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RESEARCH REPORT

Tallo: A global tree allometry and crown architecture database

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Abstract

Data capturing multiple axes of tree size and shape, such as a tree's stem diameter, height and crown size, underpin a wide range of ecological research—from developing and testing theory on forest structure and dynamics, to estimating forest carbon stocks and their uncertainties, and integrating remote sensing imagery into forest monitoring programmes. However, these data can be surprisingly hard to come by, particularly for certain regions of the world and for specific taxonomic groups, posing a real barrier to progress in these fields. To overcome this challenge, we developed the `Tallo` database, a collection of 498,838 georeferenced and taxonomically standardized records of individual trees for which stem diameter, height and/or crown radius have been measured. These data were collected at 61,856 globally distributed sites, spanning all major forested and non-forested biomes. The majority of trees in the database are identified to species (88%), and collectively `Tallo` includes data for 5163 species distributed across 1453 genera and 187 plant families. The database is publicly archived under a CC-BY 4.0 licence and can be access from: https://doi.org/10.5281/zenodo.6637599. To demonstrate its value, here we present three case studies that highlight how the `Tallo` database can be used to address a range of theoretical and applied questions in ecology—from testing the predictions of metabolic scaling theory, to exploring the limits of tree allometric plasticity along environmental gradients and modelling global variation in maximum attainable tree height. In doing so, we provide a key resource for field ecologists, remote sensing researchers and the modelling community working together to better understand the role that trees play in regulating the terrestrial carbon cycle.

KEYWORDS
allometric scaling, crown radius, forest biomass stocks, forest ecology, remote sensing, stem diameter, tree height

1 | INTRODUCTION

Trees vary enormously in the size and shape of their crowns, and accurately capturing and describing this incredible variation in tree architecture is central to numerous lines of ecological research (Verbeeck et al., 2019). For instance, data capturing the relationship between the stem diameter, height and crown radius of trees have been used to test theory linking body size and metabolism across ecological scales (Coomes et al., 2012; Enquist et al., 2009; Shenkin et al., 2020), as well as exploring the ecological, environmental and evolutionary constraints that shape allometric scaling relationships of woody plants (Banin et al., 2012; Jucker et al., 2015; Lines et al., 2012; Loubota Panzou et al., 2021). These data also underpin efforts to develop more accurate and generalizable models for estimating forest biomass stocks and their uncertainties (Chave et al., 2014; Goodman et al., 2014; Jucker et al., 2017; Ploton et al., 2016). Moreover, tree height and crown size data are increasingly being used to bridge the gap between remote sensing and traditional field ecology (Aguirre-Gutiérrez et al., 2021; Jucker et al., 2017; Marconi et al., 2021), including facilitating the integration of remote sensing data into individual-based models of forest structure and dynamics (Fischer et al., 2019, 2020; Taubert et al., 2015). However, because basic properties of tree size, such as their height and crown dimensions, are challenging and time-consuming to measure accurately on the ground, limited access to curated tree crown architectural data is often a real barrier to progress in these fields.

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Building on previous efforts to compile regional and global tree allometry databases (Falster et al., 2015; Feldpausch et al., 2011; Jucker et al., 2017; Loubota Panzou et al., 2021), here we bring together the world's largest open access collection of trees for which stem diameter, height and/or crown radius have been measured—the `Tallo` database (Figure 1). `Tallo` includes nearly 500,000 georeferenced and taxonomically standardized records from more than 5000 tree species acquired at over 60,000 sites worldwide, including data from all major terrestrial biomes and some of the world's largest ever recorded trees. After describing the key steps involved in the acquisition and standardization of the data, we showcase some of the potential applications of the `Tallo` database through a series of three case studies.

2 | COMPILING THE DATABASE

2.1 | Data aggregation

We compiled data on trees for which stem diameter (*D*, in cm), total tree height (*H*, in m) and/or crown radius (*CR*, in m) were measured. *D* was measured at breast height (1.3 m aboveground) or otherwise just above buttress roots using either diameter tape or callipers. As is common practise, for multi-stemmed trees a single pooled value of *D* was calculated by summing the diameter values of all individual stems (D_i) using the quadratic diameter: $D = \sqrt{\sum D_i^2}$ (de Souza et al., 2021; Paul et al., 2016). While care was taken to identify records from multi-stemmed individual, it is possible that for records compiled from existing databases a small number of multi-stemmed trees were mistakenly treated as separate individuals.

