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Software note

rtrees: an R package to assemble phylogenetic trees from megatrees

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Despite the increasingly available phylogenetic hypotheses for multiple taxonomic groups, most of them do not include all species. In phylogenetic ecology, there is still a strong demand to have phylogenies with all species in a study included. The existing software tools to graft species to backbone megatrees, however, are mostly limited to a specific taxonomic group such as plants or fishes. Here, I introduce a new user-friendly R package, 'rtrees', that can assemble phylogenies from existing or user-provided megatrees. For most common taxonomic groups, users can only provide a vector of species scientific names to get a phylogeny or a set of posterior phylogenies from megatrees. It is my hope that 'rtrees' can provide an easy, flexible, and reliable way to assemble phylogenies from megatrees, facilitating the progress of phylogenetic ecology.

Keywords: community ecology, phylogenetic ecology, phylogenetics, pruned phylogeny, supertree



Background

Phylogenetic trees represent hypotheses about the evolutionary history of species, providing an essential context for us to understand a wide range of ecological and evolutionary questions such as trait evolution, species interactions, and community assembly (Faith 1992, Webb et al. 2002, Cavender-Bares et al. 2009, Baum and Smith 2012). With the increasingly available genetic and fossil data, as well as the development of theories and software tools, established backbone phylogenies are now available for multiple taxonomic groups (Jetz et al. 2012, Hinchliff et al. 2015, Tonini et al. 2016, Faurby et al. 2018, Jetz and Pyron 2018, Rabosky et al. 2018, Smith and Brown 2018, Stein et al. 2018, Upham et al. 2019). The increasing availability of phylogenies has advanced multiple fields, with phylogenetic ecology being at the top of the list (Webb et al. 2002, Cavender-Bares et al. 2009, Maclvor et al. 2016, Swenson 2019).

Comprehensive phylogenies with as many of the target species to be included as possible are needed for studies in phylogenetic ecology. However, it is still common that only a fraction of the target species can be found in the available phylogenies for many taxonomic groups, because of the lack of sequence data. This situation leaves



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two options for ecologists. The first one is to collaborate with phylogeneticists to generate their own phylogenies based on sequence data so that all target species will be included. Such phylogenies were referred to as purpose-build phylogenies (Li et al. 2019). This option normally requires a large amount of effort to sample sequence data and then to assemble a phylogeny using established methods, which requires financial support that is not available for many researchers, and specific expertise to be applied appropriately. The second option is to derive their phylogenies from existing large synthetic phylogenies by grafting missing species onto the synthetic phylogenies using information such as taxonomic ranks and/or the stochastic polytomy resolution method (Chang et al. 2019). Such phylogenies were referred as synthesis-based phylogeny (Li et al. 2019), and have been demonstrated to give similar results to those based on purpose-built phylogenies for most questions asked in phylogenetic ecology, such as calculating phylogenetic diversity and estimating phylogenetic signal of traits (Swenson 2009, Cadotte 2015, Li et al. 2019).

Several computational tools exist to derive synthesis-based phylogenies. The oldest and most widely used one is phyloomatic (Webb and Donoghue 2005). Since it was published in 2005, 'phyloomatic' has been cited more than 1000 times and has contributed significantly to the development of the field of phylogenetic ecology. Phyloomatic was originally written with C but the latest version is a GNU Awk program (<https://github.com/camwebb/phyloomatic-awk>). Another recent similar tool is the set of 'S.PhyloMaker', 'V.PhyloMaker', and 'V.PhyloMaker2', a serial of R packages developed by the same group to derive phylogenies for vascular plant species (Jin and Qian 2019). These packages work well but are limited to vascular plants and require the users to provide the taxonomic classification (genus and family) of the target species. Phyloomatic requires the target taxon to share with the megatree at least one node label, which may be the terminal taxon node itself or any ancestral node supplied for the target taxon, including Linnean classification names. Another R package 'FishPhyloMaker' was developed recently to derive synthesis-based phylogenies for finned-ray fishes (Nakamura et al. 2021) based on the fish tree of life megatree (Rabosky et al. 2018). Users can simply provide a list of species names and FishPhyloMaker will retrieve the taxonomic classification information; when such information cannot be found, users are asked to enter it manually. It also will retrieve

such information for the tips in the megatree that are in the same genus (if congeneric species exist in the megatree), family (if no congeneric species exist in the megatree), or order (if no co-family species exist in the megatree) of the target species with every call of the function. Such a design, however, requires internet access and can be slow.

