FishPhyloMaker: An R package to generate phylogenies for ray-finned fishes

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Highlights

- We provide the first automated procedure to check species names, construct phylogenetic trees and calculate Darwinian shortfalls for ray-finned fishes (Actinopterygii) by the R package FishPhyloMaker.
- This package provides functions to assemble phylogenies through a fast and reproducible method, allowing its use and replicability by specialists and non-specialists in fish systematics.
- The package also provides an interactive procedure that gives more flexibility to the user when compared with other existing tools that construct phylogenetic trees for other highly speciose groups.
- The package include a new method to compute Darwinian shortfalls for ray-finned fishes, but the rationale of the provided algorithm can be extended in future studies to be used in other groups of organisms

Abstract

Phylogenies summarize evolutionary information that is essential in the investigation of ecological and evolutionary causes of diversity patterns. They allow investigating hypotheses from trait evolution to the relationship between evolutionary diversity and ecosystem functioning. However, obtaining a comprehensive phylogenetic hypothesis can be difficult for some groups, especially those with a high number of species, that is the case for fishes, particularly tropical ones. The lack of species in phylogenetic hypotheses, called Darwinian shortfalls, can hinder ecological and evolutionary studies involving this group. To tackle this problem, we developed FishPhyloMaker, an R package that facilitates the generation of phylogenetic trees through a reliable and reproducible procedure, even for a large number of species. The package adopts well-known rules of insertion based on cladistic hierarchy, allowing its use by specialists and non-specialists in fish systematics. We exemplified the use of the FishPhyloMaker package by constructing complete phylogenies for fishes inhabiting the four richest freshwater ecoregions of the world. Furthermore, we proposed a new method to calculate Darwinian shortfalls and mapped this information for the major freshwater drainages of the world. FishPhyloMaker will expand the range of evolutionary and ecological questions that can be addressed using ray-finned fishes as study models, mainly in the field of community phylogenetics, by providing an easy and reliable way to obtain comprehensive phylogenies. Further, FishPhyloMaker presents the potential to be extended to other taxonomic groups that suffer from the same difficulty in the obtention of comprehensive phylogenetic hypothesis.

Keywords: Phylogenies, community phylogenetics, Darwinian shortfall, gap-analysis.

Introduction

Phylogenies have been widely explored in ecology in the last decades due to the development of theoretical frameworks, numerical methods, and software (*e.g.*, Webb et al. 2008; Felsenstein 1985). The research agenda in ecology and evolution encompasses phylogenetic approaches from organismal to macroecological-scale, including trait evolution, invasion ecology, metacommunity ecology, and ecosystem functioning (Cavender-Bares et al., 2009). Hence, comprehensive phylogenetic trees must be available to address those topics.

Well-established phylogenies for most of the known species are available for some groups, such as terrestrial vertebrates (birds (Jetz et al., 2012), mammals (Upham et al., 2019), amphibians (Jetz and Pyron, 2018), squamates (Tonini et al., 2016), sharks (Stein et al., 2018), and plants (Magallón et al., 2015), which also have powerful tools to generate phylogenetic trees for local/regional pools of species (*e.g.*, Webb & Donoghue 2005 for mammals and plants; Jin & Qian 2019 for plants, to the others see http://vertlife.org/phylosubsets/). Inversely, available phylogenies for bony fishes (Betancur et al., 2017; Rabosky et al., 2018) display issues related to the taxonomic position of some clades (e.g., non-monophyletic groups) and the lack of species representativeness. The latter issue hampers answering some questions on the ecology and evolution of ray-finned fishes by generating inaccuracy in estimates of phylogenetic signal, trait evolution, and phylogenetic diversity (Seger et al. 2010; Boettiger et al., 2012a), or even impeding their calculation.

