

# Towards an Ecological Trait-data Standard

1  
2 Florian D. Schneider <sup>\*‡</sup> Malte Jochum <sup>§</sup> Gaëtane Le Provost <sup>‡</sup>  
3 Andreas Ostrowski <sup>||</sup> Caterina Penone <sup>§</sup> David Fichtmüller <sup>¶</sup>  
4 Martin M. Gossner <sup>††</sup> Anton Güntsch <sup>¶</sup> Birgitta König-Ries <sup>||</sup>  
5 Pete Manning <sup>‡</sup> Nadja K. Simons <sup>\*\*</sup>

---

\*Corresponding author: [florian.dirk.schneider@gmail.com](mailto:florian.dirk.schneider@gmail.com)

<sup>†</sup>Institute of Linguistics and Literary Studies, Technische Universität Darmstadt, Darmstadt, Germany

<sup>\*</sup>Senckenberg Biodiversity and Climate Research Centre (BiK-F) Frankfurt am Main, Germany

<sup>§</sup>Institute of Plant Sciences, University of Bern, Bern, Switzerland

<sup>¶</sup>Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin, Berlin, Germany

<sup>||</sup>Department of Mathematics and Computer Science, Friedrich-Schiller-Universität Jena, Jena, Germany

<sup>††</sup>Forest Entomology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

<sup>\*\*</sup>Department of Ecology and Ecosystem Management, Technische Universität München, Freising, Germany

## 6 **Abstract**

- 7 1. Trait-based approaches are widespread throughout ecological research, offering great  
8 potential for trait data to deliver general and mechanistic conclusions. Accordingly,  
9 a wealth of trait data is available for many organism groups, but, due to a lack of  
10 standardisation, these data come in heterogeneous formats.
- 11 2. We review current initiatives and infrastructures for standardising trait data and dis-  
12 cuss the importance of standardisation for trait data hosted in distributed open-access  
13 repositories.
- 14 3. In order to facilitate the standardisation and harmonisation of distributed trait  
15 datasets, we propose a general and simple vocabulary as well as a simple data  
16 structure for storing and sharing ecological trait data.
- 17 4. Additionally, we provide an R-package that enables the transformation of any tabular  
18 dataset into the proposed format. This also allows trait datasets from heterogeneous  
19 sources to be harmonised and merged, thus facilitating data compilation for any par-  
20 ticular research focus.
- 21 5. With these decentralised tools for trait-data harmonisation, we intend to facilitate  
22 the exchange and analysis of trait data within ecological research and enable global  
23 syntheses of traits across a wide range of taxa and ecosystems.

## 24 **Key-words:**

25 functional ecology, species traits, semantic web, ontologies, data standard

**Table 1** | Glossary of terms from the biodiversity data-management context as they are used in this paper; draws from Garnier et al. (2017).

Term	Definition
Term	A word that describes a particular <i>concept</i> as part of the specialised vocabulary of a field
Concept	An idea, notion or object that is made explicit in an information context by <i>name</i> , definition, <i>URI</i> or other reference ( <a href="https://www.w3.org/TR/skos-reference/">https://www.w3.org/TR/skos-reference/</a> )
Controlled vocabulary	A list of <i>terms</i> that gives all valid consensus terms for a particular context, while no unlisted entries are accepted
Terminology	The body of <i>terms</i> and <i>concepts</i> used with a particular application in a subject of study, usually formalised in a <i>thesaurus</i> or <i>ontology</i>
Data standard	A published set of instructions and <i>terminologies</i> for storing and exchanging data content of a particular type (e.g. trait data), that is recognised by a large proportion of members of the application context
Thesaurus	<i>Controlled vocabulary</i> that provides key <i>terms</i> with their associated <i>concepts</i> for a specific field or domain of interest (Laporte et al. 2013)
Ontology	<i>Controlled vocabulary</i> that (opposed to a <i>thesaurus</i> ) relates <i>concepts</i> to each other by cross-references, e.g. defines a hierarchy of terms; thus a formal model of the objects and their relationships in a domain of interest (Gruber 1995)
Semantic web	An extension of the world wide web that aims for machine-readable meaning of information via well-defined <i>data standards</i> , <i>ontologies</i> and exchange protocols (Berners-Lee et al. 2001); the World Wide Web Consortium (W3C) defines standards, i.e. specifications of protocols and technologies for the semantic web ( <a href="http://www.w3.org/standards/semanticweb/">http://www.w3.org/standards/semanticweb/</a> )
Dataset	A set of measurements and observations; often originating from a single experimental set-up or study context; can be considered as being internally homogeneous across all data entries
Data table	A two-dimensional spread-sheet containing data organised in rows and columns; in most cases these data are considered 'static', i.e. they are not altered or filtered across time
Database	A suite of data compiled from multiple <i>datasets</i> , i.e. from multiple study contexts or observation types; may take the form of a two-dimensional data table, but mostly is organised in into <i>relational databases</i> using database software;
Relational database	Usage in this paper: Two or more <i>data tables</i> that are related by common information contained in one or more columns; common information is usually labelled by <i>identifiers</i> (IDs)
Online database	A <i>relational database</i> that is made accessible on the internet; offering forms for filtering and downloading subsets of the data; some online databases offer access via a <i>webservice</i> and an <i>API</i> that can be addressed computationally
Identifier (ID)	A unique label that relates entries within and across <i>datasets</i> ; is used to connect <i>data tables</i> into a <i>relational database</i> ; can be user-specific or, as a <i>URI</i> , point to a globally valid <i>ontology</i> or <i>thesaurus</i>
Uniform Resource Identifier (URI)	An unambiguous pointer to a unique resource on the internet; used to refer to single terms of a <i>thesaurus</i> or <i>ontology</i> ; an example is ' <a href="http://t-sita.cesab.org/BETSI_vizInfo.jsp?trait=Body_length">http://t-sita.cesab.org/BETSI_vizInfo.jsp?trait=Body_length</a> '
Webservice	An exchange protocol to access <i>online databases</i> directly and programmatically, i.e. by calls from a software tool
Application Programming Interface (API)	A set of clearly defined methods of communication between software components, e.g. client software and the <i>webservice</i> of an online databases; APIs are usually documented on the website of a database provider
Online Portal	A website designed as a platform for the exchange of information, e.g. trait data; a portal may include a communication forum, data upload forms, a database access point, and advanced user management for data access
File repository	A short-term storage of <i>datasets</i> or long-term archiving on <i>file-hosting services</i> ; online repositories make data available for public access, provide <i>metadata</i> and (not always) facilitate citations via DOIs (Digital Object Identifiers)
File-hosting service	An online platform that hosts <i>datasets</i> or entire <i>repositories</i> and provides access to a wide audience on the internet; examples in biology are Figshare.com, Dryad ( <a href="http://datadryad.org">datadryad.org</a> ), Researchgate.net, or Zenodo.org
Metadata	Data documentation of the higher level information or instructions; describe the content, context, quality, structure, provenance and accessibility of a data object (Michener et al. 1997)
Darwin Core Standard (Dwc)	Body of <i>terminologies</i> providing terms intended to facilitate the sharing of information about biological diversity ( <a href="http://rs.tdwg.org/dwc/">http://rs.tdwg.org/dwc/</a> )
Darwin Core Archive (DwC-A)	A file archive, or <i>repository</i> structure, that contains <i>metadata</i> (specified using Ecological Metadata Language, EML) and primary data combined into a <i>relational database</i> via <i>identifier</i> columns.
Method handbook	A listing of consensus methodology that is to be applied to acquire a particular measure, thus formalising the precise <i>concepts</i> of measures.
Occurrence	A single observation instance of a taxon, i.e. an organism at a particular place at a particular time ( <a href="http://rs.tdwg.org/dwc/terms/Organism">http://rs.tdwg.org/dwc/terms/Organism</a> )

## 26 **Introduction**

27 Functional traits are phenotypic (i.e. morphological, physiological, behavioral) character-  
28 istics that are related to the fitness and performance of an organism (McGill et al. 2006;  
29 Violle et al. 2007). Because trait-based approaches allow studying both patterns and mech-  
30 anisms (Lavorel and Garnier 2002; Díaz et al. 2016), recent years have seen a proliferation  
31 of trait-based research in a wide range of fields. Trait-based studies have been conducted in  
32 a wide range of thematic areas ranging from the evolutionary basis of individual-level prop-  
33 erties (Salguero-Gómez et al. 2016) to global patterns of biodiversity (Díaz et al. 2016)  
34 and ecosystem functioning (Bello et al. 2010; Allan et al. 2015). The trait framework  
35 relates losses of ecosystem function to changes in the functional composition of species  
36 assemblages (Mouillot et al. 2013; Perović et al. 2015). This offers the mechanistic back-  
37 ground to relate biodiversity to climate change or local anthropogenic land use (Díaz et al.  
38 2011; Lavorel and Grigulis 2012; Allan et al. 2015). Using traits is also a promising means  
39 of bypassing taxonomic impediment, i.e. the fact that a majority of species are yet unde-  
40 scribed and little is known of their interactions with the environment and other organisms.  
41 This is because functional traits allow us to infer the ecological role of organisms from their  
42 apparent features, regardless of their taxonomic identity (Duarte et al. 2011; Schrodte et  
43 al. 2015; Le Provost et al. 2017).

44 Many issues in trait-based research arise when compiling datasets from several sources.  
45 Data may differ in taxonomic nomenclature and resolution (e.g. reported on species level or  
46 aggregated on higher taxonomical orders), the scale and place of the study context, or the  
47 accuracy of the methodology applied in measurements. These differences are not always  
48 documented in the metadata accompanying a dataset. All of these factors render trait data  
49 extremely heterogeneous and make the task of data compilation time-consuming or even  
50 prohibitive. However, fully exploiting the potential of trait-based approaches relies heavily  
51 on the broad availability and compatibility of trait data to achieve sufficient taxonomic and  
52 regional coverage, both of present-day taxa as well as in evolutionary deep-time.

