckleton, Harvey, & Pagel, 2002; Harvey, Pagel, & others, 1991), developmental biology (Delsuc et al., 2018; Laubichler & Maienschein, 2009), conservation biology and ecology (Felsenstein, 1985; Webb, 2000), historical biogeography (Posadas, Crisci, & Katinas, 2006), and species diversification (Magallon & Sanderson, 2001; Morlon, 2014).

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

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

DESCRIPTION

DateLife's core software ~~application consists of~~ applications are implemented in the R package `datelife`. ~~Its current stable version — v0.6.6, is available from The Comprehensive R Archive Network (CRAN) repository (Sanchez-Reyes et al., 2022),~~ and relies on functionalities from ~~various~~ other biological R packages: ape (Paradis, Claude, & Strimmer, 2004), bold (Chamberlain, 2018), geiger (Pennell et al., 2014), msa (Bodenhofer, Bonatesta, Horejš-Kainrath, & Hochreiter, 2015), paleotree (Bapst, 2012), phyloch (Heibl, 2008), phylocomr (Ooms & Chamberlain, 2018), phytools (Revell, 2012), rotl (Michonneau, Brown, & Winter, 2016), and taxize (Chamberlain, 2018; Chamberlain & Szöcs, 2013). Figure ~~??~~ 1 provides a graphical summary of the three main steps of the DateLife workflow: creating a search query, searching a database, and summarizing results from the search.

Creating a Search Query

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

DateLife ~~accepts scientific names that can belong to any inclusive taxonomic group (e.g., genus, family, tribe, etc.) or a binomial species name. Subspecies and variants are ignored. If an input taxon name belongs to an inclusive taxonomic group, DateLife has two alternative behaviors defined by~~ processes input scientific names using a Taxonomic Name Resolution Service (TNRS), which increases the probability of correctly finding the queried taxon names in the chronogram database. TNRS detects, corrects and standardizes name misspellings and typos, variant spellings and authorities, and nomenclatural synonyms to a single taxonomic standard (Boyle et al., 2013). TNRS also allows to correctly choose between homonyms, by considering other taxa provided as input to infer the taxonomic

120 context of the ~~flag. If the flag is active, DateLife retrieves all species names within the~~

121 ~~inclusive taxonomic group following a standard taxonomy of choice, and adds them to the~~

122 ~~input string. Taxonomies currently supported by DateLife are~~ homonym. DateLife

123 implements TNRS using the Open Tree of Life (OpenTree) unified Taxonomy (OTT, Open

124 Tree Of Life et al., 2016; Rees & Cranston, 2017) ~~,~~ as standard, storing taxonomic

125 identification numbers (OTT ids) for further processing and analysis. Other taxonomies

126 currently supported by DateLife are the National Center of Biotechnology Information

127 (NCBI) taxonomic database (Schoch et al., 2020), the Global Biodiversity Information

128 Facility (GBIF) taxonomic backbone (GBIF Secretariat, 2022), and the Interim Register of

129 Marine and ~~Nonmarine~~ Non-marine Genera (IRMNG) database (Rees et al., 2017). ~~If~~

130 Besides binomial species names, DateLife accepts scientific names from any inclusive

131 taxonomic group (e.g., genus, family, tribe), as well as subspecific taxonomic variants (e.g.,

132 subspecies, variants, strains). If a taxon name belongs to an inclusive taxonomic group,

133 DateLife has two alternative behaviors defined by the "get species from taxon" flag. If the

134 flag is active, DateLife retrieves all species names within a taxonomic group provided, from

135 a standard taxonomy of choice, and adds them to the ~~flag is inactive, DateLife excludes~~

136 ~~any taxon names above the species level from the~~ search query.

137 ~~DateLife processes input scientific names using a Taxonomic Name Resolution Service~~

138 ~~(TNRS), which increases the probability of correctly finding the queried taxon names in~~

139 ~~the chronogram database. TNRS detects, corrects and standardizes name misspellings and~~

140 ~~typos, variant spellings and authorities, and nomenclatural synonyms to a single taxonomic~~

141 ~~standard (Boyle et al., 2013). DateLife implements TNRS with OTT as standard (Open~~

142 ~~Tree Of Life et al. , 2016; Rees & Cranston, 2017), storing taxonomic identification~~

143 ~~numbers for further processing.~~

144 ~~The processed input~~ In this case, subspecific variants are excluded. If the flag is

145 inactive, DateLife excludes inclusive taxon names from the search query, and species and

146 subspecific variant names are processed as provided by the user. The processed taxon

147 names are saved as an R object of a newly defined class, `datelifeQuery`, that is used in the

148 following steps. This object contains the ~~standardized names~~ input names standardized to a

149 taxonomy of choice (OTT by default), the corresponding OTT ~~identification~~ id numbers,

150 and the topology of ~~the input treeif any~~ an input tree, if one was provided.

Searching a Chronogram Database

152 At the time of writing of this manuscript (~~Jun 22, 2022~~May 15, 2023), DateLife's

153 chronogram database latest version consist of 253 chronograms published in 187 different

154 studies. It is curated from OpenTree's phylogenetic database, the Phylesystem, which

155 constitutes an open source of expert and peer-reviewed phylogenetic knowledge with rich

156 metadata (McTavish et al., 2015), which allows automatic and reproducible assembly of our

157 chronogram database. Datelife's chronogram database is navigable as an R data object

158 within the `datelife` R package.

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

160 state-of-the-art chronograms any time, through ~~their~~ OpenTree's curator application

161 (https://tree.opentreeoflife.org/curator). As chronograms are added to Phylesystem, they ~~are~~

162 can be incorporated into the chronogram database of the `datelife` ~~package~~R package,

163 which is currently manually updated as new chronogram data is added to Phylesystem.

164 The updated database is assigned a new version number, followed by a package release on

165 CRAN. Users can directly run `datelife` ~~'s chronogram database is updated as new~~

166 ~~chronogram data is added to Phylesystem, at a minimum of once a month and a maximum~~

167 ~~of every 6 months. Users can also implement functions from the~~ `datelife` ~~R package~~

168 functions to trigger an update of ~~the~~ their local chronogram database, to incorporate any

169 new chronograms to ~~the user's~~ their DateLife analysis before an official database update is

170 released on CRAN.

¹⁷¹ A DateLife search is implemented by matching processed taxon names provided by the

¹⁷² user to tip labels in the chronogram database. Chronograms with at least two matching

¹⁷³ taxon names on their tip labels are identified and pruned down to preserve only the matched

¹⁷⁴ taxa. These matching pruned chronograms are referred to as source chronograms. Total

¹⁷⁵ distance (in units of ~~millions of years~~ million years (Myr) between taxon pairs within each

¹⁷⁶ source chronogram are stored as a patristic distance matrix (~~Figure ??~~Fig. 1). The matrix

¹⁷⁷ format speeds up extraction of pairwise taxon ages of any queried taxa, as opposed to

¹⁷⁸ searching the ancestor node of a pair of taxa in a "phylo" object or newick string. Finally,

¹⁷⁹ the patristic matrices are associated to the study citation where the original chronogram was

¹⁸⁰ published, and stored as an R object of the newly defined class `datelifeResult`.

¹⁸¹ *Summarizing Search Results*

¹⁸² Summary information is extracted from the `datelifeResult` object to inform

¹⁸³ decisions for subsequent steps in the analysis workflow. Basic summary information available

¹⁸⁴ to the user is:

¹⁸⁵ 1. The matching pruned chronograms as newick strings or "phylo" objects.

¹⁸⁶ 2. The ages of the root of all source chronograms. These ages can correspond to the age

¹⁸⁷ of the most recent common ancestor (mrca) of the user's group of interest if the source

¹⁸⁸ chronograms have all taxa belonging to the group. If not, the root corresponds to the

¹⁸⁹ mrca of a subgroup ~~withing~~ within the group of interest.

¹⁹⁰ 3. Study citations where original chronograms were published.