H and *CR*—which we mostly derived from 2 to 8 orthogonal crown radii measurements or otherwise from crown projection areas—were measured using a variety of approaches, including laser or ultrasonic range finders, clinometers, as well as tape measures and telescopic poles for smaller trees. For a very small subset of trees with fully sun-exposed crowns, *H* and *CR* were measured using a combination of high-resolution aerial photos and airborne LiDAR (Cano et al., 2019). Previous work comparing tree height measurements derived using laser range finders and clinometers—the two most common methods used to take tree biometric measurements—has shown that the two approaches provide consistent estimates, with laser rangefinders allowing for greater precision but with a tendency to slightly underestimate total tree heights (Larjavaara & Muller-Landau, 2013).

In addition to the data on tree size and shape, we also recorded the latitude and longitude of the site where each tree was measured, and any available taxonomic information. Data were obtained from a range of sources, including the published literature, online databases and unpublished data collected by co-authors of this study (see Appendix S1 in Supporting Information for a complete list of data sources). In compiling these data, we excluded records from heavily managed and industrial tree plantations, as well as agroforestry systems. Care was also taken to avoid double counting trees, which could occur either because the same data had been obtained from multiple sources or because trees were measured more than once as part of successive forest inventories. Specifically, for data obtained from public databases we made sure none had been compiled from the same primary sources. Additionally, for the small subset of trees that had been measured more than once, we only retained data from the most recent census.

2.2 | Taxonomy

Species names were cross-referenced and harmonized against those of The Plant List (TPL; http://www.theplantlist.org), using a combination of the `taxonstand` package in R (Cayuela et al., 2012; R Core Development Team, 2021) and the Taxonomic Name Resolution Service (Boyle et al., 2013). While TPL has been static since 2013, it was chosen as a reference as it remains widely used in ecology. Future versions of `Tallo` will align to the World Flora Online (http://www.worldfloraonline.org) as this becomes the new standard for plant taxonomy. Taxa that did not match TPL were reviewed manually and any misspellings or synonyms that had not been automatically detected were corrected. The small number of species for which no direct match to TPL was found (n = 43, 0.8% of the total) were checked against the Global Tree Search database (GTS; https://tools.bgci.org/global_tree_search.php), a curated list of over 60,000 plant species that meet the IUCN's Global Tree Specialist Group definition of a tree. In all, 11 species (0.2% of the total) did not match either TPL or GTS, but because all of these could be traced back to published records online, we retained them in the database. Finally, genus names were used to assign each tree to its family and group trees into major divisions of vascular plants (i.e. angiosperms and gymnosperms) following the classification of Kew Royal Botanic Gardens (http://data.kew.org/vpfg1992/genfile.html).

Having standardized taxonomic names, we then removed any records from species that did not meet our working definition of trees—perennial woody seed plants with a single dominant stem, that are self-supporting and undergo secondary growth. This included removing all ferns, palms, lianas, strangler figs, bamboos, pandans, as well as a number of shrub species that rarely exceed 2 m in height and are generally multi-stemmed.

2.3 | Geographical coordinates

Each tree in the database is associated with a set of geographical coordinates, recorded in decimal degrees of latitude and longitude. These range in precision between 1 and 3 decimal places (approximately 0.1–11 km at the equator), with the majority of trees geolocated with a precision of ≤1 km. To facilitate the integration of the `Tallo` database with other large-scale spatial datasets, we used the `CoordinateCleaner` package in R to flag and correct common issues known to affect georeferenced records obtained from online databases (Zizka et al., 2019).