53 To this end, the number of available trait datasets is increasing rapidly. In the past, trait  
54 data have been standardised and compiled in centralised databases for specific organism  
55 groups and regional scope, often centred around particular research questions (e.g. Pan-  
56 THERIA, Jones et al. 2009; TRY, Kattge et al. 2011a; AmphibiBio, Oliveira et al. 2017).  
57 These initiatives map heterogeneous data into a common scheme and, importantly, also  
58 offer access control and data usage policies. As such, they protect the rights of the original  
59 data providers while simplifying data queries for synthesis researchers. Besides initiatives  
60 aiming at assembling data, other tools to enable the compatibility of data across databases

61 are being developed. These include semantic-web standards (Page 2008; Wieczorek et  
62 al. 2012) and ontologies of standard terms (Walls et al. 2012; Garnier et al. 2017).  
63 Meanwhile, open-science reaches the mainstream: it has become the declared goal of an  
64 open biodiversity knowledge management (<http://www.bouchoutdeclaration.org/>) and is  
65 increasingly demanded by journals and public research funding (German Science Organisa-  
66 tions 2010; Centre 2012; Swan 2012; Allison and Gurney 2015; Emerson et al. 2015). As  
67 a result, an increasing number of individual research projects publish their primary data on  
68 file hosting services like Figshare.com, Dryad (datadryad.org), Researchgate.net, or Zen-  
69 odo.org, where no data standards are forced upon the uploaded material. It is likely that  
70 trait data will become increasingly available, but a lack of data and metadata standardisa-  
71 tion will hamper the efficient re-use and synthesis of published datasets.

72 In this paper, we review existing trait databases and online portals, as well as initiatives  
73 for standardisation. We discuss current practice and the importance of data standards for  
74 trait-based research, and we identify current deficits in standardisation from a pragmatic  
75 view of data providers and data users. Based on these considerations, we propose a minimal  
76 structure and vocabulary for describing trait datasets, that builds upon and is compatible  
77 with existing terminology standards for biodiversity data. Finally, we present an R package  
78 that assists the harmonisation of trait data from distributed sources. With this easy-to-use  
79 terminology and toolset, we hope to convince trait-data providers and trait-data users about  
80 the general importance of trait-data standardisation and lay out the roadmap towards an  
81 accessible ecological trait data standard.

## 82 **A review of initiatives for trait-data standardisation**

83 In this section, we review four types of initiatives that are of relevance for trait-data stan-  
84 dardisation (see Glossary in Table 1 for italicised terms):

- 85 1. Initiatives that provide *trait datasets* which have been assembled out of a particular  
86 research interest, either by measurement or collated from the literature.
- 87 2. Initiatives that aim to harmonise trait data from the literature or from direct mea-  
88 surement into *trait databases* and make those data widely available.
- 89 3. Initiatives that aim at the standardisation and development of consensus measure-  
90 ment methods and definitions for traits, and provides standard *terminologies* in the  
91 form of *thesauri* and *ontologies*.
- 92 4. Initiatives that aim to leverage *relational database* structures and *semantic web* tech-  
93 nology to link trait data to a wider set of biodiversity data.

94 We discuss these initiatives separately although often they are developed in conjunction  
95 to serve a particular database project, as for instance in the case of the TRY plant database  
96 (Kattge et al. 2011a; Kattge et al. 2011b) and the Thesaurus of Plant Traits (TOP; Garnier et  
97 al. 2017). We show how the degree of trait-data standardisation in existing datasets spans  
98 this entire spectrum and which tools and standards are applied to achieve harmonisation of  
99 data from multiple, distributed sources. The objective of this review is to raise awareness  
100 for the generic structure of trait data and aid researchers to share and publish own datasets  
101 in an appropriate form.

## 102 **Trait datasets**

103 In the field of comparative biology, morphological traits related to plant flower, leaf and  
104 stem traits or bird wing and beak measurements, as well as life-history traits such as Ellen-  
105 berg values for plants or ecological parameters of animals (e.g. reproductive traits, feeding  
106 biology, dispersal or body size) have been measured for decades, and have been published  
107 in regular journal articles or books. With the rise of ecological trait-based research, individ-  
108 ual measurements and information available from species descriptions have been compiled  
109 into project-specific datasets that typically comprise a local set of taxa and a focal set of  
110 traits. A plethora of such static datasets has been published along with scientific articles  
111 or as standalone data publications (see Kleyer et al. 2008 for a review on plant data; on  
112 animal data, see e.g., Gossner et al. 2015; Ricklefs 2017). Today, the online publication  
113 of such data is greatly facilitated by *file hosting services* (e.g. Figshare.com), which warrant  
114 long-term accessibility and citability via DOIs, and support Public Domain dedication or  
115 Creative Commons licenses. These platforms offer publicly accessible repositories at low-  
116 cost or for free, which makes them attractive for small and intermediate sized research  
117 projects that cannot dedicate extra resources for data management. However, although  
118 open for manual access, the trait datasets on data repositories might be stored in propri-  
119 etary (e.g. .xlsx, .docx) or binary (e.g. .pdf) data formats which make a programmatic  
120 extraction tedious and dependent on commercial software, putting the long-term and open  
121 accessibility of these data at risk. Most importantly, these platforms enable public hosting  
122 of data with very low thresholds for *metadata* documentation and data standardisation.

123 For trait data, there are typical issues arising from the variability of data structures. For  
124 instance, the column descriptions and terminology applied to taxa and traits are mostly  
125 project specific, and rarely chosen to allow translation into larger database initiatives. Fur-  
126 thermore, metadata varies in its detail, e.g. for documenting descriptions of variables, mea-  
127 surement procedures or sampling context (Kattge et al. 2011b). In terms of structure, trait  
128 data usually are reported in a species×traits wide-table format. In this format, each row

129 contains a species (or taxon) for which multiple traits are reported in columns. Similarly,  
130 when reporting raw data, researchers place observations of individual organisms in rows  
131 with multiple trait measurements applied to the same individual across multiple columns.  
132 Variability in the number and meaning of columns in these *data tables* requires tedious  
133 manual adjustments when merging multiple datasets (Wickham 2014).

134 A global overview of existing trait data for all taxa and trait types is difficult to obtain.  
135 Therefore, in an attempt to collate a list of existing distributed datasets, we initiated a living  
136 spreadsheet (<https://goo.gl/QxzfHy>) which lists published trait datasets, their regional and  
137 taxonomic focus, the number and scope of traits covered, their location on the internet and  
138 the terms of use (see Appendix A for a current excerpt of this list). We invite data owners  
139 and users to add further trait datasets to this spreadsheet.

140 As it stands, the decentralisation and the lack of data standardisation of low-threshold  
141 online repositories renders the compilation of data into larger collections inefficient and  
142 reduces the potential of many published datasets to be re-used and combined into broad  
143 synthesis analysis.

#### 144 **Database initiatives**

145 In the past two decades, many distributed trait datasets have been aggregated and har-  
146 monised into greater collections with particular taxonomic or regional focus (e.g. Klotz et  
147 al. 2002; Kleyer et al. 2008; Jones et al. 2009; Kissling et al. 2014; Myhrvold et al. 2015;  
148 Iversen et al. 2017; Oliveira et al. 2017, see Appendix A table A1). While mostly concerned  
149 with issues of heterogeneity in units or factor levels, and aiming for high taxonomic cov-  
150 erage, few of these datasets apply a standardised terminology for taxa or traits that would  
151 allow them to be efficiently related to other databases. Documentation of metadata and  
152 methodology differs in the level of detail, depending on the research focus of the initiative.  
153 Just as the individual datasets described above, many of these databases are published as  
154 static data tables on low-threshold file hosting platforms and are updated irregularly.

155 As they deal with much larger amounts of data, initiatives that form around natural his-  
156 tory museum collections are more concerned with standardisation. Concerning organism  
157 traits, with the digitisation efforts that are currently undertaken in many museum collec-  
158 tions (Vollmar et al. 2010; Blagoderov et al. 2012), supported by citizen science crowd-  
159 sourcing (e.g. [www.markmybird.org](http://www.markmybird.org)), data on body measurements are likely to grow expo-  
160 nentially in the near future. For example, the VertNet database compiled and harmonized  
161 large quantities of vertebrate trait data with the aim of mobilising measurements from col-  
162 lections (Guralnick et al. 2016). The resulting data are published as versioned data tables  
163 which are updated as new data sources become available.

164 More specialised trait-database platforms have been created to cover certain trait types  
165 (e.g. floral traits, seed traits, root traits or wood density traits), interaction types (e.g. pol-  
166 lination traits or feeding relationships), or a specific environmental and experimental con-  
167 text of the trait observation (e.g. location or climatic data). Such database initiatives at-  
168 tract data submissions from a defined research field and take care of the harmonisation  
169 process and thereby greatly facilitate data synthesis. For example, by aiming for a uni-  
170 versal framework for plant traits, the TRY database (Kattge et al. 2011a) attracted more  
171 data submissions and downloads than any other trait data platform. The *online database*  
172 enables selective data download and user permission and rights management. As a com-  
173 munity effort, TRY serves as a network for consensus building on trait definitions (Garnier  
174 et al. 2017) and measurement methodology (Perez-Harguindeguy et al. 2013) (see next  
175 section). Microbial ecologists also make frequent use of trait-based approaches to assess  
176 genomic function and describe functional diversity at the community level (Fierer et al.  
177 2012; Fierer et al. 2014; Krause et al. 2014). Here, ‘operational taxonomic units’ (OTUs)  
178 are derived from metagenomic analysis (Torsvik and Øvreås 2002; Langille et al. 2013).  
179 Databases are also used to interpret OTUs in terms of their functional role (e.g. the KEGG  
180 orthology, Kanehisa et al. 2012). For animals, a single unified platform and harmonising  
181 scheme for animal trait data is still lacking. The reason for this may be that harmonising  
182 trait data on animals, which span multiple trophic levels and possess diverse body plans,  
183 is a more complex task than for plants (Moretti et al. 2017). Nonetheless, initiatives for  
184 particular groups of animals, such as the BETSI database collects traits on soil invertebrates  
185 (<http://betsi.cesab.org/>; Pey et al. 2014), and the Carabids.org web portal collects traits  
186 of carabid beetles (<http://www.carabids.org/>), already exist.

187 Regarding open access, few of these centralised databases comply with the criteria de-  
188 manded by journals and funding agencies for primary data publication. The platforms  
189 incentivise data submissions by offering increased data visibility and usage, while provid-  
190 ing data use policies that secure author attribution and potentially co-authorship. With  
191 the proactive turn towards open access data (as stated in the Bouchot Declaration; <http://www.bouchoutdeclaration.org/>), it may be necessary to find other incentives for data  
192 submission.  
193

## 194 **Thesauri and Ontologies for traits**

195 A major challenge in trait-data standardisation is the lack of widely accepted and unam-  
196 biguous trait definitions. Previous standard definitions of trait *concepts* range from listings  
197 of selected definitions in *glossaries*, over well-defined methodological *handbooks* and com-  
198 prehensive *thesauri*, to relational definitions of trait concepts in *ontologies*. While glossaries



199 may be seen as specific for a study context, the initiatives behind method handbooks, the-  
200 sauri and ontologies are primarily concerned with consensus building on trait definitions  
201 in a wider community.

202 Very general classes of traits are defined within the list of GeoBON Essential Biodiver-  
203 sity Variables (Pereira et al. 2013). Assigning a more detailed and unambiguous method-  
204 ological protocol to a trait, including the units to use or the ordinal or factor levels to be  
205 assigned, is key for standardising the physical process of measuring. Efforts to develop  
206 handbooks for measurement protocols provide such a methodological standardisation for  
207 plants (Cornelissen et al. 2003; Perez-Harguindeguy et al. 2013) or invertebrates (Moretti  
208 et al. 2017), but obviously are of limited use in harmonising trait data that pre-date or  
209 ignore this standard (Kattge et al. 2011b).

210 A thesaurus provides a “controlled vocabulary designed to clarify the definition and  
211 structuring of key terms and associated concepts in a specific discipline” (Laporte et al.  
212 2013; Garnier et al. 2017). Expanding on this, ontologies link the defined terms by for-  
213 mally defining the relationships between them, with the objective of enabling a computa-  
214 tional interpretation of data. Being publicly available, it is also possible to refer to these  
215 defined terms via globally unique *Uniform Resource Identifiers (URIs)* within own datasets.  
216 For example, a measurement of seed size could be linked to the Planteome Trait Ontology  
217 (TO) definition of ‘seed size’ by referencing ‘[http://browser.planteome.org/amigo/term/](http://browser.planteome.org/amigo/term/TO:0000391)  
218 [TO:0000391](http://browser.planteome.org/amigo/term/TO:0000391)’. Ontologies define terms based on other well-defined terms from published  
219 ontologies. The TO definition of the concept ‘seed size’ contains references to other glob-  
220 ally defined terms: “A seed morphology trait (TO:0000184) which is the size of a seed  
221 (PO:0009010).” Furthermore, trait definitions may refer to related terms or synonyms de-  
222 fined in other trait ontologies or other scientific ontologies, like units as defined by the  
223 Units of Measurement Ontology (Gkoutos et al. 2012). This way, each trait definition  
224 may link to a broader or narrower term. For example, the definition of ‘femur length of  
225 first leg, left side’ is narrower than ‘femur length’ which is narrower than ‘leg trait’ which  
226 is narrower than ‘locomotion trait’. By providing this interlinkage of trait ontologies, a  
227 machine-readable web of definitions is spun across the Internet which allows researchers  
228 and search engines to relate independent trait measurements with each other and connect  
229 it to the wider *semantic web* of online data (Berners-Lee et al. 2001; Page 2008). The dis-  
230 tinction of thesauri and ontologies is not truly binary. Rather they mark idealised ends of  
231 a spectrum. While thesauri may contain defined relations between terms within the stan-  
232 dard, ontologies relate most terms to other defined concepts, and also link those to other  
233 standards.

234 Comprehensive trait thesauri have been developed in the TOP Thesaurus of plant traits,

235 which is employed in the TRY database (Garnier et al. 2017), and in the Thesaurus for Soil  
236 Invertebrate Trait-based Approaches (T-SITA, <http://t-sita.cesab.org/>, Pey et al. 2014). On-  
237 tologies of trait definitions have been developed for plants (e.g. the Plant Ontology, Jaiswal  
238 et al. 2005; the Flora Phenotype Ontology, Hoehndorf et al. 2016), as well as for animals  
239 (e.g. the Hymenoptera Anatomy Ontology, Yoder et al. 2010; the vertebrate trait ontology,  
240 Park et al. 2013). The existing thesauri and ontologies for traits differ widely in terms of  
241 hierarchical depth and detail, as well as in curation efforts and measures for peer-reviewed  
242 quality control. Meta-ontology initiatives, like Planteome.org, offer access to multiple  
243 published ontologies and build platforms for their collaborative development (Walls et al.  
244 2012). For general biodiversity data, the OBO Foundry (<http://www.obofoundry.org/>),  
245 Ontobee (<http://www.ontobee.org/>), Bioportal (<https://bioportal.bioontology.org/>), or  
246 the GFBio Terminology service (<https://terminologies.gfbio.org/>), provide centralised  
247 hosting for advanced trait ontologies and offer webservices for computational access.

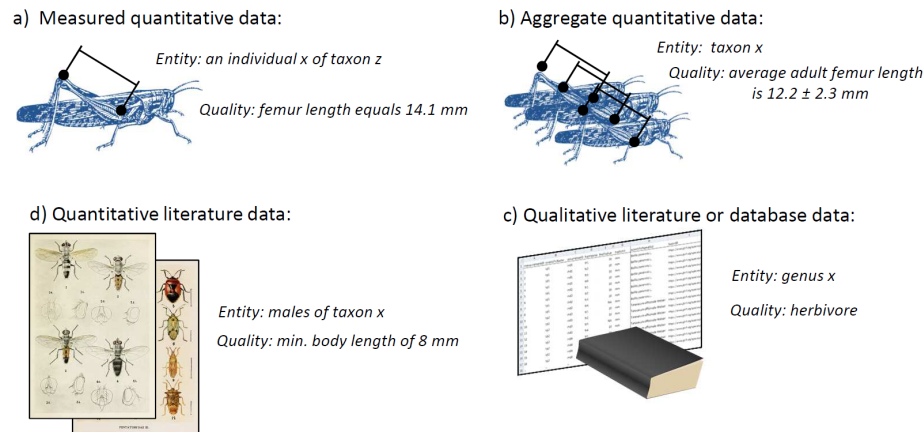
248 To conclude, there is already a suite of globally available thesauri and ontologies for  
249 traits that emerged from standardisation efforts of methodologies and community con-  
250 sensus processes. However, definitions in some domains are better covered than others.  
251 Interlinkage and accessibility of ontologies can be much improved to fulfil semantic web  
252 standards. Most importantly, while these defined vocabularies are widely used in biodi-  
253 versity data management, distributed data repositories of smaller project contexts hardly  
254 make use of them. A more widespread implementation of ontologies would advance the  
255 possibilities to aggregate datasets into databases and reduce noise and uncertainty. To  
256 achieve this, the use of ontologies and thesauri must be incentivised and facilitated for  
257 individual researchers. For example, the accessibility of ontologies will increase if open  
258 *Application Programming Interfaces (APIs)* are provided as a way to extract the definitions  
259 and higher-level trait hierarchies programmatically via software tools. Software then can  
260 assist researchers in linking own data to globally defined concepts.

## 261 **Trait-data structures for the semantic web**

262 While trait thesauri and ontologies typically define traits for focal groups of organisms, they  
263 do not specify the format or structure in which trait data should be stored and linked to  
264 further standard terminologies, such as standard taxonomy nomenclatures.

265 To make sense of trait data in the context of more general databases, a consensus definition  
266 of trait data is necessary.

267 Trait data have been defined by Garnier et al. (2017) to follow an entity-quality model  
268 (EQ), where a trait observation is ‘an entity having a quality’. More specifically, a trait  
269 dataset contains information on quantitative *measurements* or qualitative *facts* (i.e. trait



**Figure 1** | Types of ecological trait data assume different entities or reported quantities. a) morphometric or morphological measurements of individual body features (lengths, areas, volumes, weights) or other quantities related to life history (e.g. reproductive rates, life spans); b) aggregated traits are reported as means taken on multiple measures of members of a taxon; c) quantities may be extracted from literature or existing databases, referring to the entire taxon (or a subset, e.g. a sex) as the entity of description; d) Qualitative traits are categorical or binary descriptors of the entire species or higher taxonomic group.

270 values) describing the physical phenotypic characteristics relating to fitness and perfor-  
271 mance (i.e. traits) observed on a biological entity (i.e. an individual specimen, or parts of  
272 an individual specimen) that can be assigned to a biological taxon (i.e. a species or higher-  
273 level taxon). We are expanding on this definition: quantitative measurements are values  
274 obtained either by direct morphological, physiological or behavioural observations on single  
275 specimens (Fig. 1a), by aggregating replicated measurements on multiple entities (Fig.  
276 1b) or by estimating the means or ranges for the respective taxon as reported in the litera-  
277 ture or other published sources (e.g. databases, Fig. 1c). Qualitative facts are assignments  
278 of an entity to a categorical level, e.g. of a behavioural or life-history trait (Fig. 1d). The  
279 entity or observation (i.e. the *occurrence*) to which the reported measurement or fact ap-  
280 plies may differ in organisational scale – depending on the scientific question – and could  
281 be a sub-sample or bodypart, an individual specimen, an entire species or a higher-level  
282 taxon (e.g. a genus).

283 These relationships between a trait observation and an individual organism as an oc-  
284 currence of a particular taxon have been formalised in the schema for biological collection  
285 records (ABCD Schema; Holetschek et al. 2012) and the Darwin Core Standard for biodi-  
286 versity data (DwC; Wiczorek et al. 2012). For example, the Global Biodiversity Informa-  
287 tion Facility (GBIF, [www.gbif.org](http://www.gbif.org)) applies these terms. These frameworks specify terms and  
288 classes to describe the general structure of biodiversity databases, for example by defining  
289 names for columns that contains measurement values, units, taxon names, variables such

290 as sex or life stage, ancillary information of time and date of observation, and method-  
291 ological details. The terminologies provided by these standards are quite universal and  
292 even cover most use cases of trait data. An entire ecosystem of data standards links to and  
293 expands the capacities of DwC (Wieczorek et al. 2012).

294 Specifically designed for plant traits, Kattge et al. (2011a) proposed a generic database  
295 structure that covers most potential use cases of trait-based ecology. This data structure  
296 is built around a central data table that contains observations, i.e. a single event of mea-  
297 surement on the same individual plant specimen at the same point in time. This structure  
298 emphasises the fact that multiple trait data are measured on the same individual organ-  
299 isms and used to analyse correlations between these multiple traits. Identifiers link the  
300 measurements (qualities) to the same observation (entity), each measurement being well  
301 defined by additional standard tables. The observations are also linked to a taxonomy and  
302 ancillary descriptors of the observation context, like location or experimental treatment.  
303 This structure can be implemented in any relational database management system.

304 In a similar vein, the Encyclopedia of Life (EOL) project has proposed the database  
305 framework TraitBank (Parr et al. 2016) for major physiological and life-history traits of  
306 all kingdoms of life, which is to date the most general approach of an integrated structure  
307 for trait data. The framework employs established terms provided by the DwC, relates trait  
308 definitions to trait ontologies for phenotypic or anatomical terms, and maps taxa to global  
309 identifiers in taxonomic hierarchies of name service providers to capture synonyms, mis-  
310 spellings and controversies (Parr et al. 2016, [http://eol.org/info/cp\\_archives](http://eol.org/info/cp_archives)). Additional  
311 layers of information capture bibliographic reference, multimedia archives and ecological  
312 interactions. TraitBank invites data submissions to the EOL database in a structured Darwin  
313 Core Archive (DwC-A, Robertson et al. 2009), a zip-file with annotated text-files that is also  
314 preferred for observation data in GBIF (GBIF 2017, <http://tools.gbif.org/dwca-assistant/>).  
315 The archive also integrates the general framework for metadata of the Ecological Metadata  
316 Language (EML, KNB 2011). The difficulties with keeping taxonomic references intact  
317 along with continuous changes in taxonomy consensus are a central challenge of biodiver-  
318 sity data management and are beyond the scope of this review (Franz et al. 2016). Initia-  
319 tives that aim at providing a stable reference for taxa are for instance the EOL Catalogue of  
320 Life (<http://www.catalogueoflife.org/>, Roskov et al. 2018), the GBIF Backbone Taxonomy  
321 (Secretariat 2017), or the EDIT Platform for Cybertaxonomy (<https://cybertaxonomy.eu/>).

322 These proposed standards are responses to a demand from biodiversity data managers  
323 for more structured input from the research community. However, hardly any of the afore-  
324 mentioned trait datasets for birds, amphibians, or mammals employs such ontologies or se-  
325 mantic web standards. One reason for this is most certainly complexity: the data structures

326 are designed for multi-layered, relational databases rather than for standalone datasets for  
327 which a two-dimensional data table may suffice. In the eyes of the data-provider, in most  
328 cases, ancillary co-factors can be appended as extra columns to the dataset. The other rea-  
329 son is lack of awareness for the need for trait-data standardisation among data providers:  
330 many providers are not trained in the demands of biodiversity data-management and com-  
331 plying with what may be non-intuitive data structures is an investment without clear incen-  
332 tive or immediate pay-off, and hardly affordable for small and intermediate-size research  
333 projects.

334 By filling this gap, data-brokering services (e.g. the German Federation for Biolog-  
335 ical Data; [gfbio.org](http://gfbio.org); Diepenbroek et al. 2014) or data management systems for sci-  
336 entific projects (e.g. KNB and its open-source database back-end Metacat, <https://knb.ecoinformatics.org/>;  
337 Diversity Workbench, [www.diversityworkbench.net](http://www.diversityworkbench.net); BExIS, <http://bexis2.uni-jena.de/>;  
338 ) are likely to gain importance. These services simplify and di-  
339 rect the standardised upload of research data and descriptive metadata into reliable and  
340 interlinked data infrastructures. One goal of such initiatives is to facilitate data publi-  
341 cations and standardisation for researchers, for instance by providing terminologies and  
342 ontologies for biodiversity data, and by consulting on publication licenses.

### 343 **Conclusion of review**

344 Initiatives for standardisation (e.g. ontologies and data standards) and platforms for data  
345 management (e.g. database and data management platforms) provide great visibility and  
346 improve interconnectedness of datasets, but raise relatively high thresholds for data and  
347 metadata preparation. Low-threshold repositories offer the hosting of scientific primary  
348 data attracting a wealth of heterogeneous trait datasets, but data harmonisation of these  
349 distributed data sets is currently laborious. The goal must be to better integrate these dis-  
350 tributed data into the global biodiversity data-management ecosystem by creating aware-  
351 ness for data standardisation on the side of data providers. We propose the development  
352 of tools and vocabularies that impose low thresholds and offer high pay-off in the visibility  
353 and interconnectedness of published data.

### 354 **An ecological trait-data standard vocabulary**

355 As a response to the challenges outlined above, we propose a versatile vocabulary for trait-  
356 based ecological research. The aim of the vocabulary is to cover the variety of trait-based  
357 approaches and their different degrees of measurement detail. Rather than describing a

358 data structure for relational databases, the vocabulary is intended as a more inclusive ter-  
359 minology, that can be used in simple two-dimensional datasets as well as in the exchange of  
360 data between web services in the semantic web. By using this standard vocabulary, authors  
361 can ensure that the description of trait measurements that are uploaded to distributed data  
362 repositories will be unambiguous and generally applicable. It will facilitate re-use of data  
363 for future data aggregation initiatives and data synthesis and ensure long-term accessibility.

364 In designing this vocabulary, we drew on the combined expertise of empirical biodi-  
365 versity researchers (data providers), biodiversity synthesis researchers (data users), and  
366 biodiversity informatics researchers (data managers). We paid particular consideration to  
367 the work of Kattge et al. (2011a), Kattge et al. (2011b), and Garnier et al. (2017), as  
368 well as Parr et al. (2016) to ensure compatibility of our proposed data structure with ma-  
369 jor trait databases and existing standards for biodiversity data management. Here, the  
370 use of identifiers ('IDs') for the individual measurement observations ('measurementID'),  
371 specimens ('occurrenceID'), sampling events ('eventID'), or taxa ('taxonID') is key to map  
372 two-dimensional data onto the structure of relational databases. Besides being used for  
373 the publication of datasets, the standard vocabulary could be imposed in webservices or  
374 download tools, e.g. APIs that provide direct access to online databases. The vocabulary  
375 proposed is intended to form the foundations of a standard nomenclature that can be ex-  
376 panded and corrected by the wider community of researchers using trait-based approaches  
377 in ecology.

### 378 **How to apply the standard vocabulary**

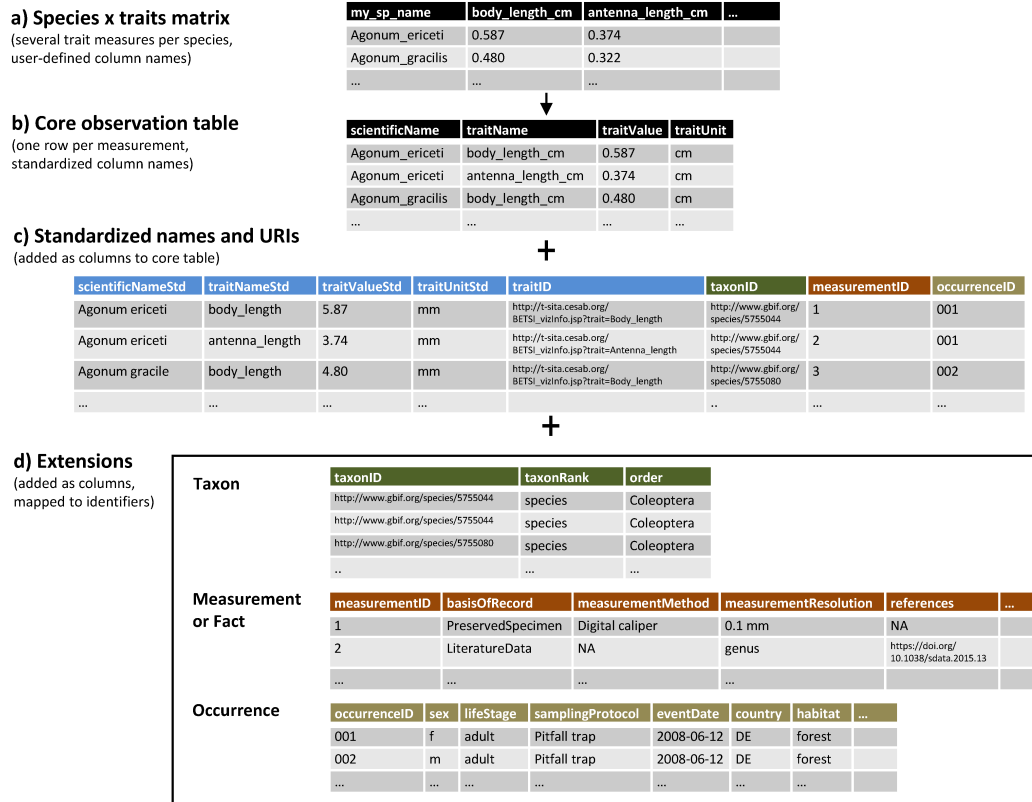
379 We suggest that any trait dataset that is published on online repositories should draw its  
380 column names and field entries from the defined vocabulary where possible. The core  
381 vocabulary lists and defines terms that describe a dataset according to the Entity-Quality  
382 model described above (Garnier et al. 2017): each entry describes a trait value (i.e. quality)  
383 observed on an individual or population (i.e. entity), of a biological taxon. When applying  
384 the vocabulary, it is implicit to use a two-dimensional observation long-table format for the  
385 data (Fig. 2 b), rather than a species $\times$ traits matrix (Fig. 2 a). As the long-table format  
386 draws from a defined set of columns, merging datasets is easier. Long-table datasets also  
387 purport multiple advantages for data manipulation (e.g. filtering, sub-setting and aggre-  
388 gating data, Wickham 2014).

389 Well-defined identifiers ('IDs') are key elements to structure the datasets and relate them  
390 to complementing datasets, if necessary (Fig. 2 c & d). For instance, for occurrence level  
391 data where multiple trait measurements are reported for each individual specimen, the  
392 same user-defined entry for 'occurrenceID' would link several measurements across the

393 rows of the dataset. Similarly, multivariate measurements, for instance gas chromatogra-  
394 phy data or x-y-z data of morphometric landmarks could be linked via a ‘measurementID’.  
395 In literature data, summarised traits are usually given at the taxon level instead of the indi-  
396 vidual organism (e.g. reported as means or factorials) and a ‘taxonID’ is the key identifier.  
397 In larger compilations, a ‘datasetID’ allow to trace data origin to the primary source. Be-  
398 yond being just of structural use for the dataset, identifiers are capable of linking own data  
399 to consensus taxonomy and trait terminology via URIs, which point to external terminology  
400 services (see above for resources). Two-dimensional spreadsheets are however limited in  
401 the number and complexity of co-variates they can contain. As such, for datasets containing  
402 multi-layered information on observations, traits, taxa and environmental context, the use  
403 of relational database structures may be indicated, like the generic trait database struc-  
404 ture proposed by Kattge et al. (2011b) or the TraitBank structure proposed by Parr et al.  
405 (2016). The trade-off is user-side readability and handling in a single table vs. avoidance  
406 of content duplication and redundancy in a relational database. The standard vocabulary  
407 proposed here may still be applied to describe columns within the individual data tables of  
408 relational databases.

409 For reasons of long-term accessibility, data should not be uploaded in proprietary spread-  
410 sheet formats (like ‘.xlsx’) but rather in comma-separated text files (‘.csv’ or ‘.txt’) that are  
411 compatible with all computing platforms and internationalisation settings by applying a  
412 unified character encoding (e.g. UTF-8 or ASCII).

413 In order to ensure traceability, the metadata of any dataset that employs this vocabu-  
414 lary should refer to the specific online version that was used to build the dataset, e.g.  
415 “Schneider, F.D., Jochum, M., Le Provost, G., Penone, C., Ostrowski, A. and Simons, N.K.,  
416 2018 Ecological Traitdata Standard v0.8, DOI: 10.5281/zenodo.1255287, URL: [https://  
417 ecologicaltraitdata.github.io/ETS/v0.8/](https://ecologicaltraitdata.github.io/ETS/v0.8/)”. In addition to this versioned online reference,  
418 the dataset should also cite this paper for an explanation of the rationale. Wherever  
419 referring to individual terms of the vocabulary in publications or metadata, this should  
420 be done via their global identifiers, which will be hosted by the GFBio Terminology Ser-  
421 vice (Karam et al. 2016, <https://terminologies.gfbio.org/>) and can be accessed program-  
422 matically (i.e. via the API; **in preparation!**). Wherever our glossary refines or dupli-  
423 cates existing terms from other ontologies for biological data, like the Glossary of EOL  
424 (<http://eol.org/info/516>) and Darwin Core (<http://rs.tdwg.org/dwc/terms/>), we indicate  
425 this in the fields ‘refines’ or ‘identical’, respectively.



**Figure 2** | Formats used for trait datasets. a) taxon-level trait data compiled from literature or aggregated from measurements are often published as a compiled species × traits matrix; b) observation long-tables are a well defined and tidy data format, reporting one single measurement per row and c) relating it to a standard trait definition and accepted taxon name using unambiguous identifiers. Additional identifiers relate each row to other layers of information on d) the taxon resolution, the specimen (occurrence) or the origin or confidence on the reported measurement or fact.

## 426 Terms of the standard vocabulary

427 The standard vocabulary is accessible at <https://ecologicaltraitdata.github.io/ETS/>. The  
 428 core terms describe minimal trait data according to the Entity-Quality model. Beyond these  
 429 core observations, further information might be available that are related to the taxonomic  
 430 assignment, or that put the reported fact, measurement or sampling event in a broader  
 431 observation context (including geolocation and date information). These information can  
 432 be useful for future analysis of the causal reasons of trait variation and should always be  
 433 published along with the core data. For this case, we offer three extensions of the core  
 434 vocabulary (“Taxon”, “Measurement or Fact”, and “Occurrence”) that expand and refine  
 435 terms of the Darwin Core Extensions (see below) which may simply be added as extra



436 columns to the core dataset. Additional terms are provided for metadata and for relating  
437 trait names to definitions and external ontologies or thesauri (see section on metadata  
438 below). The scope of the vocabulary may not yet cover all aspects of morphological and  
439 evolutionary perspectives. Also, information about interactions between species are not  
440 within the scope of the Entity-Quality Model, but may easily be combined with trait data  
441 by using other extensions of DwC. Therefore, we invite researchers to contribute to the  
442 next iterations of the standard vocabulary and develop own applications and ontologies  
443 that interact with it.

#### 444 **Specification of core terms**

445 To qualify as trait data according to the definition provided above, where each row is the  
446 reported measurement or fact for a single observation, the following columns are required  
447 at minimum (Fig. 2 b): 1. a value (column `traitValue`) and – for numeric values – a  
448 standard unit (`traitUnit`); 2. a descriptive trait name (`traitName`) that links to a well-  
449 defined definition; 3. the scientific taxon name for which the measurement or fact was  
450 obtained (`scientificName`). For these core values, unambiguous and self-explanatory  
451 vocabularies for trait names and taxa are recommended. However, to ensure compati-  
452 bility with existing databases or analytical code, it might be necessary to use abbrevia-  
453 tions or user-specific identifiers for `scientificName` and `traitName` instead. In this  
454 case, it is essential to relate the user-defined names to a consensus standard of taxon  
455 names as well as a look-up table of traits. This is achieved by adding globally valid Uni-  
456 form Resource Identifiers (URIs) for taxon (`taxonID`) and trait definitions (`traitID`),  
457 complemented by the human-readable verbatim accepted names (`ScientificNameStd`  
458 and `traitNameStd`, respectively). For example, referring to GBIF Backbone Terminol-  
459 ogy, for *Bellis perennis*, the `taxonID` would be ‘<https://www.gbif.org/species/3117424>’;  
460 the `traitID` for ‘fruit mass’ according to TOP Thesaurus of plant traits would be ‘[http://top-thesaurus.org/annotationInfo?viz=1&&trait=Fruit\\_mass](http://top-thesaurus.org/annotationInfo?viz=1&&trait=Fruit_mass)’.

462 By allowing for a double record of both user-specific and standardised entries, we acknowl-  
463 edge the fact that most authors have their own schemes for standardisation which may refer  
464 to different scientific community standards (as practised in TRY; Kattge et al. 2011a). This  
465 redundancy of data allows for continuity for data owners while also ensuring quality checks  
466 and comparability for the data user.

## 467 **Extensions for additional data layers**

468 Beyond measurement units or higher taxon information, further information might be  
469 available that may not be core data, but are related to the individual or specimen, or  
470 to the reported fact, measurement or sampling event. The data standard provides three  
471 extensions of the vocabulary that should be used to describe this information (Fig. 2\*d\*):

- 472 • The `Taxon` extension provides further terms for specifying the taxonomic resolu-  
473 tion of the observation and to ensure the correct reference in case of synonyms and  
474 homonyms. (<http://ecologicaltraitdata.github.io/ETS/#extension-taxon>)
- 475 • The `MeasurementOrFact` extension provides terms to describe information at the  
476 level of single measurements or reported facts, such as the original literature from  
477 where the value is cited, the method of measurement or statistical method of aggre-  
478 gation. It provides important information that allows for the tracking of potential  
479 sources of noise or bias in measured data (e.g. variation in measurement method) or  
480 aggregated values (e.g. statistical method applied), as well as the source of reported  
481 facts (e.g. literature source or expert reference). (<https://ecologicaltraitdata.github.io/ETS/#extension-measurement-or-fact>)
- 482 • The `Occurrence` extension contains vocabulary to describe information on the level  
483 of individual specimens, such as sex, life stage or age. This also includes the method  
484 of sampling and preservation, as well as date and geographical location, which pro-  
485 vides an important resource to analyse trait variation due to differences in space and  
486 time. (<https://ecologicaltraitdata.github.io/ETS/#extension-occurrence>)

488 Many terms of these extensions refine or copy terms of the DwC and their own `Taxon`,  
489 `MeasurementOrFact` and `Occurrence` extensions and EOL TraitBank's use of those terms  
490 ([http://eol.org/info/structured\\_data\\_archives](http://eol.org/info/structured_data_archives)). These additional layers of information  
491 can either be added as extra columns to the core dataset or kept in separate data sheets  
492 (published separately or as part of a Darwin Core Archive), thus avoiding redundancy and  
493 duplication of content. A unique identifier would link to these other datasheets, encoding  
494 each individual occurrence of a species (`occurrenceID`), single measurements or reported  
495 facts (`measurementID`), locations of sampling (`locationID`) and sampling campaigns  
496 (`eventID`). Some data-types may directly refer to existing global identifiers for occurrence  
497 IDs, e.g. a GBIF URI or a museum collection code references the precise specimen from  
498 which the measurement was taken (Groom et al. 2017; Güntsch et al. 2017).

## 499 **Specification of Metadata**

500 Wherever possible, the column `traitID` should point to a publicly available, unambigu-  
501 ous trait definition in a published ontology. If no globally available trait definition ex-  
502 ists as an external reference, trait datasets should always be accompanied by a dataset-  
503 specific list of traits as part of the metadata or as an accompanying data table. Such  
504 a controlled vocabulary would, in its simplest form, assign trait names with an unam-  
505 biguous definition of the trait and an expected format of measured values or reported  
506 facts (e.g. units or legit factor levels). Ideally, this definition refers to or refines terms  
507 from published trait ontologies. By providing a minimal vocabulary for trait lists (see  
508 <https://ecologicaltraitdata.github.io/ETS/#terms-for-trait-definitions>), we hope to facil-  
509 itate the unambiguous definition of traits for trait datasets. This vocabulary might also  
510 prove useful for the future publication of trait ontologies.

511 Information about the authorship and ownership of the data and the terms of use should  
512 be considered when sharing and working with trait datasets. We define a vocabulary  
513 (<https://ecologicaltraitdata.github.io/ETS/#metadata-vocabulary>) that allows trait data  
514 to be related to authors and owners, while also stating a bibliographic reference and li-  
515 cense model. In the case of primary measurement data, this information applies to the en-  
516 tire trait dataset, and should be stored along with the published data as metadata (e.g. in a  
517 separate metadata file, possibly applying the ecological metadata language, EML). In cases  
518 where individual data from different sources are compiled into a trait database, these in-  
519 formation must be provided at the measurement level. This can be achieved by appending  
520 the information as columns to the core dataset, or via an unambiguous `datasetID` and a  
521 descriptive `datasetName`.

## 522 **Computational tools for producing compliant data**

523 To access data from public databases, the R-package ‘traits’ (Chamberlain et al. 2017) con-  
524 tains functions to extract trait data via several open API interfaces including Birdlife, EOL  
525 TraitBank or BetyDB. The package ‘TR8’ provides similar access to plant traits from a list  
526 of databases (including LEDA, BioFlor and Ellenberg values; Bocci 2015) and aggregates  
527 them into a species×traits matrix. However, none of these packages provide the option  
528 to harmonisation trait data into a unified scheme. To close this gap, we developed the R  
529 package ‘traitdataform’, which assists the production of data compliant with the trait data  
530 standard proposed above. There are two major use cases for the package:

- 531 1. preparing trait datasets for publication on public hosting services and project databases,

532 and  
533 2. automating the harmonisation of trait datasets from different sources by moulding  
534 them into a unified format.

535 A comprehensive documentation of the package can be found on its Github repository  
536 (<https://github.com/EcologicalTraitData/traitdataform>) and the documentation website  
537 (<http://EcologicalTraitData.github.io/traitdataform/>). The package is under continuous  
538 open source development and invites participation in development, comments or bug re-  
539 ports via the Github Issue page ([https://github.com/EcologicalTraitData/traitdataform/](https://github.com/EcologicalTraitData/traitdataform/issues)  
540 issues).

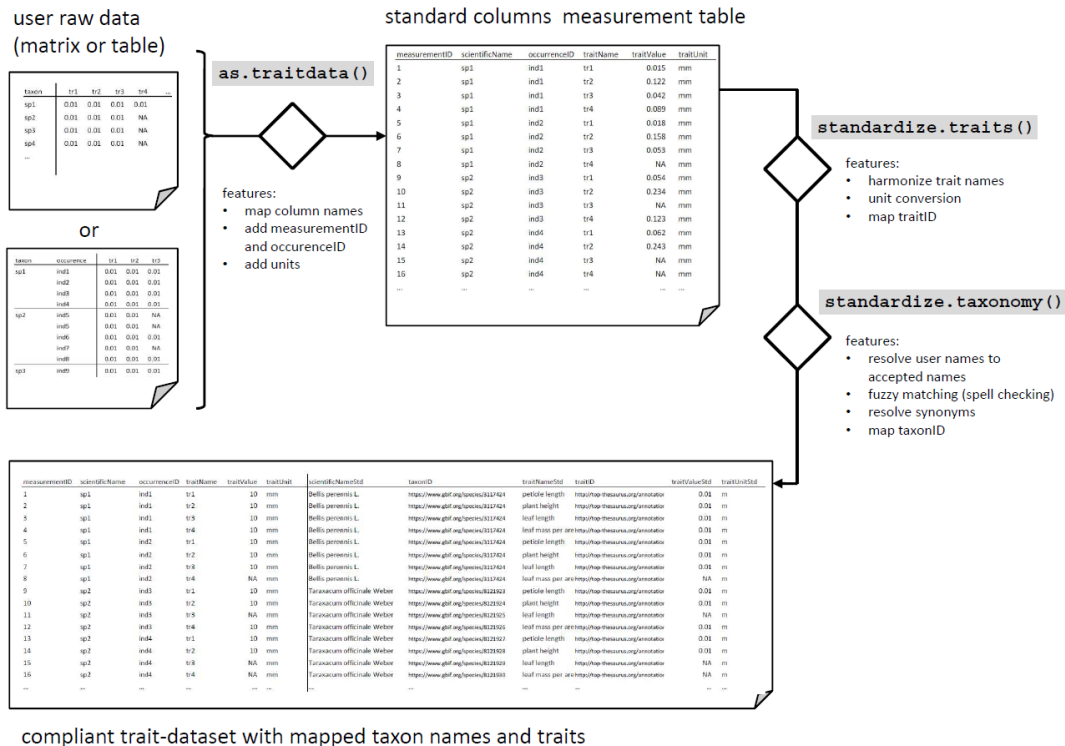
541 The key function of the package is `as.traitdata()` which moulds a species-trait-  
542 matrix or occurrence table into a measurement long-table format (Fig. 3). This function  
543 also maps column names into terms provided in the trait data standard and adds metadata  
544 as attributes to the output object. This example converts an own file ‘data.csv’ into a dataset  
545 of long-table structure that employs the standard vocabulary for core data:

```
546 library("traitdataform")  
547 dataset <- as.traitdata(read.csv("path/to/data.csv"),  
548   traits = c("body_length", "antenna_length",  
549             "metafemur_length"),  
550   units = "mm",  
551   taxa = "name_correct",  
552   keep = c(locationID = "location")  
553   )
```

554 The parameter ‘traits’ lists column names that contain trait values. The column contain-  
555 ing taxon names is given in parameter ‘taxa’. Note that the parameter ‘keep’ specifies and  
556 renames any data that should be maintained in the output. The parameter ‘units’ is used  
557 to specify the input units of measurement. In order to map user-provided names to unam-  
558 biguous and globally unique identifiers, the function `standardize.taxonomy()` matches  
559 scientific taxon names automatically to the GBIF Backbone Taxonomy and adds the column  
560 `taxonID` to the core data (Fig. 3).

561 The R-package further supports the mapping of trait names to a list of trait definitions  
562 and identifiers ( this lookup table is cast into an own object class called ‘thesaurus’). The  
563 following example harmonises traits based on a minimal list, referencing trait names with  
564 globally valid URIs provided by the BETSI thesaurus of soil invertebrate traits:

```
565 traitlist <- as.thesaurus(  
566   body_length = as.trait("body_length",
```



**Figure 3** | Process chart of the functions provided within the R package 'traitdataform' to apply the standard vocabulary to any trait-data table.

```

567     expectedUnit = "mm", valueType = "numeric",
568     identifier = "http://t-sita.cesab.org/BETSI_vizInfo.jsp?trait=Body_length"),
569     antenna_length = as.trait("antenna_length",
570     expectedUnit = "mm", valueType = "numeric",
571     identifier = "http://t-sita.cesab.org/BETSI_vizInfo.jsp?trait=Antenna_length"),
572     metafemur_length = as.trait("metafemur_length",
573     expectedUnit = "mm", valueType = "numeric",
574     identifier = "http://t-sita.cesab.org/BETSI_vizInfo.jsp?trait=Femur_length")
575 )
576
577 datasetStd <- standardize.traits(dataset, thesaurus = traitlist)

```

The function `as.thesaurus()` provides a structured object that is required by the function `standardize.traits()` (Fig. 3). Other ways of defining a 'thesaurus' object are documented in the package vignette and function documentation (?`as.thesaurus`). Future iterations of the R package will aim at automatising the generation of thesaurus objects from globally available ontologies. The package functions form a tool-chain where each function can be piped as an input into the next. A wrapper function `standardize()`

584 applies all functions sequentially, making transferring and harmonising trait data as simple  
585 as:

```
586 datasetStd <- standardize(read.csv("path/to/data.csv"),  
587                             thesaurus = traitlist,  
588                             taxa = "name_correct",  
589                             units = "mm"  
590                             )
```

591 Datasets that have been produced by these functions can easily be appended using the  
592 function `rbind()` of R base, while maintaining any available metadata information as  
593 separate column entries. To merge datasets with additional information on the occurrence  
594 or measurement level, secondary data tables can be added as columns of the core dataset  
595 according to a unique identifier using the function `merge()`. This enables an easy handling  
596 of data sources that originate in a relational database format.

597 Since the intention of the package is also to simplify the harmonisation of published trait  
598 data, the package offers direct access to trait datasets that have been released in the Public  
599 Domain or under Creative Commons licenses. We invite users and authors of datasets to  
600 add further data to the package and thereby contribute to this registry for distributed trait  
601 datasets.

## 602 Conclusion

603 To serve the demand for simple ways to standardise and harmonise ecological trait data,  
604 we propose a versatile vocabulary for simple, two-dimensional datasets as well as for the  
605 exchange and handling of trait data in the context of a ‘semantic web’. With the R-package  
606 ‘traitdataform’, we also present a toolbox in R to transfer and harmonise data into this  
607 scheme.

608 It appears to be broad consensus that an open biodiversity science is crucial for an  
609 evidence-based decision making and conservation policy on regional and global scales. In  
610 times of increasing demand for open research data and international platforms for biodi-  
611 versity data management, the development of meaningful terminologies for the standardi-  
612 sation of biodiversity data is more than essential: defined ontologies enable researchers to  
613 relate published datasets to each other to achieve a greater synthesis, thereby paving the  
614 way for a better mechanistic understanding of the relationship between drivers, commu-  
615 nities and functions and providing new insights on global biodiversity patterns. Moreover  
616 it might be also a step towards a more predictive ecology as a broader set of available

617 traits might enable more hypothesis based trait-based approaches. In terms of data sci-  
618 ence, machine-readable, ontology-based data ease the application of big-data mining and  
619 machine-learning techniques.

