

RNeXML: a package for reading and writing richly annotated phylogenetic, character, and trait data in R

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Abstract

1. NeXML is a powerful and extensible exchange standard recently proposed to better meet the expanding needs for phylogenetic data and metadata sharing. Here we present the RNeXML package, which provides users of the R programming language with easy-to-use tools for reading and writing NeXML documents, including rich metadata, in a way that interfaces seamlessly with the extensive library of phylogenetic tools already available in the R ecosystem.
2. Wherever possible, we designed RNeXML to map NeXML document contents, whose arrangement is influenced by the format's XML Schema definition, to their most intuitive or useful representation in R. To make NeXML's powerful facility for recording semantically rich machine-readable metadata accessible to R users, we designed a functional programming interface to it that hides the semantic web standards leveraged by NeXML from R users who are unfamiliar with them.
3. RNeXML can read any NeXML document that validates, and it generates valid NeXML documents from phylogeny and character data in various R representations in use. The metadata programming interface at a basic level aids fulfilling data documentation best practices, and at an advanced level preserves NeXML's nearly limitless extensibility, for which we provide a fully working demonstration. Furthermore, to lower the barriers to sharing well-documented phylogenetic data, RNeXML has started to integrate with taxonomic metadata augmentation services on the web, and with online repositories for data archiving.
4. RNeXML allows R's rich ecosystem to read and write data in the NeXML format through an interface that is no more involved than reading or writing data from other, less powerful data formats. It also provides an interface designed to feel familiar to R programmers and to be consistent with recommended practices for R package development, yet that retains the full power

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for users to add their own custom data and metadata to the phylogenies they work with, without introducing potentially incompatible changes to the exchange standard.

Introduction

Users of the popular statistical and mathematical computing platform R (R Core Team 2014) enjoy a wealth of readily installable comparative phylogenetic methods and tools (O’Meara 2014). Exploiting the opportunities arising from this wealth for complex and integrative comparative research questions relies on the ability to reuse and integrate previously generated or published data and metadata. The expanding data exchange needs of the evolutionary research community are rapidly outpacing the capabilities of most current and widely used data exchange standards (Vos *et al.* 2012), which were all developed a decade or more ago. This has resulted in a radiation of different data representations and exchange standard “flavors” that are no longer interoperable at the very time when the growth of available data and methods has made that interoperability most valuable. In response to the unmet needs for standardized data exchange in phylogenetics, a modern XML-based exchange standard, called NeXML, has recently been developed (Vos *et al.* 2012). NeXML comprehensively supports current data exchange needs, is predictably machine-readable, and is forward compatible.

The exchange problem for phylogenetic data is particularly acute in light of the challenges in finding and sharing phylogenetic data without the otherwise common loss of most data and metadata semantics (Stoltzfus *et al.* 2012; Drew *et al.* 2013; Cranston *et al.* 2014). For example, the still popular NEXUS file format (Maddison *et al.* 1997) cannot consistently represent horizontal gene transfer or ambiguity in reading a character (such as a DNA sequence base pair). This and other limitations have led to modifications of NEXUS in different ways for different needs, with the unfortunate result that NEXUS files generated by one program can be incompatible with another (Vos *et al.* 2012). Without a formal grammar, software based on NEXUS files may also make inconsistent assumptions about tokens, quoting, or element lengths. Vos *et al.* (2012) estimates that as many as 15% of the NEXUS files in the CIPRES portal contain unrecoverable but hard to diagnose errors.

