Running head: DATELIFE: REVEALING THE DATED TREE OF LIFE

Title: DateLife: Leveraging databases and analytical tools to reveal the dated Tree of Life

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abstract.- Here goes the abstract.

Keywords: Tree; Phylogeny; Scaling; Dating; Ages; Divergence times; Open Science; Congruification; Supertree; Calibrations

Time of lineage divergence constitutes a fundamental piece of information for evolutionary understanding in many areas of research, from developmental to conservation biology (Felsenstein 1985; Webb 2000), from historical biogeography to species diversification studies (Posadas et al. 2006; Morlon 2014). The primary information needed for time of lineage divergence estimation comes from the fossil record. Coupled to molecular phylogenies, molecular dating methods are used to reconstruct the time of divergence of extant lineages.

Probably encouraged by the great developments in DNA sequencing techniques, phylogenetic inference and molecular dating methods, the number of studies publishing phylogenies with branch lengths proportional to geologic time (hereafter chronograms) have constantly increased in number for the last two decades (Kumar et al. 2017). Still, generating a chronogram is not easy unless you have specialized training. That's why there has been an urge for reuse of the vast amount and still accuulating already available information for the advantage of researchers not specialized in this area.

Wide interest from the scientific community to make chronogram information available for consultation and reuse has spurred the creation of public platforms with various goals. TreeBASE (Morell 1996; Piel et al. 2002), Phylomatic (Webb and Donoghue 2005), the Dryad repository (http://datadryad.org/), and the Open Tree of Life (OToL; Hinchliff et al. 2015) platforms are dedicated to storing and making available published trees and chronograms for easy scientific reuse. For chronogram reuse for a wide range of living organisms, only OToL is generally suitable right now. Treebase does not store branch length information and dryad does not distinguish between data sets, so the time of lineage div information cannot be accessed. Phylomatic does contain chronograms but is restricted to plants and mammals, and if it tries to add more data it gives many polytomies back.

OToL also has the primary goal of synthesizing stored trees into a single tree of life, to show phylogenetic relationships among known extant species and subspecies. All or parts of OToL's synthetic tree can be reused for any purpose; however, it currently does not include information on time of divergence, so the platform does not summarize source chronogram data. The Timetree of Life platform main goal is the synthesis of a single chronogram of life (Hedges et al. 2006). However, both the latest version of their synthetic chronogram

(Kumar et al. 2017) and the thousands of chronograms compiled for synthesis are only publicly available for visual examination in their website or for download as images, but not for scientific reuse or reanalysis.

Other platforms such as SuperSmart (Antonelli et al. 2017) and phylogenerator (Pearse and Purvis 2013) are focused in *de novo* chronogram inference, by reusing DNA sequence data to reconstruct phylogenetic trees. However, expert fossil information necessary for subsequent molecular dating analyses still needs to be compiled and curated by the user, rendering them a challenging tool to obtain data on time of lineage divergence for the non-specialist. Moreover, they do not provide information from available chronograms.

A platform for efficient reuse of expert, published data on time of lineage divergence should have an open source database in a format suitable for scientific reuse, and straightforward means of accessing, comparing and summarizing the source data as needed by the user. A prototype service striving for this characteristics was initially developed over a series of hackathons at the National Evolutionary Synthesis Center (Stoltzfus et al. 2013). In here we present the first formal description of the `datelife` service. Constituted by and R package and web site, it features new methods to summarize chronograms, an improved system for chronogram database maintenance, new functions to visualize source data in the web interface (http://www.datelife.org/query/), as well as tools for comparison of source and summary trees. R packages for benchmarking of functionalities and exemplifying services were also developped.

Description

The basic `datelife` workflow is shown in figure 1 and consists of:

1) A user providing at least two taxon names as input, either as tip labels on a tree, or as a simple comma separated character string. The tree can be in newick or phylo format, and can be with or without branch lengths.
2) `datelife` then performs a search across its database of peer reviewed and curated chronograms; identifies and gets source trees with at least two matching input names; drops unmatching taxa from positively identified source trees; and finally transforms each source tree to a patristic matrix named by the citation of the original study. This format facilitates and greatly speeds up all further analyses and

summarization algorithms.