¹⁹¹ 4. A report of input taxon names matches across source chronograms.

¹⁹² 5. The source chronogram(s) with the most input taxon names.

¹⁹³ 6. Various single summary chronograms resulting from summarizing age data, generated

¹⁹⁴ using the methodology described next.

¹⁹⁵ *Choosing a Topology*

DateLife requires a tree topology to summarize age data upon. We recommend that users provide as input a tree topology from the literature, or one 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 combine topologies from source chronograms into a single summary (or supertree)topology, the DateLife workflow~~ (Criscuolo, Berry, Douzery, & Gascuel, 2006). 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. ~~If source chronograms do not form a grove, the supertree reconstruction will fail.~~ The result is a single summary (or supertree) topology, that combines topologies from source chronograms in a grove.

~~Dating the Topology~~ Applying Secondary Calibrations

~~Input topologies from OpenTree or the supertreeapproach 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~~

222 ~~branch length information provides additional data for nodes without secondary date~~

223 ~~calibrations, topologies without branch lengths can also be dated.~~

224   Once a topology is chosen, DateLife applies the congruification method (Eastman,

225 Harmon, & Tank, 2013) ~~to~~ that find nodes belonging to the same clade across source

226 chronograms, and ~~extract~~ then extracts the corresponding node ages from ~~the~~ patristic

227 distance matrices stored as a `datelifeResult` ~~. By definition, the~~ object. Note that by

228 definition, these matrices store total distance (time from tip to tip), ~~hence~~ assuming that the

229 terminal taxa are coeval and occur at the present. Hence, node ages correspond to half the

230 values stored in the ~~patristic distance matrices. This assumes that the terminal taxa are~~

231 ~~coeval and occur at the present.~~ `datelifeResult` matrices. A table of congruified node

232 ages that can be used as calibrations for a dating analysis is stored as a

233 `congruifiedCalibrations` object.

234   For each congruent node, the pairwise distances that traverse that node are

235 summarized into a single summary matrix using classic summary statistics (i.e., mean,

236 median, minimum and maximum ages), and the Supermatrix Distance Method (SDM;

237 Criscuolo ~~, Berry, Douzery, & Gascuel,~~ et al., 2006), which deforms patristic distance

238 matrices by minimizing variance and then averaging them. These single summary taxon pair

239 age matrices ~~(Summarized calibrations) can be applied as~~ are stored as summarized

240 calibrations that can be used as secondary calibrations to date a tree topology ~~, using~~

241 ~~different~~ with or without initial branch lengths, using phylogenetic dating methods

242 currently supported within DateLife: BLADJ (Webb, Ackerly, & Kembel, 2008; Webb &

243 Donoghue, 2005), MrBayes (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003),

244 PATHd8 (Britton, Anderson, Jacquet, Lundqvist, & Bremer, 2007), ~~BLADJ (Webb, Ackerly,~~

245 ~~& Kembel, 2008; Webb & Donoghue, 2005),~~ and treePL (Smith & O'Meara, 2012).

246   ~~By default, DateLife implements the~~

248   ***Dating a tree with no branch lengths.*** – When producing or obtaining a tree

249 with branch lengths for a group of interest is not possible, DateLife can date a topology

250 without branch lengths, obtained from OpenTree or by implementing the supertree

251 approach described above, by applying the Branch Length Adjuster (BLADJ) ~~algorithm to~~

252 ~~obtain a fully dated topology. BLADJ fixes node ages that have calibration data~~ , and

253 ~~distributes time between~~ ; Webb et al., 2008; Webb & Donoghue, 2005) algorithm, which

254 requires no initial branch lengths. The algorithm starts by fixing ages for nodes with

255 calibration data upon the given topology. Then, it distributes time for nodes with no data

256 evenly between ~~nodes with calibration data. This minimizes~~ calibrated nodes, minimizing

257 age variance in the resulting chronogram. This approach has proven useful for ecological

258 analyses that require a phylogenetic time context (Webb et al., 2008). ~~BLADJ does not use~~

259 ~~branch lengths even when they are present in the input tree or summarizing topology.~~

260 When there is conflict ~~in ages between nodes with calibration data~~ between ages of

261 calibrated nodes, BLADJ ignores node ages that are older than the age of a parent node.

262 ~~BLADJ~~ The BLADJ algorithm requires a root age estimate to run. If there is no

263 information on the age of the root in the chronogram database, users can provide an

264 estimate from the literature. If none is provided, DateLife ~~assigns an arbitrary age to the~~

265 ~~root as 10% older than the oldest age available within the group~~ will not return a dated

266 topology and will provide a warning message along with suggestions on how the user can

267 provide an age for the root so that a fully dated tree can be returned.

268   In the absence of genetic data, BLADJ is a very agnostic way to assign ages to nodes

269 with no available data, as it does not require any assumptions on the underlying model of

270 branch length distribution. It is however common practice in the literature to use a

271 birth-death model to assign ages to nodes with no genetic data (Jetz, Thomas, Joy,

272 Hartmann, & Mooers, 2012; Rabosky et al., 2018; Smith & Brown, 2018). To do so,

DateLife implements MrBayes (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), using nodes with published age data as calibration priors on a fixed topology, a simple birth-death model with parameters that can be determined by the user, and no genetic data.

~~Alternative phylogenetic datingoptions supported in DateLife (MrBayes, PATHD8, TreePL)~~ ***Dating a tree with branch lengths.*** – Relative branch lengths can provide key information for phylogenetic dating, specifically for nodes without any calibration data available. While using initial branch length data is the golden standard for phylogenetic dating analyses, estimating trees with branch lengths proportional to substitution rates per site requires obtaining primary data, assembling and curating a homology hypothesis, and choosing and implementing a method for phylogenetic inference. DateLife implements a workflow to streamline this process by applying open data from the Barcode of Life Data System, BOLD (Ratnasingham & Hebert, 2007) to obtain genetic markers for input taxa. By default, BOLD genetic sequences are aligned with MUSCLE (Edgar, 2004) using functions from the msa R package (Bodenhofer et al., 2015). Alternatively, sequences can be aligned with MAFFT (Katoh, Asimenos, & Toh, 2009), using functions from the ape R package (Paradis et al., 2004). The BOLD sequence alignment is then used to obtain initial branch lengths with the accelerated transformation (ACCTRAN) parsimony algorithm, which resolves ambiguous character optimization by assigning changes along branches of the tree as close to the root as possible (Agnarsson & Miller, 2008), resulting in older internal nodes as compared to other parsimony algorithms (Forest et al., 2005). The parsimony branch lengths are then optimized using Maximum Likelihood, given the alignment, the topology and a simple Jukes-Cantor model, producing a BOLD tree with branch lengths proportional to expected number of substitutions per site. Both parsimony and ML optimizations are done with functions from the `phangorn` package (Schliep, 2011). Due to the computing load it requires, the BOLD workflow is currently only supported through DateLife's R package. It is not yet available through the web application.

Phylogenetic dating methods supported in DateLife that incorporate branch length information from the input topology in combination with the ~~calibrations.~~ secondary calibrations include: PATHd8~~is~~, a non-clock, rate-smoothing method to date trees (Britton et al., 2007)~~to date trees.~~; treePL (Smith & O'Meara, 2012), ~~is~~ a semi-parametric, rate-smoothing, penalized likelihood dating method (Sanderson, 2002)~~. The~~; and MrBayes (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003)~~approach in DateLife uses the calibrations as priors on node ages~~, a Bayesian inference program implementing Markov chain Monte Carlo (MCMC) methods to estimate a posterior distribution of model parameters.

Visualizing Results

Finally, users can save all source and summary chronograms in formats ~~that permit reuse and reanalyses (newick and~~ allowing for reuse and reanalysis, such as newick and the R "phylo" format~~), as well as visualize and compare results graphically, or~~. Input and summary chronograms can be visualized and compared graphically, and users can construct their own graphs using DateLife's chronogram plot generation functions available from the R package `datelifeplot` (Sanchez-Reyes & O'Meara, 2022).