A detailed account of how the NeXML standard addresses these and other relevant challenges can be found in Vos *et al.* (2012). In brief, NeXML was designed with the following important properties. First, NeXML is defined by a precise grammar that can be programmatically **validated**; i.e., it can be verified whether a file precisely follows this grammar, and therefore whether it can be read (parsed) without

errors by software that uses the NeXML grammar (e.g. RNeXML) is predictable. Second, NeXML is **extensible**: a user can define representations of new, previously unanticipated information (as we will illustrate) without violating its defining grammar. Third and most importantly, NeXML is rich in **computable semantics**: it is designed for expressing metadata such that machines can understand their meaning and make inferences from it. For example, OTUs in a tree or character matrix for frog species can be linked to concepts in a formally defined hierarchy of taxonomic concepts such as the Vertebrate Taxonomy Ontology (Midford *et al.* 2013), which enables a machine to infer that a query for amphibia is to include the frog data in what is returned. (For a more broader discussion of the value of such capabilities for evolutionary and biodiversity science we refer the reader to Parr et al. (2011).) To make the capabilities of NeXML available to R users in an easy-to-use form, and to lower the hurdles to adoption of the standard, we present RNeXML, an R package that aims to provide easy programmatic access to reading and writing NeXML documents, tailored for the kinds of use-cases that will be common for users and developers of the wealth of evolutionary analysis methods within the R ecosystem.

The RNeXML package

The RNeXML package is written entirely in R and available under a Creative Commons Zero public domain waiver. The current development version can be found on Github at <https://github.com/ropensci/RNeXML>, and the stable version can be installed from the CRAN repository. RNeXML is part of the rOpenSci project. Users of RNeXML are encouraged to submit bug reports or feature requests in the issues log on Github, or the phylogenetics R users group list at r-sig-phylo@r-project.org for help. Vignettes with more detailed examples of specific features of RNeXML are distributed with the R package and serve as a supplement to this manuscript. Each of the vignettes can be found at <http://ropensci.github.io/RNeXML/>.

Representation of NeXML documents in R

Conceptually, a NeXML document has the following components: (1) phylogeny topology and branch length data, (2) character or trait data in matrix form, (3) operational taxonomic units (OTUs), and (4) metadata. To represent the contents of a NeXML document (currently in memory), RNeXML defines the `nexml` object type. This type therefore holds phylogenetic trees as well as character or trait matrices, and all metadata, which is similar to the phylogenetic data object types defined in the `phylobase`

89 package (NESCENT R Hackathon Team 2014), but contrasts with the more widely used ones defined
90 in the **ape** package (Paradis *et al.* 2004), which represents trees alone.

91 When reading and writing NeXML documents, **RNeXML** aims to map their components to and from,
92 respectively, their most widely used representations in R. As a result, the types of objects accepted
93 or returned by the package's methods are the **phylo** and **multiPhylo** objects from the **ape** package
94 (Paradis *et al.* 2004) for phylogenies, and R's native **data.frame** list structure for data matrices.

95 *Reading phylogenies and character data*

96 The method **nexml_read()** reads NeXML files, either from a local file, or from a remote location via
97 its URL, and returns an object of type **nexml**:

```
nex <- nexml_read("components/trees.xml")
```

98 The method **get_trees_list()** can be used to extract the phylogenies as an **ape::multiPhylo** object,
99 which can be treated as a list of **ape::phylo** objects:

```
phy <- get_trees_list(nex)
```

100 The **get_trees_list()** method is designed for use in scripts, providing a consistent and predictable
101 return type regardless of the number of phylogenies a NeXML document contains. For greater convenience
102 in interactive use, the method **get_trees()** returns the R object most intuitive given the arrangement
103 of phylogeny data in the source NeXML document. For example, the method returns an **ape::phylo**
104 object if the NeXML document contains a single phylogeny, an **ape::multiPhylo** object if it contains
105 multiple phylogenies arranged in a single **trees** block, and a list of **ape::multiPhylo** objects if it
106 contains multiple **trees** blocks (the capability for which NeXML inherits from NEXUS).

107 If the location parameter with which the **nexml_read()** method is invoked is recognized as a URL,
108 the method will automatically download the document to the local working directory and read it from
109 there. This gives convenient and rapid access to phylogenetic data published in NeXML format on the
110 web, such as the content of the phylogenetic data repository TreeBASE (Piel *et al.* 2002, 2009). For
111 example, the following plots a tree in TreeBASE (using **ape**'s **plot** function):

```
tb_nex <- nexml_read(
  "https://raw.githubusercontent.com/TreeBASE/supertreebase/master/data/treebase/S100.xml")
tb_phy <- get_trees_list(tb_nex)
plot(tb_phy[[1]])
```

112 The method `get_characters()` obtains character data matrices from a `nexml` object, and returns them
 113 as a standard `data.frame` R object with columns as characters and rows as taxa:

```
nex <- nexml_read("components/comp_analysis.xml")
get_characters(nex)
```

```
114      log snout-vent length reef-dwelling
115 taxon_8      -3.2777799           0
116 taxon_9       2.0959433           1
117 taxon_10      3.1373971           0
118 taxon_1       4.7532824           1
119 taxon_2      -2.7624146           0
120 taxon_3       2.1049413           0
121 taxon_4      -4.9504770           0
122 taxon_5       1.2714718           1
123 taxon_6       6.2593966           1
124 taxon_7       0.9099634           1
```

125 A NeXML data matrix can be of molecular (for molecular sequence alignments), discrete (for most
 126 morphological character data), or continuous type (for many trait data). To enable strict validation
 127 of data types NeXML allows, and if their data types differ requires multiple data matrices to be
 128 separated into different “blocks”. Since the `data.frame` data structure in R has no such constraints, the
 129 `get_characters()` method combines such blocks as separate columns into a single `data.frame` object,
 130 provided they correspond to the same taxa. Otherwise, a list of `data.frames` is returned, with list
 131 elements corresponding to characters blocks. Similar to the methods for obtaining trees, there is also a
 132 method `get_characters_list()`, which always returns a list of `data.frames`, one for each character
 133 block.

134 *Writing phylogenies and character data*

135 The method `nexml_write()` generates a NeXML file from its input parameters. In its simplest
136 invocation, the method writes a tree to a file:

```
data(bird.orders)
nexml_write(bird.orders, file = "birds.xml")
```

137 The first argument to `nexml_write()` is either an object of type `nexml`, or any object that can be coerced
138 to it, such as in the above example an `ape::phylo` phylogeny. Alternatively, passing a `multiPhylo`
139 object would write a list of phylogenies to the file.

140 In addition to trees, the `nexml_write()` method also allows to specify character data as another
141 parameter. The following example uses data from the comparative phylogenetics R package `geiger`
142 (Pennell *et al.* 2014).

```
library("geiger")
data(geospiza)
nexml_write(trees = geospiza$phy,
            characters = geospiza$dat,
            file="geospiza.xml")
```

143 Note that the NeXML format is well-suited for incomplete data: for instance, here it does not assume
144 the character matrix has data for every tip in the tree.

145 *Validating NeXML*

146 File validation is a central feature of the NeXML format which ensures that any properly implemented
147 NeXML parser will always be able to read the NeXML file. The function takes the path to any NeXML
148 file and returns `TRUE` to indicate a valid file, or `FALSE` otherwise, along with a display of any error
149 messages generated by the validator.

```
nexml_validate("geospiza.xml")
```

150 [1] TRUE

151 The `nexml_validate()` function performs this validation using the online NeXML validator (when a
152 network connection is available), which performs additional checks not expressed in the NeXML schema
153 itself (Vos *et al.* 2012). If a network connection is not available, the function falls back on the schema
154 validation method from the XML package (Lang 2013).

155 *Creating and populating `nexml` objects*

156 Instead of packaging the various components for a NeXML file at the time of writing the file, RNeXML
157 also allows users to create and iteratively populate in-memory `nexml` objects. The methods to do this
158 are `add_characters()`, `add_trees()`, and `add_meta()`, for adding characters, trees, and metadata,
159 respectively. Each of these functions will automatically create a new `nexml` object if not supplied with
160 an existing one as the last (optional) argument.

161 For example, here we use `add_trees()` to first create a `nexml` object with the phylogeny data, and
162 then add the character data to it:

```
nexObj <- add_trees(geospiza$phy)
nexObj <- add_characters(geospiza$dat, nexObj)
```

163 The data with which a `nexml` object is populated need not share the same OTUs. RNeXML automatically
164 adds new, separate OTU blocks into the NeXML file for each data matrix and tree that uses a different
165 set of OTUs.

166 Other than storage size, there is no limit to the number of phylogenies and character matrices that
167 can be included in a single NeXML document. This allows, for example, to capture samples from a
168 posterior probability distribution of inferred or simulated phylogenies and character states in a single
169 NeXML file.

170 *Data documentation and annotation with built-in metadata*

171 NeXML allows attaching (“*annotating*”) metadata to any data element, and even to metadata themselves.
172 Whether at the level of the document as a whole or an individual data matrix or phylogeny, metadata
173 can provide bibliographic and provenance information, for example about the study as part of which
174 the phylogeny was generated or applied, which data matrix and which methods were used to generate it.
175 Metadata can also be attached to very specific elements of the data, such as specific traits, individual
176 OTUs, nodes, or even edges of the phylogeny.

177 As described in Vos et al. (2012), to encode metadata annotations NeXML uses the “Resource
178 Description Framework in Annotations” (RDFa) (Prud’hommeaux 2014). This standard provides for
179 a strict machine-readable format yet enables future backwards compatibility with compliant NeXML
180 parsers (and thus RNeXML), because the capacity of a tool to *parse* annotations is not predicated on
181 *understanding* the meaning of annotations it has not seen before.

182 To lower the barriers to sharing well-documented phylogenetic data, RNeXML aims to make recording
183 useful and machine-readable metadata easier at several levels.

184 First, when writing a NeXML file the package adds certain basic metadata automatically if they
185 are absent, using default values consistent with recommended best practices (Cranston *et al.* 2014).
186 Currently, this includes naming the software generating the NeXML, a time-stamp of when a tree was
187 produced, and an open data license. These are merely default arguments to `add_basic_meta()` and
188 can be configured.

189 Second, RNeXML provides a simple method, called `add_basic_metadata()`, to set metadata attributes
190 commonly recommended for inclusion with data to be publicly archived or shared (Cranston *et al.*
191 2014). The currently accepted parameters include `title`, `description`, `creator`, `pubdate`, `rights`,
192 `publisher`, and `citation`. Behind the scenes the method automatically anchors these attributes in
193 common vocabularies (such as Dublin Core).

194 Third, RNeXML integrates with the R package `taxize` (Chamberlain & Szöcs 2013) to mitigate one of
195 the most common obstacles to reuse of phylogenetic data, namely the misspellings and inconsistent
196 taxonomic naming with which OTU labels are often fraught. The `taxize_nexml()` method in RNeXML
197 uses `taxize` to match OTU labels against the NCBI database, and, where a unique match is found, it
198 annotates the respective OTU with the matching NCBI identifier.

199 *Data annotation with custom metadata*

200 The RNeXML interface described above for built-in metadata allows users to create precise and semantically
201 rich annotations without confronting any of the complexity of namespaces and ontologies. Nevertheless,
202 advanced users may desire the explicit control over these semantic tools that takes full advantage of
203 the flexibility and extensibility of the NeXML specification (Parr *et al.* 2011; Vos *et al.* 2012). In this
204 section we detail how to accomplish these more complex uses in RNeXML.

205 Using a vocabulary or ontology terms rather than simple text strings to describe data is crucial for
206 allowing machines to not only parse but also interpret and potentially reason over their semantics.

207 To achieve this benefit for custom metadata extensions, the user necessarily needs to handle certain
208 technical details from which the RNeXML interface shields her otherwise, in particular the globally unique
209 identifiers (normally HTTP URIs) of metadata terms and vocabularies. To be consistent with XML
210 terminology, RNeXML calls vocabulary URIs *namespaces*, and their abbreviations *prefixes*. For example,
211 the namespace for the Dublin Core Metadata Terms vocabulary is “<http://purl.org/dc/elements/1.1/>”.
212 Using its common abbreviation “dc”, a metadata property “dc:title” expands to the identifier “<http://purl.org/dc/elements/1.1/title>”. This URI resolves to a human and machine-readable (depending on
214 access) definition of precisely what the term `title` in Dublin Core means. In contrast, just using the
215 text string “title” could also mean the title of a person, a legal title, the verb title, etc. URI identifiers
216 of metadata vocabularies and terms are not mandated to resolve, but if machines are to derive the
217 maximum benefit from them, they should resolve to a definition of their semantics in RDF.

218 RNeXML includes methods to obtain and manipulate metadata properties, values, identifiers, and
219 namespaces. The `get_namespaces()` method accepts a `nexml` object and returns a named list of
220 namespace prefixes and their corresponding identifiers known to the object:

```
birds <- nexml_read("birds.xml")
prefixes <- get_namespaces(birds)
prefixes["dc"]
```

```
221                                     dc
222 "http://purl.org/dc/elements/1.1/"
```

223 The `get_metadata()` method returns, as a named list, the metadata annotations for a given `nexml`
224 object at a given level, with the whole NeXML document being the default level ("`all`" extracts all
225 metadata objects):

```
meta <- get_metadata(birds)
otu_meta <- get_metadata(birds, level="otu")
```

226 The returned list does not include the data elements to which the metadata are attached. Therefore, a
227 different approach, documented in the metadata vignette, is recommended for accessing the metadata
228 attached to data elements.

229 The `meta()` method creates a new metadata object from a property name and content (value). For
230 example, the following creates a modification date metadata object, using a property in the PRISM
231 vocabulary:

```
modified <- meta(property = "prism:modificationDate", content = "2013-10-04")
```

232 Metadata annotations in NeXML can be nested within another annotation, which the `meta()` method
233 accommodates by accepting a parameter `children`, with the list of nested metadata objects (which can
234 themselves be nested) as value.

235 The `add_meta()` function adds metadata objects as annotations to a `nexml` object at a specified level,
236 with the default level being the NeXML document as a whole:

```
birds <- add_meta(modified, birds)
```

237 If the prefix used by the metadata property is not among the built-in ones (which can be obtained
238 using `get_namespaces()`), it has to be provided along with its URI as the `namespaces` parameter. For
239 example, the following uses the “[Simple Knowledge Organization System](http://www.w3.org/2004/02/skos/core#)” (SKOS) vocabulary to add a
240 note to the trees in the `nexml` object:

```
history <- meta(property = "skos:historyNote",  
  content = "Mapped from the bird.orders data in the ape package using RNeXML")  
birds <- add_meta(history,  
  birds,  
  level = "trees",  
  namespaces = c(skos = "http://www.w3.org/2004/02/skos/core#"))
```

241 Alternatively, additional namespaces can also be added in batch using the `add_namespaces()` method.
242 By virtue of subsetting the S4 `nexml` object, RNeXML also offers fine control of where a `meta` element is
243 added, for which the package vignette on S4 subsetting of `nexml` contains examples.

244 Because NeXML expresses all metadata using the RDF standard, and stores them compliant with
245 RDFa, they can be extracted as an RDF graph, queried, analyzed, and mashed up with other RDF data,
246 local or on the web, using a wealth of off-the-shelf tools for working with RDF (see Prud’hommeaux
247 (2014) or Hartig (2012)). Examples for these possibilities are included in the RNeXML SPARQL vignette

(a recursive acronym for SPARQL Protocol and RDF Query Language, see <http://www.w3.org/TR/rdf-sparql-query/>), and the package also comes with a demonstration that can be run from R using the following command: `demo("sparql", "RNeXML")`).

Using metadata to extend the NeXML standard

NeXML was designed to prevent the need for future non-interoperable “flavors” of the standard in response to new research directions. Its solution to this inevitable problem is a highly flexible metadata system without sacrificing strict validation of syntax and structure.

Here we illustrate how RNeXML’s interface to NeXML’s metadata system can be used to record and share a type of phylogenetic data not taken into account when NeXML was designed, in this case stochastic character maps (Huelsenbeck *et al.* 2003). Such data assign certain parts (corresponding to time) of each branch in a time-calibrated phylogeny to a particular “state” (typically of a morphological characteristic). The current de-facto format for sharing stochastic character maps, created by `simmap` (Bollback 2006), a widely used tool for creating such maps, is a non-interoperable modification of the standard Newick tree format. This means that computer programs designed to read Newick or NEXUS formats may fail when trying to read in a phylogeny that includes `simmap` annotations.

In contrast, by allowing new data types to be added as — sometimes complex — metadata annotations NeXML can accommodate data extensions without compromise to its grammar and thus syntax. In NeXML. To illustrate how RNeXML facilitates extending the NeXML standard in this way, we have implemented two functions in the package, `nexml_to_simmap` and `simmap_to_nexml`. These functions show how `simmap` data can be represented as `meta` annotations on the branch length elements of a NeXML tree, and provide routines to convert between this NeXML representation and the extended `ape::phylo` representation of a `simmap` tree in R that was introduced by Revell (2012). We encourage readers interested in this capability to consult the example code in `simmap_to_nexml` to see how this is implemented.

Extensions to NeXML must also be defined in the file’s namespace in order to valid. This provides a way to ensure that a URI providing documentation of the extension is always included. Our examples here use the prefix, `simmap`, to group the newly introduced metadata properties in a vocabulary, for which the `add_namespace()` method can be used to give a URI as an identifier:

```
nex <- add_namespaces(c(simmap =  
  "https://github.com/ropensci/RNeXML/tree/master/inst/simmap.md"))
```

Here the URI does not resolve to a fully machine-readable definition of the terms and their semantics, but it can nonetheless be used to provide at least a human-readable informal definition of the terms.

Publishing NeXML files from R

Data archiving is increasingly required by scientific journals, including in evolutionary biology, ecology, and biodiversity (e.g. Rausher et al. (2010)). The effort involved with preparing and submitting properly annotated data to archives remains a notable barrier to the broad adoption of data archiving and sharing as a normal part of the scholarly publication workflow (Tenopir *et al.* 2011; Stodden 2014). In particular, the majority of phylogenetic trees published in the scholarly record are inaccessible or lost to the research community (Drew *et al.* 2013).

One of RNeXML's aims is to promote the archival of well-documented phylogenetic data in scientific data repositories, in the form of NeXML files. To this end, the method `nexml_publish()` provides an API directly from within R that allows data archival to become a step programmed into data management scripts. Initially, the method supports the data repository Figshare (<http://figshare.com>):

```
doi <- nexml_publish(birds, repository="figshare")
```

This method reserves a permanent identifier (DOI) on the figshare repository that can later be made public through the figshare web interface. This also acts as a secure backup of the data to a repository and a way to share with collaborators prior to public release.

Conclusions and future directions

RNeXML allows R's ecosystem to read and write data in the NeXML format through an interface that is no more involved than reading or writing data from other phylogenetic data formats. It also carries immediate benefits for its users compared to other formats. For example, comparative analysis R packages and users frequently add their own metadata annotations to the phylogenies they work with, such as annotations of species, stochastic character maps, trait values, model estimates and parameter values. RNeXML affords R the capability to harness machine-readable semantics and an extensible

299 metadata schema to capture, preserve, and share these and other kinds of information, all through an
300 API instead of having to understand in detail the schema underlying the NeXML standard. To assist
301 users in meeting the rising bar for best practices in data sharing in phylogenetic research (Cranston *et*
302 *al.* 2014), RNeXML captures metadata information from the R environment to the extent possible, and
303 applies reasonable defaults.

304 The goals for continued development of RNeXML revolve primarily around better interoperability with
305 other existing phylogenetic data representations in R, such as those found in the **phylobase** package
306 (NESCENT R Hackathon Team 2014); and better integration of the rich metadata semantics found in
307 ontologies defined in the Web Ontology Language (OWL), including programmatic access to machine
308 reasoning with such metadata.

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316 their behest, the reviews of FitzJohn and Pennell can be found in this project's GitHub page at
317 github.com/ropensci/RNeXML/issues/120 and github.com/ropensci/RNeXML/issues/120, together
318 with our replies and a record of our revisions.

319 *Data Accessibility*

320 All software, scripts and data used in this paper can be found in the permanent data archive Zenodo under
321 the digital object identifier [doi:10.5281/zenodo.13131](https://doi.org/10.5281/zenodo.13131) (Boettiger *et al.* 2014). This DOI corresponds to
322 a snapshot of the GitHub repository at github.com/ropensci/RNeXML.

323 **References**

324 Boettiger, C., Vos, R., Chamberlain, S. & Lapp, H. (2014). RNeXML v2.0.0. Retrieved from [http:](http://dx.doi.org/10.5281/zenodo.13131)
325 [//dx.doi.org/10.5281/zenodo.13131](http://dx.doi.org/10.5281/zenodo.13131)

326 Bollback, J. (2006). *BMC Bioinformatics*, **7**, 88. Retrieved from [http://dx.doi.org/10.1186/1471-2105-7-](http://dx.doi.org/10.1186/1471-2105-7-88)
327 88

328 Chamberlain, S.A. & Szöcs, E. (2013). Taxize: Taxonomic search and retrieval in r. *F1000Research*.
329 Retrieved from <http://dx.doi.org/10.12688/f1000research.2-191.v2>

330 Cranston, K., Harmon, L.J., O’Leary, M.A. & Lisle, C. (2014). Best practices for data shar-
331 ing in phylogenetic research. *PLoS Curr.* Retrieved from [http://dx.doi.org/10.1371/currents.tol.](http://dx.doi.org/10.1371/currents.tol.bf01eff4a6b60ca4825c69293dc59645)
332 [bf01eff4a6b60ca4825c69293dc59645](http://dx.doi.org/10.1371/currents.tol.bf01eff4a6b60ca4825c69293dc59645)

333 Drew, B.T., Gazis, R., Cabezas, P., Swithers, K.S., Deng, J., Rodriguez, R., Katz, L.A., Crandall,
334 K.A., Hibbett, D.S. & Soltis, D.E. (2013). Lost branches on the tree of life. *PLoS Biol*, **11**, e1001636.
335 Retrieved from <http://dx.doi.org/10.1371/journal.pbio.1001636>

336 Hartig, O. (2012). An introduction to sPARQL and queries over linked data. *Web engineering* pp.
337 506–507. Springer Science + Business Media. Retrieved from [http://dx.doi.org/10.1007/978-3-642-](http://dx.doi.org/10.1007/978-3-642-31753-8_56)
338 [31753-8_56](http://dx.doi.org/10.1007/978-3-642-31753-8_56)

339 Huelsenbeck, J.P., Nielsen, R. & Bollback, J.P. (2003). Stochastic mapping of morphological characters.
340 *Systematic Biology*, **52**, 131–158. Retrieved from <http://dx.doi.org/10.1080/10635150390192780>

341 Lang, D.T. (2013). *XML: Tools for parsing and generating xML within r and s-plus*. Retrieved from
342 <http://CRAN.R-project.org/package=XML>

343 Maddison, D., Swofford, D. & Maddison, W. (1997). NEXUS: An extensible file format for systematic
344 information. *Syst. Biol.*, **46**, 590–621. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/11975335>