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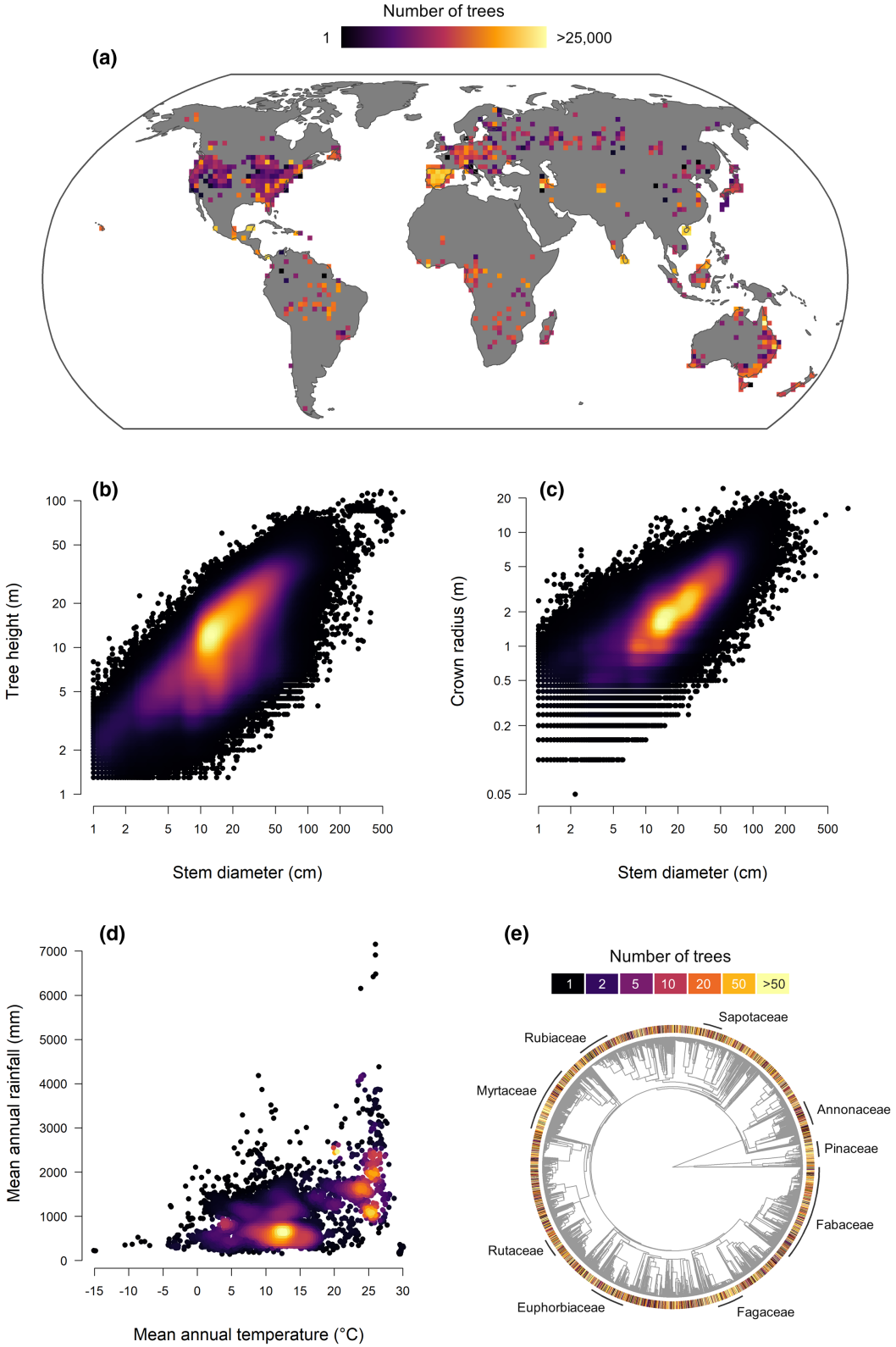