Benchmark

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

325 a very large number of taxon names (Fig. ~~??~~2).

326   `datelife`'s code performance was evaluated with a set of unit tests designed and

327 implemented with the R package testthat (R Core Team, 2018) that were run both locally

328 with the devtools package (R Core Team, 2018), and on a public server using the continuous

329 integration tool of GitHub actions (https://docs.github.com/en/actions). At present, unit

330 tests cover more than 40% of `datelife`'s code (https://codecov.io/gh/phylotastic/datelife).

331 Unit testing helps identify potential issues as code is updated or, more critically, as services

332 code relies upon may change.

Case Studies

334   We illustrate the DateLife workflow using a family within the ~~Passeriform~~ passeriform

335 birds encompassing the true finches, Fringillidae, as case study. On a small example, we

336 analysed 6 bird species, and results from each step of the workflow are shown in ~~Fig. ??.~~

337 Figure 3. As a second example, we analysed 289 bird species in the family Fringillidae that

338 are included in the NCBI taxonomy. The resulting summary chronogram is shown in ~~Fig.~~

339 ~~??~~Figure 4, and results from previous steps of the workflow are available as Supplementary

340 Figures.

A Small Example

342   ***Creating a search query.***– We chose 6 bird species within the Passeriformes. The

343 sample includes two species of cardinals: the black-thighed grosbeak – *Pheucticus tibialis*

344 and the crimson-collared grosbeak – *Rhodothraupis celaeno*; three species of buntings: the

345 yellowhammer – *Emberiza citrinella*, the pine bunting – *Emberiza leucocephalos* and the

346 yellow-throated bunting – *Emberiza elegans*; and one species of tanager, the vegetarian finch –

347 *Platyspiza crassirostris*. Processing of input names found that *Emberiza elegans* is synonym

348 for *Schoeniclus elegans* in the default reference taxonomy (OTT v3.3, June 1, 2021). For a

349 detailed discussion on the state of the synonym, refer to Avibase (Avibase, 2022; Lepage,

350 2004; Lepage, Vaidya, & Guralnick, 2014). Discovering this synonym allowed assigning five

351 age data points for the parent node of *Emberiza elegans*, shown as *Schoeniclus elegans* in

352 ~~figure ??A~~Figure 3A, which would not have had any data otherwise.

353   ***Searching the database.***– DateLife used the processed input names to search the

354 local chronogram database and found 9 matching chronograms ~~in~~ from 6 different studies

355 (Fig. ~~??B~~3B). Three studies matched five input names (Barker, Burns, Klicka, Lanyon, &

356 Lovette, 2015; Hedges, Marin, Suleski, Paymer, & Kumar, 2015; Jetz ~~, Thomas, Joy,~~

357 ~~Hartmann, & Mooers,~~ et al., 2012), one study matched four input names (Hooper & Price,

358 2017) and two studies matched two input names (Barker, Burns, Klicka, Lanyon, & Lovette,

359 2013; Burns et al., 2014). No studies matched all input names. Together, source

360 chronograms provide 28 unique age data points, covering all nodes on our chosen tree

361 topology to date (Table ~~??~~1).

362   ***Summarizing search results.***– DateLife obtained OpenTree's synthetic tree

363 topology for these taxa (Fig. ~~??C~~3C), and congruified and mapped age data to nodes in this

364 chosen topology (Table ~~??~~1). The name processing step allowed including five data points

365 for node "n4" (parent of *Schoeniclus elegans*; Fig. ~~??A~~3A) that would not have had any

366 data otherwise due to name mismatch. Age summary statistics per node were calculated

367 (Table ~~??~~2) and used as calibrations to date the tree topology using the BLADJ algorithm.

368 As expected, more inclusive nodes (e.g., node "n1") have more variance in age data than less

369 inclusive nodes (e.g., node "n5"). Summary age data for node "n2" were excluded as final

370 calibration because they are older than age data of the more inclusive node, "n1" (Fig.

371 ~~??C4~~3C4).

₃₇₂   *An Example with the Family of True Finches*

₃₇₃   ***Creating a query.***– To obtain ages for all species within the family of true finches,

₃₇₄ Fringillidae, we ran a DateLife query using the "get species from taxon" flag, which gets all

₃₇₅ recognized species names within a named group from a taxonomy of choice. Following the

₃₇₆ NCBI taxonomy, our DateLife query has 289 Fringillidae species names. This

₃₇₇ taxon-constrained approach implies that the ~~final results of a~~ full DateLife analysis will be

₃₇₈ ~~done~~ performed using a tree topology and ages ~~for the species in a named~~ available for

₃₇₉ species names from a given taxonomic group, which do not necessarily correspond to a

₃₈₀ monophyletic group. Users can change this ~~behaviour by providing a monophyletic tree~~

₃₈₁ behavior by providing all species names corresponding to a monophyletic group as input for

₃₈₂ a DateLife search, or ~~as a tree topology for~~ a monophyletic tree to construct a DateLife

₃₈₃ summary.

₃₈₄   ***Searching the database.***– Next, we used the processed species names in our

₃₈₅ DateLife query to identify chronograms with at least two Fringillidae species as tip taxa.

₃₈₆ The DateLife search identified ~~13 chronograms containing at least two Fringillidae species~~19

₃₈₇ chronograms matching this criteria, published in ~~9~~13 different studies (Barker et al., 2013,

₃₈₈ 2015; Burns et al., 2014; Claramunt & Cracraft, 2015; Gibb et al., 2015; Hedges et al., 2015;

₃₈₉ Hooper & Price, 2017; Jetz et al., 2012; Kimball et al., 2019; Oliveros et al., 2019; Price et

₃₉₀ al., 2014; Roquet, Lavergne, & Thuiller, 2014; Uyeda, Pennell, Miller, Maia, & McClain,

₃₉₁ 2017). Once identified, DateLife pruned these matching chronograms to ~~keep Fringillidae~~

₃₉₂ ~~species names on tips only~~remove tips that do not belong to the queried taxon names, and

₃₉₃ transformed these pruned chronograms to pairwise distance matrices, revealing 1, 206

₃₉₄ different age data points available for species within the Fringillidae (~~Supplementray~~

₃₉₅ Supplementary Table S1).

₃₉₆   ***Summarizing search results.***– The final step ~~is to congruify and summarize~~

₃₉₇ entailed congruifying and summarizing the age data available for the Fringillidae species

into two single summary chronograms, using two different types of summary ages, median and SDM. As explained in the "Description" section, a tree topology to summarize age data upon is required. By default, DateLife uses the topology from OpenTree's synthetic tree that contains ~~the species in the search query~~ ~~to summarize age data upon~~ all taxa from the search query. According to OpenTree's synthetic tree, species belonging to the family Fringillidae do not form a monophyletic group (Fig. ~~??).~~ 5). Hence, a topology containing only the 289 species from the original query was extracted from Open Tree of Life's synthetic tree v12.3 (Open Tree Of Life et al., 2019).

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

Cross-Validation Test

We performed a cross validation ~~analysis of the DateLife workflow~~ test of a DateLife analysis using the Fringillidae ~~chronograms. We used the~~ source chronograms obtained above (Supplementary Figs. S2-S20). We used as inputs for a DateLife analysis all individual tree topologies from each of the 19 source chronograms from 13 studies~~as inputs~~, treating their node ages as unknown. We ~~then estimated dates for these topologies using~~ ~~the node ages~~ congruified node ages extracted from chronograms from ~~the chronograms~~ ~~from the other studies as calibrations and smoothing using BLADJ~~ all other studies upon the individual topologies, effectively excluding original ages from each topology. Finally, average node ages per node were applied as secondary calibrations and smoothed with the BLADJ algorithm. We found that node ages from ~~original study~~the original studies, and ages estimated using all other age data available are largely correlated (Fig. ~~??~~5). For five studies, ~~Datelife~~ DateLife tended to underestimate ages for topologically deeper nodes (those

with many descendant taxa, aka "closer to the root") relative to the original estimate, and overestimate ages for nodes closer to the tips. Accordingly, root ages are generally older in the original study than estimated using cross-validated ages (Supplementary Fig. S1). In general, topologically deeper nodes display the largest age variation between node ages from the original chronograms and ages summarized with DateLife.