Ray-finned fishes (Actinopterygii) exhibit a complex evolutionary history and high ecological diversity (Albert et al., 2020), making them an interesting group to address questions in the interface of ecology and evolution (*e.g.*, Roa-Fuentes et al. 2019; Nakamura et al. 2020). The difficulty in obtaining phylogenetic information can hinder our efforts to understand fish ecology and evolution. Additionally, the lack of phylogenetic information for species, *i.e.*, Darwinian shortfalls, is currently investigated in few lineages (*e.g.*, Freitas et al.,

2021), which impedes the mapping of the relative demand of additional efforts needed in entire regions or clades to uncover the phylogenetic history of fishes. This problem urges a rapid solution in the context of the accelerated loss of species (Chase et al., 2020).

A short-term solution to tackle the Darwinian shortfall for ray-finned fishes would be coupling the phylogenetic information with cladistic classification to produce comprehensive phylogenies (Diniz-Filho et al., 2013). This solution is laborious and lacks reproducibility when adding many species, and the specific steps are not precisely documented when did "by hand" procedures (Webb et al., 2008). An alternative would be the use of molecular techniques to generate comprehensive phylogenies. However, it demands high expertise and high financial investment (Roquet et al., 2013), limiting factors for several institutions. Therefore, automatizing the procedures of constructing comprehensive phylogenies using the information from cladistic hierarchy, as suggested by Diniz-Filho et al (2013), provides a more reliable, accessible, and short-term solution for evolutionary ecologists. The technique produces reliable phylogenetic information for community phylogenetics (Li et al., 2019).

In order to tackle the problem of obtention of comprehensive fish phylogenies in a reliable and reproducible way, we developed the FishPhyloMaker. This freely available R package facilitates the obtention of phylogenetic trees for ray-finned fishes. FishPhyloMaker automates the insertion procedure of species in the most comprehensive phylogeny (Rabosky et al., 2018) of ray-finned fishes following their taxonomic hierarchy. We illustrated how the FishPhyloMaker package solves the problem of obtaining comprehensive phylogenies by constructing phylogenetic trees for species inhabiting the four major freshwater ecoregions (Afrotropics, Indo-Malay, Nearctic and Neotropics, sensu Tedesco et al., (2017)). Further, we developed a new method to quantify the Darwinian shortfalls and illustrate the use of this method by mapping the Darwinian shortfalls of all the major freshwater drainages in the world. Our package overcomes the main problems associated with manually building

phylogenies for ray-finned fishes by following a specific and documented procedure and reducing the manual labor in large phylogenies.

Methods

Inside the Fish(PhyloMaker): an overview of the package

FishPhyloMaker is a freely available R package containing three main functions, *FishTaxaMaker*, *FishPhyloMaker*, and *Darwinian_deficit*. Below, we describe the functions to generate phylogenetic trees, highlighting the input data, intermediate steps, and output objects. Brief descriptions of the package functions are available in Table 1.

FishTaxaMaker

The *FishTaxaMaker* function checks the validity of species names provided by the user and prepares a formatted data frame for the *FishPhyloMaker* function. The input data must be a string vector or a data frame containing a list of species from the regional pool or an occurrence matrix (sites x species). The genus and specific epithet (or subspecies) must be separated by underline (e.g., *Genus_epithet*). The function first classifies the provided species names as valid or synonymies based on Fishbase (Froese & Pauly, 2006) using the *rfishbase* package (Boettiger et al., 2012b). A new column summarizes names initially valid and the current valid names substituting identified synonymies. Unknown species to Fishbase are printed in the command line, and the user must manually inform the Family and the Order of the species. The output of the function is a list containing three elements: 1) a data frame displaying the taxonomic information (Valid name, Subfamily, Family, Order, Class, and SuperClass) for each provided species; 2) a data frame displaying the taxonomic information (Species, Family, and Order), only for the valid species; 3) a character vector displaying the species names not found in Fishbase.

Table 1: Functions presented in the package FishPhyloMaker and their descriptions.