FIGURE 1 Overview of the `Tallo` database, including (a) geographical coverage, (b–c) size range of sampled trees, (d) climatic range of the data and (e) taxonomic coverage in phylogenetic space. Panel (a) shows the total number of trees recorded in grid cells of approximately 200 × 200 km. In (b–d), the density of overlapping points is reflected by a colour gradient ranging from black (low point density) to yellow (high point density). Data on mean annual rainfall and temperature show in (d) were obtained from WorldClim2 database (Fick & Hijmans, 2017) at a spatial resolution of 30 arc-seconds (approximately 1 km). Panel (e) shows a phylogenetic tree constructed from all species in the `Tallo` database (n = 5163). Branch tips have been colour coded to reflect the number of trees sampled for each species and the position of several seed plant families on the tree has been labelled. The phylogenetic tree was generated using the `V.PhyloMaker` package in R (Jin & Qian, 2019), the backbone of which is a phylogeny of 79,881 taxa of seed plants developed by Smith and Brown (2018).

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First, we checked for any coordinates that were either invalid or had zero values for longitude or latitude. Data from two locations with a longitude of zero were retained after being checked against primary sources. Next, we checked for coordinates that did not fall on land by overlaying them onto a map of the world's coastlines obtained from the Natural Earth database at 1:10, 1:50 and 1:110 million scales (https://www.naturalearthdata.com). A small number of locations ($n = 13$ sites, 0.02% of the total) were located at sea at all three scales. These records were all from the Balearic Islands in Spain and were manually corrected to the nearest land point using the 1:10 million scale map as a reference. Lastly, we also checked that all coordinates aligned to high-resolution (30 arc-seconds, approximately 1 km) gridded climate data from the WorldClim2 database (Fick & Hijmans, 2017).

2.4 | Data quality control

As a quality control measure, we first removed any trees recorded as dead or damaged and then filtered the database to exclude trees with $D < 1$ cm and $H < 1.3$ m. We then used Mahalanobis distance as implemented in the `OutlierDetection` package in R to identify trees with unrealistically large or small *H* and *CR* values given the size of their trunk, their biome association and their functional group (see Appendix S2 for details). These outliers could be the result of a data entry error (e.g. shift in decimal place or mistaken conversion between m, cm and mm) or possibly reflect a tree with substantial damage to its crown which went unrecorded. In total, 508 trees were identified as outliers based on *H* (Figure S1) and a further 490 based on *CR* (Figure S2). These records were retained in the `Tallo` database but flagged as outliers, allowing them to be easily removed by users depending on the application.

3 | DATABASE OVERVIEW AND ACCESS

The `Tallo` database includes a total of 498,838 trees from 61,856 unique sites across the world for which *D*, *H* and/or *CR* have been measured (Figure 1a), including 311,326 trees where all three dimensions are recorded. These represent all major forested and non-forested biomes (Table 1) and cover a gradient of over 45°C in mean annual temperature and more than 7000 mm in annual rainfall (Figure 1d). Trees in the database span multiple orders of magnitude in size (Figure 1b–c and Table 1), with *D* ranging from 1.0 to 770.0 cm, *H* from 1.3 to 115.8 m and *CR* from 0.05 to 24.25 m. The majority of trees (88%) are identified to species, and overall the `Tallo` database includes records for 5163 species, 1453 genera and 187 plant families (Figure 1e).

The version of the `Tallo` database described in this article is publicly archived on Zenodo under a CC-BY 4.0 licence so that it can be freely used, shared and modified so long as appropriate credit is given (https://doi.org/10.5281/zenodo.6637599). Major version updates will be periodically uploaded to Zenodo, in addition to which we will also maintain an up-to-date version of the database on GitHub (https://github.com/selva-lab-repo/TALLO). `Tallo` should be referenced by citing this paper and users are also encouraged to report the version of the database they have accessed and to cite the original data sources whenever possible. The database is stored as a csv file which contains the individual tree morphological data, the geographical coordinates of each tree, any available taxonomic information, an identifier flagging any records classified as outliers and a reference code linking to the source from which records were obtained. A look-up table with full bibliographical sources is provided separately in Table S1 and as a csv file on the GitHub repository. Additionally, metadata files with a detailed description of each field in `Tallo` database can also be found on GitHub.

4 | CASE STUDIES

To showcase a few of the possible applications of the `Tallo` database, we developed three case studies that explore a range of theoretical and applied questions in ecology related to tree allometry. To enable users to replicate and build on these examples, all R code and ancillary environmental data used in the case studies have been archived on the GitHub repository.