Discussion

DateLifemakes 's goal is to improve availability and accessibility of state-of-the-art data on evolutionary time frame easily accessible for comparison, reuse, and reanalysis, to researchers in of organisms, to allow users from all areas of science and with all levels of expertise in the matter. It is to compare, reuse, and reanalyse expert age data for their own applications. As such, it is designed as an open service that does not require any expert biological knowledge from users besides the scientific names of the species or group they users want to work with, for to use any of its functionalityfunctionalities.

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

As we envision that DateLife will have many interesting applications in research and beyond, we emphasize that DateLife's results –as well as any insights gleaned from them,

largely depend on the quality of the source chronograms: low quality chronograms will produce low quality results. This "garbage in, garbage out" problem has long been recognised in supertree methods for summarizing phylogenetic trees (Bininda-Emonds et al., 2004). We note that this is a surfacing issue of any automated tool for biological data analysis. For example, DNA riddled with sequencing errors will produce generally poor alignments that will return biased evolutionary hypothesis, independently of the quality of the analysis software used. Again, we urge readers and DateLife users to explore all input chronograms before using a summary chronogram resulting from a DateLife workflow. Finally, uncertainty and variability of chronogram node age estimates might pose larger issues in some research areas than others. For example, in ecological and conservation biology studies, it has been shown that incorporating some chronogram data provides better results than when not using any age data at all, even if the node ages are not good quality (Webb et al., 2008). In the following sections we discuss the particularities of divergence times from DateLife's summary chronograms and their impact on certain evolutionary analyses, for consideration of the readers and users in different research areas.

Age Variation in Source Chronograms

Conflict in estimated ages among alternative studies is common in the literature. See, for example, the robust ongoing debate about crown group age of angiosperms (Barba-Montoya, Reis, Schneider, Donoghue, & Yang, 2018; Magallón, Gómez-Acevedo, Sánchez-Reyes, & Hernández-Hernández, 2015; Ramshaw et al., 1972; Sanderson & Doyle, 2001; Sauquet, Ramírez-Barahona, & Magallón, 2021). ~~Source~~ Alternative source chronograms available for the same ~~organisms~~ taxa have potentially been estimated implementing ~~calibrations very differently~~ different types of calibrations, which affects the resulting node age estimates. For example, ~~the chronograms from~~ in the DateLife analysis of the Fringillidae shown above, the chronograms from one study (Burns et al.~~,~~ 2014) were inferred using molecular substitution rate estimates across birds (Weir & Schluter, 2008),

and have much older age estimates for the same nodes than chronograms that were inferred using ~~fossils as~~ fossil calibrations (Figs. **??, ??**4, 5; Supplementary Figs. S1, S5).

~~Different calibrationimplementations might also~~ Another source of conflict in estimated node ages can arise from different placements for the same calibration, which would imply fundamentally distinct evolutionary hypotheses (Antonelli et al., 2017). For example, two independent researchers working on the same clade should both carefully select and justify their choices of fossil calibration placement. Yet, if one researcher concludes that a fossil should calibrate the ingroup of a clade, while another researcher concludes that the same fossil should calibrate the outgroup of the clade, the resulting age estimates will differ, as the placement of calibrations as stem or crown group ~~has been proven~~ is known to significantly affect estimates of time of lineage divergence ~~estimates~~ (Sauquet, 2013). Finally, placement of calibrations also affects uncertainty of node age estimates. For example, nodes that are sandwiched between a calibrated node and a calibrated root have less freedom of movement and hence narrower confidence intervals (Vos & Mooers, 2004), which inflates precision for nodes without calibrations but does not necessarily improve accuracy of the estimated ages.

DateLife's summary chronograms are intended to represent all variation in estimated node ages from source chronograms. Node age distribution ranges allow to visually explore ages from source chronograms individually and contextualize and compare them against other chronograms. Researchers that wish to use summary chronograms in downstream evolutionary analysis may select multiple trees sampled from the summary distribution of node ages, to account for variation in source chronograms.

Primary vs Secondary Calibrations

While most chronograms in DateLife's database are constructed using primary calibrations~~(~~, i.e., molecular substitution rates or ~~ages~~ absolute ages in Myr obtained from

the fossil record or geological events~~), DateLife summarizes~~, DateLife also constructs summary chronograms using secondary calibrations~~(ages coming from other chronograms).Graur and Martin (2004) cautioned on the increased error and uncertainty in estimated ages when using secondary calibrations in dating analyses.Schenk (2016) showed that, in simulations, divergence times inferred using secondary calibrations are significantly younger than those inferred with primary calibrations, when obtained with Bayesian inference methods, and when priors are implemented in similar ways in both analyses. Accordingly, the scientific community seems to have~~, i.e., node ages in Myr extracted from existing chronograms. The scientific community has generally more confidence in chronograms ~~obtained~~ generated from a single analysis, ~~using fossil data as primary sources of calibrations~~ (where carefully chosen primary calibrations constitute the main source of absolute time information used in the dating analysis (Antonelli et al., 2017; Garzón-Orduña, Silva-Brandão, Willmott, Freitas, & Brower, 2015; Graur & Martin, 2004; Sauquet, 2013; Sauquet et al., 2012; Schenk, 2016~~)~~; Shaul & Graur, 2002). However, implementation of primary calibrations does not come without difficulties: it requires high expertise and training to discover, place and apply calibrations appropriately (Hipsley & Müller, ~~and using~~ 2014; Ksepka et al., 2011). One way around it is to use fossils that have been widely discussed and previously curated as calibrations to date other trees ~~,~~ (Ksepka et al., 2011; Sauquet, 2013), and making sure that all data reflect a coherent evolutionary history (Sauquet, 2013), as for example done by Antonelli et al. (2017). ~~There have been attempts to create fossil calibration databases~~ The Fossil Calibration Database provides availability of 220 primary calibration points encompassing flowering plants and metazoans, that have been curated by experts and used for dating analysis in peer-reviewd publications (Ksepka et al., 2015)~~, though these still~~. This database facilitates the use of expert primary fossil calibrations in new phylogenetic dating analyses. Yet, users still require the expertise to locate appropriate nodes in their phylogenies to corresponding fossils available in the database, potentially delaying increased usage of the database in

research. Open databases for effective reuse of fossil calibration data still have room to grow and should constitute a key addition to the phylogenetics tool set.

In some cases, secondary calibrations might represent the only information available for a dating analysis (e.g., groups with a poor fossil record). Recently, Powell, Waskin, and Battistuzzi (2020) showed in a simulation analysis that secondary calibrations are as good as primary calibrations. It seems that using several secondary calibrations (as opposed to just ~~a few) secondary calibrations~~ one) can provide sufficient information to alleviate or even neutralize potential biases ~~(described before~~ (Graur & Martin, 2004; Sauquet, 2013~~).~~ ~~Certainly, further studies are required to~~ ; Shaul & Graur, 2002). Our cross validation analysis also provides some insight into the application of secondary calibrations. In general, node ages summarized with DateLife and those from the original studies appear positively correlated (Supplementary Figs. S2-S20). We also note that nodes closer to the root tend to be slightly younger than ages from the original studies. In contrast, nodes closer to the tips tend to be slightly older when estimated using secondary calibrations than ages from the original studies. The only exception to this trend was observed in Burns et al. (2014) chronogram, which generally displays much younger node ages when estimated using secondary calibrations than the original study (Supplementary Figs. S1, S5), supporting previous observations (Sauquet et al., 2012; Schenk, 2016).