Function	Description
FishTaxaMaker()	Checks species names according to Fishbase and prepares the species list for the other functions in the package.
whichFishAdd()	Identifies the species already included in the mega-tree and in which taxonomic level each remaining species will be inserted.
FishPhyloMaker()	Builds the phylogeny and may return a data frame identifying step-by-step the performed insertions.
Darwinian_deficit()	Calculates the Darwinian shortfall for the provided species list through a Phylogenetic Diversity (PD Faith (1992)) ratio

FishPhyloMaker

FishPhyloMaker is the core function of the package. This function builds a phylogenetic hypothesis for the provided species list by inserting in and pruning species from the Rabosky's et al. (2020) phylogenetic tree (Figure 1) downloaded by the fishtreeoflife R package (Chang et al. 2019). This phylogeny is the most up-to-date and comprehensive phylogenetic hypothesis for ray-finned fishes.

The input for the *FishPhyloMaker* function can be the second element in the list returned by the *FishTaxaMaker* function or a manually constructed data frame with the same configuration (species, family, and order names for each taxon). The function also contains three logical arguments: insert.base.node, return.insertions and progress.bar. These three

arguments are set by default as FALSE, TRUE, and TRUE, respectively, and allow the user to choose if the species must be inserted at the base node of families/orders, if the insertions made by each species must be shown in the output and if a progress bar must be shown in the console.

The function works sequentially, first identifying which of the provided species are in the backbone phylogenetic tree. If all of them are already present in the backbone tree, the function returns a pruned one. If any of the provided species is not in the backbone tree, the function performs a four-level insertion routine. First, species from genera already included in the backbone tree are inserted as polytomies at the most recent ancestral node that links all congeneric species (or as the sister species of the only species representing a genus in the backbone tree, as shown in *i* in Figure 1). Second, species not inserted in the previous step are then inserted at the family level by an interactive procedure using a returned list of all the genera within the same family of the target species. The user has the option to insert the target species as a sister taxon to a genus (*ii* in Figure 1, option 1, near to *Loricaria* genus), between two genera (*ii* in Figure 1, option 2, between genus *Loricaria* and *Hypostomus*), or at the node of the family (*ii* in Figure 1, option 3). If the user enters a single genus from the list, the function splits its branch and inserts the target species as a sister taxon (option 1). If the user enters two genera separated by a blank space, the function inserts the target species as a polytomy at the most recent node that links the selected genera (option 2). If the user enters the family name, the function inserts the target species at the family node as a polytomy (option 3). Third, if any remaining species can now be inserted at the genus level, the function repeats the first procedure but records it as a Congeneric family-level insertion (*iii* in Figure 1). Fourth, remnant species are inserted at the order level following similar to the second step, by an interactive procedure using a returned list of all the families within the order of the target species. Hence, the user may specify a family to insert the target species as

sister taxon (option 1), two families to insert it as a polytomy at the most recent node linking them (option 2), or the order to insert it as a sister taxon (option 3). The function will not perform insertions steps beyond the order level because it would add too much uncertainty to the phylogenetic tree.

Setting the argument `insert.base.node` as TRUE automatically inserts the target species from the second and fourth steps in the family and order nodes, respectively. This setting facilitates the insertion of a large number of species or species with the phylogenetic position unknown. The default output is a list with two objects: (i) the pruned tree including only the provided species list (Final tree in Figure 1); (ii) a data frame identifying if each provided species was initially present in the backbone tree, in which step it was inserted, or not inserted at all. This data frame will tag each species with one of the six classification based on the insertion procedure: 1 – Present in tree will indicate species that were already present in the backbone tree; 2 – Congeneric insertion will indicate species that present at least one species of the same genus in the backbone tree and was inserted as congeneric of this species; 3 – Family insertion will indicate inserted species that did not present any congeneric species at backbone tree, but had at least one species of the same family in backbone tree; 4 – Congeneric at Family-level will indicate species that was added as congeneric after another species of the same genus was inserted at the Family level; 5 – Order insertion will indicate inserted species that did not presented any species of the same family in the backbone tree and must be inserted near to an extant family or in node corresponding to the order root in the backbone tree; 6 – not inserted will indicate species that did not present any species of the same order in the backbone tree, therefore was not inserted due their high uncertainty in the phylogenetic position.