3) The user can obtain different types of summaries from the source data including: a) all source chronograms, b) mrca ages of source chronograms, c) citations of studies where source chronograms were originally published, d) a summary table with all of the above, e) a single summary tree of all source chronograms, and f) a report of succesful matches per input taxon name across source chronograms.
4) At this point, users can choose to use all or some source data as calibration points to date a tree of their own making or choosing.
5) Users can also simulate age and/or phylogenetic data of input taxa not found in the database. A variety of algorithms are available for this purpose.
6) Finally, users can easily view results graphically as well as construct their own graphs using inbuilt `datelife` graphic generators.

`datelife`'s chronogram database is currently built from OToL's tree repository. Among currently existing repositories (i.e., TreeBASE, Dryad), OToL's metadata rich tree store is the only one meeting the requirements for automatized handling of source trees. TreeBASE trees are stored without branch lengths. Dryad metadata does not allow differentiating between different types of data sets, and trees would need to be manually curated anyways. `datelife` currently accepts scientific names, from named clades to binomial specifics. Taxon searches are performed at the species level, so when input names correspond to named clades, `datelife` pulls all accepted species names within the clade from OToL's reference taxonomy to perform the search. Currently, searches at the infraspecies level are not allowed, so input names belonging to subspecies or any other infraspecific category are collapsed to the species level. `datelife` also processes input names with the taxon name resolution service (TNRS; Boyle et al. 2013), which corrects potentially misspelled names and typos, and standardizes spelling variations and synonyms , increasing the probability to correctly find the queried taxa in `datelife`'s chronogram database.

Source chronogram summary tree can be assembled using the Super Distance Matrix (SDM) supertree construction approach (Criscuolo et al. 2006) or using the median of branch lengths . Tree dating and simulation options are performed with various algorithms: Branch Length Adjuster (BLADJ) is a simple

algorithm to distribute ages of undated nodes evenly, which minimizes age variance in the chronogram (Webb et al. 2008). PATHd8 is a non-clock, rate-smoothing method (Britton et al. 2007) to date trees. treePL, is a semi-parametric, rate-smoothing, penalized likelihood dating method (Smith and O'Meara 2012). MrBayes (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) can be used when adding taxa at random, following a reference taxonomy or a topological constraint. It draws ages from a pure birth model, as implemented by Jetz and collaborators (2012). To apply calibrations to a tree, the congruification algorithm described by Eastman et al. (2013) is implemented to find shared nodes between trees (congruent nodes).

To gather, process, and present information, `datelife` builds up from functions available in several R packages including rotl (Michonneau et al. 2016), ape (Paradis et al. 2004), geiger (Harmon et al. 2008), paleotree (Bapst 2012), bold (Chamberlain 2018), phytools (Revell 2012), taxize (Chamberlain and Szöcs 2013; Chamberlain 2018), phyloch (Heibl 2008), phylocomr (Ooms and Chamberlain 2018) and rphylotastic (O'Meara et al. 2019).

Benchmark

`datelife`'s code speed was tested on an Apple iMac with one 3.4 GHz Intel Core i5 processor. We registered variation in computing time of query processing and search through the database relative to number of queried taxon names. Query processing increases roughly linearly with number of input taxon names, and increases considerably if TNRS service is activated. Up to ten thousand names can be processed and searched in less than 30 minutes. A name search through the chronogram database with an already processed query can be performed in less than a minute, even with a very large number of taxon names (Fig. 2). `datelife`'s code performance was evaluated with a set of unit tests designed and implemented with the R package testthat (R Core Team 2018) that were run locally –using the devtools package (R Core Team 2018), and on a public server –via GitHub, using the continuous integration tool Travis CI (https://travis-ci.org). At present, unit tests cover more than 50% of `datelife`'s code (https://codecov.io/gh/phylotastic/datelife).

Example

In this section we demonstrate the types of outputs that can be obtained with `datelife`, using as an example

the bird family Fringillidae of true finches. We performed a higher-taxon search to obtain all data on lineage divergence available in `datelife`'s database for all recognised species within the Fringillidae (475 spp. according to the Open Tree of Life taxonomy). There are 13 chronograms containing at least two Fringillidae species, published in 9 different studies (Fig. 3). Data from these source chronograms was used to generate two types of summary chronograms, median and SDM. As explained in the `Description`, data from source chronograms was first summarised into a single distance matrix (using either the median or the SDM method) and then the available node ages were used as calibrations points over a consensus tree topology, to obtain a dated tree with the program BLADJ (Fig. 4). Median summary chronograms are older and have wider variation in maximum ages than chronograms obtained with SDM. In both cases, ages are coherent with source ages. It is not certain if these chronograms can be used to perform downstream evolutionary analyses. There is currently wide interest in determining this. However, we know that these chronograms are useful for...