What is missing from the tool box of phylogenetic ecologists is a user-friendly program that can derive synthesis-based phylogenies for most common taxonomic groups with available megatrees by taking just a species list. If a large set of posterior phylogenies exists for some taxonomic groups, the tool should be able to derive phylogenies from a small number of randomly selected megatrees (e.g. 50–100) so that uncertainties can be accounted for in the downstream analyses. To fill this gap, I developed an R package named 'rtrees' (<https://github.com/daijiang/rtrees>). With 'rtrees', users only need to provide a species list to derive phylogeny or phylogenies for taxonomic groups with existing, established megatrees, which have been processed and hosted in a separate R data package 'megatrees'. Users can also provide their own megatrees if needed.

Software availability

The 'rtrees' package can be installed using the R code below. This code will also install the data package 'megatrees', which hosts a collection of existing synthetic megatrees for amphibians, birds, fishes, mammals, plants, reptiles, and sharks (Table 1).

```
install.packages('rtrees', repos=c(
  rtrees = 'https://daijiang.r-universe.dev',
  CRAN = 'https://cloud.r-project.org'
))
```

I have also developed a shiny app (https://dli.shinyapps.io/rtrees_shiny/) to get phylogenies quickly without using R when the number of missing species is small (< 1000).

Package structure

The general workflow of 'rtrees' is described in Fig. 1. In this section, instead of going through each step of the workflow, I have focused on four major components: taxonomic classification information, megatrees, species names processing, and the grafting process.

Table 1. Brief information about the megatrees included in the 'megatrees' package, which will be installed automatically when 'rtrees' is installed.

Taxon	No. of species	No. of trees	R object	Reference
Amphibian	7238	100	tree_amphibian_n100	Jetz and Pyron (2018)
Bird	9993	100	tree_bird_n100	Jetz et al. (2012)
Fish	11 638	1	tree_fish_12k	Rabosky et al. (2018)
	31 516	50	tree_fish_32k_n50	Rabosky et al. (2018)
Mammal	5831	100	tree_mammal_n100_phylacine	Faury et al. (2018)
	5911	100	tree_mammal_n100_vertlife	Upham et al. (2019)
Plant	74 531	1	tree_plant_ottl	Smith and Brown (2018), Jin and Qian (2019)
Reptile (squamate)	9755	100	tree_reptile_n100	Tonini et al. (2016)
Shark, ray, and chimaera	1192	100	tree_shark_ray_n100	Stein et al. (2018)