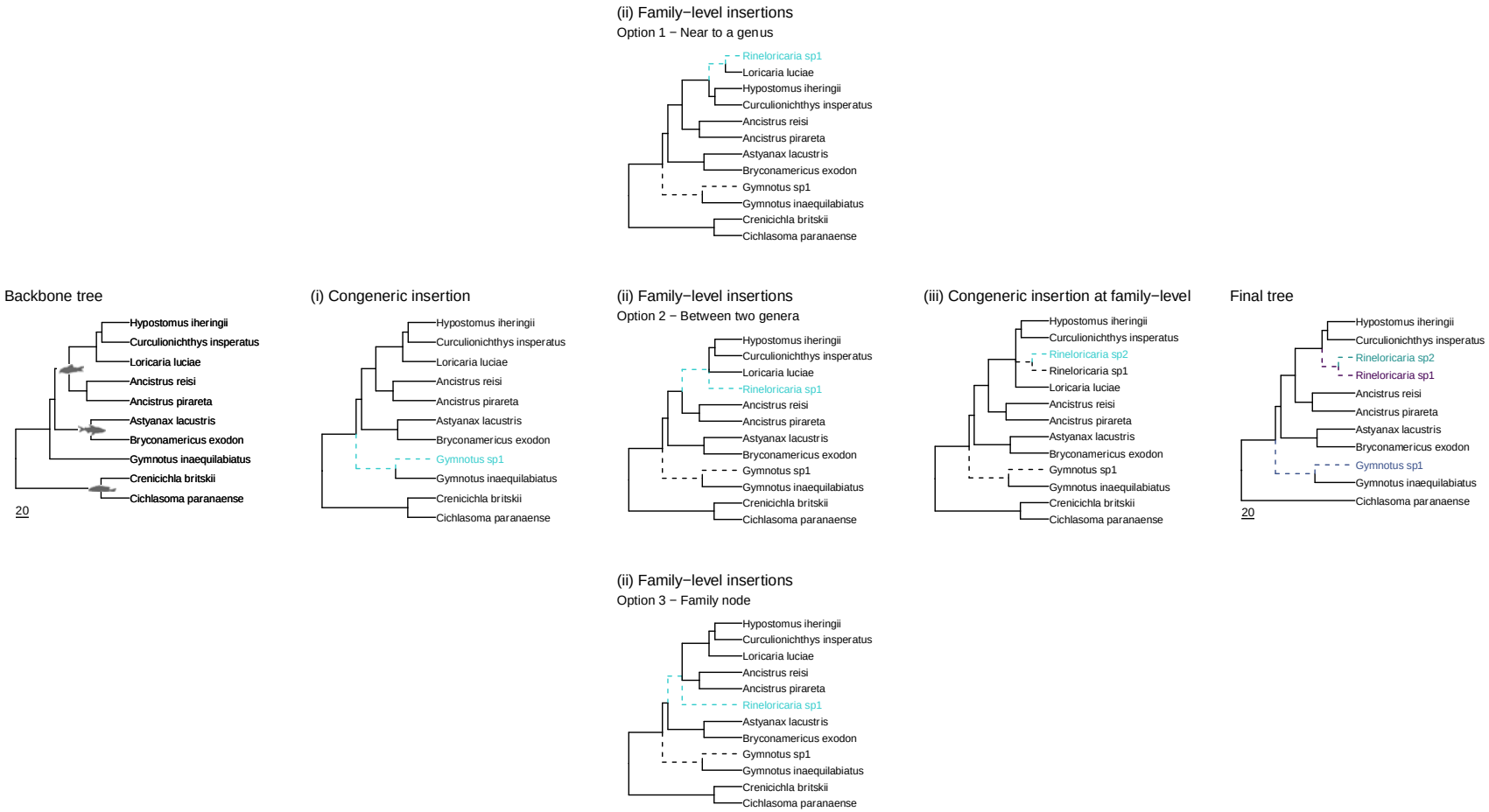

Figure 1: Schematic representation of insertion and subsetting procedure performed by the FishPhyloMaker() function. Here we used a hypothetical phylogeny containing ten species and four families (silhouettes inside the tree) as the backbone phylogeny. Step (i) represents the

congeneric level of insertion. Step (ii) represents the three options that the user may choose in the Family-level round of insertions (Option 1 – near to a genus; Option 2 – between two genera; Option 3 – at the family node). (iii) represents the congeneric insertions at the family level and, finally, the final pruned tree containing only the species of interest.