Data from source chronograms was also used to date tree topologies with no branch length information and trees with branch lengths in relative substitution rates (Figs. 5 and 6). As a form of cross validation, we used tree topologies from each study and calibrated them using information from all other source chronograms. In the absence of branch length data, the ages of internal nodes were approximately recovered in almost all cases (except for studies 3, and 5; Fig. 5). Maximum tree ages were only approximately recovered in one case (study 2; Fig. 5). Branch lengths were successfully generated using the BOLD database for all source chronograms. However, dating with PATHd8 (using congruified calibrations) was only successful in three cases (studies 3, 5, and 9; Fig. 6). From these, two trees have a different sampling than the original source chronogram, mainly because DNA data for some species is absent from the BOLD. Maximum ages are quite different from source chronograms, but this might be explained also by the differences in sampling between source chronograms and BOLD trees. More examples and details can be consulted in https://github.com/LunaSare/datelife_examples.

Conclusions

Taxon ages are key to many areas of evolutionary studies: trait evolution, species diversification, biogeography,

macroecology and more. Obtaining these ages is difficult, especially for those who want to use phylogenies but who are not systematists, or do not have the time to develop the necessary knowledge and data curation skills to produce new chronograms. Knowledge on taxon ages is also important for non-biological studies and the non-academic community. The combination of new analytical techniques, availability of more fossil and molecular data, and better practices in data sharing has resulted in a steady accumulation of chronograms in public and open databases such as Dryad, TreeBASE or Open Tree of Life, for a large quantity and diversity of organisms. However, this information remains difficult to synthesize for many biologists and the non-academic community.

Here, we have shown that `datelife` allows an easy and fast obtention of all publicly available information on taxon ages, which can be used to generate new data. This information can be used to account for the effect of phylogenetic signal in studies of trait evolution; to explore potential speciation and extinction dynamics of interest within a clade; to obtain a time frame of biogeographical events; for science communication and outreach, amongst others. Compared to similar platforms such as time tree of life and supermart, it offers several advantages. It is fast; source data is completely open; it requires no expert biological knowledge from users for any of its functionalities; it allows exploration of alternative taxonomic and phylogenetic schemes; it allows rapid exploration of the effect of alternative divergence time hypothesis; it allows rapid synthesis in a number of different formats; it facilitates reproducibility of analyses;

Improvements, short and long-term: * fossils as calibrations: Using secondary calibrations can generate biased ages when using bayesian methods, mainly because we don't know what prior to give to secondary calibrations (Schenk 2016). * bayesian congruification * topological congruification

Problems and caveats: Not many databases, only OToL Why TreeBase is not very useful for us? Be precise. Are these chronograms reliable to study evolutionary patterns, such as species diversification? `datelife` can be seen as an open resource to know the current state of knowledge on lineage divergence times. Whether chronograms obtained using this original data can be used reliably to study complicated patterns of evolution is still uncertain. If all, la facilidad para obtener hipotesis de tiempo de divergencia nos ayudará a evaluar la capacidad de los cronogramas para estudiar otros fenomenos evolutivos. Por ahora, no podemos aseverar que

estos cronogramas puedan usarse para todo tipo de analisis.

Availability

`datelife` is free and open source and it can be used through its current website http://www.datelife.org/query/, through its R package, and through Phylotastic's project web portal http://phylo.cs.nmsu.edu:3000/. `datelife`'s website is maintained by RStudio's shiny server and the shiny package open infrastructure, as well as Docker. `datelife`'s R package stable version is available for installation from the CRAN repository (https://cran.r-project.org/package=datelife) using the command `install.packages(pkgs = "datelife")` from within R. Development versions are available from the GitHub repository (https://github.com/phylotastic/datelife) and can be installed using the command `devtools::install_github("phylotastic/datelife")`.

Supplementary Material

Code used to generate all versions of this manuscript, the biological examples, as well as the software benchmark can be found in GitHub repositories at https://github.com/LunaSare/datelife_paper1, https://github.com/LunaSare/datelife_examples, and https://github.com/LunaSare/datelife_benchmark, respectively.

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metadata rich repository of trees used for `datelife`. The many scientists who publish their chronograms in an open, reusable form, and the scientists who curate them for deposition in OpenTree. The NSF for funding nearly all the above, in addition to the ABI grant that funded this project itself.

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Figure 1

Stylized DateLife workflow. This shows the general worflows and analyses that can be performed with `datelife`, via the R package or through the website. Details on the functions involved on each workflow are shown in `datelife`'s R package vignette.