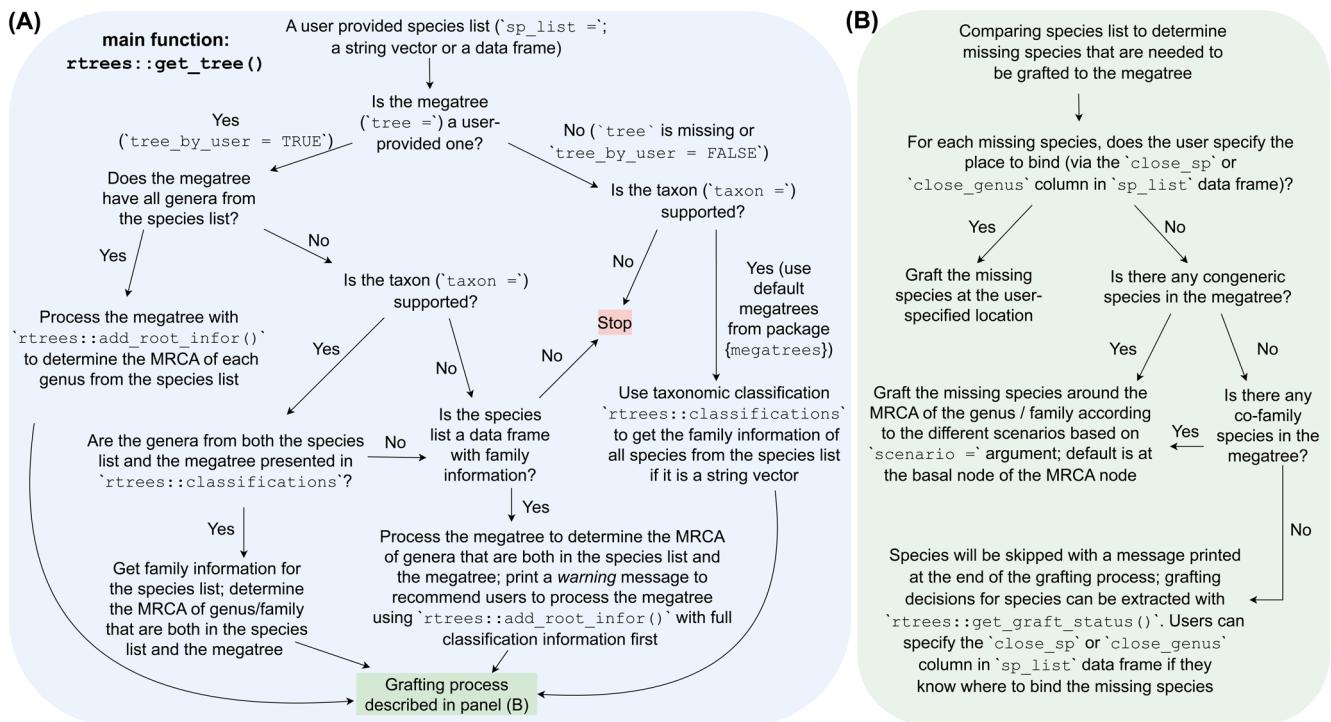


Figure 1. Schematic description of the general workflow of 'rtrees'. Detailed documentation of the different arguments of the main function `rtrees::get_tree()` and other functions can be found in the R documentation after installing the package. It is also available from the package website <https://daijiang.github.io/rtrees/>.

Classification information

The taxonomic classification information (e.g. genus and family of each species) is critical for the pre-process of megatrees (below) and to determine where a new species should be grafted onto a megatree. Therefore, 'rtrees' provides the classification information in the R object `rtrees::classifications` for common taxonomic groups. In the current version of 'rtrees' (ver. 1.0.1), the object `rtrees::classifications` includes 24 222 unique genera of plants, 4833 unique genera of fishes, 2508 unique genera of birds, 1419 unique genera of mammals, 1237 unique genera of reptiles, 543 unique genera of amphibians, and 198 unique genera of sharks, rays, and chimaeras. I did not include classification information above the family level (e.g. order) because grafting species above family level may bring too much uncertainty.

For plants, I extracted genus and family information from multiple sources, including the Plant List (<http://www.theplantlist.org/>, superseded by the World Flora Online), the Plants of the World Online (<https://powo.science.kew.org/>), and Catalogue of Life (<https://www.catalogueoflife.org/>) 2019. When different sources give different family information for the same genus, I used the information provided by the Plants of the World Online. For fish, I used the taxonomic information provided by the fish tree of life (Rabosky et al. 2018). Jetz et al. (2012) built the bird phylogenies based on the Handbook of the Birds of the World (HBW) and BirdLife International digital checklist ver. 3, and later updated the

taxonomy based on ver. 5. I downloaded the bird taxonomy from Birdtree.org. Information on mammal taxonomy came from two sources: PHYLACINE 1.2 (Faurby et al. 2018) and the mammal diversity database of VertLife (<https://vertlife.org/>, Upham et al. 2019). For genera with different family information from these two sources, I used the information provided by VertLife. Taxonomy information for amphibians, reptiles, sharks, rays, and chimaeras were all provided by VertLife.

Sources and preparation of megatrees

Sources of existing megatrees for different taxonomic groups are described in Table 1. For some taxonomic groups, if published phylogenetic analyses provided multiple posterior phylogenies, a subset of phylogenies (100 for taxonomic groups except fish, see the column of # of trees in Table 1) were randomly selected. For most analyses, 50–100 randomly selected posterior phylogenies were enough to account for the uncertainties in phylogenetic spaces (Li et al. 2018, Nakagawa and De Villemereuil 2019, Upham et al. 2019). All megatrees were stored in the 'megatrees' R data package with class of `phylo` or `multiPhylo`, the most common data structures of phylogenies used in R.