345 Midford, P., Dececchi, T., Balhoff, J., Dahdul, W., Ibrahim, N., Lapp, H., Lundberg, J., Mabee, P.,
346 Sereno, P., Westerfield, M., Vision, T. & Blackburn, D. (2013). The vertebrate taxonomy ontology: A
347 framework for reasoning across model organism and species phenotypes. *J. Biomed. Semantics*, **4**, 34.
348 Retrieved from <http://dx.doi.org/10.1186/2041-1480-4-34>

349 NESCENT R Hackathon Team. (2014). *Phylobase: Base package for phylogenetic structures and*
350 *comparative data*. Retrieved from <http://CRAN.R-project.org/package=phylobase>

351 O’Meara, B. (2014). CRAN task view: Phylogenetics, especially comparative methods. Retrieved from
352 <http://cran.r-project.org/web/views/Phylogenetics.html>

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

355 Parr, C.S., Guralnick, R., Cellinese, N. & Page, R.D.M. (2011). Evolutionary informatics: unifying
 356 knowledge about the diversity of life. *Trends in ecology & evolution*, **27**, 94–103. Retrieved from
 357 <http://www.ncbi.nlm.nih.gov/pubmed/22154516>

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

361 Piel, W.H., Chan, L., Dominus, M.J., Ruan, J., Vos, R.A. & Tannen, V. (2009). TreeBASE v. 2: A
 362 database of phylogenetic knowledge. Retrieved from <http://www.e-biosphere09.org>

363 Piel, W.H., Donoghue, M.J. & Sanderson, M.J. (2002). TreeBASE: A database of phylogenetic
 364 information. *The interoperable ‘catalog of life’* (eds J. Shimura, K.L. Wilson & D. Gordon), pp. 41–47.
 365 Research report. National Institute for Environmental Studies, Tsukuba, Japan. Retrieved from
 366 http://donoghuelab.yale.edu/sites/default/files/124_piel_shimura02.pdf

367 Prud’hommeaux, E. (2014). SPARQL query language for rDF. *W3C*. Retrieved from <http://www.w3.org/TR/rdf-sparql-query/>
 368

369 R Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for
 370 Statistical Computing, Vienna, Austria. Retrieved from <http://www.R-project.org/>

371 Rausher, M.D., McPeck, M.A., Moore, A.J., Rieseberg, L. & Whitlock, M.C. (2010). Data archiving.
 372 *Evolution*, **64**, 603–604. Retrieved from <http://dx.doi.org/10.1111/j.1558-5646.2009.00940.x>

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

375 Stodden, V. (2014). The scientific method in practice: Reproducibility in the computational sciences.
 376 *SSRN Journal*. Retrieved from <http://dx.doi.org/10.2139/ssrn.1550193>

377 Stoltzfus, A., O’Meara, B., Whitacre, J., Mounce, R., Gillespie, E.L., Kumar, S., Rosauer, D.F. & Vos,
 378 R.A. (2012). Sharing and re-use of phylogenetic trees (and associated data) to facilitate synthesis. *BMC*
 379 *Research Notes*, **5**, 574. Retrieved from <http://dx.doi.org/10.1186/1756-0500-5-574>

380 Tenopir, C., Allard, S., Douglass, K., Aydinoglu, A.U., Wu, L., Read, E., Manoff, M. & Frame, M.
 381 (2011). Data sharing by scientists: Practices and perceptions (C. Neylon, Ed.). *PLoS ONE*, **6**, e21101.
 382 Retrieved from <http://dx.doi.org/10.1371/journal.pone.0021101>

383 Vos, R.A., Balhoff, J.P., Caravas, J.A., Holder, M.T., Lapp, H., Maddison, W.P., Midford, P.E.,

384 Priyam, A., Sukumaran, J., Xia, X. & Stoltzfus, A. (2012). NeXML: Rich, extensible, and verifiable
385 representation of comparative data and metadata. *Systematic Biology*, **61**, 675–689. Retrieved from
386 <http://dx.doi.org/10.1093/sysbio/sys025>