Figure 2

Computation time of query processing and search across `datelife`'s chronogram database relative to number of input taxon names. We sampled N names from the class Aves for each cohort 100 times and then performed a search with query processing not using the Taxon Names Resoultion Service (TNRS; dark gray), and using TNRS (light gray). We also performed a search using the already processed query for comparison (light blue).

Figure 3

Lineage through time (LTT) plots of source chronograms containing all or a subset of species from the bird family Fringillidae of true finches. Arrows indicate maximum age of each chronogram. Numbers reference to chronograms' original publications 1: Barker et al. (2012), 2: Barker et al. (2015), 3: Burns et al. (2014), 4: Claramunt and Cracraft (2015), 5: Gibb et al. (2015), 6: Hedges et al. (2015), 7: Hooper and Price (2017), 8: Jetz et al. (2012), 9: Price et al. (2014).

Figure 4

LTT plots of median and Supermatrix Distance Method (SDM) chronograms summarising information from source chronograms found for the Fringillidae. Arrows indicate maximum age.

Figure 5

LTT plots showing results from the cross-validation analyses of trees without branch lengths dated using BLADJ. The dating analysis can only be performed in trees with more than 2 tips, thus excluding chronogram from study 4; its data was still used as calibration for the other source chronograms.

Figure 6

LTT plots showing results from the cross-validation analyses of trees with branch length reconstructed with data from the Barcode of Life Database (BOLD) dated using PATHd8. We could construct a tree with branch lengths for all source chronograms. However, dating with PATHd8 was only successful in three source chronograms shown here.

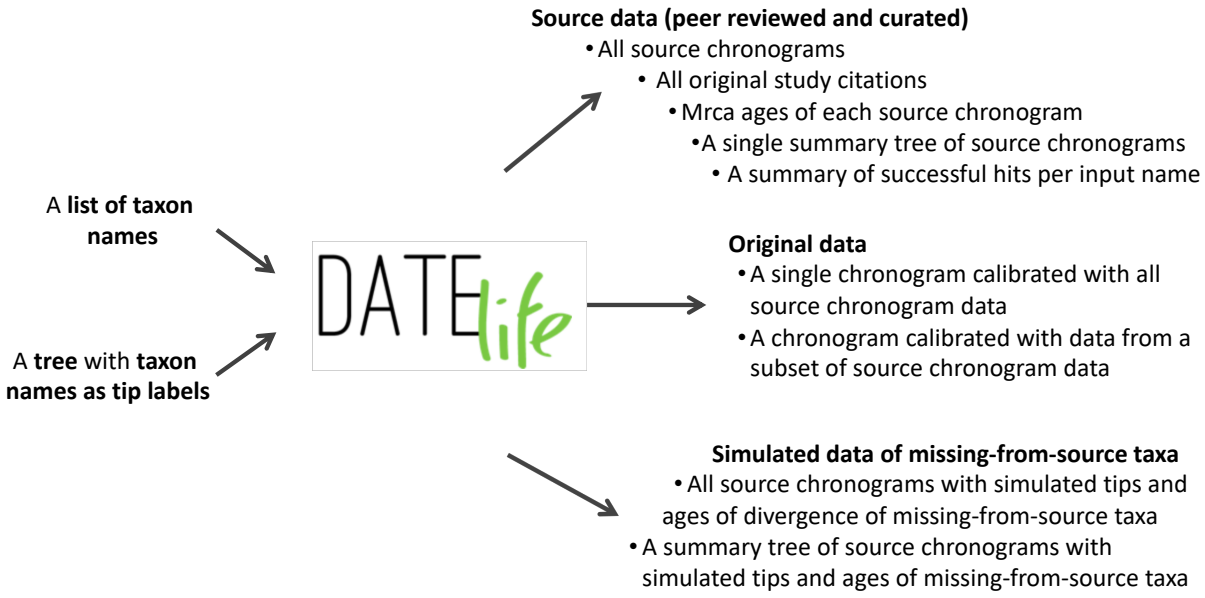
Source data (peer reviewed and curated)
• All source chronograms
• All original study citations
• Mrca ages of each source chronogram
• A single summary tree of source chronograms
• A summary of successful hits per input name
A list of taxon names
A tree with taxon names as tip labels
DATElife
Original data
• A single chronogram calibrated with all source chronogram data
• A chronogram calibrated with data from a subset of source chronogram data
Simulated data of missing-from-source taxa
• All source chronograms with simulated tips and ages of divergence of missing-from-source taxa
• A summary tree of source chronograms with simulated tips and ages of missing-from-source taxa