Each megatree was processed so that the most recent common ancestors (MRCA) of all the genera and families in the megatrees were determined using the function `rtrees::add_root_info()`. If a genus or a family was not monophyletic, I used the most inclusive MRCA for that genus or

family. The MRCA information of each megatree was saved as an extra component named `genus_family_root` in the corresponding R object (Table 1; e.g. `tree_plant_otl$genus_family_root`). The function `rtrees::add_root_info()` is also used by `rtrees::get_tree()` to process user-provided megatrees (Fig. 1). Users can also process their own megatrees with the function `rtrees::add_root_info()` if they have family information for all genera in the megatrees.

Species names processing

R package 'rtrees' does not provide functions to standardize taxonomic names because existing packages such as 'taxize' already provide such features. Users should use such existing tools to standardize their species names first, ideally using the same taxonomy backbone as the corresponding megatrees described in Table 1. When users provide a list of standardized species without information about genus and family (can be a character vector or a data frame with one column named as 'species'), function `rtrees::get_tree()` will automatically call function `rtrees::sp_list_df()` to use the classification information described above to extract the genus and family information needed for grafting missing species

to the megatrees if the taxonomic group is one of those in Table 1. Note that if all genera in the species list are already in the megatrees, no classification information will be needed to finish the grafting process. Users can also pass prepared classification information to `rtrees::get_tree()`. To do so, the input data frame should have at least three columns: `species`, `genus`, and `family`. Two extra optional columns (`close_sp` and `close_genus`) can also be included in the input data frame to specify where the target species should be grafted into the megatrees. If users provided the classification and/or location information, 'rtrees' will honor the user provided information.

The grafting process

Once the megatrees are processed and the classification information of species is ready, the grafting process begins (Fig. 2B). If all species are already present in the megatrees, no grafting is needed and a pruned phylogeny is returned. Otherwise, for species that are missing from the megatrees, 'rtrees' first looks for congeneric species in the megatrees. If there is no congeneric species in the megatrees, 'rtrees' then looks for co-family species in the megatrees. If neither congeneric nor co-family species are found, the target species is skipped