We unite to the call of our colleagues: further research is needed to fully understand the ~~effect of secondary calibrations on outputs from different~~ effects of using secondary calibrations with alternative tree dating methods, ~~and on downstream analyses .~~ as well as usage of resulting chronograms in downstream analyses (Hipsley & Müller, 2014; Powell et al., 2020; Schenk, 2016; Shaul & Graur, 2002). It is possible that secondary calibrations can be ~~safely used~~ used successfully with dating methods that do not require setting priors, such as penalized likelihood (Sanderson, 2003)~~,~~; with methods that do not make any assumptions on the ages and fix them to a node on a tree topology, such as BLADJ (Webb et al., 2008;

553 Webb & Donoghue, 2005)~~, or~~ ; and with methods that summarize age data unto a tree

554 topology~~.~~

555   ~~Our cross validation analysis might provide some insight in this regard. When ages~~

556 ~~are estimated with secondary calibrations, nodes closer to the root do tend to be slightly~~

557 ~~younger than ages estimated with primary calibrations. However, nodes closer to the tip~~

558 ~~tend to be older when estimated using secondary calibrations with a dating method that~~

559 ~~does not make any prior assumptions on the nature of the calibrations themselves~~

560 ~~(Supplementary Figures S2-S20). The only excpetion to tjis was observed on results of the~~

561 ~~cross validation analysis of the Burns et al. (2014) chronogram, which results in much~~

562 ~~younger node ages when estimated using secondary calibrations (Supplementary Figs. S1,~~

563 ~~S5).~~ such as DateLife.

564   *Sumarizing Chronograms*

565   By default, DateLife currently summarizes all source chronograms that overlap with at

566 least two species names. Users can exclude source chronograms if they have reasons to do so.

567 Strictly speaking, a good chronogram should reflect the real time of lineage divergence

568 accurately and precisely. To our knowledge, there are no tested measures to determine

569 independently when a chronogram is better than another. Yet, several characteristics of the

570 data used for dating analyses, as well as from the output chronogram itself, could be used to

571 score the quality of source chronograms.

572   Some measures that have been proposed are the proportion of lineage sampling and the

573 number of calibrations used (Magallón, 2010; Magallón et al., 2015). Some characteristics

574 that are often cited in published studies as a measure of improved age estimates as compared

575 to previously published estimates are: quality of alignment (missing data, GC content),

576 lineage sampling (strategy and proportion), phylogenetic and dating inference method,

577 number of fossils used as calibrations, support for nodes and ages, and magnitude of

578 confidence intervals.

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

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

Effects of Taxon Sampling on Downstream Analyses

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

597 ~~In ecology and conservation biology, incorporating at least some data on lineage~~
598 ~~divergence times represents a relevant improvement for testing alternative hypothesis using~~
599 ~~phylogenetic distance (Webb~~ Analysis of species diversification of simulated and empirical
600 phylogenies suggest that using a more completely sampled phylogeny provides estimates
601 that are closer to the true diversification history than when analysing incompletely
602 sampled phylogenies (Chang, Rabosky, & Alfaro, 2020; Cusimano, Stadler, & Renner, 2012;

Sun et al., 2008). 2020). Ideally, phylogenies should be completed using genetic data, but this is a time-consuming and difficult task to achieve for many biological groups. Hence, DateLife's workflow features different ways of estimating node ages in assigning divergence times to taxa with missing the absence of branch length data and calibrations and branch length information lengths for certain taxa. branch lengths

Completing a phylogeny using a stochastic birth-death polytomy resolver and a backbone taxonomy is a common practice in scientific publications: Jetz et al. (2012), created a chronogram of all 9, 993 bird species, where 67% had molecular data and the rest was simulated; Rabosky et al. (2018) created a chronogram of 31, 536 ray-finned fishes, of which only 37% had molecular data; Smith and Brown (2018) constructed a chronogram of 353, 185 seed plants where only 23% had molecular data. These stochastically resolved chronograms return diversification rates estimates that appear less biased than those estimated from their incompletely sampled counterparts, even with methods that account for missing lineages by using sampling fractions (Chang et al., 2020; Cusimano et al., 2012), but can also introduce spurious patterns of early bursts of diversification (Cusimano & Renner, 2010; Sun et al., 2020).

Notably, Taxonomy-based stochastic polytomy resolvers also introduce topological differences in phylogenetic trees. The study of macroevolutionary processes largely depends on an understanding of the timing of species diversification events, and different phylogenetic and chronogram hypothesis can provide very different overviews of the macroevolutionary history of a biological group. For example, alternative topologies in chronograms from the same biological group can infer very different species diversification patterns (Rabosky, 2015; Title & Rabosky, 2016). Similarly, there are worries that patterns of morphological evolution cannot be accurately inferred with phylogenies that have been resolved stochastically over a taxonomic backbone, as any patterns would be erased by randomization (Rabosky, 2015). We note that the same applies for geography- and

morphology-dependent diversification analysis. Hence, we suggest that phylogenies that have been processed with taxonomy-based stochastic polytomy resolvers, including certain summary chronograms from a DateLife analysis, can be useful as null or neutral models, representing the case of a diversification process that is independent of traits and geographical scenario.

Taxonomy-based stochastic polytomy resolvers have been used to advance research in evolution, still, risks come with this practice. Taken to the extreme, one could ~~make~~ generate a fully resolved, calibrated tree of all modern and extinct taxa using a single taxonomy~~and~~, a single calibration, ~~using polytomy resolution and branch estimation methods. There has yet to be a thorough analysis of what can go wrong when one extends inferences beyond the data in this way, so we urge caution; we also urge readers~~ and assigning branch lengths following a birth-death diversification model. Clearly, this can lead to a misrepresentation of the true evolutionary history. We urge DateLife users to follow the example of the large tree papers cited above, by carefully considering the statistical assumptions being made, potential biases, and assessing the consistency of ~~the~~ DateLife's results with prior work.

Conclusions

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

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

Availability

The DateLife software is free and open source ~~and it~~. It can be used online through its R shiny web application hosted at http://www.datelife.org, and locally through the `datelife` R package, ~~and through Phylotastic's project web portal~~ available from Zenodo (https://doi.org/10.5281/zenodo.593938 and the CRAN repository (Sanchez-Reyes et al., 2022). DateLife's web application is maintained using RStudio's shiny server and the shiny package open infrastructure, as well as Docker and OpenTree's infrastructure (~~dates~~datelife.opentreeoflife.org~~/datelife~~). `datelife`'s ~~R package stable version is available for installation~~ stable version can be installed from the CRAN repository ~~()~~ using the command `install.packages(pkgs = "datelife")` from within R. Development versions are available from ~~the~~ DateLife's GitHub repository (https://github.com/phylotastic/datelife) and can be installed using the command `devtools::install_github("phylotastic/datelife")`.

Supplementary Material

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References

713

714 Agnarsson, I., & Miller, J. A. (2008). Is ACCTRAN better than DELTRAN? *Cladistics*,
715   *24*(6), 1032–1038.

716 Alström, P., Hooper, D. M., Liu, Y., Olsson, U., Mohan, D., Gelang, M., . . . Price, T. D.
717   (2014). Discovery of a relict lineage and monotypic family of passerine birds. *Biology*
718   *Letters*, *10*(3), 20131067.

719 Ané, C., Eulenstein, O., Piaggio-Talice, R., & Sanderson, M. J. (2009). Groves of
720   phylogenetic trees. *Annals of Combinatorics*, *13*(2), 139–167.