Figure 1:

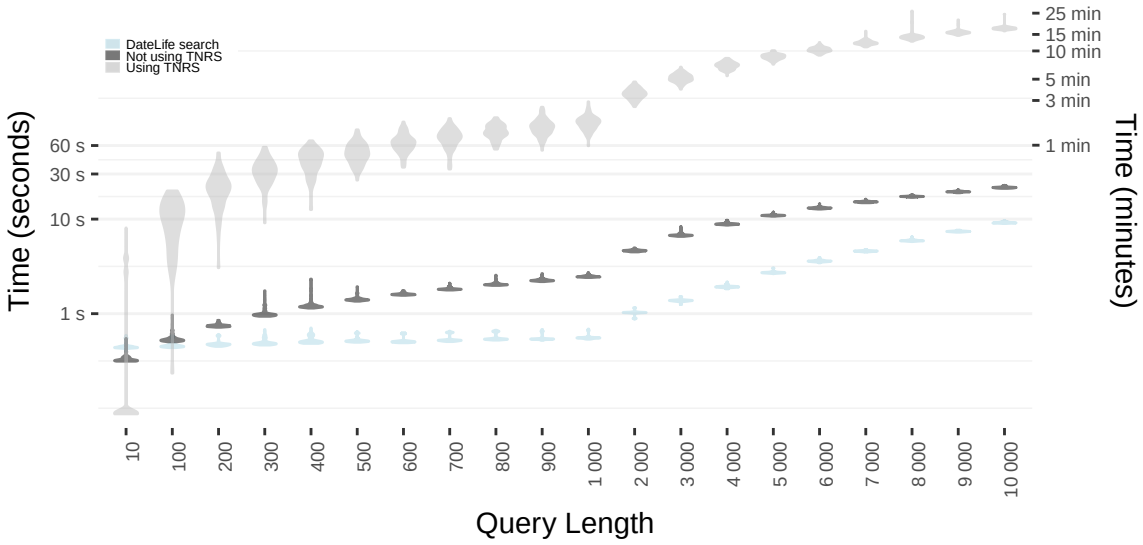
DateLife search
Not using TNRS
Using TNRS
Time (seconds)
60 s
30 s
10 s
1 s
25 min
15 min
10 min
5 min
3 min
1 min
Time (minutes)
10
100
200
300
400
500
600
700
800
900
1 000
2 000
3 000
4 000
5 000
6 000
7 000
8 000
9 000
10 000
Query Length

Figure 2:

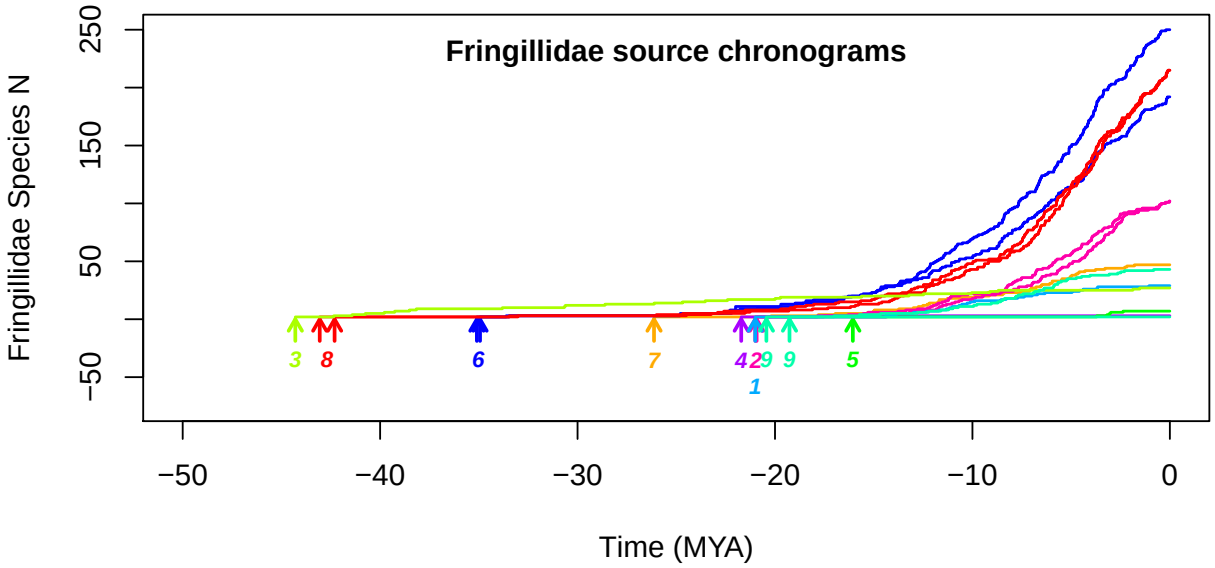
Fringillidae source chronograms
Fringillidae Species N
250
150
50
−50
−50
−40
−30
−20
−10
0
Time (MYA)
3
8
6
7
4
2
9
9
1
5