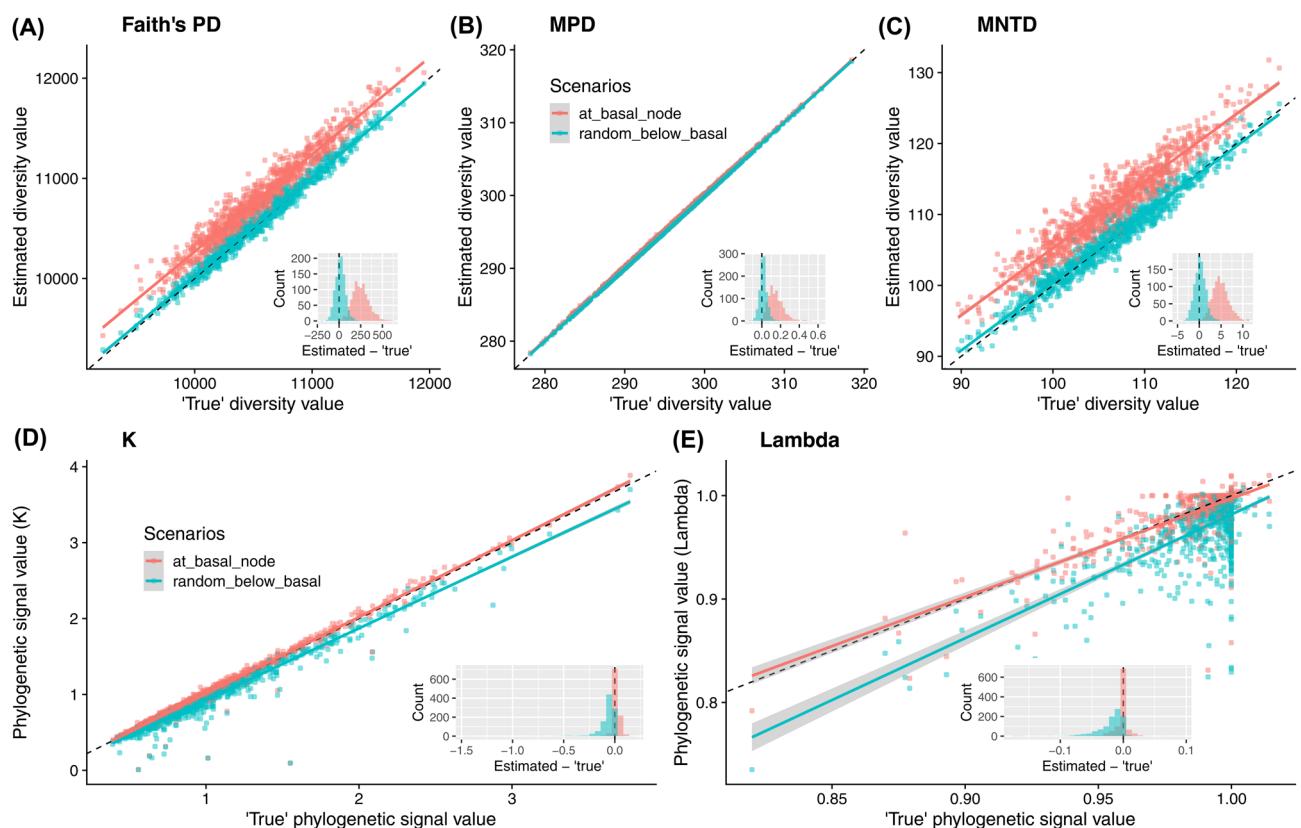


Figure 2. Effects of different grafting scenarios on results of community phylogenetic diversity (A–C) and phylogenetic signal of traits (D–E). Black dashed lines in the larger regression plots represent 1-to-1 relationships (intercept = 0, slope = 1). Nested histograms present the distributions of differences between estimated values based on the phylogenies derived with different grafting scenarios and the 'true' phylogeny. In most cases, simulations suggest that the default option (i.e. scenario = 'at_basal_node') works well when downstream analysis involves community phylogenetic diversity or trait phylogenetic signal.

and is included in the output message with other skipped target species. If either congeneric or co-family species are found in the megatrees, users have two options to graft the target species into the megatrees by setting the `scenario` argument within `rtrees::get_tree()`:

- 1) The default way is to graft the missing target species as a polytomy at the basal node of the MRCA of the genus or family in the megatrees (`scenario = 'at_basal_node'`); if the megatrees have only one species in that genus or family, then the missing target species is grafted to the half of this only species' branch length.
- 2) If users set `scenario` to 'random_below_basal', a randomly selected node within the genus or family is used to graft the missing target species; the probability of a node being selected is proportional to its branch length. Because of the randomness involved with this option, users may want to repeat this process multiple time (e.g. 50–100) to generate a set of phylogenies to account for the randomness.

In most cases, simulations suggest that the default option (i.e. `scenario = 'at_basal_node'`) works well when downstream analysis involves community phylogenetic diversity or trait phylogenetic signal (Fig. 2; see Supporting information for simulation methods). Although phylogenies derived with the 'random_below_basal' scenario work better in recovering the 'true' community phylogenetic diversity (Fig. 2A–C), it takes much longer to finish, as hundreds of such derived phylogenies are needed to account for the randomness by calculating an average value. Given that most biodiversity studies care more about the relative diversity across communities within a region instead of their absolute 'true' values, such computational cost may not be justified. In addition, estimated phylogenetic diversity values based on the default scenario 'at_basal_node', despite being slightly overestimated for Faith's PD (Fig. 2A) and MNTD (Fig. 2C), have a slope of ~ 1 when regressed with the 'true' values, suggesting that phylogenies derived with the default scenario work appropriately for most phylogenetic diversity studies. For trait phylogenetic signal, the default scenario works better than the 'random_below_basal' scenario (Fig. 2D–E). Together, simulations suggest that, for most phylogenetic ecological studies, the default scenario is justified.