Darwinian_deficit

The *Darwinian_deficit* function calculates a measure of Darwinian shortfalls following Equation 1:

$$PD_{inserted} \Big/ PD_{inserted} + PD_{present\ in\ tree} \qquad \text{Equation 1}$$

In this function, $PD_{inserted}$ is the sum of the branch lengths of species in the phylogenetic tree before the insertion procedure. $PD_{present\ in\ tree}$ is the sum of branch lengths of the species inserted in the tree. The Darwinian deficit ranges from 0 (most species already present in the tree before the insertion procedure) to 1 (all the species in the phylogenetic tree were inserted an was not presented in backbone phylogeny). To calculate the Darwinian shortfall through the *Darwinian_deficit* function, the user must provide a phylogenetic tree and a table of insertions, both obtained from the *FishPhyloMaker* function. For further explanations regarding the usage of functions in FishPhyloMaker package the user can assess the package website https://gabrielnakamura.github.io/FishPhyloMaker/index.html and see the Articles section.

Illustrating the use of FishPhyloMaker package

We provide an example of the usage of the *FishPhyloMaker* package by creating phylogenetic trees using a global dataset of freshwater fishes inhabiting 3,119 drainage basins that cover more than 80% of the Earth surface (Tedesco et al., 2017). This dataset allowed in-depth investigation on the global patterns of species distribution and their evolutionary determinants (*e.g.*, Miller & Román-Palácios, 2021). We built phylogenetic trees for the four major freshwater ecoregions based on species richness: Afrotropics, Indo-Malay, Nearctic, and Neotropics. Moreover, we used this same dataset to demonstrate how to map the Darwinian shortfalls, calculated following Equation 1 through *Darwinian_deficit* function,

for all the drainage basins in the Tedesco et al. (2017) dataset. First, the user must download the package from the online GitHub repository, using the following command line:

```
devtools::install_github("GabrielNakamura/FishPhyloMaker", ref = "main",
build_vignettes = TRUE)
```

We recommend that the user updates all the requested packages to avoid errors related to packages versions. We prepared the fish occurrence by checking the validity of its names by using the function *FishTaxaMaker*. The occurrence matrix encompassed 2,478 species, from which 2,477 were valid names. We applied the *FishPhyloMaker* function separately for each ecoregion using the valid names retrieved from the *FishTaxaMaker* (Figure 2). For simplicity and reproducibility, we set the argument `insert.base.node` as TRUE, thus, inserting all species at the base node of its corresponding family and order. We also set the argument `return.insertions = TRUE` for retrieving the insertion information of each species. Then, we applied the *Darwinian_deficit* functional to calculate the Darwinian shortfall for all the freshwater basins of the world harboring at least three species (Tedesco et al. 2017). The *Darwinian_deficit* function was calculate considering only congeneric insertions, however, the function may also include other levels of phylogenetic insertion, like family and order insertions. All the codes need to fully reproduce these analysis is provided at GitHub (GabrielNakamura/MS_FishPhyloMaker) repository.

Results

The entire insertion procedure lasted approximately two hours using one core from a computer machine with an i5 processor. A total of 821 species were inserted, with the Afrotropics exhibiting the largest number of insertions (359 from 767, Figure 2). On the contrary, the Nearctic displayed the least number of insertions, being only six species inserted at the genus level (2.7% of missing species in the phylogenetic tree). Indo-Malay and

Neotropics presented 30.3% and 30% of insertions, respectively. Except for the Nearctic, all the remaining ecoregions exhibited insertions in all considered taxonomic levels (Figure 2).