Figure 3:

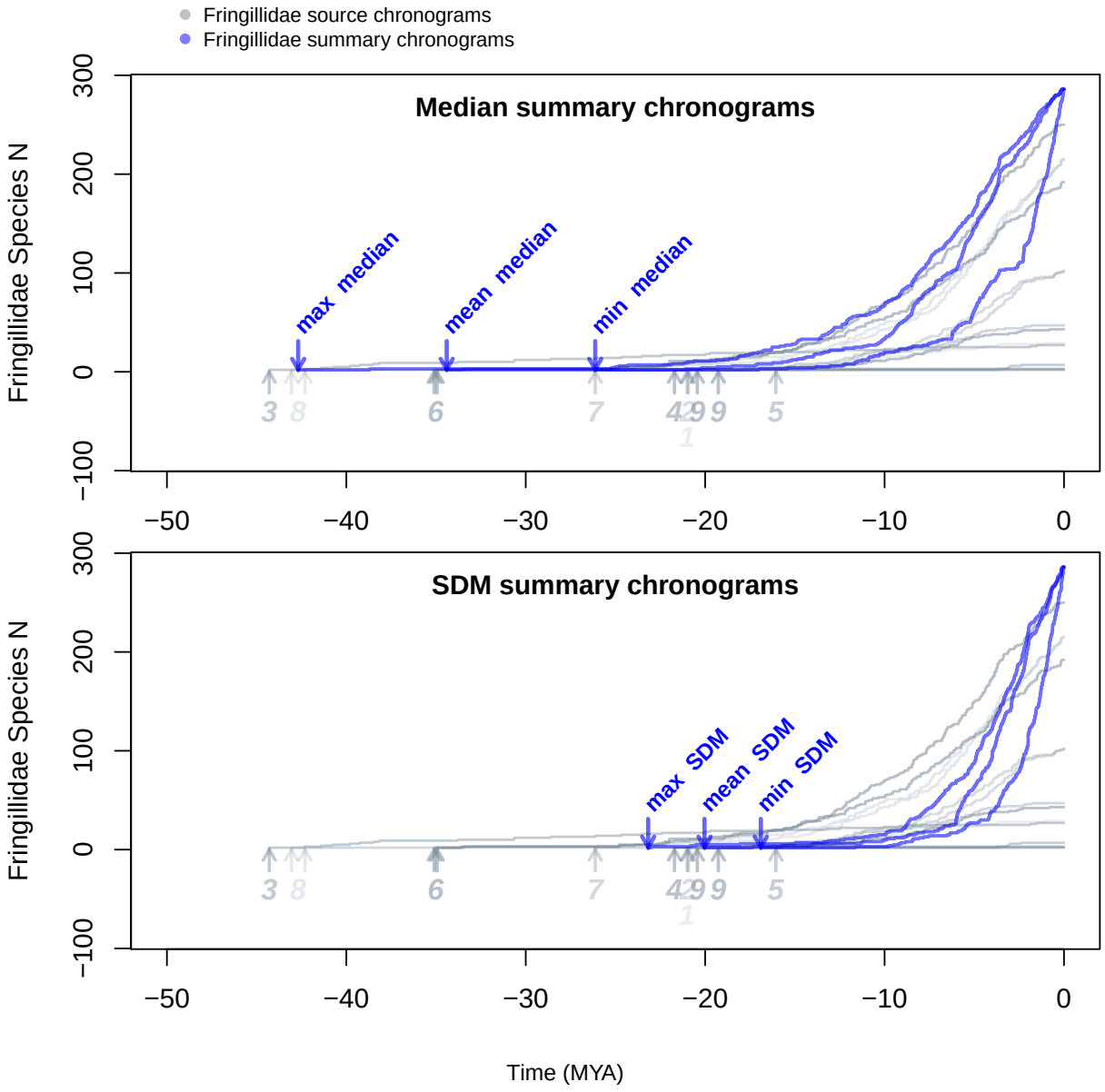
Fringillidae source chronograms
Fringillidae summary chronograms
Median summary chronograms
max median
mean median
min median
SDM summary chronograms
max SDM
mean SDM
min SDM
Fringillidae Species N
Time (MYA)