TABLE 1 Breakdown of the `Tallo` database by biome, including number of tree records and species, as well as the median and range of stem diameter (*D*, in cm), tree height (*H*, in m) and crown radius (*CR*, in m) values. Biome classifications follow those of Olson et al. (2001), with boreal and montane biomes grouped together

Biome	N° trees	N° species	*D* (in cm)	*H* (in m)	*CR* (in m)
Tropical rain forests	179,175	3547	13.5 [1–475.3]	12.5 [1.3–100.8]	1.5 [0.05–24.25]
Tropical dry forests	30,117	526	6.6 [1–175.0]	6.0 [1.3–65]	1.25 [0.05–21.0]
Temperate broadleaf forests	126,517	781	16.3 [1–652.0]	11.0 [1.3–99.7]	2.0 [0.05–17.5]
Temperate conifer forests	26,849	208	15.2 [1–770.0]	11.1 [1.3–115.8]	1.7 [0.05–16.25]
Boreal & montane forests	21,631	37	17.0 [1–181.0]	12.9 [1.3–76]	1.35 [0.05–5.1]
Mediterranean woodlands	80,882	140	21.4 [1–403.0]	7.5 [1.4–76.7]	2.0 [0.25–16]
Tropical savannas	22,818	587	12.9 [1–251.0]	8.7 [1.3–66.2]	1.5 [0.1–22.05]
Temperate grasslands	9572	126	11.1 [1–117.0]	8.4 [1.3–48.6]	1.2 [0.05–9.6]
Drylands	538	17	9.3 [1–40.3]	2.8 [1.3–10.7]	1.5 [0.4–4.95]
Mangroves	739	3	13.2 [1–103.3]	10.0 [1.3–32.2]	1.5 [0.2–7.4]

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4.1 | Case study 1: Testing the predictions of metabolic scaling theory across biomes and functional groups

Metabolic scaling theory (MST) makes a number of predictions about how different axes of tree size should scale against one another based on first principles of plant water transport, branching architecture and stem biomechanics (Anderson-Teixeira et al., 2015; Shenkin et al., 2020; West et al., 2009). Specifically, both *H* and *CR* are expected to be proportional to the $\frac{2}{3}$ power of *D* (i.e. $H \propto D^{\frac{2}{3}}$ and $CR \propto D^{\frac{2}{3}}$), while *CR* is assumed to scale isometrically with *H* (i.e. $CR \propto H^{1}$). However, there is substantial evidence that real-world scaling relationships can depart substantially and systematically from the theoretical predictions of MST due to the environmental context in which a tree is growing (e.g. water availability, competition for light, browsing, disturbance regime), as well as its evolutionary history (Jucker et al., 2017; Lines et al., 2012; Moncrieff et al., 2011; Muller-Landau et al., 2006; Shenkin et al., 2020).

Using `Tallo`, we tested whether crown allometric scaling relationships can be reconciled with the predictions of MST or if instead they vary systematically and predictably among major plant lineages (i.e. angiosperms and gymnosperms) and biome types. We modelled *H*–*D*, *CR*–*D* and *CR*–*H* scaling relationships using a power-law function by fitting linear mixed-effects regressions to log–log transformed data and allowing both the normalization constant (intercept) and scaling exponent (slope) to vary among biomes for both angiosperm and gymnosperm lineages. Models were fit using the `lme4` package in R and took the following general form:

```
lmer(log(Y) ~ log(X) + (log(X)|Biome:Lineage))
```

Additionally, we also tested whether biome-level scaling exponents varied in relation to the degree of aridity experienced by trees within a biome, quantified as the ratio between mean annual precipitation and potential evapotranspiration. Aridity data for this analysis were obtained at 30-arc second resolution from the Global Aridity Index and PET Database (Trabucco & Zomer, 2019) and matched to each tree based on its geographical coordinates.