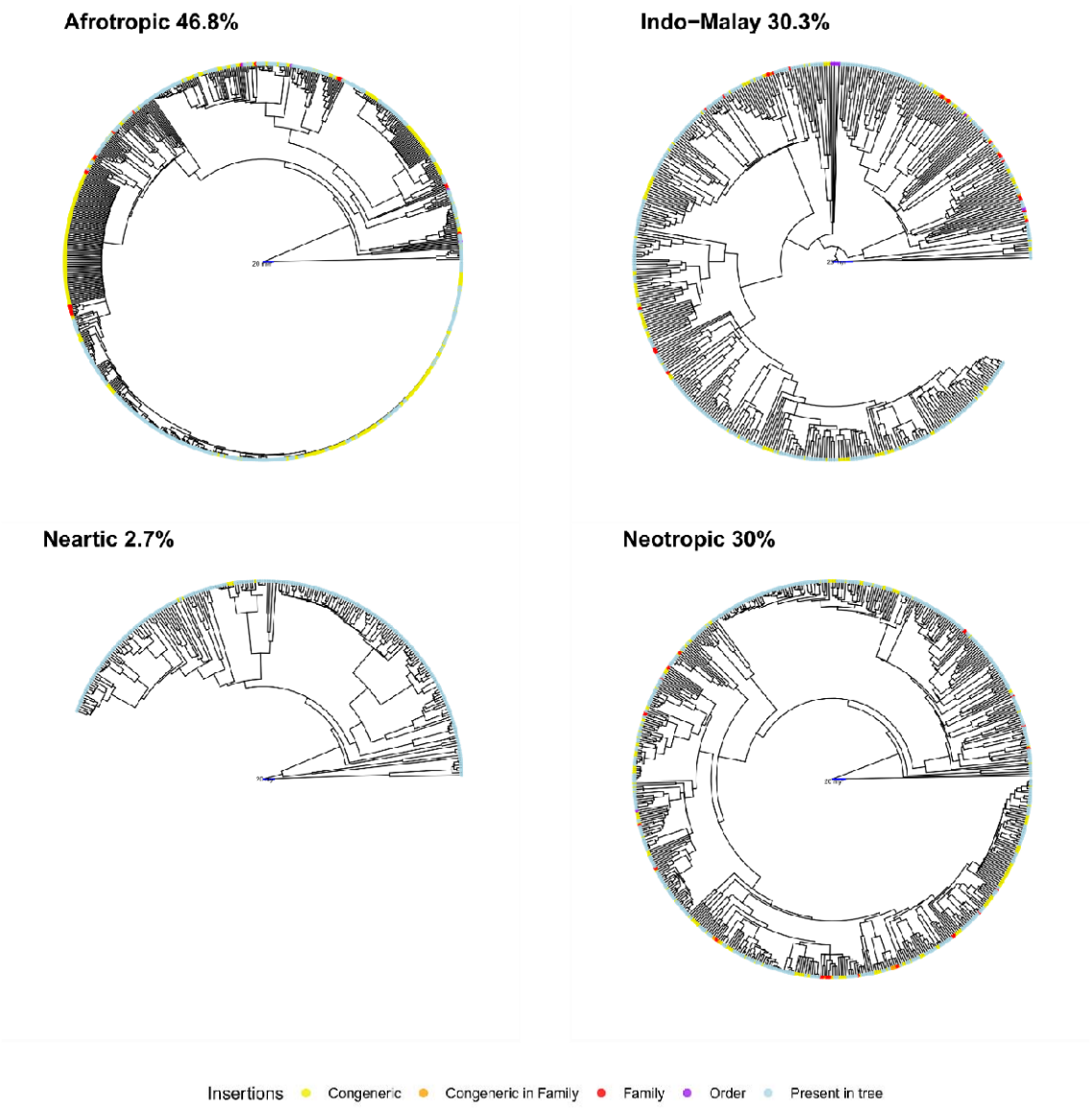

Figure 2: Phylogenetic trees generated with the FishPhyloMaker package for freshwater fishes inhabiting four ecoregions (Afrotropics, Indo-Malay, Nearctic, and Neotropic). The colored tip-points indicate if species were present in the backbone tree (Present in tree) or at which level they were inserted (the code indicating the insertion level was explained in

Methods section). The percentages of insertions over the total number of species for each ecoregion are shown.

We observed that tropical regions exhibited larger Darwinian shortfalls, while northern sites had lower values of shortfalls (Figure 3). The highest values of Darwinian shortfalls were found in Afrotropics and Neotropics, as some drainages did not harbor any (or few) species in the original Rabosky's phylogeny. The grey areas correspond to sites that do not presented species occurrences accordingly to Tedesco et al (2017) study.

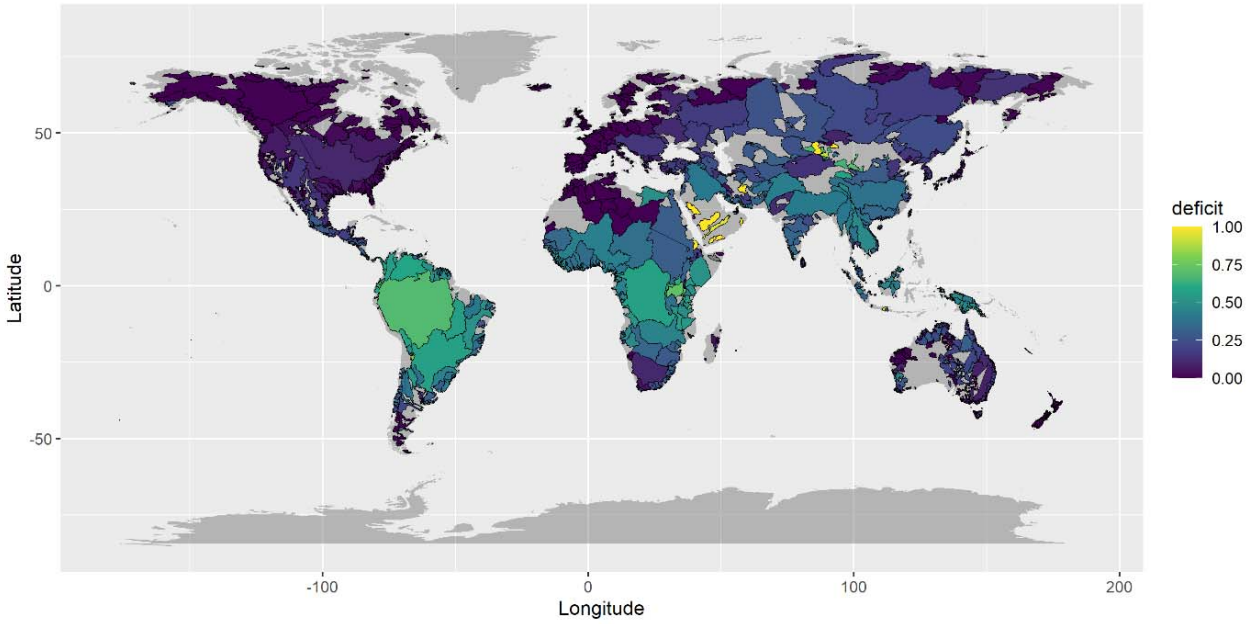

Figure 3: Global distribution of the Darwinian Shortfalls for ray-finned fishes, based on dataset available from Tedesco et al (2017). Values near to 1 indicate a high Darwinian shortfall (a large amount of congeneric insertions), while values near zero indicate a low shortfall. Gray color indicates unsampled areas.

Discussion

We provided a user-friendly, efficient and reproducible way to construct phylogenetic trees for a megadiverse group (Actinopterygii). The FishPhyloMaker package is in line with tools developed for plants, such as Phylomatic (C++ application) and V.PhyloMaker (R package)

(Jin and Qian, 2019; Webb and Donoghue, 2005), but includes different features. These features include new options for inserting species through a interactive procedure in phylogenies and recording insertions. The latter feature allows a better systematization of building supertrees and calculating the first, to our knowledge, quantitative measure of the Darwinian shortfall.

Whereas Phylomatic allows the insertion of absent species only as congeneric or at the node corresponding to the family of the focal species (Webb and Donoghue, 2005), the FishPhyloMaker package delivers options through an interactive procedure of insertion. The performed insertions can be easily recorded in an R script, providing flexibility and the same level of reproducibility as other algorithms designed for similar purposes (*e.g.*, Jin and Qian, 2019). This interactive option is a novelty when compared to similar insertion algorithms (*e.g.*, Phylomatic).

Map the spatial distribution of the Darwinian shortfall is paramount to guide our future efforts to understand the history of life. The phylogenetic gaps in the knowledge of ray-finned fishes are geographically biased, with tropical basins presenting the higher levels of Darwinian shortfalls, as we evidenced in this study. This gap in evolutionary knowledge could lead to a bias in evaluating the effects of evolutionary history and the interpretation of macroecological patterns for fish assemblages in these regions, which in turn can affect conservation decision based on phylogenetic dimension of diversity (Assis, 2018).

Several biological and sociological factors can explain the observed bias in Darwinian shortfalls. First, the regions exhibiting the largest Darwinian gaps exhibit the largest freshwater fish diversity, which we can not describe at the same speed as less biologically rich areas (Hortal et al., 2015). Second, on-ground accessibility, human occupation, and economic development constrain investments in biodiversity research (Moura et al., 2018;

Moura and Jetz, 2021), that is probably more pronounced in tropical regions than temperate ones, which may hamper field sampling and phylogenetic analyses.

Limitations and possible applications

Future developments of the package should consider the Catalog of Fishes (Fricke & Eschemeyer, 2021) to improve the nomenclature checking procedures. Despite Fishbase being a widely used database to check for the taxonomic classification of fishes, it may present delays in updating taxonomic information because it is not its primary purpose. Inversely, the Catalog of Fishes is an authoritative taxonomic list frequently updated.

An inherent limitation of the phylogenetic hypothesis produced by FishPhyloMaker is the large number of polytomies resulting from the insertion procedures. We recommend that users directly assess how the phylogenetic uncertainty affects further analysis when not using a fully solved phylogenetic tree (Martins et al., 2013).

These limitations do not preclude the package applicability for studies in phylogenetic community ecology since synthesis phylogenies do not significantly impact phylogenetic diversity indices (Li et al., 2019). Moreover, this is the only automated tool able to provide a complete phylogenetic tree that can easily handle large datasets. FishPhyloMaker can be relevant for addressing several critical questions in ecology and evolution by facilitating the obtention of phylogenetic hypotheses for local pools of ray-finned fishes. This facilitation can be essential for regions with a large gap in the phylogenetic knowledge of fishes, such as the Neotropical region (Albert et al., 2020). Such phylogenetic hypotheses allow understanding how ecological traits evolved or how the current and past environmental conditions selected the lineages in different areas.

Biogeographical studies are usually restricted to one or a few lineages at larger scales due to the availability of molecular phylogenies (e.g. Garcia-Andrade et al. 2021). The FishPhyloMaker package facilitates large-scale investigations on the biogeographic history of

the most diverse group of vertebrates on Earth, the Actinopterygians, helping us understand the processes that drive this high diversity. Finally, we can map where the lack of phylogenetic information is the most critical once the function returns the insertion level of species. This information can directly elucidate the patterns of the Darwinian shortfalls for ray-finned fishes, contributing not only to direct sampling and studying efforts but also to evidence the need for increased efforts to decolonize science (Trisos et al., 2021). Therefore, we expect that the FishPhyloMaker package reduces the gaps and barriers to addressing ecological and evolutionary questions due to the difficulty or lack of a reliable phylogenetic hypothesis for local and regional pools of ray-finned fishes.

Contributions

GN Conceptualization; Data curation; Formal Analysis; Methodology; Software; Writing – original draft. AR Data curation; Methodology; Software, Writing – review and editing. BES Writing – original draft; Methodology.

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