Figure 4:

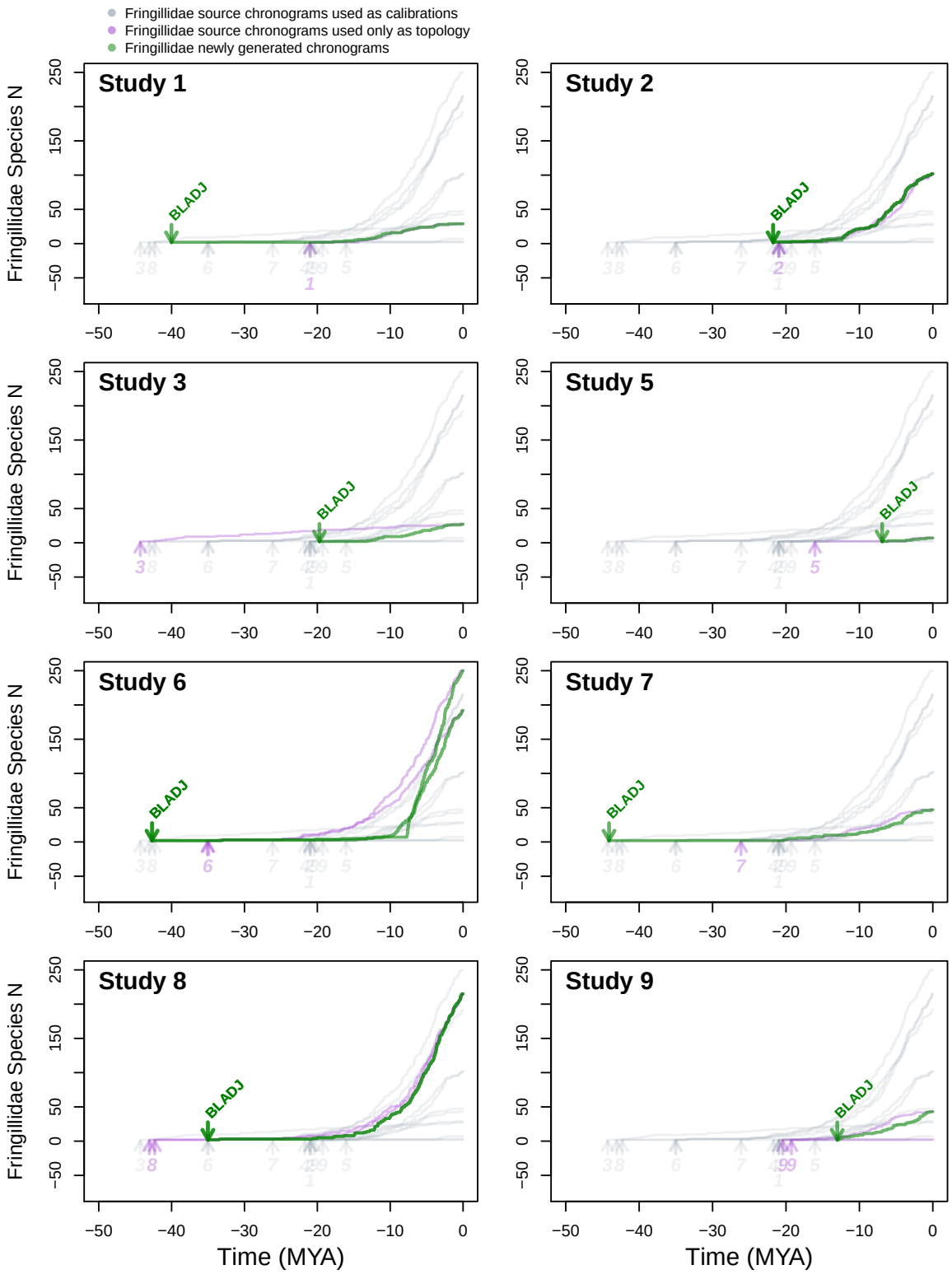
Fringillidae source chronograms used as calibrations
Fringillidae source chronograms used only as topology
Fringillidae newly generated chronograms
Study 1
Study 2
Study 3
Study 5
Study 6
Study 7
Study 8
Study 9
BLADJ
Fringillidae Species N
Time (MYA)