721 Antonelli, A., Hettling, H., Condamine, F. L., Vos, K., Nilsson, R. H., Sanderson, M. J., . . .
722   Vos, R. A. (2017). Toward a self-updating platform for estimating rates of speciation
723   and migration, ages, and relationships of Taxa. *Systematic Biology*, *66*(2), 153–166.
724   https://doi.org/10.1093/sysbio/syw066

725 Archie, J., Day, W. H., Felsenstein, J., Maddison, W., Meacham, C., Rohlf, F. J., &
726   Swofford, D. (1986). The Newick tree format. Retrieved from
727   {https://evolution.genetics.washington.edu/phylip/newicktree.html}

728 Avibase. (2022). Yellow-throated Bunting. *Avibase - the World Bird Database*, (Online
729   Resource). Retrieved from
730   {https://avibase.bsc-eoc.org/species.jsp?lang=EN&avibaseid=82D1EE0049D8D927}

731 Bapst, D. W. (2012). Paleotree: An R package for paleontological and phylogenetic analyses
732   of evolution. *Methods in Ecology and Evolution*, *3*(5), 803–807.
733   https://doi.org/10.1111/j.2041-210X.2012.00223.x

734 Barba-Montoya, J., Reis, M. dos, Schneider, H., Donoghue, P. C., & Yang, Z. (2018).
735   Constraining uncertainty in the timescale of angiosperm evolution and the veracity of

736   a cretaceous terrestrial revolution. *New Phytologist, 218*(2), 819–834.

737   Barker, F. K. (2014). Mitogenomic data resolve basal relationships among passeriform and

738   passeridan birds. *Molecular Phylogenetics and Evolution, 79*, 313–324.

739   Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2013). Going to

740   extremes: Contrasting rates of diversification in a recent radiation of new world

741   passerine birds. *Systematic Biology, 62*(2), 298–320.

742   Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2015). New insights

743   into new world biogeography: An integrated view from the phylogeny of blackbirds,

744   cardinals, sparrows, tanagers, warblers, and allies. *The Auk: Ornithological Advances*,

745   *132*(2), 333–348.

746   Barker, F. K., Cibois, A., Schikler, P., Feinstein, J., & Cracraft, J. (2004). Phylogeny and

747   diversification of the largest avian radiation. *Proceedings of the National Academy of*

748   *Sciences, 101*(30), 11040–11045.

749   Beresford, P., Barker, F., Ryan, P., & Crowe, T. (2005). African endemics span the tree of

750   songbirds (passeri): Molecular systematics of several evolutionary "enigmas".

751   *Proceedings of the Royal Society B: Biological Sciences, 272*(1565), 849–858.

752   Bininda-Emonds, O. R., Jones, K. E., Price, S. A., Cardillo, M., Grenyer, R., & Purvis, A.

753   (2004). Garbage in, garbage out: Data issues in supertree construction. *Phylogenetic*

754   *Supertrees: Combining Information to Reveal the Tree of Life*, 267–280.

755   Bodenhofer, U., Bonatesta, E., Horejš-Kainrath, C., & Hochreiter, S. (2015). Msa: An r

756   package for multiple sequence alignment. *Bioinformatics, 31*(24), 3997–3999.

757   Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J. A., Mozzherin, D., Rees, T., . . . Enquist,

758   B. J. (2013). The taxonomic name resolution service: An online tool for automated

standardization of plant names. *BMC Bioinformatics*, *14*(1).

https://doi.org/10.1186/1471-2105-14-16

Britton, T., Anderson, C. L., Jacquet, D., Lundqvist, S., & Bremer, K. (2007). Estimating

Divergence Times in Large Phylogenetic Trees. *Systematic Biology*, *56*(788777878),

741–752. https://doi.org/10.1080/10635150701613783

Bryson Jr, R. W., Chaves, J., Smith, B. T., Miller, M. J., Winker, K., Pérez-Emán, J. L., &

Klicka, J. (2014). Diversification across the new world within the 'blue'cardinalids

(aves: Cardinalidae). *Journal of Biogeography*, *41*(3), 587–599.

Burleigh, J. G., Kimball, R. T., & Braun, E. L. (2015). Building the avian tree of life using a

large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution*, *84*, 53–63.

Burns, K. J., Shultz, A. J., Title, P. O., Mason, N. A., Barker, F. K., Klicka, J., . . . Lovette,

I. J. (2014). Phylogenetics and diversification of tanagers (passeriformes:

Thraupidae), the largest radiation of neotropical songbirds. *Molecular Phylogenetics

and Evolution*, *75*, 41–77.

Chamberlain, S. (2018). *bold: Interface to Bold Systems API*. Retrieved from

https://CRAN.R-project.org/package=bold

Chamberlain, S. A., & Szöcs, E. (2013). taxize : taxonomic search and retrieval in R [version

2; referees: 3 approved]. *F1000Research*, *2*(191), 1–29.

https://doi.org/10.12688/f1000research.2-191.v2

Chang, J., Rabosky, D. L., & Alfaro, M. E. (2020). Estimating diversification rates on

incompletely sampled phylogenies: Theoretical concerns and practical solutions.

Systematic Biology, *69*(3), 602–611.

Chaves, J. A., Hidalgo, J. R., & Klicka, J. (2013). Biogeography and evolutionary history of

the n eotropical genus s altator (a ves: T hraupini). *Journal of Biogeography*, *40*(11), 2180–2190.

Claramunt, S., & Cracraft, J. (2015). A new time tree reveals earth history's imprint on the evolution of modern birds. *Science Advances*, *1*(11), e1501005.

Criscuolo, A., Berry, V., Douzery, E. J., & Gascuel, O. (2006). SDM: A fast distance-based approach for (super)tree building in phylogenomics. *Systematic Biology*, *55*(5), 740–755. https://doi.org/10.1080/10635150600969872

Cusimano, N., & Renner, S. S. (2010). Slowdowns in diversification rates from real phylogenies may not be real. *Systematic Biology*, *59*(4), 458–464.

Cusimano, N., Stadler, T., & Renner, S. S. (2012). A new method for handling missing species in diversification analysis applicable to randomly or nonrandomly sampled phylogenies. *Systematic Biology*, *61*(5), 785–792.

Delsuc, F., Philippe, H., Tsagkogeorga, G., Simion, P., Tilak, M.-K., Turon, X., . . . Douzery, E. J. (2018). A phylogenomic framework and timescale for comparative studies of tunicates. *BMC Biology*, *16*(1), 1–14.

Eastman, J. M., Harmon, L. J., & Tank, D. C. (2013). Congruification: Support for time scaling large phylogenetic trees. *Methods in Ecology and Evolution*, *4*(7), 688–691. https://doi.org/10.1111/2041-210X.12051

Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, *32*(5), 1792–1797.

Felsenstein, J. (1985). Phylogenies and the Comparative Method. *The American Naturalist*, *125*(1), 1–15. Retrieved from http://www.jstor.org/stable/2461605

Forest, F., Savolainen, V., Chase, M. W., Lupia, R., Bruneau, A., & Crane, P. R. (2005).

805   Teasing apart molecular-versus fossil-based error estimates when dating

806   phylogenetic trees: A case study in the birch family (betulaceae). *Systematic*

807   *Botany*, *30*(1), 118–133.

808   Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and

809   comparative data: A test and review of evidence. *The American Naturalist.*

810   Garzón-Orduña, I. J., Silva-Brandão, K. L., Willmott, K. R., Freitas, A. V., & Brower, A.

811   V. (2015). Incompatible ages for clearwing butterflies based on alternative

812   secondary calibrations. *Systematic Biology*, *64*(5), 752–767.

813   GBIF Secretariat. (2022). GBIF Backbone Taxonomy. *Checklist dataset*, (Online Resource

814   accessed via GBIF.org). Retrieved from {https://doi.org/10.15468/39omei }

815   Gibb, G. C., England, R., Hartig, G., McLenachan, P. A., Taylor Smith, B. L., McComish,

816   B. J., . . . Penny, D. (2015). New zealand passerines help clarify the diversification of

817   major songbird lineages during the oligocene. *Genome Biology and Evolution*, *7*(11),

818   2983–2995.

819   Graur, D., & Martin, W. (2004). Reading the entrails of chickens: Molecular timescales of

820   evolution and the illusion of precision. *TRENDS in Genetics*, *20*(2), 80–86.