620 To date, a rich distributed body of independently published trait datasets focus on par-  
621 ticular organism groups, ecosystem types or regions. However, these distributed data are  
622 heterogeneous in form and description and initiatives to harmonise and compile these data  
623 require significant amounts of funding and personnel. To support the long-term rewards  
624 of standardisation efforts, incentives should be sought to mitigate the cost of readying trait  
625 data for the ‘semantic web’ of biodiversity data and knowledge. This can be software tools  
626 or supporting infrastructures. The tools proposed here help to standardise trait datasets  
627 before upload to central as well as distributed data repositories. By using a constrained  
628 vocabulary with globally accessible definitions of terms, distributed trait data can be ac-  
629 cessed more easily by other researchers and harmonised into aggregated datasets. Also, it  
630 will ease the exchange of data between databases and facilitate the development computa-  
631 tional methods and software tools that access and handle the data, based on the standard  
632 vocabulary. We also encourage the advancement of trait thesauri into more interrelated  
633 and complete ontologies. The biggest challenge in community efforts of standardisation  
634 of traits may be the investment in consensus building which leads to an acceptance and  
635 establishment of the methodological and conceptual definitions of traits. This requires sig-  
636 nificant effort, but it returns great scientific benefit by enabling synthesis on our general  
637 understanding of biodiversity and ecosystem function.

## 638 **Acknowledgements**

639 Thanks to all respondents to an internal online survey on trait data for the Biodiversity  
640 Exploratories project and to Matthias Biber, Kristin Bohn, Diana Bowler, Klaus Birkhofer,  
641 Runa Boeddinghaus, Catrin Westphal, Markus Fischer and Jens Kattge for comments on the  
642 manuscript drafts, the trait data standard vocabulary and the pre-releases of the R-package.

643 We thank the managers of the three Exploratories, Kirsten Reichel-Jung, Katrin Loren-  
644 zen, Juliane Vogt, Miriam Teuscher, and all former managers for their work in maintaining  
645 the plot and project infrastructure; Christiane Fischer and Jule Mangels for giving sup-  
646 port through the central office, and Markus Fischer, Eduard Linsenmair, Dominik Hes-  
647 senmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, Wolfgang  
648 W. Weisser and the late Elisabeth Kalko for their role in setting up the Biodiversity Ex-  
649 ploratories project. The work has been partly funded by the DFG Priority Program 1374  
650 “Infrastructure-Biodiversity-Exploratories” (DFG-Refno.).

651 M.J. was supported by the German Research Foundation within the framework of the  
652 Jena Experiment (FOR 1451) and by the Swiss National Science Foundation.

## 653 **Authors' contributions**

654 FDS, AO, CP, and NKS conceived the idea and developed the vocabulary for the trait data  
655 standard with significant contributions of MJ and GLP (forming the first tier of the author  
656 list); NKS authored the example list of traits; FDS developed the R package 'traitdataform';  
657 CP and FDS curated the living spreadsheet. All contributing authors appear in alphabetical  
658 order in a second tier of the author list. AG and DF implemented the vocabulary in the  
659 GFBio terminology service. All authors contributed critically to the structure and content  
660 of the manuscript and gave final approval for publication.

## 661 **Online Resources**

662 The Appendix A contains a static excerpt of the living spreadsheet on existing trait datasets  
663 and databases, which can be found at <https://goo.gl/QxzfHy>.

664 The online reference for the Ecological Trait-data Standard Vocabulary described in this  
665 paper is <https://ecologicaltraitdata.github.io/ETS/>, stable DOI representing all versions:  
666 10.5281/zenodo.1041732.

667 The development website for the R-package 'traitdataform' is [https://github.com/  
668 EcologicalTraitData/traitdataform](https://github.com/EcologicalTraitData/traitdataform).

669 Any future development of the vocabulary and the R-package is coordinated via [https:  
670 //github.com/EcologicalTraitData/](https://github.com/EcologicalTraitData/).

## 671 **References**

672 Allan, E., P. Manning, F. Alt, J. Binkenstein, S. Blaser, N. Blüthgen, S. Böhm, et al. 2015. Land use intensification  
673 alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecology  
674 Letters* 18:834–843.

675 Allison, L., and R. Gurney, eds. 2015. *A Place to Stand: E-Infrastructures and Data Management for Global  
676 Change Research (COMMUNITY EDITION)*.

677 Bello, F. de, S. Lavorel, S. Díaz, R. Harrington, J. H. C. Cornelissen, R. D. Bardgett, M. P. Berg, et al. 2010.  
678 Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and  
679 Conservation* 19:2873–2893.

680 Berners-Lee, T., J. Hendler, and O. Lassila. 2001. The semantic web. *Scientific american* 284:28–37.



- 681 Blagoderov, V., I. J. Kitching, L. Livermore, T. J. Simonsen, and V. S. Smith. 2012. No specimen left behind:  
682 Industrial scale digitization of natural history collections. *ZooKeys* 133–146.
- 683 Bocci, G. 2015. TR8: An R package for easily retrieving plant species traits. *Methods in Ecology and Evolution*  
684 6:347–350.
- 685 Centre, R. S. S. P. 2012. *Science as an open enterprise*. The Royal Society, London, UK.
- 686 Chamberlain, S., Z. Foster, I. Bartomeus, D. LeBauer, and D. Harris. 2017. *Traits: Species Trait Data from*  
687 *Around the Web*.
- 688 Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, et al. 2003. A  
689 handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian*  
690 *journal of Botany* 51:335–380.
- 691 Diepenbroek, M., F. O. Glöckner, P. Grobe, A. Güntsch, R. Huber, B. König-Ries, I. Kostadinov, et al. 2014.  
692 Towards an Integrated Biodiversity and Ecological Research Data Management and Archiving Platform: The  
693 German Federation for the Curation of Biological Data (GFBio). In *GI-Jahrestagung* (pp. 1711–1721).
- 694 Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, et al. 2016. The global spectrum  
695 of plant form and function. *Nature* 529:167–171.
- 696 Díaz, S., F. Quétier, D. M. Cáceres, S. F. Trainor, N. Pérez-Harguindeguy, M. S. Bret-Harte, B. Finegan, et al.  
697 2011. Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of  
698 nature's benefits to society. *Proceedings of the National Academy of Sciences* 108:895–902.
- 699 Duarte, L., M. Carlucci, C. Fontana, S. Hartz, and V. Pillar. 2011. Plant diaspore traits as indicators of mutual-  
700 istic interactions in woody vegetation patches developing into a grassland-forest mosaic. *Community Ecology*  
701 12:126–134.
- 702 Emerson, C., E. M. Faustman, M. Mokrane, and S. Harrison. 2015. *World Data System (WDS) Data Sharing*  
703 *Principles*. Zenodo.
- 704 Fierer, N., A. Barberán, and D. C. Laughlin. 2014. Seeing the forest for the genes: Using metagenomics to  
705 infer the aggregated traits of microbial communities. *Frontiers in Microbiology* 5.
- 706 Fierer, N., J. W. Leff, B. J. Adams, U. N. Nielsen, S. T. Bates, C. L. Lauber, S. Owens, et al. 2012. Cross-  
707 biome metagenomic analyses of soil microbial communities and their functional attributes. *Proceedings of the*  
708 *National Academy of Sciences of the United States of America* 109:21390–21395.
- 709 Franz, N. M., M. Chen, P. Kianmajd, S. Yu, S. Bowers, A. S. Weakley, and B. Ludäscher. 2016. Names are not  
710 good enough: Reasoning over taxonomic change in the *Andropogon* complex1. (K. Janowicz, B. Adams, B.  
711 König-Ries, D. McGuinness, & M. Schildhauer, eds.) *Semantic Web* 7:645–667.
- 712 Garnier, E., U. Stahl, M.-A. Laporte, J. Kattge, I. Mougnot, I. Kühn, B. Laporte, et al. 2017. Towards a  
713 thesaurus of plant characteristics: An ecological contribution. *Journal of Ecology* 105:298–309.
- 714 GBIF. 2017. *Darwin Core Archives - How-to Guide*.
- 715 German Science Organisations, A. of. 2010. *Principles for the Handling of Research Data*. Schwerpunktinitia-  
716 tive "Digitale Information".
- 717 Gkoutos, G. V., P. N. Schofield, and R. Hoehndorf. 2012. *The Units Ontology: A tool for integrating units of*  
718 *measurement in science*. Database 2012.