Figure 5:

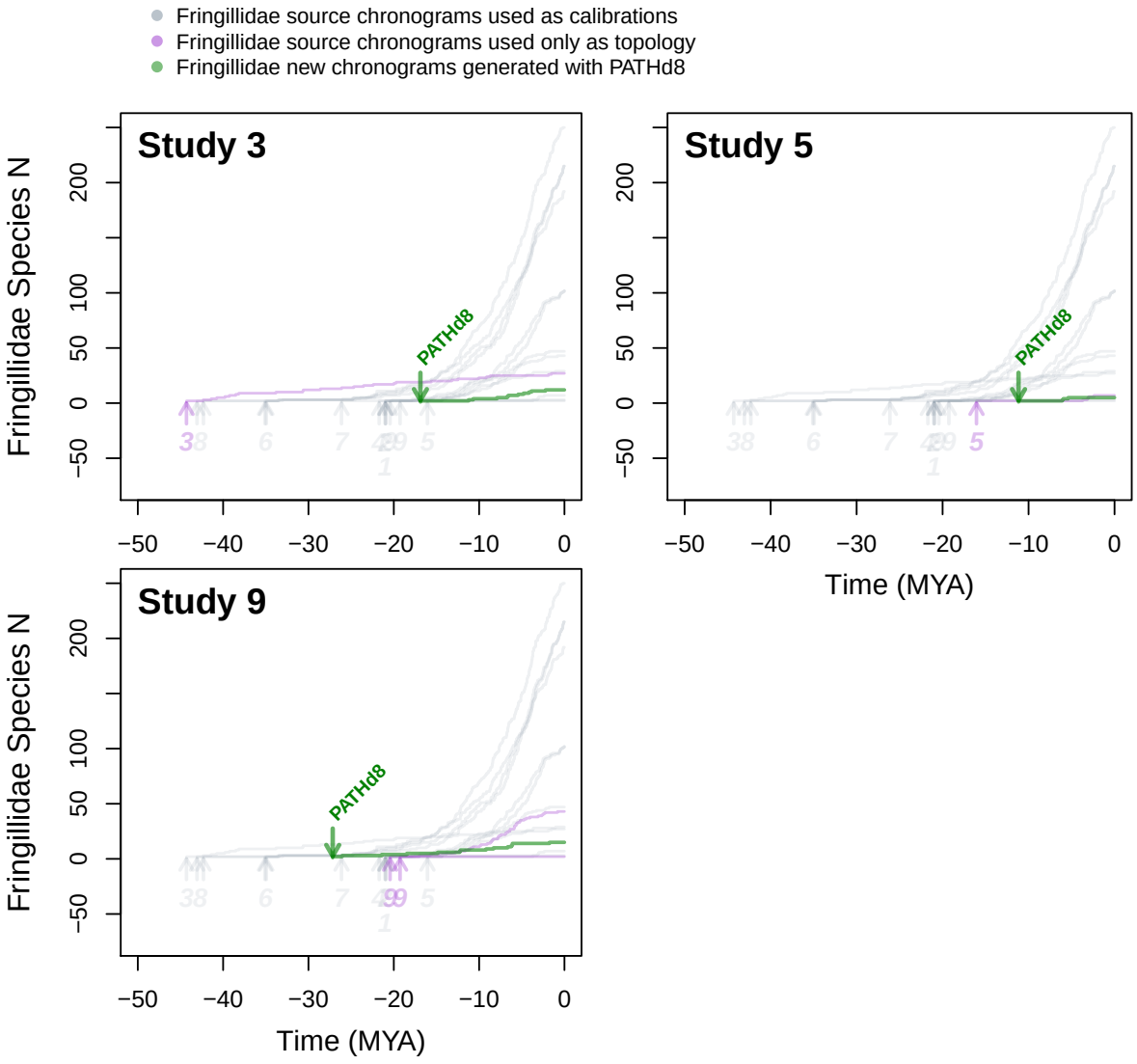
Fringillidae source chronograms used as calibrations
Fringillidae source chronograms used only as topology
Fringillidae new chronograms generated with PATHd8
Study 3
Study 5
Study 9
PATHd8
Fringillidae Species N
Time (MYA)
−50
−40
−30
−20
−10
0
−50
0
50
100
200

Figure 6: