



OPEN

# AusTraits, a curated plant trait database for the Australian flora

DATA DESCRIPTOR

We introduce the AusTraits database - a compilation of values of plant traits for taxa in the Australian flora (hereafter AusTraits). AusTraits synthesises data on 448 traits across 28,640 taxa from field campaigns, published literature, taxonomic monographs, and individual taxon descriptions. Traits vary in scope from physiological measures of performance (e.g. photosynthetic gas exchange, water-use efficiency) to morphological attributes (e.g. leaf area, seed mass, plant height) which link to aspects of ecological variation. AusTraits contains curated and harmonised individual- and species-level measurements coupled to, where available, contextual information on site properties and experimental conditions. This article provides information on version 3.0.2 of AusTraits which contains data for 997,808 trait-by-taxon combinations. We envision AusTraits as an ongoing collaborative initiative for easily archiving and sharing trait data, which also provides a template for other national or regional initiatives globally to fill persistent gaps in trait knowledge.

## Background & Summary

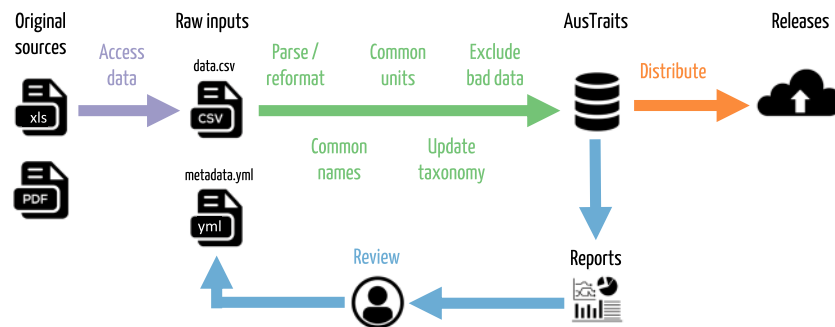
Species traits are essential for comparing ecological strategies among plants, both within any given vegetation and across environmental space or evolutionary lineages<sup>1–4</sup>. Broadly, a trait is any measurable property of a plant capturing aspects of its structure or function<sup>5–8</sup>. Traits thereby provide useful indicators of species' behaviours in communities and ecosystems, regardless of their taxonomy<sup>8–10</sup>. Through global initiatives the volume of available trait information for plants has grown rapidly in the last two decades<sup>11,12</sup>. However, the geographic coverage of trait measurements across the globe is patchy, limiting detailed analyses of trait variation and diversity in some regions, and, more generally, development of theory accounting for the diversity of plant strategies.

One such region where trait data is sparsely documented is Australia; a continent with a flora of c. 28,900 native vascular plant taxa<sup>13</sup> (including species, subspecies, varieties and forma). While significant investment has been made in curating and digitising herbarium collections and observation records in Australia over the last two decades (e.g. The Australian Virtual Herbarium houses ~7 million specimen occurrence records; <https://avh.ala.org.au>), no complementary resource yet exists for consolidating information on plant traits. Moreover, relatively few Australian species are represented in the leading global databases. For example, the international TRY database<sup>12</sup> has measurements for only 3830 Australian species across all collated traits. This level of species coverage limits our ability to use traits to understand and ultimately manage Australian vegetation<sup>14</sup>. While initiatives such as TRY<sup>12</sup> and the Open Traits Network<sup>15</sup> are working towards global synthesis of trait data, a stronger representation of Australian plant taxa in these efforts is essential, especially given the high richness and endemism of this continental flora, and the unique contribution this makes to global floral diversity<sup>16,17</sup>.

Here we introduce the AusTraits database (hereafter AusTraits), a compilation of plant traits for the Australian flora. Currently, AusTraits draws together 283 distinct sources and contains 997,808 measurements spread across 448 different traits for 28,640 taxa. To assemble AusTraits from diverse primary sources and make data available for reuse, we needed to overcome three main types of challenges (Fig. 1): (1) Accessing data from diverse original sources, including field studies, online databases, scientific articles, and published taxonomic floras; (2) Harmonising these diverse sources into a federated resource, with common taxon names, units, trait names, and data formats; and (3) Distributing versions of the data under suitable license. To meet this challenge, we developed a workflow which draws on emerging community standards and our collective experience building trait databases.

By providing a harmonised and curated dataset on 448 plant traits, AusTraits contributes substantially to filling the gap in Australian and global biodiversity resources. Prior to the development of AusTraits, data on Australian plant traits existed largely as a series of disconnected datasets collected by individual laboratories or initiatives.

A full list of authors and their affiliations appears at the end of the paper.



**Fig. 1** The data curation pathway used to assemble the AusTraits database. Trait measurements are accessed from original data sources, including published floras and field campaigns. Features such as variable names, units and taxonomy are harmonised to a common standard. Versioned releases are distributed to users, allowing the dataset to be used and re-used in a reproducible way.

AusTraits has been developed as a standalone database, rather than as part of the existing global database TRY<sup>12</sup>, for three reasons. First, we sought to establish an engaged and localised community, actively collaborating to enhance coverage of plant trait data within Australia. We envisioned that a community would form more readily to fill gaps in national knowledge of traits with local ownership of the resource. While we will never have a counterfactual, a vibrant community excited to be part of this initiative has indeed been established and coverage is much higher for Australian species than has been achieved since TRY's inception. Local ownership also aligns well with funding opportunities and national research priorities, and enables database coordinators to progress at their own speed. Second, we wanted to apply an entirely open-source approach to the aggregation workflow. All the code and raw files used to create the compiled database are available, and this database is freely available via a third party data repository (Zenodo) which is itself built for long term data archiving, with an established API. Finally, we targeted primary data sources, where possible, whereas TRY accepts aggregated datasets. The hope was that this would increase data quality, by removing intermediaries and easier identification of duplicates.

While independent, the overall structure of AusTraits is similar to that of TRY, ensuring the two databases will be interoperable. Both databases are founded on similar principles and terminology<sup>18,19</sup>. Increasingly, researchers and biodiversity portals are seeking to connect diverse datasets<sup>15</sup>, which is possible if they share a common foundation.

We envision AusTraits as an on-going collaborative initiative for easily archiving and sharing trait data about the Australian flora. Open access to a comprehensive resource like this will generate significant new knowledge about the Australian flora across multiple scales of interest, as well as reduce duplication of effort in the compilation of plant trait data, particularly for research students and government agencies seeking to access information on traits. In coming years, AusTraits will continue to be expanded, with integrations into other biodiversity platforms and expansion of coverage into historically neglected plant lineages in trait science, such as pteridophytes (lycophytes and ferns). Further, through international initiatives, such as the Open Traits Network, linkages are being forged between plant datasets and a variety of other organismal databases<sup>15</sup>.

## Methods

**Primary sources.** AusTraits version 3.0.2 was assembled from 283 distinct sources, including published papers, field measurements, glasshouse and field experiments, botanical collections, and taxonomic treatments. Initially we identified a list of candidate traits of interest, then identified primary sources containing measurements for these traits, before contacting authors for access. As the compilation grew, we expanded the list of traits considered to include any measurable quantity that had been quantified for at least a moderate number of taxa ( $n > 20$ ).

For a small subset of sources from herbaria, providing a text description of taxa, we used regular expressions in R to extract measurements of traits from the text. A variety of expressions were developed to extract height, leaf/seed dimensions and growth form. Error checking was completed on approximately 60% of mined measurements by visually inspecting the extracted values relative to the textual descriptions.

**Trait definitions.** A full list of traits and their sources appears in Supplementary Table 1<sup>20–354</sup>. The list of sources in AusTraits was developed gradually as new datasets were incorporated, drawing from original source publications and a published thesaurus of plant characteristics<sup>19</sup>. We categorised traits based on the tissue where it is measured (bark, leaf, reproductive, root, stem, whole plant) and the type of measurement (allocation, life history, morphology, nutrient, physiological). Version 3.0.2 of AusTraits includes 358 numeric and 90 categorical traits.

**Database structure.** The schema of AusTraits broadly follows the principles of the established Observation and Measurement Ontology<sup>18</sup> in that, where available, trait data are connected to contextual information about the collection (e.g. location coordinates, light levels, whether data were collected in the field or lab) and information about the methods used to derive measurements (e.g. number of replicates, equipment used). The database

Element	Contents
traits	A table containing measurements of plant traits.
sites	A table containing observations of site characteristics associated with information in 'traits'. Cross referencing between the two dataframes is possible using combinations of the variables 'dataset_id', 'site_name'.
contexts	A table containing observations of contextual characteristics associated with information in 'traits'. Cross referencing between the two dataframes is possible using combinations of the variables 'dataset_id', 'context_name'.
methods	A table containing details on methods with which data were collected, including time frame and source.
excluded_data	A table of data that did not pass quality test and so were excluded from the master dataset.
taxa	A table containing details on taxa associated with information in 'traits'. This information has been sourced from the APC (Australian Plant Census) and APNI (Australian Plant Name Index) and is released under a CC-BY3 license.
definitions	A copy of the definitions for all tables and terms. Information included here was used to process data and generate any documentation for the study.
sources	Bibtex entries for all primary and secondary sources in the compilation.
contributors	A table of people contributing to each study.
taxonomic_updates	A table of all taxonomic changes implemented in the construction of AusTraits. Changes are determined by comparing against the APC (Australian Plant Census) and APNI (Australian Plant Name Index).
build_info	A description of the computing environment used to create this version of the dataset, including version number, git commit and R session_info.

**Table 1.** Main elements of the harmonised AusTraits database. See Tables 2–8 for details on each component.

key	value
dataset_id	Primary identifier for each study contributed into AusTraits; most often these are scientific papers, books, or online resources. By default should be name of first author and year of publication, e.g. 'Falster_2005'.
taxon_name	Currently accepted name of taxon in the Australian Plant Census or in the Australian Plant Name Index.
site_name	Name of site where individual was sampled. Cross-references to identical columns in 'sites' and 'traits'.
context_name	Name of contextual scenario where individual was sampled. Cross-references to identical columns in 'contexts' and 'traits'.
observation_id	A unique identifier for the observation, useful for joining traits coming from the same 'observation_id'. These are assigned automatically, based on the 'dataset_id' and row number of the raw data.
trait_name	Name of trait sampled.
value	Measured value.
unit	Units of the sampled trait value after aligning with AusTraits standards.
date	Date sample was taken, in the format 'yyyy-mm-dd', but with days and months only when specified.
value_type	A categorical variable describing the type of trait value recorded.
replicates	Number of replicate measurements that comprise the data points for the trait for each measurement. A numeric value (or range) is ideal and appropriate if the value type is a 'mean', 'median', 'min' or 'max'. For these value types, if replication is unknown the entry should be 'unknown'. If the value type is 'raw_value' the replicate value should be 1. If the value type is 'expert_mean', 'expert_min', or 'expert_max' the replicate value should be 'na'.
original_name	Name given to taxon in the original data supplied by the authors

**Table 2.** Structure of the `traits` table, containing measurements of plant traits.

contains 11 elements, as described in Table 1. This format was developed to include information about the trait measurements, taxon, methods, sites, contextual information, people involved, and citation sources.

For storage efficiency, the main table of traits contains relatively little information (Table 2), but can be cross linked against other tables (Tables 3–8) using identifiers for dataset, site, context, observation, and taxon (Table 1). The `dataset_id` is ordinarily the surname of the first author and year of publication associated with the source's primary citation (e.g. `Blackman_2014`). Trait values were also recorded as being one of several possible value types (`value_type`) (Table 9), reflecting the type of measurement submitted by the contributor, as different sources provide different levels of detail. Possible values include `raw_value`, `individual_mean`, `site_mean`, `multisite_mean`, `expert_mean`, `experiment_mean`. Further details on the methods used for collecting each trait are provided in a `methods` table (Table 5).

**Harmonisation.** To harmonise each source into the common AusTraits format we applied a reproducible and transparent workflow (Fig. 1), written in R<sup>355</sup>, using custom code, and the packages `tidyverse`<sup>356</sup>, `yaml`<sup>357</sup>, `remake`<sup>358</sup>, `knitr`<sup>359</sup>, and `rmarkdown`<sup>360</sup>. In this workflow, we performed a series of operations, including reformatting data into a standardised format, generating observation ids for each set of linked measurements, transforming variable names into common terms, transforming data into common units, standardising terms (trait values) for categorical variables, encoding suitable metadata, and flagging data that did not pass quality checks. Details from each primary source were saved with minimal modification into two plain text files. The first file, `data.csv`, contains the actual trait data in comma-separated values format. The second file, `metadata.yml`, contains relevant metadata for the study, as well as options for mapping trait names and units onto standard types, and any substitutions applied to the data in processing. These two files provide all the information needed to compile each study into

key	value
dataset_id	Primary identifier for each study contributed into AusTraits; most often these are scientific papers, books, or online resources. By default should be name of first author and year of publication, e.g. 'Falster_2005'.
site_name	Name of site where individual was sampled. Cross-references to identical columns in 'sites' and 'traits'.
site_property	The site characteristic being recorded. Name should include units of measurement, e.g. 'longitude (deg)'. Ideally we have at least these variables for each site - 'longitude (deg)', 'latitude (deg)', 'description'.
value	Measured value.

**Table 3.** Structure of the `sites` table, containing observations of site characteristics associated with information in `traits`.

key	value
dataset_id	Primary identifier for each study contributed into AusTraits; most often these are scientific papers, books, or online resources. By default should be name of first author and year of publication, e.g. 'Falster_2005'.
context_name	Name of contextual scenario where individual was sampled. Cross-references to identical columns in 'contexts' and 'traits'.
context_property	The contextual characteristic being recorded. Name should include units of measurement, e.g. 'CO2 concentration (ppm)'.
value	Measured value.

**Table 4.** Structure of the `contexts` table, containing observations of contextual characteristics associated with information in `traits`.

key	value
dataset_id	Primary identifier for each study contributed into AusTraits; most often these are scientific papers, books, or online resources. By default should be name of first author and year of publication, e.g. 'Falster_2005'.
trait_name	Name of trait sampled. Allowable values specified in the table 'traits'.
methods	A textual description of the methods used to collect the trait data. Whenever available, methods are taken near-verbatim from referenced source. Methods can include descriptions such as 'measured on botanical collections', 'data from the literature', or a detailed description of the field or lab methods used to collect the data.
year_collected_start	The year data collection commenced.
year_collected_end	The year data collection was completed.
description	A 1–2 sentence description of the purpose of the study.
collection_type	A field to indicate where the majority of plants on which traits were measured were collected - in the 'field', 'lab', 'glasshouse', 'botanical collection', or 'literature'. The latter should only be used when the data were sourced from the literature and the collection type is unknown.
sample_age_class	A field to indicate if the study was completed on 'adult' or 'juvenile' plants.
sampling_strategy	A written description of how study sites were selected and how study individuals were selected. When available, this information is copied verbatim from a published manuscript. For botanical collections, this field ideally indicates which records were 'sampled' to measure a specific trait.
source_primary_citation	Citation for primary source. This detail is generated from the primary source in the metadata.
source_primary_key	Citation key for primary source in 'sources'. The key is typically of format 'Surname_year'.
source_secondary_citation	Citations for secondary source. This detail is generated from the secondary source in the metadata.
source_secondary_key	Citation key for secondary source in 'sources'. The key is typically of format 'Surname_year'.

**Table 5.** Structure of the `methods` table, containing details on methods with which data were collected, including time frame and source.

a standardised AusTraits format. Successive versions of AusTraits iterate through the steps in Fig. 1, to incorporate new data and correct identified errors, leading to a high-quality, harmonised dataset.

After importing a study, we generated a detailed report which summarised the study's metadata and compared the study's data values to those collected by other studies for the same traits. Data for continuous and categorical variables are presented in scatter plots and tables respectively. These reports allow first the AusTraits data curator, followed by the data contributor, to rapidly scan the metadata to confirm it has been entered correctly and the trait data to ensure it has been assigned the correct units and their categorical traits values are properly aligned with AusTraits trait values.

**Taxonomy.** We developed a custom workflow to clean and standardise taxonomic names using the latest and most comprehensive taxonomic resources for the Australian flora: the Australian Plant Census (APC)<sup>13</sup> and the Australian Plant Name Index (APNI)<sup>361</sup>. These resources document all known taxonomic names for Australian plants, including currently accepted names and synonyms. While several automated tools exist for updating taxonomy, such as `taxize`<sup>362</sup>, these do not currently include up to date information for Australian taxa. Updates were completed in two steps. In the first step, we used both direct and then fuzzy matching (with up

key	value
dataset_id	Primary identifier for each study contributed into AusTraits; most often these are scientific papers, books, or online resources. By default should be name of first author and year of publication, e.g. 'Falster_2005'.
original_name	Name given to taxon in the original data supplied by the authors
cleaned_name	Name of the taxon after implementing any changes encoded for this taxon in the metadata file for the corresponding 'dataset_id'.
taxonIDClean	Where it could be identified, the 'taxonID' of the 'cleaned_name' for this taxon in the APC.
taxonomicStatusClean	Taxonomic status of the taxon identified by 'taxonIDClean' in the APC.
alternativeTaxonomicStatusClean	The status of alternative records with the name 'cleaned_name' in the APC.
acceptedNameUsageID	ID of the accepted name for taxon in the APC or APNI.
taxon_name	Currently accepted name of taxon in the APC or in the APNI.

**Table 6.** Structure of the `taxonomic_updates` table, of all taxonomic changes implemented in the construction of AusTraits. Changes are determined by comparing against the APC (Australian Plant Census) and APNI (Australian Plant Name Index).

key	value
taxon_name	Currently accepted name of taxon in the APC or in the APNI.
source	Source of taxonomic information, either APC or APNI.
acceptedNameUsageID	ID of the accepted name for taxon in the APC or APNI.
scientificNameAuthorship	Authority for taxon indicated under <code>taxon_name</code> .
taxonRank	Rank of the taxon.
taxonomicStatus	Taxonomic status of the taxon.
family	Family of the taxon.
genus	Genus of the taxon.
taxonDistribution	Known distribution of the taxon, by state.
ccAttributionIRI	Source of taxonomic information.

**Table 7.** Structure of the `taxa` table, containing details on taxa associated with information in the traits table. This information has been sourced from the APC (Australian Plant Census) and APNI (Australian Plant Name Index) and is released under a CC-BY3 license.

key	value
dataset_id	Primary identifier for each study contributed into AusTraits; most often these are scientific papers, books, or online resources. By default should be name of first author and year of publication, e.g. 'Falster_2005'.
name	Name of contributor
institution	Last known institution or affiliation
role	Their role in the study

**Table 8.** Structure of the `contributors` table, of people contributing to each study.

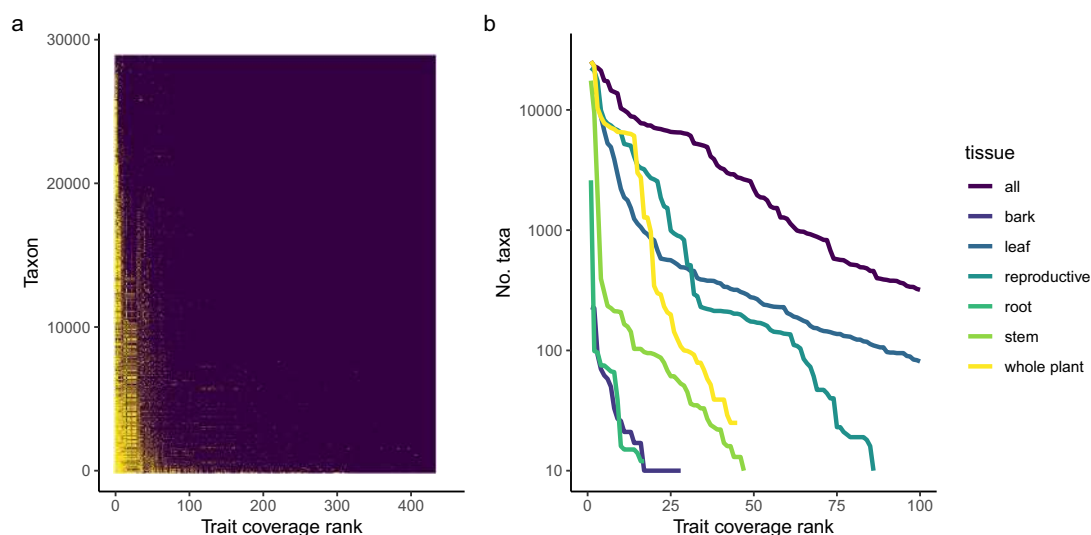
to 2 characters difference) to search for an alignment between reported names and those in three name sets: 1) All accepted taxa in the APC, 2) All known names in the APC, 3) All names in the APNI. Names were aligned without name authorities, as we found this information was rarely reported in the raw datasets provided to us. Second, we used the aligned name to update any outdated names to their current accepted name, using the information provided in the APC. If a name was recorded as being both an accepted name and an alternative (e.g. synonym) we preferred the accepted name, but also noted the alternative records. For phrase names, when a suitable match could not be found, we manually reviewed near matches via web portals such as the Atlas of Living Australia to find a suitable match. The final resource reports both the original and the updated taxon name alongside each trait record (Table 2), as well as an additional table summarising all taxonomic name changes (Table 6) and further information from the APC and APNI on all taxa included (Table 7). Any changes in taxonomy are exposed within the compiled dataset, enabling researchers to review these as needed.

### Data Records

**Access.** Static versions of AusTraits, including version 3.0.2 used in this descriptor, are available via Zenodo<sup>363</sup>. Data is released under a CC-BY license enabling reuse with attribution – being a citation of this descriptor and, where possible, original sources. Deposition within Zenodo helps makes the dataset consistent with FAIR principles<sup>364</sup>. As an evolving data product, successive versions of AusTraits are being released, containing updates and corrections. Versions are labeled using semantic versioning to indicate the change between versions<sup>365</sup>. As

key	value
raw_value	Value is a direct measurement
site_min	Value is the minimum of measurements on multiple individuals of the taxon at a single site
site_mean	Value is the mean or median of measurements on multiple individuals of the taxon at a single site
site_max	Value is the maximum of measurements on multiple individuals of the taxon at a single site
multisite_min	Value is the minimum of measurements on multiple individuals of the taxon across multiple sites
multisite_mean	Value is the mean or median of measurements on multiple individuals of the taxon across multiple sites
multisite_max	Value is the maximum of measurements on multiple individuals of the taxon across multiple sites
expert_min	Value is the minimum observed for a taxon across its range or in this particular dataset, as estimated by an expert based on their knowledge of the taxon. Data fitting this category include estimates from floras that represent a taxon's entire range.
expert_mean	Value is the mean observed for a taxon across its range or in this particular dataset, as estimated by an expert based on their knowledge of the taxon. Data fitting this category include estimates from floras that represent a taxon's entire range, and values for categorical variables obtained from a reference book, or identified by an expert.
expert_max	Value is the maximum observed for a taxon across its range or in this particular dataset, as estimated by an expert based on their knowledge of the taxon. Data fitting this category include estimates from floras that represent a taxon's entire range.
experiment_min	Value is the minimum of measurements from an experimental study either in the field or a glasshouse
experiment_mean	Value is the mean or median of measurements from an experimental study either in the field or a glasshouse
experiment_max	Value is the maximum of measurements from an experimental study either in the field or a glasshouse
individual_mean	Value is a mean of replicate measurements on an individual (usually for experimental ecophysiology studies)
individual_max	Value is a maximum of replicate measurements on an individual (usually for experimental ecophysiology studies)
literature_source	Value is a site or multi-site mean that has been sourced from an unknown literature source
unknown	Value type is not currently known

**Table 9.** Possible value types of trait records.

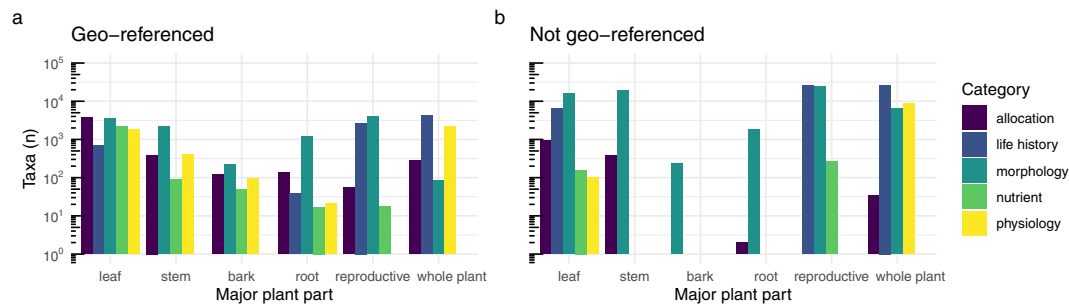


**Fig. 2** Coverage of traits by taxa. (a) Matrix showing the coverage of taxa for each trait, with yellow indicating presence of data. The figure was generated with a subset of 500 randomly selected taxa. (b) Number of taxa with data for first 100 traits for all traits and separated by tissue.

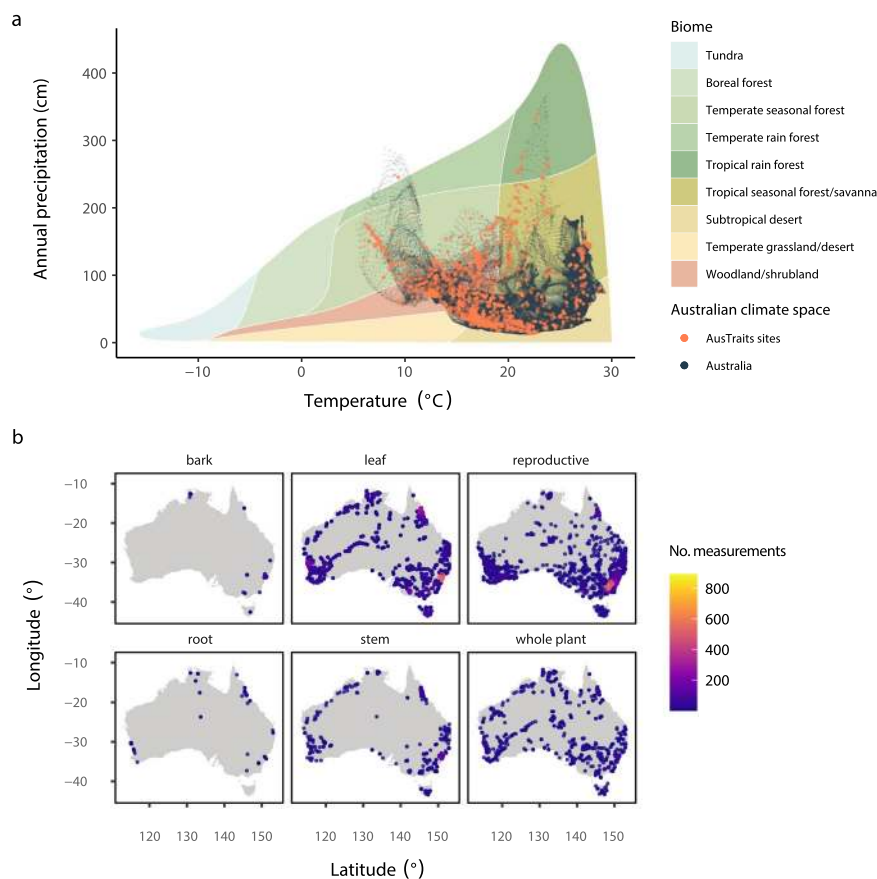
validation (see Technical Validation, below) and data entry are ongoing, users are recommended to pull data from release, to ensure results in their downstream analyses remain consistent as the database is updated.

The R package *austraits* (<https://github.com/traitecoevo/austraits>) provides easy access to data and examples on manipulating data (e.g. joining tables, subsetting) for those using this platform.

**Data coverage.** The number of accepted vascular plant taxa in the APC (as of May 2020) is around 28,981<sup>13</sup>. Version 3.0.2 of *AusTraits* includes at least one record for 26,852 taxa (~93% of known taxa). Five traits (leaf\_length, leaf\_width, plant\_height, life\_history, plant\_growth\_form) have records for more than 50% of known species (Fig. 2a). Across all traits, the median number of taxa with records is 62. Supplementary Table 1 shows the number of studies, taxa, and families with data in *AusTraits*, as well as the number of geo-referenced records, for each trait. Looking across traits and tissue categories, coverage declined gradually, with moderate



**Fig. 3** Number of taxa with trait records by plant tissue and trait category, for data that are (a) Geo-referenced, and (b) Not geo-referenced. Many records without a geo-reference come from botanical collections, such as floras.

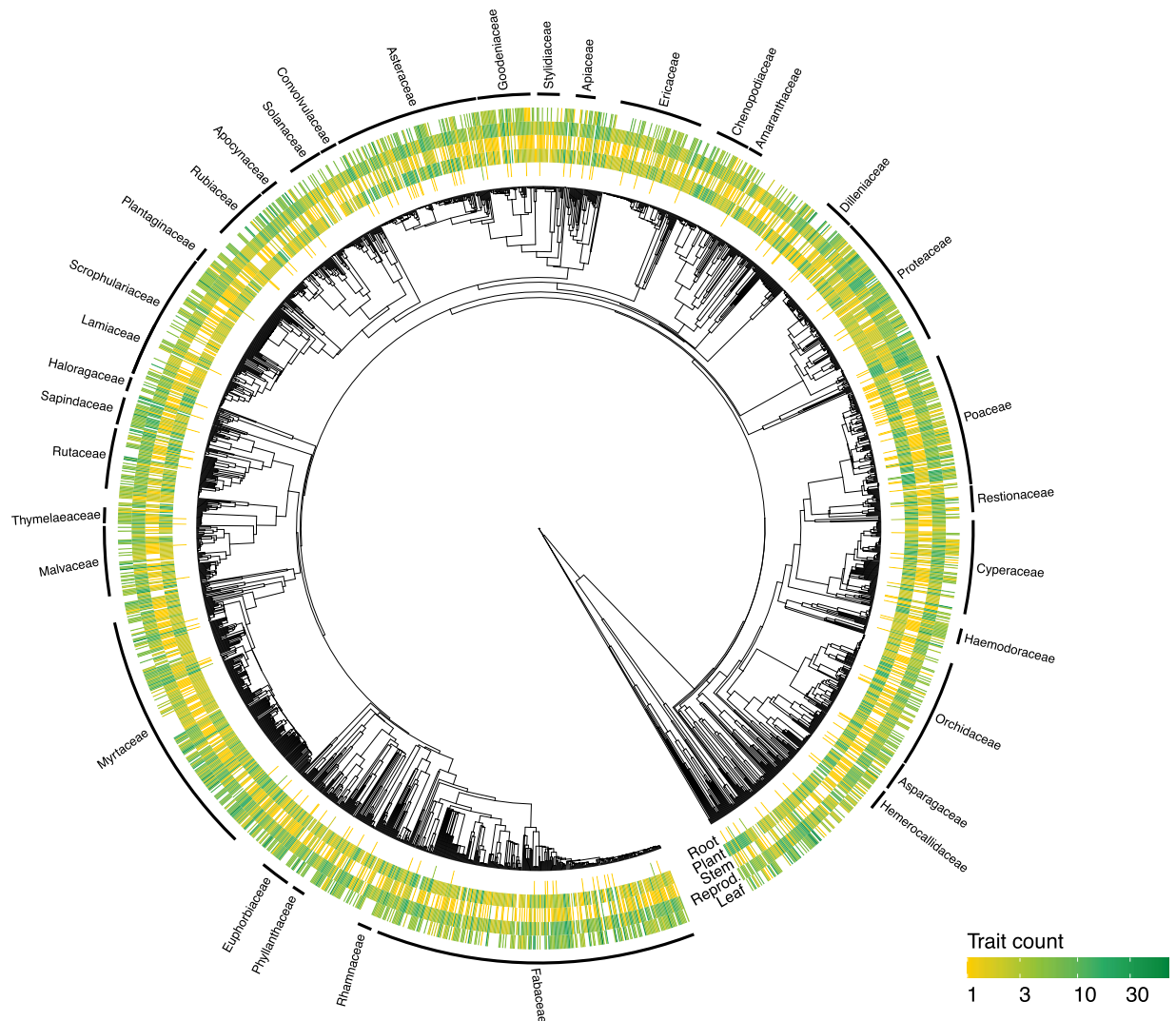


**Fig. 4** Coverage of geo-referenced trait records across Australian climatic and geographic space for traits in different categories. (a) AusTraits' sites (orange) within Australia's precipitation-temperature space (dark-grey) superimposed upon Whittaker's classification of major biomes by climate<sup>370</sup>. Climate data were extracted at 10'' resolution from WorldClim<sup>371</sup>. (b) Locations of geo-referenced records for different plant tissues.

coverage (>20%) for more than 50 traits (Fig. 2). Coverage for root, stem and bark traits declined much faster than trait measurements for other plant tissues (Fig. 2b).

The most common traits are non geo-referenced records from floras; these are trait values representing a continental or region mean (or spread) and hence are not linked to a location. Yet, geo-referenced records were available for several traits for more than 10% of the flora (Fig. 3a). Coverage is notably higher for geo-referenced measurements of some tissues and trait types - such as bark stems and roots - relative to non-geo-referenced measurements (Fig. 3).

Trait records are spread across the climate space of Australia (Fig. 4a), as well as geographic locations (Fig. 4b). As with most data in Australia, the density of records was somewhat concentrated around cities or roads in remote regions.



**Fig. 5** Phylogenetic distribution of trait data in AusTraits for a subset of 2000 randomly sampled taxa. The heatmap colour intensity denotes the number of traits measured within a family for each plant tissue. The most widespread family names (with more than ten taxa) are labelled on the edge of the tree.

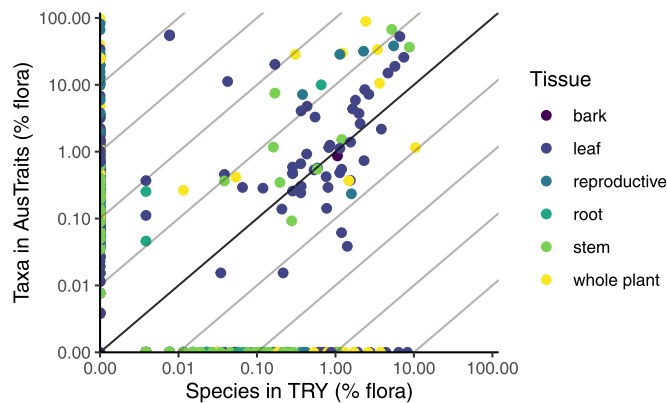
Overall trait coverage across an estimated phylogenetic tree of Australian plant species is relatively unbiased (Fig. 5), though there are some notable exceptions. One exception is for root traits, where taxa within Poaceae have large amounts of information available relative to other plant families. A cluster of taxa within the family Myrtaceae which are largely from Western Australia have little leaf information available.

Comparing coverage in AusTraits to the global database TRY, there were 76 traits overlapping. Of these, AusTraits tended to contain records for more taxa, but not always; multiple traits had more than 10 times the number of taxa represented in AusTraits (Fig. 6). However, there were more records in TRY for 25 traits, in particular physiological leaf traits. Many traits were not overlapping between the two databases (Fig. 6). We noted that AusTraits includes more seed and fruit nutrient data; possibly reflecting the interest in Australia in understanding how fruit and seeds are provisioned in nutrient-depauperate environments. AusTraits includes more categorical values, especially variables documenting different components of species' fire response strategies, reflecting the importance of fire in shaping Australian communities and the research to document different strategies species have evolved to succeed in fire-prone environments.

### Technical Validation

We implemented three strategies to maintain data quality. First, we conducted a detailed review of each source based on a bespoke report, showing all data and metadata, by both an AusTraits curator (primarily Wenk) and the original contributor (where possible). Measurements for each trait were plotted against all other values for the trait in AusTraits, allowing quick identification of outliers. Corrections suggested by contributors were combined back into AusTraits and made available with the next release. Version 3.0.2 of AusTraits, described here, is the sixth release.





**Fig. 6** The number of taxa with trait records in AusTraits and global TRY database (accessed 28 May 2020). Each point shows a separate trait.

Second, we implemented automated tests for each dataset, to confirm that values for continuous traits fall within the accepted range for the trait, and that values for categorical traits are on a list of allowed values. Data that did not pass these tests were moved to a separate spreadsheet (“excluded\_data”) that is also made available for use and review.

Third, we provide a pathway for user feedback. AusTraits is an open-source community resource and we encourage engagement from users on maintaining the quality and usability of the dataset. As such, we welcome reporting of possible errors, as well as additions and edits to the online documentation for AusTraits that make using the existing data, or adding new data, easier for the community. Feedback can be posted as an issue directly at the project’s GitHub page (<http://traitecoevo.github.io/austraits.build>).

### Usage Notes

Each data release is available in multiple formats: first, as a compressed folder containing text files for each of the main components, second, as a compressed R object, enabling easy loading into R for those using that platform.

Using the taxon names aligned with the APC, data can be queried against location data from the Atlas of Living Australia. To create the phylogenetic tree in Fig. 6, we pruned a master tree for all higher plants<sup>366</sup> using the package `V. PhyloMaker`<sup>367</sup> and visualising via `ggtree`<sup>368</sup>. To create Fig. 3a, we used the package `plotbiomes`<sup>369</sup> to create the baseline plot of biomes.

### Code availability

All code, raw and compiled data are hosted within GitHub repositories under the Trait Ecology and Evolution organisation (<http://traitecoevo.github.io/austraits.build/>). The archived material includes all data sources and code for rebuilding the compiled dataset. The code used to produce this paper is available at [http://github.com/traitecoevo/austraits\\_ms](http://github.com/traitecoevo/austraits_ms).

Received: 14 December 2020; Accepted: 5 August 2021;

Published online: 30 September 2021

### References

- Zanne, A. E. *et al.* Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**, 89 (2014).
- Cornwell, W. K. *et al.* Functional distinctiveness of major plant lineages. *J. Ecol.* **102**, 345–356 (2014).
- Diaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167 (2016).
- Kunstler, G. *et al.* Plant functional traits have globally consistent effects on competition. *Nature* **529**, 204 (2016).
- Chapin, F. S. III, Autumn, K. & Pugnaire, F. Evolution of suites of traits in response to environmental stress. *Am. Nat.* **142**, S78–S92 (1993).
- Adler, P. B. *et al.* Functional traits explain variation in plant life history strategies. *Proc. Natl. Acad. Sci. USA* **111**, 740–745 (2014).
- Diaz, S., Cabido, M. & Casanoves, F. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* **9**, 113–122 (1998).
- Violle, C. *et al.* Let the concept of trait be functional! *Oikos* **116**, 882–892 (2007).
- Westoby, M. A leaf-height-seed (LHS) plant ecol. *Strategy scheme. Plant Soil* **199**, 213–227 (1998).
- Funk, J. L. *et al.* Revisiting the holy grail: Using plant functional traits to understand ecological processes. *Biol. Rev.* **92**, 1156–1173 (2017).
- Kattge, J. *et al.* TRY a global database of plant traits. *Glob. Chang. Biol.* **17**, 2905–2935 (2011).
- Kattge, J. *et al.* TRY plant trait database enhanced coverage and open access. *Glob. Chang. Biol.* **26**, 119–188 (2020).
- CHAH. *Australian Plant Census*, Centre of Australian National Biodiversity Research. <https://id.biodiversity.org.au/tree/51354547> (2020).
- Kissling, W. D. *et al.* Towards global data products of Essential Biodiversity Variables on species traits. *Nat. Ecol. Evol.* **2**, 1531–1540 (2018).
- Gallagher, R. V. *et al.* Open Science principles for accelerating trait-based science across the Tree of Life. *Nat. Ecol. Evol.* **4**, 294–303 (2020).
- Chapman, A. D. *et al.* *Numbers of living species in Australia and the world.* (Australian Government, 2009).
- Hopper, S. D. & Gioia, P. The Southwest Australian Floristic Region: Evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **35**, 623–650 (2004).

18. Madin, J. *et al.* An ontology for describing and synthesizing ecological observation data. *Ecol. Inform.* **2**, 279–296 (2007).
19. Garnier, E. *et al.* Towards a thesaurus of plant characteristics: An ecological contribution. *J. Ecol.* **105**, 298–309 (2017).
20. Adams, M. A. M., P. & Attiwill. Role of *Acacia* spp. in nutrient balance and cycling in regenerating *Eucalyptus regnans* F. Muell. forests. I. *Temporal changes in biomass and nutrient content*. *Aust. J. Bot.* **32**, 205–215 (1984).
21. Ahrens, C. W. *et al.* Plant functional traits differ in adaptability and are predicted to be differentially affected by climate change. *Ecol. Evo.* **10**, 232–248 (2019).
22. Australian National Botanic Gardens. The National Seed Bank. <http://www.anbg.gov.au/gardens/living/seedbank/> (2018).
23. Angevin, T. *Species richness and functional trait diversity response to land use in a temperate eucalypt woodland community*. (La Trobe University, 2011).
24. Apgaua, D. M. G. *et al.* Functional traits and water transport strategies in lowland tropical rainforest trees. *PLoS One* **10**, e0130799 (2015).
25. Apgaua, D. M. G. *et al.* Plant functional groups within a tropical forest exhibit different wood functional anatomy. *Funct. Ecol.* **31**, 582–591 (2017).
26. Ashton, D. H. Studies of litter in *Eucalyptus regnans* forests. *Aust. J. Bot.* **23**, 413–433 (1975).
27. Ashton, D. H. Phosphorus in forest ecosystems at Beenak, Victoria. *The J. Ecol.* **64**, 171–186 (1976).
28. Attiwill, P. M. Nutrient cycling in a *Eucalyptus obliqua* (L'Herit.) forest IV: Nutrient uptake and nutrient return. *Aust. J. Bot.* **28**, 199–222 (1980).
29. Barlow, B. A., Clifford, H. T., George, A. S. & McCusker, A. K. A. *Flora of Australia*. <http://www.environment.gov.au/biodiversity/abrs/online-resources/flora/main/> (1981).
30. Bean, A. R. A revision of *Baeckea* (Myrtaceae) in eastern Australia, Malesia and south-east Asia. *Telopea* **7**, 245–268 (1997).
31. Bell, L. C. *Nutrient requirements for the establishment of native flora at Weipa*. (Comalco Aluminium Ltd., 1985).
32. Bennett, L. T. & Attiwill, P. M. The nutritional status of healthy and declining stands of *Banksia integrifolia* on the Yanakie Isthmus, Victoria. *Aust. J. Bot.* **45**, 15–30 (1997).
33. Bevege, D. I. *Biomass and nutrient distribution in indigenous forest ecosystems*. vol. 6 20 (Queensland Department of Forestry, 1978).
34. Birk, E. M. & Turner, J. Response of flooded gum (*E. grandis*) to intensive cultural treatments: biomass and nutrient content of eucalypt plantations and native forests. *For. Ecol. Manage.* **47**, 1–28 (1992).
35. Blackman, C. J., Brodribb, T. J. & Jordan, G. J. Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. *New Phytol.* **188**, 1113–1123 (2010).
36. Blackman, C. J. *et al.* Leaf hydraulic vulnerability to drought is linked to site water availability across a broad range of species and climates. *Ann. Bot.* **114**, 435–440 (2014).
37. Blackman, C. J. *et al.* The links between leaf hydraulic vulnerability to drought and key aspects of leaf venation and xylem anatomy among 26 Australian woody angiosperms from contrasting climates. *Ann. Bot.* **122**, 59–67 (2018).
38. Bloomfield, K. J. *et al.* A continental-scale assessment of variability in leaf traits: Within species, across sites and between seasons. *Funct. Ecol.* **32**, 1492–1506 (2018).
39. Bolza, E. *Properties and uses of 175 timber species from Papua New Guinea and West Irian*. (Victoria (Australia) CSIRO, Div. of Building Research, 1975).
40. Bragg, J. G. & Westoby, M. Leaf size and foraging for light in a sclerophyll woodland. *Funct. Ecol.* **16**, 633–639 (2002).
41. Brisbane Rainforest Action and Information Network. Trait measurements for Australian rainforest species. <http://www.brisrain.org.au/> (2016).
42. Briggs, A. L. & Morgan, J. W. Seed characteristics and soil surface patch type interact to affect germination of semi-arid woodland species. *Plant Ecol.* **212**, 91–103 (2010).
43. Brock, J. & Dunlop, A. *Native plants of northern Australia*. (Reed New Holland, 1993).
44. Brodribb, T. J. & Cochard, H. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiol.* **149**, 575–584 (2009).
45. Buckton, G. *et al.* Functional traits of lianas in an Australian lowland rainforest align with post-disturbance rather than dry season advantage. *Austral Ecol.* **44**, 983–994 (2019).
46. Burgess, S. S. O. & Dawson, T. E. Predicting the limits to tree height using statistical regressions of leaf traits. *New Phytol.* **174**, 626–636 (2007).
47. Burrows, G. E. Comparative anatomy of the photosynthetic organs of 39 xeromorphic species from subhumid New South Wales, Australia. *Int. J. Plant Sci.* **162**, 411–430 (2001).
48. Butler, D. W., Gleason, S. M., Davidson, I., Onoda, Y. & Westoby, M. Safety and streamlining of woody shoots in wind: an empirical study across 39 species in tropical Australia. *New Phytol.* **193**, 137–149 (2011).
49. CAB International. Forestry Compendium. <http://www.cabi.org/fc/> (2009).
50. Caldwell, E., Read, J. & Sanson, G. D. Which leaf mechanical traits correlate with insect herbivory among feeding guilds? *Ann. Bot.* **117**, 349–361 (2015).
51. Canham, C. A., Froend, R. H. & Stock, W. D. Water stress vulnerability of four *Banksia* species in contrasting ecohydrological habitats on the Gnaragara Mound. *Western Australia. Plant Cell Environ.* **32**, 64–72 (2009).
52. Carpenter, R. J. Cuticular morphology and aspects of the ecology and fossil history of North Queensland rainforest Proteaceae. *Bot. J. Linn. Soc.* **116**, 249–303 (1994).
53. Carpenter, R. J., Hill, R. S. & Jordan, G. J. Leaf Cuticular Morphology Links Platanaceae and Proteaceae. *Int. J. Plant Sci.* **166**, 843–855 (2005).
54. Catford, J. A., Downes, B. J., Gippel, C. J. & Vesk, P. A. Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. *J. Appl. Ecol.* **48**, 432–442 (2011).
55. Catford, J. A., Morris, W. K., Vesk, P. A., Gippel, C. J. & Downes, B. J. Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion. *Divers. Distrib.* **20**, 1084–1096 (2014).
56. Cernusak, L. A., Hutley, L. B., Beringer, J. & Tapper, N. J. Stem and leaf gas exchange and their responses to fire in a north Australian tropical savanna. *Plant Cell Environ.* **29**, 632–646 (2006).
57. Cernusak, L. A., Hutley, L. B., Beringer, J., Holtum, J. A. M. & Turner, B. L. Photosynthetic physiology of eucalypts along a sub-continental rainfall gradient in northern Australia. *Agric. For. Meteorol.* **151**, 1462–1470 (2011).
58. Chandler, G. T., Crisp, M. D., Cayzer, L. W. & Bayer, R. J. Monograph of *Gastrolobium* (Fabaceae: Mirbelieae). *Aust. Syst. Bot.* **15**, 619–739 (2002).
59. Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecol. Lett.* **12**, 351–366 (2009).
60. Cheal, D. *Growth stages and tolerable fire intervals for Victoria's native vegetation data sets*. (Victorian Government Department of Sustainability; Environment Melbourne, 2010).
61. Cheesman, A. W., Duff, H., Hill, K., Cernusak, L. A. & McNerney, F. A. Isotopic and morphologic proxies for reconstructing light environment and leaf function of fossil leaves: A modern calibration in the Daintree Rainforest, Australia. *Am. J. Bot.* **107**, 1165–1176 (2020).
62. Chen *et al.* Plants show more flesh in the tropics: Variation in fruit type along latitudinal and climatic gradients. *Ecography* **40**, 531–538 (2017).
63. Chinnock, R. J. *Eremophila and allied genera: A monograph of the plant family Myoporaceae*. (Rosenberg, 2007).

64. Choat, B., Ball, M. C., Luly, J. G. & Holtum, J. A. M. Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. *Trees* **19**, 305–311 (2005).
65. Choat, B., Ball, M. C., Luly, J. G., Donnelly, C. F. & Holtum, J. A. M. Seasonal patterns of leaf gas exchange and water relations in dry rain forest trees of contrasting leaf phenology. *Tree Physiol.* **26**, 657–664 (2006).
66. Choat, B. *et al.* Global convergence in the vulnerability of forests to drought. *Nature* **491**, 752–755 (2012).
67. Chudnoff, M. *Tropical timbers of the world*. 472 (US Department of Agriculture, Forest Service, 1984).
68. The French agricultural research and international cooperation organization (CIRAD). Wood density data. <http://www.cirad.fr/> (2009).
69. Clarke, P. J. *et al.* A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Sci. Total Environ.* **534**, 31–42 (2015).
70. Cooper, W. & Cooper, W. T. *Fruits of the Australian tropical rainforest*. (Nokomis Editions, 2004).
71. Cooper, W. & Cooper, W. T. *Australian rainforest fruits*. 272 (CSIRO Publishing, 2013).
72. Cornwell, W. K. *Causes and consequences of functional trait diversity: plant community assembly and leaf decomposition*. (Stanford University, California, 2006).
73. Centre for Plant Biodiversity Research. EUCLID 2.0: Eucalypts of Australia. <http://apps.lucidcentral.org/euclid/text/intro/index.html> (2002).
74. Craven, L. A., A taxonomic revision of *Calytrix* Labill. (Myrtaceae). *Brunonia* **10**, 1–138 (1987).
75. Craven, L. A., Lepschi, B. J. & Cowley, K. J. *Melaleuca* (Myrtaceae) of Western Australia: Five new species, three new combinations, one new name and a new state record. *Nuytsia* **20**, 27–36 (2010).
76. Crisp, M. D., Cayzer, L., Chandler, G. T. & Cook, L. G. A monograph of *Daviesia* (Mirbelieae, Faboideae, Fabaceae). *Phytotaxa* **300**, 1–308 (2017).
77. Cromer, R. N., Raupach, M., Clarke, A. R. P. & Cameron, J. N. Eucalypt plantations in Australia - the potential for intensive production and utilization. *Appita J.* **29**, 165–173 (1975).
78. Cross, E. *The characteristics of natives and invaders: A trait-based investigation into the theory of limiting similarity*. (La Trobe University, 2009).
79. Crous, K. Y. *et al.* Photosynthesis of temperate *Eucalyptus globulus* trees outside their native range has limited adjustment to elevated CO<sub>2</sub> and climate warming. *Glob. Chang. Biol.* **19**, 3790–3807 (2013).
80. Crous, K. Y., Wujeska-Klaue, A., Jiang, M., Medlyn, B. E. & Ellsworth, D. S. Nitrogen and phosphorus retranslocation of leaves and stemwood in a mature *Eucalyptus* forest exposed to 5 years of elevated CO<sub>2</sub>. *Front. Plant. Sci.* **10**, art664 (2019).
81. Cunningham, S. A., Summerhayes, B. & Westoby, M. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecol. Monogr.* **69**, 569–588 (1999).
82. Curran, T. J., Clarke, P. J. & Warwick, N. W. M. Water relations of woody plants on contrasting soils during drought: does edaphic compensation account for dry rainforest distribution? *Aust. J. Bot.* **57**, 629–639 (2009).
83. Curtis, E. M., Leigh, A. & Rayburg, S. Relationships among leaf traits of Australian arid zone plants: alternative modes of thermal protection. *Aust. J. Bot.* **60**, 471–483 (2012).
84. Denton, M. D., Veneklaas, E. J., Freimoser, F. M. & Lambers, H. *Banksia* species (Proteaceae) from severely phosphorus-impooverished soils exhibit extreme efficiency in the use and re-mobilization of phosphorus. *Plant Cell Environ.* **30**, 1557–1565 (2007).
85. Desch, H. E. & Dinwoodie, J. M. *Timber structure, properties, conversion and use*. (Palgrave Macmillan, 1996).
86. de Tombour, F. *et al.* A shift from phenol to silica-based leaf defenses during long-term soil and ecosystem development. *Ecol. Lett.* **24**, 984–995 (2021).
87. Dong, N. *et al.* Leaf nitrogen from first principles: field evidence for adaptive variation with climate. *Biogeosciences* **14**, 481–495 (2017).
88. Dong, N. *et al.* Components of leaf-trait variation along environmental gradients. *New Phytol.* **228**, 82–94 (2020).
89. Du, P., Arndt, S. K. & Farrell, C. Relationships between plant drought response, traits, and climate of origin for green roof plant selection. *Ecol. Appl.* **28**, 1752–1761 (2018).
90. Du, P., Arndt, S. K. & Farrell, C. Can the turgor loss point be used to assess drought response to select plants for green roofs in hot and dry climates? *Plant Soil* **441**, 399–408 (2019).
91. Duan, H. *et al.* Drought responses of two gymnosperm species with contrasting stomatal regulation strategies under elevated [CO<sub>2</sub>] and temperature. *Tree Physiol.* **35**, 756–770 (2015).
92. Duncan, R. P. *et al.* Plant traits and extinction in urban areas: a meta-analysis of 11 cities. *Glob. Ecol. Biog.* **20**, 509–519 (2011).
93. Dwyer, J. M. & Laughlin, D. C. Constraints on trait combinations explain climatic drivers of biodiversity: The importance of trait covariance in community assembly. *Ecol. Lett.* **20**, 872–882 (2017).
94. Dwyer, J. M. & Mason, R. Plant community responses to thinning in densely regenerating *Acacia harpophylla* forest. *Restor. Ecol.* **26**, 97–105 (2018).
95. Eamus, D. & Prichard, H. A cost-benefit analysis of leaves of four Australian savanna species. *Tree Physiol.* **18**, 537–545 (1998).
96. Eamus, D., Myers, B., Duff, G. & Williams, D. Seasonal changes in photosynthesis of eight savanna tree species. *Tree Physiol.* **19**, 665–671 (1999).
97. Myers, B., E., D. & Duff, G. A cost-benefit analysis of leaves of eight Australian savanna tree species of differing life-span. *Photosynthetica* **36**, 575–586 (1999).
98. Edwards, C., Read, J. & Sanson, G. D. Characterising sclerophylly: some mechanical properties of leaves from heath and forest. *Oecologia* **123**, 158–167 (2000).
99. Edwards, C., Sanson, G. D., Aranwela, N. & Read, J. Relationships between sclerophylly, leaf biomechanical properties and leaf anatomy in some Australian heath and forest species. *Plant Biosyst.* **134**, 261–277 (2000).
100. Schöenenberger, J. *et al.* Phylogenetic analysis of fossil flowers using an angiosperm-wide data set: proof-of-concept and challenges ahead. *Am. J. Bot.* **107**, 1433–1448 (2020).
101. Esperon-Rodriguez, M. *et al.* Functional adaptations and trait plasticity of urban trees along a climatic gradient. *Urban For. Urban Green.* **54**, art126771 (2020).
102. Everingham, S. E., Offord, C. A., Sabot, M. E. B. & Moles, A. T. Time travelling seeds reveal that plant regeneration and growth traits are responding to climate change. *Ecology* **102**, e03272 (2020).
103. Falster, D. S. & Westoby, M. Leaf size and angle vary widely across species: what consequences for light interception? *New Phytol.* **158**, 509–525 (2003).
104. Falster, D. S. & Westoby, M. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *J. Ecol.* **93**, 521–535 (2005).
105. Falster, D. S. & Westoby, M. Tradeoffs between height growth rate, stem persistence and maximum height among plant species in a post-fire succession. *Oikos* **111**, 57–66 (2005).
106. Farrell, C., Mitchell, R. E., Szota, C., Rayner, J. P. & Williams, N. S. G. Green roofs for hot and dry climates: Interacting effects of plant water use, succulence and substrate. *Ecol. Eng.* **49**, 270–276 (2012).
107. Farrell, C., Szota, C., Williams, N. S. G. & Arndt, S. K. High water users can be drought tolerant: using physiological traits for green roof plant selection. *Plant Soil* **372**, 177–193 (2013).

108. Farrell, C., Szota, C. & Arndt, S. K. Does the turgor loss point characterize drought response in dryland plants? *Plant Cell Environ.* **40**, 1500–1511 (2017).
109. Feller, M. C. Biomass and nutrient distribution in two eucalypt forest ecosystems. *Austral Ecol.* **5**, 309–333 (1980).
110. Firn, J. *et al.* Leaf nutrients, not specific leaf area, are consistent indicators of elevated nutrient inputs. *Nature Ecol. Evo.* **3**, 400–406 (2019).
111. Flynn, J. H. & Holder, C. D. *A guide to useful woods of the world.* (Forest Products Society, 2001).
112. Fonseca, C. R., Overton, J. M. C., Collins, B. & Westoby, M. Shifts in trait-combinations along rainfall and phosphorus gradients. *J. Ecol.* **88**, 964–977 (2000).
113. McDonald, P. G., Fonseca, C. R., Overton, J. M. C. & Westoby, M. Leaf-size divergence along rainfall and soil-nutrient gradients: is the method of size reduction common among clades? *Funct. Ecol.* **17**, 50–57 (2003).
114. Forster, P. I. A taxonomic revision of *Alyxia* (Apocynaceae) in Australia. *Aust. Syst. Bot.* **5**, 547–580 (1992).
115. Forster, P. I. New names and combinations in *Marsdenia* (Asclepiadaceae: Marsdenieae) from Asia and Malesia (excluding Papusia). *Aust. Syst. Bot.* **8**, 691–701 (1995).
116. French, B. J., Prior, L. D., Williamson, G. J. & Bowman, D. M. J. S. Cause and effects of a megafire in sedge-heathland in the Tasmanian temperate wilderness. *Aust. J. Bot.* **64**, 513–525 (2016).
117. Froend, R. H. & Drake, P. L. Defining phreatophyte response to reduced water availability: preliminary investigations on the use of xylem cavitation vulnerability in *Banksia* woodland species. *Aust. J. Bot.* **54**, 173–179 (2006).
118. Funk, J. L., Standish, R. J., Stock, W. D. & Valladares, F. Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology* **97**, 75–83 (2016).
119. Gallagher, R. V. *et al.* Invasiveness in introduced Australian acacias: The role of species traits and genome size. *Divers. Distrib.* **17**, 884–897 (2011).
120. Gallagher, R. V. & Leishman, M. R. A global analysis of trait variation and evolution in climbing plants. *J. Biogeogr.* **39**, 1757–1771 (2012).
121. Gardiner, R., Shoo, L. P. & Dwyer John, M. Look to seedling heights, rather than functional traits, to explain survival during extreme heat stress in the early stages of subtropical rainforest restoration. *J. Appl. Ecol.* **56**, 2687–2697 (2019).
122. Geange, S. R. *et al.* Phenotypic plasticity and water availability: responses of alpine herb species along an elevation gradient. *Clim. Change Responses* **4**, 1–12 (2017).
123. Geange, S. R., Holloway-Phillips, M.-M., Briceno, V. F. & Nicotra, A. B. *Aciphylla glacialis* mortality, growth and frost resistance: a field warming experiment. *Aust. J. Bot.* **67**, 599–609 (2020).
124. Ghannoum, O. *et al.* Exposure to preindustrial, current and future atmospheric CO<sub>2</sub> and temperature differentially affects growth and photosynthesis in *Eucalyptus*. *Glob. Chang. Biol.* **16**, 303–319 (2010).
125. Gleason, S. M., Butler, D. W., Zieminska, K., Waryszak, P. & Westoby, M. Stem xylem conductivity is key to plant water balance across Australian angiosperm species. *Funct. Ecol.* **26**, 343–352 (2012).
126. Gleason, S. M., Butler, D. W. & Waryszak, P. Shifts in leaf and stem hydraulic traits across aridity gradients in eastern Australia. *Int. J. Plant Sci.* **174**, 1292–1301 (2013).
127. Gleason, S. M., Blackman, C. J., Cook, A. M., Laws, C. A. & Westoby, M. Whole-plant capacitance, embolism resistance and slow transpiration rates all contribute to longer desiccation times in woody angiosperms from arid and wet habitats. *Tree Physiol.* **34**, 275–284 (2014).
128. Gleason, S. M. *et al.* Vessel scaling in evergreen angiosperm leaves conforms with Murray’s law and area-filling assumptions: implications for plant size, leaf size and cold tolerance. *New Phytol.* **218**, 1360–1370 (2018).
129. Goble-Garratt, E., Bell, D. & Loneragan, W. Floristic and leaf structure patterns along a shallow elevational gradient. *Aust. J. Bot.* **29**, 329–347 (1981).
130. Gosper, C. R. Fruit characteristics of invasive bitou bush, *Chrysanthemoides monilifera* (Asteraceae), and a comparison with co-occurring native plant species. *Aust. J. Bot.* **52**, 223–230 (2004).
131. Gosper, C. R., Yates, C. J. & Prober, S. M. Changes in plant species and functional composition with time since fire in two mediterranean climate plant communities. *J. Veg. Sci.* **23**, 1071–1081 (2012).
132. Gosper, C. R., Prober, S. M. & Yates, C. J. Estimating fire interval bounds using vital attributes: implications of uncertainty and among-population variability. *Ecol. Appl.* **23**, 924–935 (2013).
133. Gosper, C. R., Yates, C. J. & Prober, S. M. Floristic diversity in fire-sensitive eucalypt woodlands shows a “U”-shaped relationship with time since fire. *J. Appl. Ecol.* **50**, 1187–1196 (2013).
134. Gosper, C. R. *et al.* A conceptual model of vegetation dynamics for the unique obligate-seeder eucalypt woodlands of southwestern Australia. *Austral Ecol.* **43**, 681–695 (2018).
135. Clayton, W. D., Vorontsova, M. S., Harman, K. T. & Williamson, H. GrassBase - The online world grass flora. <http://www.kew.org/data/grasses-db.html> (2006).
136. Gray, E. F. *et al.* Leaf:wood allometry and functional traits together explain substantial growth rate variation in rainforest trees. *AoB Plants* **11**, 1–11 (2019).
137. Groom, P. K. & Lamont, B. B. Reproductive ecology of non-sprouting and re-sprouting *Hakea* species (Proteaceae) in southwestern Australia. In *Gondwanan heritage* (eds S.D. Hopper M. Harvey, J. C. & George, A. S.) (Surrey Beatty, Chipping Norton, 1996).
138. Groom, P. K. & Lamont, B. B. Fruit-seed relations in *Hakea*: serotinous species invest more dry matter in predispersal seed protection. *Austral Ecol.* **22**, 352–355 (1997).
139. Groom, P. K. & Lamont, B. B. Phosphorus accumulation in Proteaceae seeds: A synthesis. *Plant Soil* **334**, 61–72 (2010).
140. Grootemaat, S., Wright, I. J., van Bodegom, P. M., Cornelissen, J. H. C. & Cornwell, W. K. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. *Funct. Ecol.* **29**, 1486–1497 (2015).
141. Grootemaat, S., Wright, I. J., van Bodegom, P. M., Cornelissen, J. H. C. & Shaw, V. Bark traits, decomposition and flammability of Australian forest trees. *Aust. J. Bot.* **65**, 327 (2017).
142. Grootemaat, S., Wright, I. J., van Bodegom, P. M. & Cornelissen, J. H. C. Scaling up flammability from individual leaves to fuel beds. *Oikos* **126**, 1428–1438 (2017).
143. Gross, C. L. The reproductive ecology of *Canavalia rosea* (Fabaceae) on Anak Krakatau. *Indonesia. Aust. J. Bot.* **41**, 591–599 (1993).
144. Gross, C. L. A comparison of the sexual systems in the trees from the Australian tropics with other tropical biomes—more monoecy but why? *Am. J. Bot.* **92**, 907–919 (2005).
145. Grubb, P. J. & Metcalfe, D. J. Adaptation and inertia in the Australian tropical lowland rain-forest flora: Contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. *Funct. Ecol.* **10**, 512–520 (1996).
146. Grubb, P. J. *et al.* Monocot leaves are eaten less than dicot leaves in tropical lowland rain forests: Correlations with toughness and leaf presentation. *Ann. Bot.* **101**, 1379–1389 (2008).
147. Guilherme Pereira, C., Clode, P. L., Oliveira, R. S. & Lambers, H. Eudicots from severely phosphorus-impooverished environments preferentially allocate phosphorus to their mesophyll. *New Phytol.* **218**, 959–973 (2018).
148. Guilherme Pereira, C. *et al.* Trait convergence in photosynthetic nutrient-use efficiency along a 2-million year dune chronosequence in a global biodiversity hotspot. *J. Ecol.* **107**, 2006–2023 (2019).
149. Hacke, U. G. *et al.* Water transport in vesselless Angiosperms: Conducting efficiency and cavitation safety. *Int. J. Plant Sci.* **168**, 1113–1126 (2007).

150. Hall, T. J. The nitrogen and phosphorus concentrations of some pasture species in the Dichanthium-Eulalia Grasslands of North-West Queensland. *Rangeland J.* **3**, 67–73 (1981).
151. Harrison, M. T., Edwards, E. J., Farquhar, G. D., Nicotra, A. B. & Evans, J. R. Nitrogen in cell walls of sclerophyllous leaves accounts for little of the variation in photosynthetic nitrogen-use efficiency. *Plant Cell Environ.* **32**, 259–270 (2009).
152. Hassiotou, F., Evans, J. R., Ludwig, M. & Veneklaas, E. J. Stomatal crypts may facilitate diffusion of CO<sub>2</sub> to adaxial mesophyll cells in thick sclerophylls. *Plant Cell Environ.* **32**, 1596–1611 (2009).
153. Hatch, A. B. Influence of plant litter on the Jarrah forest soils of the Dwellingup region. *West. Aust. For. Timber Bur. Leaflet* **18** (1955).
154. Hayes, P., Turner, B. L., Lambers, H. & Laliberté, E. Foliar nutrient concentrations and resorption efficiency in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. *J. Ecol.* **102**, 396–410 (2013).
155. Hayes, P. E., Clode, P. L., Oliveira, R. S. & Lambers, H. Proteaceae from phosphorus-impooverished habitats preferentially allocate phosphorus to photosynthetic cells: an adaptation improving phosphorus-use efficiency. *Plant Cell Environ.* **41**, 605–619 (2018).
156. Henery, M. L. & Westoby, M. Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* **92**, 479–490 (2001).
157. Hocking, P. J. The nutrition of fruits of two proteaceous shrubs, *Grevillea wilsonii* and *Hakea undulata*, from south-western Australia. *Aust. J. Bot.* **30**, 219–230 (1982).
158. Hocking, P. J. Mineral nutrient composition of leaves and fruits of selected species of *Grevillea* from southwestern Australia, with special reference to *Grevillea leucoptera* Meissn. *Aust. J. Bot.* **34**, 155–164 (1986).
159. Hong, L. T. *et al.* *Plant resources of south east Asia: Timber trees*. World biodiversity Database CD rom series (Springer-Verlag Berlin; Heidelberg GmbH; Co. KG, 1999).
160. Hopmans, P., Stewart, H. T. L. & Flinn, D. W. Impacts of harvesting on nutrients in a eucalypt ecosystem in southeastern Australia. *For. Ecol. Manage.* **59**, 29–51 (1993).
161. Huang, G., Rymer, P. D., Duan, H., Smith, R. A. & Tissue, D. T. Elevated temperature is more effective than elevated CO<sub>2</sub> in exposing genotypic variation in *Telopea speciosissima* growth plasticity: implications for woody plant populations under climate change. *Glob. Chang. Biol.* **21**, 3800–3813 (2015).
162. Hyland, B. P. M., Whiffin, T., Christophel, D., Gray, B. & Elick, R. W. *Australian tropical rain forest plants trees, shrubs and vines*. (CSIRO Publishing, 2003).
163. World Agroforestry Centre (ICRAF). The wood density database. <http://www.worldagroforestry.org/output/wood-density-database> (2009).
164. Ilic, J., Boland, D., McDonald, M., G., D. & Blakemore, P. *Woody density phase 1 - State of knowledge*. National Carbon Accounting System. Technical Report 18. (Australian Greenhouse Office, Canberra, Australia, 2000).
165. Islam, M., Turner, D. W. & Adams, M. A. Phosphorus availability and the growth, mineral composition and nutritive value of ephemeral forbs and associated perennials from the Pilbara, Western Australia. *Aust. J. Exp. Agric.* **39**, 149–159 (1999).
166. Islam, M. & Adams, M. A. Mineral content and nutritive value of native grasses and the response to added phosphorus in a Pilbara rangeland. *Trop. Grassl.* **33**, 193–200 (1999).
167. Jordan, G. J. An investigation of long-distance dispersal based on species native to both Tasmania and New Zealand. *Aust. J. Bot.* **49**, 333–340 (2001).
168. Jordan, G. J., Weston, P. H., Carpenter, R. J., Dillon, R. A. & Brodribb, T. J. The evolutionary relations of sunken, covered, and encrypted stomata to dry habitats in Proteaceae. *Am. J. Bot.* **95**, 521–530 (2008).
169. Jordan, G. J., Carpenter, R. J., Koutoulis, A., Price, A. & Brodribb, T. J. Environmental adaptation in stomatal size independent of the effects of genome size. *New Phytol.* **205**, 608–617 (2015).
170. Jordan, G. J. *et al.* Links between environment and stomatal size through evolutionary time in Proteaceae. *Proc. R. Soc. Lond. B Biol. Sci.* **287**, 20192876 (2020).
171. Jurado, E. Diaspore weight, dispersal, growth form and perenniality of central Australian plants. *J. Ecol.* **79**, 811–828 (1991).
172. Jurado, E. & Westoby, M. Germination biology of selected central Australian plants. *Austral Ecol.* **17**, 341–348 (1992).
173. Kanowski, J. *Ecological determinants of the distribution and abundance of the folivorous marsupials endemic to the rainforests of the Atherton uplands, north Queensland*. (James Cook University, Townsville, 1999).
174. Keighery, G. Taxonomy of the *Calytrix ecalycata* complex (Myrtaceae). *Nuytsia* **15**, 261–268 (2004).
175. Royal Botanic Gardens Kew. Seed Information Database (SID) and Seed Bank Database. <http://data.kew.org/sid/> (2019).
176. Royal Botanic Gardens Kew. Seed protein data from Seed Information Database (SID) and Seed Bank Database. <http://data.kew.org/sid/> (2019).
177. Royal Botanic Gardens Kew. Oil content data from Seed Information Database (SID) and Seed Bank Database. <http://data.kew.org/sid/> (2019).
178. Royal Botanic Gardens Kew. Seed dispersal data from the Seed Information Database (SID) and Seed Bank Database. <http://data.kew.org/sid/> (2019).
179. Royal Botanic Gardens Kew. Germination data from the Seed Information Database (SID) and Seed Bank Database. <http://data.kew.org/sid/> (2019).
180. Knox, K. J. E. & Clarke, P. J. Fire severity and nutrient availability do not constrain resprouting in forest shrubs. *Plant Ecol.* **212**, 1967–1978 (2011).
181. Körner, C. & Cochrane, P. M. Stomatal responses and water relations of *Eucalyptus pauciflora* in summer along an elevational gradient. *Oecologia* **66**, 443–455 (1985).
182. Kooyman, R., Rossetto, M., Cornwell, W. & Westoby, M. Phylogenetic tests of community assembly across regional to continental scales in tropical and subtropical rain forests. *Glob. Ecol. Biog.* **20**, 707–716 (2011).
183. Kotowska, M. M., Wright, I. J. & Westoby, M. Parenchyma abundance in wood of evergreen trees varies independently of nutrients. *Front. Plant. Sci.* **11**, art86 (2020).
184. Kuo, J., Hocking, P. & Pate, J. Nutrient reserves in seeds of selected Proteaceous species from South-western Australia. *Aust. J. Bot.* **30**, 231–249 (1982).
185. Laliberté, E. *et al.* Experimental assessment of nutrient limitation along a 2-million-year dune chronosequence in the south-western Australia biodiversity hotspot. *J. Ecol.* **100**, 631–642 (2012).
186. Lambert, M. J. *Sulphur relationships of native and exotic tree species*. (Macquarie University, Sydney, 1979).
187. Lamont, B. B., Groom, P. K. & Cowling, R. M. High leaf mass per area of related species assemblages may reflect low rainfall and carbon isotope discrimination rather than low phosphorus and nitrogen concentrations. *Funct. Ecol.* **16**, 403–412 (2002).
188. Lamont, B. B., Groom, P. K., Williams, M. & He, T. LMA, density and thickness: recognizing different leaf shapes and correcting for their nonlaminarity. *New Phytol.* **207**, 942–947 (2015).
189. Landsberg, J. Dieback of rural eucalypts: response of foliar dietary quality and herbivory to defoliation. *Austral Ecol.* **15**, 89–96 (1990).
190. Landsberg, J. & Gillieson, D. S. Regional and local variation in insect herbivory, vegetation and soils of eucalypt associations in contrasted landscape positions along a climatic gradient. *Aust. J. Ecol.* **20**, 299–315 (1995).
191. Lawes, M. J., Adie, H., Russell-Smith, J., Murphy, B. & Midgley, J. J. How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. *Ecosphere* **2**, 1–13 (2011).

192. Lawes, M. J., Richards, A., Dathe, J. & Midgley, J. J. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecol.* **212**, 2057–2069 (2011).
193. Lawes, M. J., Midgley, J. J. & Clarke, P. J. Costs and benefits of relative bark thickness in relation to fire damage: A savanna/forest contrast. *J. Ecol.* **101**, 517–524 (2012).
194. Lawson, J. R., Fryirs, K. A. & Leishman, M. R. Data from: Hydrological conditions explain wood density in riparian plants of south-eastern Australia. *Dryad Digital Repository* <https://doi.org/10.5061/dryad.72h45> (2015).
195. Laxton, E. *Relationship between leaf traits, insect communities and resource availability*. (Macquarie University, 2005).
196. Lee, M. R. *et al.* Good neighbors aplenty: fungal endophytes rarely exhibit competitive exclusion patterns across a span of woody habitats. *Ecology* **100**, e02790 (2019).
197. Leigh, A. & Nicotra, A. B. Sexual dimorphism in reproductive allocation and water use efficiency in *Maireana pyramidata* (Chenopodiaceae), a dioecious, semi-arid shrub. *Aust. J. Bot.* **51**, 509–514 (2003).
198. Leigh, A., Cosgrove, M. J. & Nicotra, A. B. Reproductive allocation in a gender dimorphic shrub: anomalous female investment in *Gynatrix pulchella*? *J. Ecol.* **94**, 1261–1271 (2006).
199. Leishman, M. R. & Westoby, M. Classifying plants into groups on the basis of associations of individual traits—Evidence from Australian semi-arid woodlands. *J. Ecol.* **80**, 417–424 (1992).
200. Leishman, M. R., Westoby, M. & Jurado, E. Correlates of seed size variation: A comparison among five temperate floras. *J. Ecol.* **83**, 517–529 (1995).
201. Leishman, M. R., Haslehurst, T., Ares, A. & Baruch, Z. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytol.* **176**, 635–643 (2007).
202. Lemmens, R. H. M. J. & Soerjanegara, I. *Prosea, Volume 5/1: Timber Trees - Major Commercial Timbers*. (Pudoc/Prosea, 1993).
203. Lenz, T. I., Wright, I. J. & Westoby, M. Interrelations among pressure-volume curve traits across species and water availability gradients. *Physiol. Plant.* **127**, 423–433 (2006).
204. Leuning, R., Cromer, R. N. & Rance, S. Spatial distributions of foliar nitrogen and phosphorus in crowns of *Eucalyptus grandis*. *Oecologia* **88**, 504–510 (1991).
205. Lewis, J. D. *et al.* Rising temperature may negate the stimulatory effect of rising CO<sub>2</sub> on growth and physiology of *Wollemi pine* (*Wollemia nobilis*). *Funct. Plant. Bio.* **42**, 836–850 (2015).
206. Lim, F. K. S., Pollock, L. J. & Veski, P. A. The role of plant functional traits in shrub distribution around alpine frost hollows. *J. Veg. Sci.* **28**, 585–594 (2017).
207. Lord, J. *et al.* Larger seeds in tropical floras: Consistent patterns independent of growth form and dispersal mode. *J. Biogeogr.* **24**, 205–211 (1997).
208. Lusk, C. H., Onoda, Y., Kooyman, R. & Gutierrez-Giron, A. Reconciling species-level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. *New Phytol.* **186**, 429–438 (2010).
209. Lusk, C. H., Kelly, J. W. G. & Gleason, S. M. Light requirements of Australian tropical vs. cool-temperate rainforest tree species show different relationships with seedling growth and functional traits. *Ann. Bot.* **111**, 479–488 (2012).
210. Lusk, C. H., Sendall, K. M. & Clarke, P. J. Seedling growth rates and light requirements of subtropical rainforest trees associated with basaltic and rhyolitic soils. *Aust. J. Bot.* **62**, 48–55 (2014).
211. Macinnis-Ng, C., McClenahan, K. & Eamus, D. Convergence in hydraulic architecture, water relations and primary productivity amongst habitats and across seasons in Sydney. *Funct. Plant. Bio.* **31**, 429–439 (2004).
212. Macinnis-Ng, C. M. O., Zeppel, M. J. B., Palmer, A. R. & Eamus, D. Seasonal variations in tree water use and physiology correlate with soil salinity and soil water content in remnant woodlands on saline soils. *J. Arid Environ.* **129**, 102–110 (2016).
213. Marsh, N. R. & Adams, M. A. Decline of *Eucalyptus tereticornis* near Bairnsdale, Victoria: insect herbivory and nitrogen fractions in sap and foliage. *Aust. J. Bot.* **43**, 39–49 (1995).
214. Maslin, B. *WATTLE, Interactive Identification of Australian Acacia. Version 2*. (Australian Biological Resources Study, Canberra, 2014).
215. McCarthy, J. K., Dwyer, J. M. & Mokany, K. A regional-scale assessment of using metabolic scaling theory to predict ecosystem properties. *Proc. R. Soc. Lond. B Biol. Sci.* **286**, 20192221 (2019).
216. McClenahan, K., Macinnis-Ng, C. & Eamus, D. Hydraulic architecture and water relations of several species at diverse sites around Sydney. *Aust. J. Bot.* **52**, 509–518 (2004).
217. McGlone, M. S., Richardson, S. J. & Jordan, G. J. Comparative biogeography of New Zealand trees: Species richness, height, leaf traits and range sizes. *New Zealand J. Ecol.* **34**, 137–151 (2010).
218. McGlone, M. S., Richardson, S. J., Jordan, G. J. & Perry, G. L. W. Is there a “suboptimal” woody species height? A response to Scheffer *et al.* *Trends in Ecol. Evo.* **30**, 4–5 (2015).
219. McIntyre, S., Lavorel, S. & Tremont, R. M. Plant life-history attributes: Their relationship to disturbance response in herbaceous vegetation. *The J. Ecol.* **83**, 31–44 (1995).
220. Meers, T. *Role of plant functional traits in determining the response of vegetation to land use change on the Delatite Peninsula, Victoria*. (University of Melbourne, 2007).
221. Meers, T. L., Bell, T. L., Enright, N. J. & Kasel, S. Role of plant functional traits in determining vegetation composition of abandoned grazing land in north-eastern Victoria, Australia. *J. Veg. Sci.* **19**, 515–524 (2008).
222. Meers, T. L., Bell, T. L., Enright, N. J. & Kasel, S. Do generalisations of global trade-offs in plant design apply to an Australian sclerophyllous flora? *Aust. J. Bot.* **58**, 257–270 (2010).
223. Meers, T. L., Kasel, S., Bell, T. L. & Enright, N. J. Conversion of native forest to exotic *Pinus radiata* plantation: response of understorey plant composition using a plant functional trait approach. *For. Ecol. Manage.* **259**, 399–409 (2010).
224. Meier, E. The wood database. <http://www.wood-database.com/> (2007).
225. Laliberté, E. *et al.* Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol. Lett.* **13**, 76–86 (2010).
226. Milberg, P. & Lamont, B. B. Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. *New Phytol.* **137**, 665–672 (1997).
227. Milberg, P., Pérez-Fernández, M. A. & Lamont, B. B. Seedling growth response to added nutrients depends on seed size in three woody genera. *J. Ecol.* **86**, 624–632 (1998).
228. Mokany, K. & Ash, J. Are traits measured on pot grown plants representative of those in natural communities? *J. Veg. Sci.* **19**, 119–126 (2008).
229. Mokany, K., Thomson, J. J., Lynch, A. J. J., Jordan, G. J. & Ferrier, S. Linking changes in community composition and function under climate change. *Ecol. Appl.* **25**, 2132–2141 (2015).
230. Moles, A. T. & Westoby, M. Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage? *Oikos* **90**, 517–524 (2000).
231. Moles, A. T., Warton, D. I. & Westoby, M. Seed size and survival in the soil in arid Australia. *Austral Ecol.* **28**, 575–585 (2003).
232. Moles, A. T. *et al.* Putting plant resistance traits on the map: A test of the idea that plants are better defended at lower latitudes. *New Phytol.* **191**, 777–788 (2011).
233. Mooney, H. A., Ferrar, P. J. & Slatyer, R. O. Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia* **36**, 103–111 (1978).