821   Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C., Braun, E. L., Braun, M. J., . . .

822   others. (2008). A phylogenomic study of birds reveals their evolutionary history.

823   *Science*, *320*(5884), 1763–1768.

824   Harvey, P. H., Pagel, M. D., & others. (1991). *The comparative method in evolutionary*

825   *biology* (Vol. 239). Oxford university press Oxford.

826   Hedges, S. B., Marin, J., Suleski, M., Paymer, M., & Kumar, S. (2015). Tree of life reveals

827   clock-like speciation and diversification. *Molecular Biology and Evolution*, *32*(4),

835–845. https://doi.org/10.1093/molbev/msv037

Heibl, C. (2008). *PHYLOCH: R language tree plotting tools and interfaces to diverse phylogenetic software packages.* Retrieved from http://www.christophheibl.de/Rpackages.html

Hipsley, C. A., & Müller, J. (2014). Beyond fossil calibrations: Realities of molecular clock practices in evolutionary biology. *Frontiers in Genetics, 5,* 138.

Hooper, D. M., & Price, T. D. (2017). Chromosomal inversion differences correlate with range overlap in passerine birds. *Nature Ecology & Evolution*, *1*(10), 1526.

Huelsenbeck, J. P., & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, *17*(8), 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Jetz, W., Thomas, G., Joy, J. J., Hartmann, K., & Mooers, A. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448. https://doi.org/10.1038/nature11631

Johansson, U. S., Fjeldså, J., & Bowie, R. C. (2008). Phylogenetic relationships within passerida (aves: Passeriformes): A review and a new molecular phylogeny based on three nuclear intron markers. *Molecular Phylogenetics and Evolution*, *48*(3), 858–876.

Katoh, K., Asimenos, G., & Toh, H. (2009). Multiple alignment of dna sequences with mafft. In *Bioinformatics for dna sequence analysis* (pp. 39–64). Springer.

Kimball, R. T., Oliveros, C. H., Wang, N., White, N. D., Barker, F. K., Field, D. J., . . . others. (2019). A phylogenomic supertree of birds. *Diversity*, *11*(7), 109.

Klicka, J., Barker, F. K., Burns, K. J., Lanyon, S. M., Lovette, I. J., Chaves, J. A., & Bryson Jr, R. W. (2014). A comprehensive multilocus assessment of sparrow (aves:

Passerellidae) relationships. *Molecular Phylogenetics and Evolution*, *77*, 177–182.

Ksepka, D. T., Benton, M. J., Carrano, M. T., Gandolfo, M. A., Head, J. J., Hermsen, E. J., . . . others. (2011). *Synthesizing and databasing fossil calibrations: Divergence dating and beyond.* The Royal Society.

Ksepka, D. T., Parham, J. F., Allman, J. F., Benton, M. J., Carrano, M. T., Cranston, K. A., . . . others. (2015). The fossil calibration database—a new resource for divergence dating. *Systematic Biology*, *64*(5), 853–859.

Lamichhaney, S., Berglund, J., Almén, M. S., Maqbool, K., Grabherr, M., Martinez-Barrio, A., . . . others. (2015). Evolution of darwin's finches and their beaks revealed by genome sequencing. *Nature*, *518*(7539), 371–375.

Laubichler, M. D., & Maienschein, J. (2009). *Form and function in developmental evolution.* Cambridge University Press.

Lepage, D. (2004). *Avibase: The world bird database.* Bird Studies Canada.

Lepage, D., Vaidya, G., & Guralnick, R. (2014). Avibase–a database system for managing and organizing taxonomic concepts. *ZooKeys*, (420), 117.

Lerner, H. R., Meyer, M., James, H. F., Hofreiter, M., & Fleischer, R. C. (2011). Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of hawaiian honeycreepers. *Current Biology*, *21*(21), 1838–1844.

Lovette, I. J., Pérez-Emán, J. L., Sullivan, J. P., Banks, R. C., Fiorentino, I., Córdoba-Córdoba, S., . . . others. (2010). A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the parulidae (aves). *Molecular Phylogenetics and Evolution*, *57*(2), 753–770.

Magallon, S., & Sanderson, M. (2001). Absolute diversification rates in angiosperm clades.

874 *Evolution*, *55*(9), 1762–1780.

875 Magallón, S. (2010). Using fossils to break long branches in molecular dating: A comparison

876   of relaxed clocks applied to the origin of angiosperms. *Systematic Biology*, *59*(4),

877   384–399.

878 Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L., & Hernández-Hernández, T. (2015).

879   A metacalibrated time-tree documents the early rise of flowering plant phylogenetic

880   diversity. *New Phytologist*, *207*(2), 437–453.

881 McTavish, E. J., Hinchliff, C. E., Allman, J. F., Brown, J. W., Cranston, K. A., Holder, M.

882   T., . . . Smith, S. (2015). Phylesystem: A git-based data store for community-curated

883   phylogenetic estimates. *Bioinformatics*, *31*(17), 2794–2800.

884 Michonneau, F., Brown, J. W., & Winter, D. J. (2016). rotl: an R package to interact with

885   the Open Tree of Life data. *Methods in Ecology and Evolution*, *7*(12), 1476–1481.

886   https://doi.org/10.1111/2041-210X.12593

887 Morlon, H. (2014). Phylogenetic approaches for studying diversification. *Ecology Letters*,

888   *17*(4), 508–525. https://doi.org/10.1111/ele.12251

889 Moyle, R. G., Oliveros, C. H., Andersen, M. J., Hosner, P. A., Benz, B. W., Manthey, J. D.,

890   . . . Faircloth, B. C. (2016). Tectonic collision and uplift of wallacea triggered the

891   global songbird radiation. *Nature Communications*, *7*(1), 1–7.

892 Oliveros, C. H., Field, D. J., Ksepka, D. T., Barker, F. K., Aleixo, A., Andersen, M. J., . . .

893   others. (2019). Earth history and the passerine superradiation. *Proceedings of the*

894   *National Academy of Sciences*, *116*(16), 7916–7925.

895 Ooms, J., & Chamberlain, S. (2018). *Phylocomr: Interface to 'phylocom'*. Retrieved from

896   https://CRAN.R-project.org/package=phylocomr

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

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

Ödeen, A., Håstad, O., & Alström, P. (2011). Evolution of ultraviolet vision in the largest avian radiation-the passerines. *BMC Evolutionary Biology*, *11*(1), 1–8.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*(2), 289–290.

Parchman, T. L., Benkman, C. W., & Mezquida, E. T. (2007). Coevolution between hispaniolan crossbills and pine: Does more time allow for greater phenotypic escalation at lower latitude? *Evolution*, *61*(9), 2142–2153.

Päckert, M., Martens, J., Sun, Y.-H., Severinghaus, L. L., Nazarenko, A. A., Ting, J., . . . Tietze, D. T. (2012). Horizontal and elevational phylogeographic patterns of himalayan and southeast asian forest passerines (aves: Passeriformes). *Journal of Biogeography*, *39*(3), 556–573.

Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G., . . . Harmon, L. J. (2014). Geiger v2. 0: An expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics*, *30*(15), 2216–2218.

Posadas, P., Crisci, J. V., & Katinas, L. (2006). Historical biogeography: A review of its basic concepts and critical issues. *Journal of Arid Environments*, *66*(3), 389–403.

Powell, A. F., Barker, F. K., Lanyon, S. M., Burns, K. J., Klicka, J., & Lovette, I. J. (2014). A comprehensive species-level molecular phylogeny of the new world blackbirds (icteridae). *Molecular Phylogenetics and Evolution*, *71*, 94–112.

Powell, C. L. E., Waskin, S., & Battistuzzi, F. U. (2020). Quantifying the error of secondary vs. Distant primary calibrations in a simulated environment. *Frontiers in Genetics, 11*, 252.

Price, T. D., Hooper, D. M., Buchanan, C. D., Johansson, U. S., Tietze, D. T., Alström, P., . . . others. (2014). Niche filling slows the diversification of himalayan songbirds. *Nature*, *509*(7499), 222.