By default, if the number of missing target species is over 200, a progress bar is shown in the console. Once the grafting process is finished, the megatrees are pruned to only keep the target species. When there is only one megatree used, the generated phylogeny has a class of 'phylo'; when multiple posterior megatrees are used, the generated phylogenies have a class of 'multiPhylo'. When `show_grafted` is set to TRUE (default is FALSE) within `rtrees::get_tree()`, grafted species are indicated with trailing * or ** in the tip labels of the generated phylogeny, indicating that a species is grafted at the genus and family level, respectively. If such information is important for downstream analyses, users can extract such information as its own data frame using

`rtrees::get_graft_status()`. Users can use `rtrees::rm_stars()` to remove all trailing stars from the tip labels of the generated phylogeny.

Applied examples

R package 'rtrees' can be used in the following exemplary scenarios.

- 1) Deriving phylogenies with a species list based on one megatree. Users can use 'rtrees' to derive a phylogeny from an existing megatree (i.e. synthetic phylogeny) based on a list of species names for downstream analyses such as estimating phylogenetic signal of species traits, or calculating phylogenetic diversity and investigating phylogenetic structures of communities. For these kinds of analyses, a phylogeny derived from a synthetic megatree provides robust results (Li et al. 2019).
- 2) Deriving phylogenies with a species list based on multiple megatrees. In this scenario, users can find a set of existing posterior phylogenies that include all or most of their species. However, there are thousands of such posterior phylogenies in the datasets (e.g. phylogenies provided by VertLife). However, for most phylogenetic analyses, a smaller number (50–100) of randomly selected posterior phylogenies is generally enough to capture the uncertainties of phylogenetic hypotheses (Li et al. 2018, Nakagawa and De Villemereuil 2019, Upham et al. 2019). R package 'rtrees' can save users time to repeat this download-subset-graft process by providing 50–100 randomly selected posterior phylogenies and derive phylogenies for the user-provided species list based on these randomly selected posterior phylogenies.
- 3) Grafting species to phylogenies. If users have a phylogeny, either one that is purpose-built or synthetic, and they want to insert more species in the phylogeny – potentially as polytomies with their congeneric or co-family species in the phylogeny because of the lack of sequence data – 'rtrees' can help. For example, in some cases, users already have a phylogeny for the species pool. However, users also have species that cannot be identified at species level with certainty, e.g. *Carex* spp. Such morphological species can be grafted into the phylogeny using 'rtrees' so that users do not need to throw them away for the downstream analysis. These taxa can be given dummy species names, e.g. *Carex* sp1.

In all scenarios above, the main function to use is `rtrees::get_tree()`. Users can see detailed documentation and examples by visiting the package website (<https://daijiang.github.io/rtrees>).

Discussion

With the recent advances in phylogenetics of multiple taxonomic groups, more megatrees will be available in the near future, such as for Lepidoptera (Kawahara et al. 2019). It

is relatively easy to include more megatrees beyond those described in [Table 1](#), as the R package ‘*rtrees*’ was designed with expandability in mind. Including a new megatree requires two steps. First, the new megatree needs to be processed with the function *rtrees::add_root_info()* and to be stored in the R data package ‘*megatrees*’, which is a dependency of ‘*rtrees*’. Second, the classification information (genus and family) of tips of the new megatree needs to be saved within ‘*rtrees*’ if it is a new taxonomic group. No further change will be needed for other components of ‘*rtrees*’.

It is my hope that ‘*rtrees*’ will make it much easier to derive phylogenies from existing megatrees for all common taxonomic groups. Such synthesis-based phylogenies are reliable for most ecological questions such as calculating phylogenetic diversity and estimating phylogenetic signals ([Li et al. 2019](#)). Note that such phylogenies may not be suitable for evolutionary studies such as estimating diversification rates if a large proportion of missing species is included in the derived phylogenies. Therefore, it is also my hope that ‘*rtrees*’ will facilitate research in phylogenetic ecology. I am committed to maintain and update ‘*rtrees*’ in the foreseeable future. Since ‘*rtrees*’ is an open source software, others are more than welcome to contribute by submitting pull requests or opening issues to its GitHub repository (<https://github.com/daijiang/rtrees>).

To cite ‘*rtrees*’ or acknowledge its use, cite this Software note as follows, substituting the version of the application that you used for ‘ver. 1.0’:

Li, D. 2023. *rtrees*: an R package to assemble phylogenetic trees from megatrees. – *Ecography* 2023: e06643 (ver. 1.0).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.18931zd2f> ([Li 2023](#)).

Supporting information

The Supporting information associated with this article is available with the online version.

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