234. Moore, A. W., Russell, J. S. & Coaldrake, J. E. Dry matter and nutrient content of a subtropical semiarid forest of *Acacia harpophylla* F. Muell. (Brigalow). *Aust. J. Bot.* **15**, 11–24 (1967).
235. Moore, N. A., Camac, J. S. & Morgan, J. W. Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses. *New Phytol.* **221**, 1424–1433 (2018).
236. Morgan, H. *Root system architecture, water use and rainfall responses of perennial species*. (Macquarie University, 2005).
237. Muir, A. M., Vesk, P. A. & Hepworth, G. Reproductive trajectories over decadal time-spans after fire for eight obligate-seeder shrub species in south-eastern Australia. *Aust. J. Bot.* **62**, 369–379 (2014).
238. Munroe, S. E. M. *et al.* The photosynthetic pathways of plant species surveyed in Australia's national terrestrial monitoring network. *Scientific Data* **8**, 97 (2021).
239. National Herbarium of NSW. Trait measurements for NSW rainforest species from PLantNET. <http://plantnet.rbg Syd.nsw.gov.au/> (2016).
240. Nicholson, A., Prior, L. D., Perry, G. L. W. & Bowman, D. M. J. S. High post-fire mortality of resprouting woody plants in Tasmanian Mediterranean-type vegetation. *Int. J. Wildland Fire* **26**, 532–537 (2017).
241. Nicolle, D. A classification and census of regenerative strategies in the eucalypts (*Angophora*, *Corymbia* and *Eucalyptus* - Myrtaceae), with special reference to the obligate seeders. *Aust. J. Bot.* **54**, 391–407 (2006).
242. Nicolle, D. *Classification of the Eucalypts (Angophora, Corymbia and Eucalyptus) Version 3*. (Currency Creek Arboretum Eucalypt Research, 2018).
243. Ninemets, U., Wright, I. J. & Evans, J. R. Leaf mesophyll diffusion conductance in 35 Australian sclerophylls covering a broad range of foliage structural and physiological variation. *J. Exp. Bot.* **60**, 2433–2449 (2009).
244. Kenny, B., Orscheg, C., Tasker, E., Gill, M. A. & Bradstock, R. *NSW Flora Fire Response Database, v2.1*. (NSW Department of Planning Industry; Environment, 2014).
245. Northern Territory Herbarium. Flora of the Darwin Region Online. [http://www.lrm.nt.gov.au/plants-and-animals/herbarium/darwin\\_flora\\_online](http://www.lrm.nt.gov.au/plants-and-animals/herbarium/darwin_flora_online) (2014).
246. Onoda, Y., Richards, A. E. & Westoby, M. The relationship between stem biomechanics and wood density is modified by rainfall in 32 Australian woody plant species. *New Phytol.* **185**, 493–501 (2009).
247. O'Reilly-Nugent, A. *et al.* Measuring competitive impact: Joint-species modelling of invaded plant communities. *J. Ecol.* **108**, 449–459 (2018).
248. Osborne, C. P. *et al.* A global database of C4 photosynthesis in grasses. *New Phytol.* **204**, 441–446 (2014).
249. Paczkowska G. & Chapman, A.R. *The Western Australian flora: A descriptive catalogue*. 652 (CALM, Kings Park; Botanic Gardens; Wildflower Society of Western Australia, 2000).
250. Palma, E. *et al.* Functional trait changes in the floras of 11 cities across the globe in response to urbanization. *Ecography* **40**, 875–886 (2017).
251. Pate, J. S., Rasins, E., Rullo, J. & Kuo, J. Seed nutrient reserves of Proteaceae with special reference to protein bodies and their inclusions. *Ann. Bot.* **57**, 747–770 (1986).
252. Pearcy, R. W. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. *Funct. Ecol.* **1**, 169–178 (1987).
253. Peeters, P. J. Correlations between leaf structural traits and the densities of herbivorous insect guilds. *Biol. J. Linn. Soc.* **77**, 43–65 (2002).
254. Pekin, B. K., Wittkuhn, R. S., Boer, M. M., Macfarlane, C. & Grierson, P. F. Plant functional traits along environmental gradients in seasonally dry and fire-prone ecosystem. *J. Veg. Sci.* **22**, 1009–1020 (2011).
255. Pickering, C., Green, K., Barros, A. A. & Venn, S. A resurvey of late-lying snowpatches reveals changes in both species and functional composition across snowmelt zones. *Alp. Bot.* **124**, 93–103 (2014).
256. Pickup, M., Westoby, M. & Basden, A. Dry mass costs of deploying leaf area in relation to leaf size. *Funct. Ecol.* **19**, 88–97 (2005).
257. Pollock, L. J., Morris, W. K. & Vesk, P. A. The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* **35**, 716–725 (2011).
258. Pollock, L. J. *et al.* Combining functional traits, the environment and multiple surveys to understand semi-arid tree distributions. *J. Veg. Sci.* **29**, 967–977 (2018).
259. Prior, L. D., Eamus, D. & Bowman, D. M. J. S. Leaf attributes in the seasonally dry tropics: A comparison of four habitats in northern Australia. *Funct. Ecol.* **17**, 504–515 (2003).
260. Prior, L. D., Bowman, D. M. J. S. & Eamus, D. Seasonal differences in leaf attributes in Australian tropical tree species: family and habitat comparisons. *Funct. Ecol.* **18**, 707–718 (2004).
261. Prior, L. D., Williamson, G. J. & Bowman, D. M. J. S. Impact of high-severity fire in a Tasmanian dry eucalypt forest. *Aust. J. Bot.* **64**, 193–205 (2016).
262. Oxford Forestry Institute. Prospect: The wood database. <http://dps.plants.ox.ac.uk/ofi/prospect/index.htm> (2009).
263. Royal Botanic Gardens Kew. Seed Information Database (SID). <http://data.kew.org/sid/> (2014).
264. Royal Botanic Gardens Sydney. PLantNET. <http://plantnet.rbg Syd.nsw.gov.au/search/simple.htm> (2014).
265. Royal Botanic Gardens Sydney. PLantNET: NSW flora online. <http://plantnet.rbg Syd.nsw.gov.au/> (2014).
266. Read, J. & Sanson, G. D. Characterizing sclerophylly: the mechanical properties of a diverse range of leaf types. *New Phytol.* **160**, 81–99 (2003).
267. Read, J., Sanson, G. D. & Lamont, B. B. Leaf mechanical properties in sclerophyll woodland and shrubland on contrasting soils. *Plant Soil* **276**, 95–113 (2005).
268. Reid, J. B., Hill, R., Brown, M. & and M. Hovenden. *Vegetation of Tasmania*. **456** (1999).
269. Reynolds, V. A., Anderegg, L. D. L., Loy, X., HilleRisLambers, J. & Mayfield, M. M. Unexpected drought resistance strategies in seedlings of four Brachychiton species. *Tree Physiol.* **38**, 664–677 (2017).
270. Rice, K. J., Matzner, S. L., Byer, W. & Brown, J. R. Patterns of tree dieback in Queensland, Australia: The importance of drought stress and the role of resistance to cavitation. *Oecologia* **139**, 190–198 (2004).
271. Richards, A. E. *et al.* Physiological profiles of restricted endemic plants and their widespread congeners in the North Queensland wet tropics, Australia. *Biol. Conserv.* **111**, 41–52 (2003).
272. Roderick, M. L., Berry, S. L. & Noble, I. R. The relationship between leaf composition and morphology at elevated CO2 concentrations. *New Phytol.* **143**, 63–72 (1999).
273. Roderick, M. L. & Cochrane, M. J. On the conservative nature of the leaf mass-area relationship. *Ann. Bot.* **89**, 537–542 (2002).
274. Rosell, J. A., Gleason, S., Mendez-Alonzo, R., Chang, Y. & Westoby, M. Bark functional ecology: Evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytol.* **201**, 486–497 (2014).
275. Rye, B. L. A revision of south-western Australian species of *Micromyrtus* (Myrtaceae) with five antisepalous ribs on the hypanthium. *Nuytsia* **15**, 101–122 (2002).
276. Rye, B. L. A partial revision of the south-western Australian species of *Micromyrtus* (Myrtaceae: Chamelaucieae). *Nuytsia* **16**, 117–147 (2006).
277. Rye, B. L. Reinstatement of the Western Australian genus *Oxymyrrhine* (Myrtaceae: Chamelaucieae) with three new species. *Nuytsia* **19**, 149–165 (2009).
278. Rye, B. L. A revision of the *Micromyrtus racemosa* complex (Myrtaceae: Chamelaucieae) of south-western Australia. *Nuytsia* **20**, 37–56 (2010).
279. Rye, B. L., Wilson, P. G. & Keighery, G. J. A revision of the species of *Hypocalymma* (Myrtaceae: Chamelaucieae) with smooth or colliculate seeds. *Nuytsia* **23**, 283–312 (2013).

280. Rye, B. L. An update to the taxonomy of some western Australian genera of Myrtaceae tribe Chamelaucieae. 1. *Calytrix*. *Nuytsia* **23**, 483–501 (2013).
281. Rye, B. L. A revision of the south-western Australian genus *Babingtonia* (Myrtaceae: Chamelaucieae). *Nuytsia* **25**, 219–250 (2015).
282. Jessop, J. P. & Toelken, H. R. *Flora of South Australia, 4th edition, 4 vols.* (Government Printer, Adelaide, 1986).
283. Sams, M. A. *et al.* Landscape context explains changes in the functional diversity of regenerating forests better than climate or species richness. *Glob. Ecol. Biog.* **26**, 1165–1176 (2017).
284. Sauquet, H. *et al.* The ancestral flower of angiosperms and its early diversification. *Nat. Commun.* **8**, 1–10 (2017).
285. Schmidt, S. & Stewart, G. R. Waterlogging and fire impacts on nitrogen availability and utilization in a subtropical wet heathland (wallum). *Plant Cell Environ.* **20**, 1231–1241 (1997).
286. Schmidt, S. & Stewart, G. R.  $\delta^{15}\text{N}$  values of tropical savanna and monsoon forest species reflect root specialisations and soil nitrogen status. *Oecologia* **134**, 569–577 (2003).
287. Schmidt, S., Lamble, R. E., Fensham, R. J. & Siddique, I. Effect of woody vegetation clearing on nutrient and carbon relations of semi-arid dystrophic savanna. *Plant Soil* **331**, 79–90 (2009).
288. Schulze, E., Kelliher, F. M., Körner, C., Lloyd, J. & Leuning, R. Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: A global ecology scaling exercise. *Annu. Rev. Ecol. Syst.* **25**, 629–662 (1994).
289. Schulze, E.-D. *et al.* Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. *Aust. J. Plant. Physiol.* **25**, 413–425 (1998).
290. Schulze, E.-D., Turner, N. C., Nicolle, D. & Schumacher, J. Species differences in carbon isotope ratios, specific leaf area and nitrogen concentrations in leaves of *Eucalyptus* growing in a common garden compared with along an aridity gradient. *Physiol. Plant.* **127**, 434–444 (2006).
291. Schulze, E.-D., Turner, N. C., Nicolle, D. & Schumacher, J. Leaf and wood carbon isotope ratios, specific leaf areas and wood growth of *Eucalyptus* species across a rainfall gradient in Australia. *Tree Physiol.* **26**, 479–492 (2006).
292. Turner, N. C., Schulze, E.-D., Nicolle, D., Schumacher, J. & Kuhlmann, I. Annual rainfall does not directly determine the carbon isotope ratio of leaves of *Eucalyptus* species. *Physiol. Plant.* **132**, 440–445 (2008).
293. Schulze, E. D. *et al.* Stable carbon and nitrogen isotope ratios of *Eucalyptus* and *Acacia* species along a seasonal rainfall gradient in Western Australia. *Trees* **28**, 1125–1135 (2014).
294. Scott, A. J. *Vegetation recovery and recruitment processes in south-eastern Australian semi-arid old fields.* (La Trobe University, 2010).
295. Sendall, K. M., Lusk, C. H. & Reich, P. B. Trade-offs in juvenile growth potential vs. shade tolerance among subtropical rain forest trees on soils of contrasting fertility. *Funct. Ecol.* **30**, 845–855 (2015).
296. Seng, O. D. *Specific gravity of Indonesian Woods and its significance for practical use.* (FPRDC Forestry Department, Bogor, Indonesia, 1951).
297. Sjöström, A. & Gross, C. L. Life-history characters and phylogeny are correlated with extinction risk in the Australian angiosperms. *J. Biogeogr.* **33**, 271–290 (2006).
298. Smith, B. *Community-level Convergence and Community Structure of temperate Nothofagus forests.* (University of Otago, Dunedin, New Zealand, 1996).
299. Smith, R. A., Lewis, J. D., Ghannoum, O. & Tissue, D. T. Leaf structural responses to pre-industrial, current and elevated atmospheric CO<sub>2</sub> and temperature affect leaf function in *Eucalyptus sideroxylon*. *Funct. Plant. Bio.* **39**, 285–296 (2012).
300. Soliveres, S., Eldridge, D. J., Hemmings, F. & Maestre, F. T. Nurse plant effects on plant species richness in drylands: The role of grazing, rainfall and species specificity. *Perspect. Plant Ecol. Evol. Syst.* **14**, 402–410 (2012).
301. Soper, F. M. *et al.* Natural abundance ( $\delta^{15}\text{N}$ ) indicates shifts in nitrogen relations of woody taxa along a savanna-woodland continental rainfall gradient. *Oecologia* **178**, 297–308 (2014).
302. Specht, R. L. *et al.* *Mediterranean-type ecosystems: A data source book.* 248 (Springer, 1988).
303. Specht, R. L. & Rundel, P. W. Sclerophylly and foliar nutrient status of Mediterranean-climate plant communities in southern Australia. *Aust. J. Bot.* **38**, 459–474 (1990).
304. Sperry, J. S., Hacke, U. G., Feild, T. S., Sano, Y. & Sikkema, E. H. Hydraulic consequences of vessel evolution in Angiosperms. *Int. J. Plant Sci.* **168**, 1127–1139 (2007).
305. Staples, T., Dwyer, J. M., England, J. R. & Mayfield, M. M. Productivity does not correlate with species and functional diversity in Australian reforestation plantings across a wide climate gradient. *Glob. Ecol. Biog.* **28**, 1417–1429 (2019).
306. Stewart, G., Turnbull, M., Schmidt, S. & Erskine, P.  $^{13}\text{C}$  natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. *Funct. Plant. Bio.* **22**, 51–55 (1995).
307. Stock, W. D., Pate, J. S. & Rasins, E. Seed developmental patterns in *Banksia attenuata* R. Br. and *B. loricata* C. Gardner in relation to mechanical defence costs. *New Phytol.* **117**, 109–114 (1991).
308. Tait, C. J., Daniels, C. B. & Hill, R. S. Changes in species assemblages within the Adelaide metropolitan area, Australia, 1836–2002. *Ecol. Appl.* **15**, 346–359 (2005).
309. Taseski, G., Keith, D. A., Dalrymple, R. L. & Cornwell, W. K. *Shifts in fine root traits within and among species along a small-scale hydrological gradient.* (University of New South Wales, 2017).
310. Taylor, D. & Eamus, D. Coordinating leaf functional traits with branch hydraulic conductivity: Resource substitution and implications for carbon gain. *Tree Physiol.* **28**, 1169–1177 (2008).
311. Thomas, F. M. & Veski, P. A. Growth rates in The Mallee: Height growth in woody plants examined with a trait-based model. *Austral Ecol.* **42**, 790–800 (2017).
312. Thomas, F. M. & Veski, P. A. Are trait-growth models transferable? Predicting multi-species growth trajectories between ecosystems using plant functional traits. *PLoS One* **12**, e0176959 (2017).
313. Thompson, I. R. Morphometric analysis and revision of eastern Australian *Hovea* (Brongniartieae-Fabaceae). *Aust. Syst. Bot.* **14**, 1–99 (2001).
314. Tasmanian Herbarium. Flora of Tasmania Online. <http://www.tmag.tas.gov.au/floratasmania> (2009).
315. Tng, D. Y. P., Jordan, G. J. & Bowman, D. M. J. S. Plant traits demonstrate that temperate and tropical giant *Eucalypt* forests are ecologically convergent with rainforest not savanna. *PLoS One* **8**, e84378 (2013).
316. Toelken, H. R. A revision of the genus *Kunzea* (Myrtaceae) I. The western Australian section *Zeanuk*. *J. Adel. Bot. Gard.* **17**, 29–106 (1996).
317. Tomlinson, K. W. *et al.* Biomass partitioning and root morphology of savanna trees across a water gradient. *J. Ecol.* **100**, 1113–1121 (2012).
318. Tomlinson, K. W. *et al.* Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents. *J. Ecol.* **101**, 430–440 (2013).
319. Tomlinson, K. W. *et al.* Seedling growth of savanna tree species from three continents under grass competition and nutrient limitation in a greenhouse experiment. *J. Ecol.* **107**, 1051–1066 (2019).
320. Tremont, R. M. Life-history attributes of plants in grazed and ungrazed grasslands on the Northern Tablelands of New South Wales. *Aust. J. Bot.* **42**, 511–530 (1994).
321. Trudgen, M. E. & Rye, B. L. *Astus*, a new western Australian genus of Myrtaceae with heterocarpic fruits. *Nuytsia* **14**, 495–512 (2005).
322. Trudgen, M. E. & Rye, B. L. An update to the taxonomy of some western Australian genera of Myrtaceae tribe Chamelaucieae. 2. *Cyathostemon*. *Nuytsia* **24**, 7–16 (2014).



323. Turner, J. & Lambert, M. J. Nutrient cycling within a 27-year-old *Eucalyptus grandis* plantation in New South Wales. *For. Ecol. Manage.* **6**, 155–168 (1983).
324. Turner, N. C., Schulze, E.-D., Nicolle, D. & Kuhlmann, I. Growth in two common gardens reveals species by environment interaction in carbon isotope discrimination of *Eucalyptus*. *Tree Physiol.* **30**, 741–747 (2010).
325. Veneklaas, E. J. & Poot, P. Seasonal patterns in water use and leaf turnover of different plant functional types in a species-rich woodland, south-western Australia. *Plant Soil* **257**, 295–304 (2003).
326. Venn, S. E., Green, K., Pickering, C. M. & Morgan, J. W. Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. *Plant Ecol.* **212**, 1491–1499 (2011).
327. Venn, S., Pickering, C. & Green, K. Spatial and temporal functional changes in alpine summit vegetation are driven by increases in shrubs and graminoids. *AoB Plants* **6**, plu008 (2014).
328. Vesk, P. A., Leishman, M. R. & Westoby, M. Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *J. Appl. Ecol.* **41**, 22–31 (2004).
329. Vesk, P. A. & Yen, J. D. L. Plant resprouting: How many sprouts and how deep? Flexible modelling of multispecies experimental disturbances. *Perspect. Plant Ecol. Evol. Syst.* **41**, 125497 (2019).
330. Vlasveld, C., O’Leary, B., Udovicic, F. & Burd, M. Leaf heteroblasty in eucalypts: biogeographic evidence of ecological function. *Aust. J. Bot.* **66**, 191–201 (2018).
331. Western Australian Herbarium. FloraBase: The Western Australian flora. <http://florabase.dpaw.wa.gov.au> (1998).
332. Western Australian Herbarium. FloraBase: The Western Australian flora. <http://florabase.dpaw.wa.gov.au/> (2016).
333. Warren, C. R., Tausz, M. & Adams, M. A. Does rainfall explain variation in leaf morphology and physiology among populations of red ironbark (*Eucalyptus sideroxylon* subsp. *tricarpa*) grown in a common garden? *Tree Physiol.* **25**, 1369–1378 (2005).
334. Warren, C. R., Dreyer, E., Tausz, M. & Adams, M. A. Ecotype adaptation and acclimation of leaf traits to rainfall in 29 species of 16-year-old *Eucalyptus* at two common gardens. *Funct. Ecol.* **20**, 929–940 (2006).
335. Weerasinghe, L. K. *et al.* Canopy position affects the relationships between leaf respiration and associated traits in a tropical rainforest in Far North Queensland. *Tree Physiol.* **34**, 564–584 (2014).
336. Wells, J. A. *Phylogeny and inter-relations of ecological traits and seed dispersal in rainforest plants: Exploring aspects of functional diversity in primary and secondary rainforests in Australia’s Wet Tropics.* (University of Queensland, 2012).
337. Westman, W. E. & Roggers, R. V. Nutrient stocks in a subtropical eucalypt forest, North Stradbroke Island. *Austral Ecol.* **2**, 447–460 (1977).
338. Westoby, M. *et al.* Seed size and plant growth form as factors in dispersal spectra. *Ecology* **71**, 1307–1315 (1990).
339. Westoby, M. & Wright, I. J. The leaf size – twig size spectrum and its relationship to other important spectra of variation among species. *Oecologia* **135**, 621–628 (2003).
340. Wheeler, J. R., Marchant, N. G. & Lewington, M. *Flora of the south west: Bunbury, Augusta, Denmark.* (Australian Biological Resources Study; University of Western Australia Press, 2002).
341. White, M., Sinclair, S. & Frood, D. *Victorian Vital Attributes Database.* (Department of Environment, Land, Water; Planning, Victoria, 2020).
342. Williams, N. S. G., Morgan, J. W., McDonnell, M. J. & McCarthy, M. A. Plant traits and local extinctions in natural grasslands along an urban-rural gradient. *J. Ecol.* **93**, 1203–1213 (2005).
343. Wills, J. *et al.* Tree leaf trade-offs are stronger for sub-canopy trees: leaf traits reveal little about growth rates in canopy trees. *Ecol. Appl.* **28**, 1116–1125 (2018).
344. Wilson, P. G. & Rowe, R. A revision of the Indigofereae (Fabaceae) in Australia. 2. Indigofera species with trifoliolate and alternately pinnate leaves. *Telopea* **12**, 293–307 (2008).
345. Wright, I. J. *et al.* A survey of seed and seedling characters in 1744 Australian dicotyledon species: Cross-species trait correlations and correlated trait-shifts within evolutionary lineages. *Biol. J. Linn. Soc.* **69**, 521–547 (2000).
346. Wright, I. J., Reich, P. B. & Westoby, M. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Funct. Ecol.* **15**, 423–434 (2001).
347. Wright, I. J. & Westoby, M. Leaves at low versus high rainfall: Coordination of structure, lifespan and physiology. *New Phytol.* **155**, 403–416 (2002).
348. Wright, I. J., Westoby, M. & Reich, P. B. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *J. Ecol.* **90**, 534–543 (2002).
349. Wright, I. J., Falster, D. S., Pickup, M. & Westoby, M. Cross-species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics. *Physiol. Plant.* **127**, 445–456 (2006).
350. Wright, I. J. *et al.* Stem diameter growth rates in a fire-prone savanna correlate with photosynthetic rate and branch-scale biomass allocation, but not specific leaf area. *Austral Ecol.* **44**, 339–350 (2018).
351. Yates, C. J. *et al.* Mallee woodlands and shrublands: the mallee, muruk/muert and maalok vegetation of Southern Australia. in *Australian Vegetation* (Cambridge University Press, 2017).
352. Zanne, A. E. *et al.* Data from: Towards a worldwide wood economics spectrum. *Dryad* <https://doi.org/10.5061/dryad.234> (2009).
353. Zieminska, K., Butler, D. W., Gleason, S. M., Wright, I. J. & Westoby, M. Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB Plants* **5**, plt046 (2013).
354. Zieminska, K., Westoby, M. & Wright, I. J. Broad anatomical variation within a narrow wood density range - A study of twig wood across 69 Australian Angiosperms. *PLoS One* **10**, e0124892 (2015).
355. R Core Team. *R: A language and environment for statistical computing.* (R Foundation for Statistical Computing, 2020).
356. Wickham, H. *et al.* Welcome to the tidyverse. *Journal of Open Source Software* **4**, 1686 (2019).
357. Stephens, J. *Yaml: Methods to convert r data to YAML and back (r package version 2.1.13).* (2014).
358. FitzJohn, R. *Remake: Make-like build management.* R package version 0.2.0. (2016).
359. Xie, Y. *Dynamic documents with R and Knitr.* (2015).
360. Allaire, J. *et al.* *Rmarkdown: Dynamic documents for R.* R package version 0.5.1. (2015).
361. CHAH. *Australian Plant Name Index (continuously updated), Centre of Australian National Biodiversity Research.* (<https://www.biodiversity.org.au/nsl/services/apni> (14/05/2020), 2020).
362. Chamberlain, S. A. & Szöcs, E. Taxize: Taxonomic search and retrieval in R. *F1000Res.* **2**, 191 (2013).
363. Falster, D. *et al.* AusTraits: a curated plant trait database for the Australian flora. *Zenodo* <https://doi.org/10.5281/zenodo.3568417> (2021).
364. Wilkinson, M. D. *et al.* The FAIR guiding principles for scientific data management and stewardship. *Sci. Data* **3** (2016).
365. Falster, D. S., FitzJohn, R. G., Pennell, M. W. & Cornwell, W. K. Datastorr: A workflow and package for delivering successive versions of ‘evolving data’ directly into R. *GigaScience* **8**, giz035 (2019).
366. Smith, S. A. & Brown, J. W. Constructing a broadly inclusive seed plant phylogeny. *Am. J. Bot.* **105**, 302–314 (2018).
367. Jin, Y. *VPhyloMaker: Make phylogenetic hypotheses for vascular plants, etc..* R package version 0.1.0. (2020).
368. Yu, G., Smith, D. K., Zhu, H., Guan, Y. & Lam, T. T.-Y. Gtree: An r package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecol. Evol.* **8**, 28–36 (2017).
369. Stefan, V. & Levin, S. Plotbiomes: Plot Whittaker biomes with ggplot2. R package version 0.0.0.9001. (2020).
370. Whittaker, R. H. *Communities and ecosystems.* (MacMillan Publishers, 1975).
371. Fick, S. E. & Hijmans, R. J. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).

## Acknowledgements

We acknowledge the work of all Australian taxonomists and their supporting institutions, whose long-term work on describing the flora has provided a rich source of data for AusTraits, including: Australian National Botanic Gardens; Australian National Herbarium; Biodiversity Science, Parks Australia; Centre for Australian National Biodiversity Research; Department of Biodiversity, Conservation and Attractions, Western Australia; Department of Environment, Land, Water and Planning, Victoria; Flora of Australia; Kew; National Herbarium of NSW; National Herbarium of Victoria; Northern Territory Herbarium; NSW Department of Planning, Industry, and Environment; Queensland Herbarium; State Herbarium of South Australia; Tasmanian Herbarium; and the Western Australian Herbarium. We gratefully acknowledge input from the following persons who contributed to data collection: Sophia Amini, Julian Ash, Tara Boreham, Ross Bradstock, Willi A. Brand, Amber Briggs, John Brock, Don Butler, Robert Chinnock, Peter Clarke, Derek Clayton, Steven Clemants, Harold Trevor Clifford, Michelle Cochrane, Bronwyn Collins, Alessandro Conti, Wendy Cooper, William Cooper, Ian Cowie, Lyn Craven, Ian Davidson, Derek Eamus, Judy Egan, Chris Fahey, Paul Irwin Forster, John Foster, Tony French, Allison Frith, Ronald Gardiner, Malcolm Gill, Ethel Goble-Garratt, Peter Grubb, Chris Guinane, TJ Hall, Monique Hallet, Tammy Haslehurst, Foteini Hassiotou, John Herbohn, Peter Hocking, Jing Hu, Kate Hughes, Muhammad Islam, Ian Kealley, Greg Keighery, James Kirkpatrick, Kirsten Knox, Luka Kovac, Kaely Kreger, John Kuo, Martin Lambert, Dana Lanceman, Michael Lawes, Claire Laws, Emma Laxton, Liz Lindsay, Daniel Montoya Londono, Christiane Ludwig, Ian Lunt, Mary Maconochie, Karen Marais, Bruce Maslin, Riah Mason, Richard Mazanec, Elissa McFarlane, Huw Morgan, Peter Myerscough, Des Nelson, Dominic Neyland, Mike Olsen, Corinna Orscheg, Jacob McC. Overton, Paula Peeters, George Perry, Aaron Phillips, Loren Pollitt, Rob Polmear, Hugh Possingham, Aina Price, Thomas Pyne, R.J. Williams, Barbara Rice, Jessica L. Rigg, Bryan Roberts, Miguel de Salas, Anna Salomaa, Inge Schulze, Waltraud Schulze, Andrew John Scott, Alison Shapcott, Veronica Shaw, Luke Shoo, Anne Sjoström, Santiago Soliveres, Amanda Spooner, George Stewart, Jan Suda, Catherine Tait, Daniel Taylor, Ian Thompson, Hellmut R. Toelken, Malcolm Trudgen, W.E. Westman, Erica Williams, Kathryn Willis, J. Bastow Wilson, Jian Yen. We thank H Cornelissen, H Poorter, SC McColl-Gausden, and one anonymous reviewer for feedback on an earlier draft, and K Levett for advice on data structures. This work was supported by fellowship grants from Australian Research Council to Falster (FT160100113), Gallagher (DE170100208) and Wright (FT100100910). The AusTraits project received investment (<https://doi.org/10.47486/TD044>, <https://doi.org/10.47486/DP720>) from the Australian Research Data Commons (ARDC). The ARDC is funded by the National Collaborative Research Infrastructure Strategy (NCRIS).

## Author contributions

R.V.G., I.J.W. conceived the original idea; R.V.G., E.H.W., C.B., S.A. collated data from primary sources; D.S.F. developed the workflow for the harmonising of data and led all coding; E.H.W., D.I., S.C.A., J.L. contributed to coding; E.H.W., S.C.A., C.B., J.L. error-checked trait measurements; A.M., A.F. assisted with workflow for updating taxonomy; D.I. developed figures for the paper; F.K., D.S.F. developed the R package; D.S.F., R.V.G., D.I., E.H.W. wrote the first draft of the paper. All other authors contributed the raw data and metadata underpinning the resource, reviewed the harmonised data for errors, and reviewed the final paper for publication.

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41597-021-01006-6>.

**Correspondence** and requests for materials should be addressed to D.F.

**Reprints and permissions information** is available at [www.nature.com/reprints](http://www.nature.com/reprints).

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

The Creative Commons Public Domain Dedication waiver <http://creativecommons.org/publicdomain/zero/1.0/> applies to the metadata files associated with this article.