Pulgarín-R, P. C., Smith, B. T., Bryson Jr, R. W., Spellman, G. M., & Klicka, J. (2013). Multilocus phylogeny and biogeography of the new world pheucticus grosbeaks (aves: Cardinalidae). *Molecular Phylogenetics and Evolution*, *69*(3), 1222–1227.

Rabosky, D. L. (2015). No substitute for real data: A cautionary note on the use of phylogenies from birth–death polytomy resolvers for downstream comparative analyses. *Evolution, 69*(12), 3207–3216.

Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., . . . others. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, *559*(7714), 392.

Ramshaw, J., Richardson, D., Meatyard, B., Brown, R., Richardson, M., Thompson, E., & Boulter, D. (1972). The time of origin of the flowering plants determined by using amino acid sequence data of cytochrome c. *New Phytologist*, *71*(5), 773–779.

Ratnasingham, S., & Hebert, P. D. (2007). BOLD: The barcode of life data system (http://www. Barcodinglife. Org). *Molecular Ecology Notes*, *7*(3), 355–364.

R Core Team. (2018). *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Rees, & Cranston, K. (2017). Automated assembly of a reference taxonomy for phylogenetic data synthesis. *Biodiversity Data Journal*, (5).

Rees, Vandepitte, L., Decock, W., & Vanhoorne, B. (2017). IRMNG 2006–2016: 10 Years of a Global Taxonomic Database. *Biodiversity Informatics*, *12*.

Revell, L. J. (2012). Phytools: An r package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223.

Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*(12), 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Roquet, C., Lavergne, S., & Thuiller, W. (2014). One tree to link them all: A phylogenetic dataset for the european tetrapoda. *PLoS Currents, 6.*

Sanchez-Reyes, L. L., & O'Meara, B. (2022). `datelifeplot`: Methods to plot chronograms and outputs of the `datelife` package. *R Package Release V0.2.2.* Retrieved from https://zenodo.org/badge/latestdoi/381501451

Sanchez-Reyes, L. L., O'Meara, B., Eastman, J., Heath, T., Wright, A., Schliep, K., . . . Alfaro, M. (2022). `datelife`: Scientific Data on Time of Lineage Divergence for Your Taxa. In *R package version 0.6.6.* Retrieved from https://CRAN.R-project.org/package=datelife and https://doi.org/10.5281/zenodo.593938

Sanderson, M. (2002). Estimating Absolute Rates of Molecular Evolution and Divergence Times: A Penalized Likelihood Approach. *Molecular Biology and Evolution*, *19*(1),

101–109. https://doi.org/10.1093/oxfordjournals.molbev.a003974

Sanderson, M. (2003). r8s: Inferring Absolute Rates of Molecular Evolution and Divergence Times in the Absence of a Molecular Clock. *Bioinformatics*, *19*(2), 301–302.

Sanderson, M., & Doyle, J. (2001). Sources of error and confidence intervals in estimating the age of angiosperms from rbcL and 18S rDNA data. *American Journal of Botany*, *88*(8), 1499–1516.

Sauquet, H. (2013). A practical guide to molecular dating. *Comptes Rendus Palevol*, *12*(6), 355–367.

Sauquet, H., Ho, S. Y. W., Gandolfo, M. a, Jordan, G. J., Wilf, P., Cantrill, D. J., . . . Udovicic, F. (2012). Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of Nothofagus (Fagales). *Systematic Biology*, *61*(2), 289–313. https://doi.org/10.1093/sysbio/syr116

Sauquet, H., Ramírez-Barahona, S., & Magallón, S. (2021). *The age of flowering plants is unknown.*

Schenk, J. J. (2016). Consequences of secondary calibrations on divergence time estimates. *PLoS ONE*, *11*(1). https://doi.org/10.1371/journal.pone.0148228

Schliep, K. P. (2011). Phangorn: Phylogenetic analysis in r. *Bioinformatics*, *27*(4), 592–593.

Schoch, C. L., Ciufo, S., Domrachev, M., Hotton, C. L., Kannan, S., Khovanskaya, R., . . . others. (2020). NCBI Taxonomy: a Comprehensive Update on Curation, Resources and Tools. *Database*, *2020*.

Selvatti, A. P., Gonzaga, L. P., & Moraes Russo, C. A. de. (2015). A paleogene origin for crown passerines and the diversification of the oscines in the new world. *Molecular Phylogenetics and Evolution*, *88*, 1–15.

Shaul, S., & Graur, D. (2002). Playing chicken (gallus gallus): Methodological inconsistencies of molecular divergence date estimates due to secondary calibration points. *Gene*, *300*(1-2), 59–61.

Smith, S., & Brown, J. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, *105*(3), 302–314.

Smith, S., & O'Meara, B. (2012). TreePL: Divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics*, *28*(20), 2689–2690. https://doi.org/10.1093/bioinformatics/bts492

Stoltzfus, A., Lapp, H., Matasci, N., Deus, H., Sidlauskas, B., Zmasek, C. M., . . . Jordan, G. (2013). Phylotastic! Making tree-of-life knowledge accessible, reusable and convenient. *BMC Bioinformatics*, *14*. https://doi.org/10.1186/1471-2105-14-158

Sun, M., Folk, R. A., Gitzendanner, M. A., Soltis, P. S., Chen, Z., Soltis, D. E., & Guralnick, R. P. (2020). Estimating rates and patterns of diversification with incomplete sampling: A case study in the rosids. *American Journal of Botany*, *107*(6), 895–909.

Tietze, D. T., Päckert, M., Martens, J., Lehmann, H., & Sun, Y.-H. (2013). Complete phylogeny and historical biogeography of true rosefinches (aves: Carpodacus). *Zoological Journal of the Linnean Society*, *169*(1), 215–234.

Title, P. O., & Rabosky, D. L. (2016). Do Macrophylogenies Yield Stable Macroevolutionary Inferences? An Example from Squamate Reptiles. *Systematic Biology*, syw102. https://doi.org/10.1093/sysbio/syw102

Treplin, S., Siegert, R., Bleidorn, C., Thompson, H. S., Fotso, R., & Tiedemann, R. (2008). Molecular phylogeny of songbirds (aves: Passeriformes) and the relative utility of common nuclear marker loci. *Cladistics*, *24*(3), 328–349.

Uyeda, J. C., Pennell, M. W., Miller, E. T., Maia, R., & McClain, C. R. (2017). The evolution of energetic scaling across the vertebrate tree of life. *The American Naturalist, 190*(2), 185–199.

Vos, R. A., Balhoff, J. P., Caravas, J. A., Holder, M. T., Lapp, H., Maddison, W. P., . . . others. (2012). NeXML: Rich, extensible, and verifiable representation of comparative data and metadata. *Systematic Biology, 61*(4), 675–689. https://doi.org/10.1093/sysbio/sys025

Vos, R. A., & Mooers, A. Ø. (2004). Reconstructing divergence times for supertrees: A molecular approach. *Phylogenetic Supertrees: Combining Information to Reveal the Tree of Life*, 281–299.

Webb, C. (2000). Exploring the Phylogenetic Structure of Ecological Communities : An Example for Rain Forest Trees. *The American Naturalist, 156*(2), 145–155.

Webb, C., Ackerly, D., & Kembel, S. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics, 24*(18), 2098–2100. https://doi.org/10.1093/bioinformatics/btn358

Webb, C., & Donoghue, M. (2005). Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes, 5*(1), 181–183.

Weir, J., & Schluter, D. (2008). Calibrating the avian molecular clock. *Molecular Ecology, 17*(10), 2321–2328.

Zuccon, D., Prŷs-Jones, R., Rasmussen, P. C., & Ericson, P. G. (2012). The phylogenetic relationships and generic limits of finches (fringillidae). *Molecular Phylogenetics and Evolution, 62*(2), 581–596.