- 719 Gossner, M. M., N. K. Simons, R. Achtziger, T. Blick, W. H. Dorow, F. Dziock, F. Köhler, et al. 2015. A summary of  
720 eight traits of Coleoptera, Hemiptera, Orthoptera and Araneae, occurring in grasslands in Germany. *Scientific*  
721 *Data* 2:150013.
- 722 Groom, Q., R. Hyam, and A. Güntsch. 2017. Data management: Stable identifiers for collection specimens.  
723 *Nature* 546:33.
- 724 Gruber, T. R. 1995. Toward principles for the design of ontologies used for knowledge sharing? *International*  
725 *Journal of Human-Computer Studies* 43:907–928.
- 726 Guralnick, R. P., P. F. Zermoglio, J. Wieczorek, R. LaFrance, D. Bloom, and L. Russell. 2016. The importance of  
727 digitized biocollections as a source of trait data and a new VertNet resource. *Database* 2016.
- 728 Güntsch, A., R. Hyam, G. Hagedorn, S. Chagnoux, D. Röpert, A. Casino, G. Droege, et al. 2017. Actionable,  
729 long-term stable and semantic web compatible identifiers for access to biological collection objects. *Database*  
730 2017.
- 731 Hoehndorf, R., M. Alshahrani, G. V. Gkoutos, G. Gosline, Q. Groom, T. Hamann, J. Kattge, et al. 2016. The  
732 flora phenotype ontology (FLOPO): Tool for integrating morphological traits and phenotypes of vascular plants.  
733 *Journal of Biomedical Semantics* 7:65.
- 734 Holetschek, J., G. Dröge, A. Güntsch, and W. G. Berendsohn. 2012. The ABCD of primary biodiversity data  
735 access. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology* 146:771–779.
- 736 Iversen, C. M., M. L. McCormack, A. S. Powell, C. B. Blackwood, G. T. Freschet, J. Kattge, C. Roumet, et al. 2017.  
737 A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*  
738 215:15–26.
- 739 Jaiswal, P., S. Avraham, K. Ilic, E. A. Kellogg, S. McCouch, A. Pujar, L. Reiser, et al. 2005. Plant Ontology (PO):  
740 A Controlled Vocabulary of Plant Structures and Growth Stages. *International Journal of Genomics*. Research  
741 article.
- 742 Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, et al. 2009. PanTHERIA: A  
743 species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*  
744 90:2648–2648.
- 745 Kanehisa, M., S. Goto, Y. Sato, M. Furumichi, and M. Tanabe. 2012. KEGG for integration and interpretation  
746 of large-scale molecular data sets. *Nucleic Acids Research* 40:D109–D114.
- 747 Karam, N., C. Müller-Birn, M. Gleisberg, D. Fichtmüller, R. Tolksdorf, and A. Güntsch. 2016. A terminology  
748 service supporting semantic annotation, integration, discovery and analysis of interdisciplinary research data.  
749 *Datenbank-Spektrum* 16:195–205.
- 750 Kattge, J., S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönisch, E. Garnier, et al. 2011a. TRY – a global  
751 database of plant traits. *Global Change Biology* 17:2905–2935.
- 752 Kattge, J., K. Ogle, G. Bönisch, S. Díaz, S. Lavorel, J. Madin, K. Nadrowski, et al. 2011b. A generic structure  
753 for plant trait databases. *Methods in Ecology and Evolution* 2:202–213.
- 754 Kissling, W. D., L. Dalby, C. Fløjgaard, J. Lenoir, B. Sandel, C. Sandom, K. Trøjelsgaard, et al. 2014. Establishing  
755 macroecological trait datasets: Digitalization, extrapolation, and validation of diet preferences in terrestrial  
756 mammals worldwide. *Ecology and Evolution* 4:2913–2930.

- 757 Kleyer, M., R. Bekker, I. Knevel, J. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, et al. 2008. The LEDA  
758 Traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology* 96:1266–1274.
- 759 Klotz, S., I. Kühn, W. Durka, and G. Briemle. 2002. BIOLFLOR: Eine Datenbank mit biologisch-ökologischen  
760 Merkmalen zur Flora von Deutschland (Vol. 38). Bundesamt für naturschutz Bonn.
- 761 KNB. 2011. Ecological Metadata Language (EML) Specification. The Knowledge Network for Biocomplexity.
- 762 Krause, S., X. Le Roux, P. A. Niklaus, P. M. Van Bodegom, J. T. Lennon, S. Bertilsson, H.-P. Grossart, et al.  
763 2014. Trait-based approaches for understanding microbial biodiversity and ecosystem functioning. *Frontiers  
764 in Microbiology* 5.
- 765 Langille, M. G. I., J. Zaneveld, J. G. Caporaso, D. McDonald, D. Knights, J. A. Reyes, J. C. Clemente, et al.  
766 2013. Predictive functional profiling of microbial communities using 16S rRNA marker gene sequences. *Nature  
767 Biotechnology* 31:814–821.
- 768 Laporte, M.-A., E. Garnier, and I. Mougenot. 2013. A faceted search system for facilitating discovery-driven  
769 scientific activities: A use case from functional ecology. *Semantics for Biodiversity (S4BioDiv 2013)* 25.
- 770 Lavorel, S., and É. Garnier. 2002. Predicting changes in community composition and ecosystem functioning  
771 from plant traits: Revisiting the Holy Grail. *Functional ecology* 16:545–556.
- 772 Lavorel, S., and K. Grigulis. 2012. How fundamental plant functional trait relationships scale-up to trade-offs  
773 and synergies in ecosystem services. *Journal of Ecology* 100:128–140.
- 774 Le Provost, G., N. Gross, L. Börger, H. Deraison, M. Roncoroni, and I. Badenhausser. 2017. Trait-matching and  
775 mass effect determine the functional response of herbivore communities to land-use intensification. *Functional  
776 Ecology*.
- 777 McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional  
778 traits. *Trends in Ecology & Evolution* 21:178–185.
- 779 Michener, W. K., J. W. Brunt, J. J. Helly, T. B. Kirchner, and S. G. Stafford. 1997. Nongeospatial metadata for  
780 the ecological sciences. *Ecological Applications* 7:330–342.
- 781 Moretti, M., A. T. Dias, F. Bello, F. Altermatt, S. L. Chown, F. M. Azcárate, J. R. Bell, et al. 2017. Handbook  
782 of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*  
783 31:558–567.
- 784 Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach  
785 reveals community responses to disturbances. *Trends in Ecology & Evolution* 28:167–177.
- 786 Myhrvold, N. P., E. Baldrige, B. Chan, D. Sivam, D. L. Freeman, and S. K. M. Ernest. 2015. An amniote life-  
787 history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* 96:3109–3109.
- 788 Oliveira, B. F., V. A. São-Pedro, G. Santos-Barrera, C. Penone, and G. C. Costa. 2017. AmphiBIO, a global  
789 database for amphibian ecological traits. *Scientific Data* 4:sdata2017123.
- 790 Page, R. D. M. 2008. Biodiversity informatics: The challenge of linking data and the role of shared identifiers.  
791 *Briefings in Bioinformatics* 9:345–354.
- 792 Park, C. A., S. M. Bello, C. L. Smith, Z.-L. Hu, D. H. Munzenmaier, R. Nigam, J. R. Smith, et al. 2013. The  
793 Vertebrate Trait Ontology: A controlled vocabulary for the annotation of trait data across species. *Journal of  
794 Biomedical Semantics* 4:13.

- 795 Parr, C. S., K. S. Schulz, J. Hammock, N. Wilson, P. Leary, J. Rice, C. Jr, et al. 2016. TraitBank: Practical  
796 semantics for organism attribute data. *Semantic Web* 7:577–588.
- 797 Pereira, H. M., S. Ferrier, M. Walters, G. N. Geller, R. H. G. Jongman, R. J. Scholes, M. W. Bruford, et al. 2013.  
798 Essential biodiversity variables. *Science* 339:277–278.
- 799 Perez-Harguindeguy, N., S. Diaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, et al.  
800 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal*  
801 *of botany* 61:167–234.
- 802 Perović, D., S. Gámez-Virués, C. Börschig, A.-M. Klein, J. Krauss, J. Steckel, C. Rothenwöhler, et al. 2015.  
803 Configurational landscape heterogeneity shapes functional community composition of grassland butterflies.  
804 *Journal of applied ecology* 52:505–513.
- 805 Pey, B., M.-A. Laporte, J. Nahmani, A. Auclerc, Y. Capowiez, G. Caro, D. Cluzeau, et al. 2014. A Thesaurus for  
806 Soil Invertebrate Trait-Based Approaches. *PLOS ONE* 9:e108985.
- 807 Ricklefs, R. E. 2017. Passerine morphology: External measurements of approximately one-quarter of passerine  
808 bird species. *Ecology* 98:1472–1472.
- 809 Robertson, T., M. Döring, J. Wiczorek, R. De Giovanni, and D. Vieglais. 2009. Darwin Core Text Guide.
- 810 Roskov, Y., L. Abucay, T. Orrell, D. Nicolson, N. Bailly, P. Kirk, T. Bourgoin, et al., eds. 2018. Species 2000 &  
811 ITIS Catalogue of Life. Species 2000: Naturalis, Leiden, NL.
- 812 Salguero-Gómez, R., O. R. Jones, E. Jongejans, S. P. Blomberg, D. J. Hodgson, C. Mbeau-Ache, P. A. Zuidema,  
813 et al. 2016. Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide.  
814 *Proceedings of the National Academy of Sciences* 113:230–235.
- 815 Schrod, F., J. Kattge, H. Shan, F. Fazayeli, J. Joswig, A. Banerjee, M. Reichstein, et al. 2015. BHPMF – a hier-  
816 archical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography.  
817 *Global Ecology and Biogeography* 24:1510–1521.
- 818 Secretariat, G. 2017. GBIF Backbone Taxonomy.
- 819 Swan, A. 2012. Policy guidelines for the development and promotion of open access. Open guidelines series.  
820 UNESCO, Paris, France.
- 821 Torsvik, V., and L. Øvreås. 2002. Microbial diversity and function in soil: From genes to ecosystems. *Current*  
822 *Opinion in Microbiology* 5:240–245.
- 823 Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of  
824 trait be functional! *Oikos* 116:882–892.
- 825 Vollmar, A., J. A. Macklin, and L. Ford. 2010. Natural history specimen digitization: Challenges and concerns.  
826 *Biodiversity informatics* 7.
- 827 Walls, R. L., B. Athreya, L. Cooper, J. Elser, M. A. Gandolfo, P. Jaiswal, C. J. Mungall, et al. 2012. Ontologies  
828 as integrative tools for plant science. *American Journal of Botany* 99:1263–1275.
- 829 Wickham, H. 2014. Tidy data. *Journal of Statistical Software* 59:1–23.
- 830 Wiczorek, J., D. Bloom, R. Guralnick, S. Blum, M. Döring, R. Giovanni, T. Robertson, et al. 2012. Darwin  
831 Core: An evolving community-developed biodiversity data standard. *PloS one* 7:e29715.
- 832 Yoder, M. J., I. Miko, K. C. Seltmann, M. A. Bertone, and A. R. Deans. 2010. A gross anatomy ontology for  
833 Hymenoptera. *PloS one* 5:e15991.