© The Author(s) 2021

Daniel Falster<sup>1,106</sup> , Rachael Gallagher<sup>2,104,106</sup> , Elizabeth H. Wenk<sup>1</sup> , Ian J. Wright<sup>2</sup> , Dony Indiarto<sup>1</sup>, Samuel C. Andrew<sup>3</sup>, Caitlan Baxter<sup>1</sup>, James Lawson<sup>4</sup>, Stuart Allen<sup>2</sup>, Anne Fuchs<sup>5</sup>, Anna Monro<sup>5</sup>, Fonti Kar<sup>1</sup>, Mark A. Adams<sup>6</sup> , Collin W. Ahrens<sup>7</sup>, Matthew Alfonzetti<sup>2</sup> , Tara Angevin<sup>8</sup>, Deborah M. G. Apgaua<sup>9</sup> , Stefan Arndt<sup>10</sup> , Owen K. Atkin<sup>11</sup> , Joe Atkinson<sup>1</sup> , Tony Auld<sup>12</sup>, Andrew Baker<sup>13</sup>, Maria von Balthazar<sup>14</sup>, Anthony Bean<sup>15</sup>, Chris J. Blackman<sup>16</sup>, Keith Bloomfield<sup>17</sup>, David M. J. S. Bowman<sup>16</sup> , Jason Bragg<sup>18</sup>, Timothy J. Brodribb<sup>16</sup> , Genevieve Buckton<sup>19</sup>, Geoff Burrows<sup>20</sup>, Elizabeth Caldwell<sup>21</sup>, James Camac<sup>16</sup> , Raymond Carpenter<sup>23</sup>, Jane A. Catford<sup>16</sup> , Gregory R. Cawthray<sup>16</sup> , Lucas A. Cernusak<sup>16</sup> , Gregory Chandler<sup>27</sup>, Alex R. Chapman<sup>16</sup> , David Cheal<sup>29</sup>, Alexander W. Cheesman<sup>19</sup>, Si-Chong Chen<sup>30</sup>, Brendan Choat<sup>16</sup> , Brook Clinton<sup>5</sup>, Peta L. Clode<sup>16</sup> , Helen Coleman<sup>28</sup>, William K. Cornwell<sup>16</sup> , Meredith Cosgrove<sup>11</sup>, Michael Crisp<sup>11</sup>, Erika Cross<sup>20</sup>, Kristine Y. Crous<sup>7</sup>, Saul Cunningham<sup>16</sup> , Timothy Curran<sup>16</sup> , Ellen Curtis<sup>33</sup>, Matthew I. Daws<sup>34</sup>, Jane L. DeGabriel<sup>35</sup>, Matthew D. Denton<sup>16</sup> , Ning Dong<sup>2</sup>, Pengzhen Du<sup>37</sup>, Honglang Duan<sup>38</sup>, David H. Duncan<sup>10</sup>, Richard P. Duncan<sup>39</sup>, Marco Duretto<sup>16</sup> , John M. Dwyer<sup>16</sup> , Cheryl Edwards<sup>42</sup>, Manuel Esperon-Rodriguez<sup>16</sup> , John R. Evans<sup>16</sup> , Susan E. Everingham<sup>1</sup>, Claire Farrell<sup>10</sup>, Jennifer Firn<sup>16</sup> , Carlos Roberto Fonseca<sup>16</sup> , Ben J. French<sup>16</sup> , Doug Froud<sup>45</sup>, Jennifer L. Funk<sup>46</sup>, Sonya R. Geange<sup>16</sup> , Oula Ghannoum<sup>7</sup>, Sean M. Gleason<sup>47</sup>, Carl R. Gosper<sup>16</sup> , Emma Gray<sup>16</sup> , Philip K. Groom<sup>49</sup>, Saskia Grootemaat<sup>1</sup>, Caroline Gross<sup>50</sup>, Greg Guerin<sup>51</sup>, Lydia Guja<sup>5</sup>, Amy K. Hahs<sup>16</sup> , Matthew Tom Harrison<sup>16</sup> , Patrick E. Hayes<sup>16</sup> , Martin Henery<sup>54</sup>, Dieter Hochuli<sup>16</sup> , Jocelyn Howell<sup>56</sup>, Guomin Huang<sup>57</sup>, Lesley Hughes<sup>2</sup>, John Huisman<sup>58</sup>, Jugoslav Ilic<sup>10</sup>, Ashika Jagdish<sup>1</sup>, Daniel Jin<sup>16</sup> , Gregory Jordan<sup>16</sup>, Enrique Jurado<sup>16</sup> , John Kanowski<sup>60</sup>, Sabine Kasel<sup>16</sup> , Jürgen Kellermann<sup>61</sup>, Belinda Kenny<sup>62</sup>, Michele Kohout<sup>63</sup>, Robert M. Kooyman<sup>16</sup> , Martyna M. Kotowska<sup>16</sup> , Hao Ran Lai<sup>16</sup> , Etienne Laliberté<sup>16</sup> , Hans Lambers<sup>16</sup> , Byron B. Lamont<sup>16</sup> , Robert Lanfear<sup>67</sup>, Frank van Langevelde<sup>16</sup> , Daniel C. Laughlin<sup>16</sup> , Bree-Anne Laugier-Kitchener<sup>2</sup>, Susan Laurance<sup>16</sup> , Caroline E. R. Lehmann<sup>16</sup> , Andrea Leigh<sup>16</sup> , Michelle R. Leishman<sup>2</sup>, Tanja Lenz<sup>2</sup>, Brendan Lepschi<sup>5</sup>, James D. Lewis<sup>16</sup> , Felix Lim<sup>16</sup> , Udayangani Liu<sup>16</sup> , Janice Lord<sup>16</sup> , Christopher H. Lusk<sup>74</sup>, Cate Macinnis-Ng<sup>16</sup> , Hannah McPherson<sup>40</sup>, Susana Magallón<sup>16</sup> , Anthony Manea<sup>2</sup>, Andrea López-Martinez<sup>76</sup>, Margaret Mayfield<sup>16</sup> , James K. McCarthy<sup>16</sup> , Trevor Meers<sup>78</sup>, Marlien van der Merwe<sup>16</sup> , Daniel J. Metcalfe<sup>3</sup>, Per Milberg<sup>16</sup> , Karel Mokany<sup>3</sup>, Angela T. Moles<sup>16</sup> , Ben D. Moore<sup>16</sup> , Nicholas Moore<sup>8</sup>, John W. Morgan<sup>8</sup>, William Morris<sup>16</sup> , Annette Muir<sup>63</sup>, Samantha Munroe<sup>16</sup> , Áine Nicholson<sup>16</sup>, Dean Nicolle<sup>80</sup>, Adrienne B. Nicotra<sup>11</sup>, Ülo Niinemets<sup>81</sup>, Tom North<sup>5</sup>, Andrew O'Reilly-Nugent<sup>39</sup>, Odhran S. O'Sullivan<sup>82</sup>, Brad Oberle<sup>83</sup>, Yusuke Onoda<sup>84</sup>, Mark K. J. Ooi<sup>16</sup> , Colin P. Osborne<sup>16</sup> , Grazyna Paczkowska<sup>28</sup>, Burak Pekin<sup>87</sup>, Caio Guilherme Pereira<sup>88</sup>, Catherine Pickering<sup>89</sup>, Melinda Pickup<sup>90</sup>, Laura J. Pollock<sup>91</sup>, Pieter Poot<sup>26</sup>, Jeff R. Powell<sup>7</sup>, Sally A. Power<sup>16</sup> , Iain Colin Prentice<sup>16</sup> , Lynda Prior<sup>16</sup>, Suzanne M. Prober<sup>3</sup>, Jennifer Read<sup>21</sup>, Victoria Reynolds<sup>41</sup>, Anna E. Richards<sup>3</sup>, Ben Richardson<sup>92</sup>, Michael L. Roderick<sup>16</sup> , Julieta A. Rosell<sup>16</sup> , Maurizio Rossetto<sup>40</sup>, Barbara Rye<sup>92</sup>, Paul D. Rymer<sup>7</sup>, Michael A. Sams<sup>41</sup>, Gordon Sanson<sup>21</sup>, Hervé Sauquet<sup>16</sup> , Susanne Schmidt<sup>16</sup> , Jürg Schönenberger<sup>16</sup> , Ernst-Detlef Schulze<sup>94</sup>, Kerrie Sendall<sup>16</sup> , Steve Sinclair<sup>16</sup> , Benjamin Smith<sup>7</sup>, Renee Smith<sup>7</sup>, Fiona Soper<sup>96</sup>, Ben Sparrow<sup>16</sup> , Rachel J. Standish<sup>16</sup> , Timothy L. Staples<sup>41</sup>, Ruby Stephens<sup>2</sup>, Christopher Szota<sup>10</sup>, Guy Taseski<sup>1</sup>, Elizabeth Tasker<sup>12</sup>, Freya Thomas<sup>10</sup>, David T. Tissue<sup>7</sup>, Mark G. Tjoelker<sup>16</sup> , David Yue Phin Tng<sup>16</sup> , Félix de Tombeur<sup>16</sup> , Kyle Tomlinson<sup>99</sup>, Neil C. Turner<sup>16</sup> , Erik J. Veneklaas<sup>16</sup> , Susanna Venn<sup>16</sup> , Peter Vesk<sup>16</sup> , Carolyn Vlasveld<sup>16</sup> , Maria S. Vorontsova<sup>16</sup> , Charles A. Warren<sup>55</sup>, Nigel Warwick<sup>16</sup> , Lasantha K. Weerasinghe<sup>16</sup> , Jessie Wells<sup>16</sup> , Mark Westoby<sup>16</sup> , Matthew White<sup>63</sup>, Nicholas S. G. Williams<sup>10</sup>, Jarrah Wills<sup>55</sup>, Peter G. Wilson<sup>102</sup>, Colin Yates<sup>48</sup>, Amy E. Zanne<sup>103,105</sup>, Graham Zemunik<sup>16</sup>  & Kasia Ziemińska<sup>16</sup> 

<sup>1</sup>Evolution & Ecology Research Centre, School of Biological, Earth, and Environmental Sciences, UNSW Sydney, Sydney, Australia. <sup>2</sup>Department of Biological Sciences, Macquarie University, Sydney, Australia. <sup>3</sup>CSIRO Land and Water, Canberra, Australia. <sup>4</sup>NSW Department of Primary Industries, Orange, Australia. <sup>5</sup>Centre for Australian National Biodiversity Research (a joint venture between Parks Australia and CSIRO), Canberra, ACT, Australia. <sup>6</sup>Swinburne University of Technology, Hawthorn, Australia. <sup>7</sup>Hawkesbury Institute for the Environment, Western Sydney University, Sydney, Australia. <sup>8</sup>La Trobe University, Bundoora, Australia. <sup>9</sup>Centre for Rainforest Studies, School for Field Studies,

Yungaburra, Queensland, 4872, Australia. <sup>10</sup>University of Melbourne, Melbourne, Australia. <sup>11</sup>The Australian National University, Canberra, Australia. <sup>12</sup>NSW Department of Planning Industry and Environment, Parramatta, Australia. <sup>13</sup>Southern Cross University, Lismore, Australia. <sup>14</sup>Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria. <sup>15</sup>Queensland Herbarium, Toowong, Australia. <sup>16</sup>University of Tasmania, Hobart, Australia. <sup>17</sup>Imperial College, London, United Kingdom. <sup>18</sup>Research Centre for Ecosystem Resilience, Australian Institute of Botanical Science, Royal Botanic Gardens and Domain Trust, Sydney, Australia. <sup>19</sup>James Cook University, Douglas, Australia. <sup>20</sup>Charles Sturt University, Bathurst, Australia. <sup>21</sup>School of Biological Sciences, Monash University, Clayton, Australia. <sup>22</sup>Centre of Excellence for Biosecurity Risk Analysis, The University of Melbourne, Melbourne, Australia. <sup>23</sup>University of Adelaide, Adelaide, Australia. <sup>24</sup>King's College London, London, United Kingdom. <sup>25</sup>University of Western Australia, Crawley, Australia. <sup>26</sup>College of Science and Engineering, James Cook University, Cairns, QLD, Australia. <sup>27</sup>Department of Agriculture, Sydney, Australia. <sup>28</sup>Western Australian Herbarium, Keiran McNamara Conservation Science Centre, Department of Biodiversity, Conservation and Attractions, Western Australia, Kensington, Australia. <sup>29</sup>Centre for Environmental Management, School of Health & Life Sciences, Federation University, Mount Helen, Australia. <sup>30</sup>Royal Botanic Gardens, Richmond, Kew, United Kingdom. <sup>31</sup>Fenner School of Environment and Society, The Australian National University, Canberra, Australia. <sup>32</sup>Lincoln University, Lincoln, New Zealand. <sup>33</sup>University of Technology Sydney, Sydney, Australia. <sup>34</sup>Environment Department, Alcoa of Australia, Huntly, Western Australia, Australia. <sup>35</sup>School of Marine and Tropical Biology, James Cook University, Douglas, Australia. <sup>36</sup>School of Agriculture, Food and Wine, University of Adelaide, Adelaide, Australia. <sup>37</sup>Lanzhou University, Lanzhou, China. <sup>38</sup>Institute for Forest Resources & Environment of Guizhou, Guizhou University, Guiyang, China. <sup>39</sup>Institute for Applied Ecology, University of Canberra, ACT, 2617, Canberra, Australia. <sup>40</sup>National Herbarium of New South Wales, Australian Institute of Botanical Science, Royal Botanic Gardens and Domain Trust, Sydney, Australia. <sup>41</sup>School of Biological Sciences, The University of Queensland, St Lucia, Australia. <sup>42</sup>Melbourne Water, Melbourne, Australia. <sup>43</sup>Queensland University of Technology, Brisbane, Australia. <sup>44</sup>Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, Natal – RN, Brazil. <sup>45</sup>Pathways Bushland and Environment Consultancy, Sydney, Australia. <sup>46</sup>Department of Plant Sciences, University of California, Davis, USA. <sup>47</sup>USDA-ARS, WMSRU, Fort Collins, Colorado, 80526, USA. <sup>48</sup>Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia. <sup>49</sup>Curtin University, Bentley, Australia. <sup>50</sup>University of New England, Armidale, Australia. <sup>51</sup>Terrestrial Ecosystem Research Network, The School of Biological Sciences, The University of Adelaide, Adelaide, SA, 5005, Australia. <sup>52</sup>School of Ecosystem and Forest Sciences, The University of Melbourne, Melbourne, Australia. <sup>53</sup>Tasmanian Institute of Agriculture, University of Tasmania, Hobart, Australia. <sup>54</sup>arks Australia, Department of Agriculture, Water and the Environment, Hobart, Australia. <sup>55</sup>School of Life and Environmental Sciences, The University of Sydney, Camperdown, Australia. <sup>56</sup>Berowa NSW, Berowa, Australia. <sup>57</sup>Nanchang Institute of Technology, Nanchang, China. <sup>58</sup>Western Australian Herbarium, Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Kensington, Western Australia, Australia. <sup>59</sup>Universidad Autonoma de Nuevo Leon, San Nicolás de los Garza, Mexico. <sup>60</sup>Australian Wildlife Conservancy, Sydney, Australia. <sup>61</sup>State Herbarium of South Australia, Botanic Gardens and State Herbarium, Hackney Road, Adelaide, SA, 5000, Australia. <sup>62</sup>NSW Rural Fire Service, Sydney, Australia. <sup>63</sup>Department of Environment, Land, Water and Planning, Victoria, Australia. <sup>64</sup>Department of Plant Ecology and Ecosystems Research, University of Goettingen, Göttingen, Germany. <sup>65</sup>University of Canterbury, Christchurch, New Zealand. <sup>66</sup>Institut de recherche en biologie végétale, Université de Montréal, 4101 Sherbrooke Est, Montréal, H1X 2B2, Canada. <sup>67</sup>Ecology and Evolution, Research School of Biology, Australian National University, Canberra, Australia. <sup>68</sup>Wildlife Ecology & Conservation Group, Wageningen University, Wageningen, The Netherlands. <sup>69</sup>Department of Botany, University of Wyoming, Laramie, WY, 82071, USA. <sup>70</sup>Royal Botanic Garden Edinburgh, Edinburgh, United Kingdom. <sup>71</sup>Fordham University, New York City, NY, USA. <sup>72</sup>AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), Université de Montpellier, CIRAD, CNRS, INRA, IRD, Montpellier, France. <sup>73</sup>University of Otago, Dunedin, New Zealand. <sup>74</sup>Environmental Research Institute, University of Waikato, Hamilton, New Zealand. <sup>75</sup>University of Auckland, Auckland, New Zealand. <sup>76</sup>Laboratorio Nacional de Ciencias de la Sostenibilidad, Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico. <sup>77</sup>Manaaki Whenua – Landcare Research, Lincoln, 7640, New Zealand. <sup>78</sup>Cumberland Ecology, Cumberland, Australia. <sup>79</sup>Linköping University, Linköping, Sweden. <sup>80</sup>Currency Creek Arboretum, Currency Creek, Australia. <sup>81</sup>Estonian University of Life Sciences, Tartu, Estonia. <sup>82</sup>Leistershire County Council, Leicester, United Kingdom. <sup>83</sup>Division of Natural Sciences, New College of Florida, Sarasota, USA. <sup>84</sup>Graduate School of Agriculture, Kyoto University, Kyoto, Japan. <sup>85</sup>Centre for Ecosystem Science, School of Biological, Earth, and Environmental Sciences, UNSW, Sydney, Australia. <sup>86</sup>University of Sheffield, Department of Animal and Plant Sciences, Sheffield, United Kingdom. <sup>87</sup>Istanbul Technical University, Eurasia Institute of Earth Sciences, Istanbul, Turkey. <sup>88</sup>Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, USA. <sup>89</sup>School of Environment and Science, Griffith University, Brisbane, Australia. <sup>90</sup>Greening Australia, Brisbane, Australia. <sup>91</sup>Department of Biology, McGill University, Montréal, Canada. <sup>92</sup>Western Australian Herbarium, Department of Biodiversity, Conservation and Attractions, Western Australia, Kensington, Australia. <sup>93</sup>School of Agriculture and Food Science, University of Queensland, St Lucia, Australia. <sup>94</sup>Max-Planck Institute for Biogeochemistry, Jena, Germany. <sup>95</sup>Rider University, Lawrence Township, Lawrenceville, NJ, USA. <sup>96</sup>McGill University, Montreal, Canada. <sup>97</sup>Environmental and Conservation Sciences, Murdoch University, Murdoch, Australia. <sup>98</sup>TERRA Teaching and Research Centre, Gembloux Agro-Bio Tech, University of Liege, Gembloux, Belgium. <sup>99</sup>Xishuangbanna Tropical Botanic Garden, Yunnan, China. <sup>100</sup>Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Australia. <sup>101</sup>Faculty of Agriculture, University of Peradeniya, Peradeniya, 20400, Sri Lanka. <sup>102</sup>National Herbarium of NSW and Royal Botanic Gardens and Domain Trust, Sydney, Australia. <sup>103</sup>Department of Biological Sciences, George Washington University, Washington, DC, 20052, USA. <sup>104</sup>Present address: Hawkesbury Institute for the Environment, Western Sydney University, Sydney, Australia. <sup>105</sup>Present address: Department of Biology, University of Miami, Coral Gables, Florida 33146 USA, George Washington University, Washington, DC, 20052, USA. <sup>106</sup>These authors contributed equally: Daniel Falster, Rachael Gallagher.

✉e-mail: [daniel.falster@unsw.edu.au](mailto:daniel.falster@unsw.edu.au)