We found that agreement with MST varied considerably among the two plant lineages and biomes, as well as the allometric relationship being examined (Figure 2). Overall, observed *H*–*D* scaling exponents were lower than the $\frac{2}{3}$ predicted by MST (exponent estimate ±95% confidence intervals = 0.581±0.068). This was especially true for angiosperm trees, whose *H*–*D* scaling exponents were on average substantially lower than those of gymnosperms across biomes (0.537 and 0.637, respectively). However, for both lineages departure from MST was most pronounced in arid biomes, whereas *H*–*D* scaling exponents of trees growing in non-water limited ecosystems such as tropical and temperate forests were consistent with the predictions of MST (Figure 2a). This trend was reflected in a significantly positive correlation between a biome's *H*–*D* scaling exponent and the mean aridity index experience by trees with that biome (Pearson's correlation coefficient, $\rho = 0.56$, $p = .017$).

A similar picture emerged for *CR*–*D*, where once again observed scaling exponents were on average lower than those predicted by MST (Figure 2b), although in this case 95% confidence intervals of the parameter estimate overlapped with $\frac{2}{3}$ (0.620±0.062). On average, gymnosperms had higher *CR*–*D* scaling exponents than angiosperms (0.648 and 0.597, respectively) and trees growing in drylands had *CR*–*D* scaling exponents that were furthest from those predicted by MST (although in this case the correlation with aridity was not statistically significant; $\rho = 0.35$, $p = .15$). By contrast, *CR*–*H* scaling relationships showed a much bigger departure from MST predictions, with an overall scaling exponent well below 1 (0.695±0.077). This was true for both angiosperms and gymnosperms (0.708 and 0.676 on average,

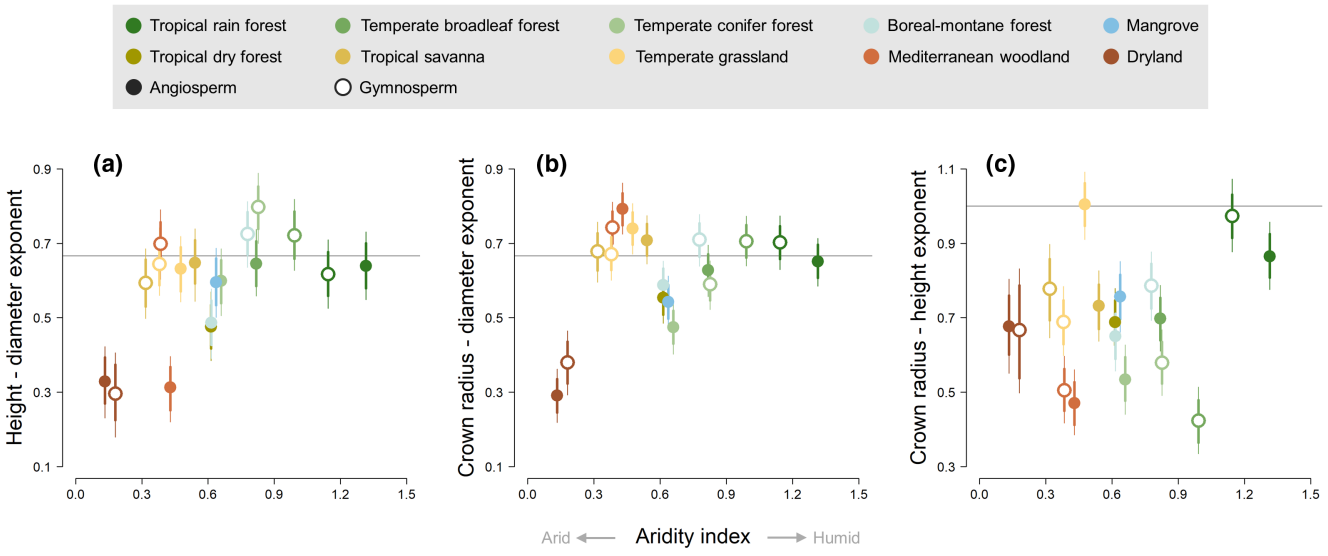


FIGURE 2 Variation in height–diameter (a), crown radius–diameter (b) and crown radius–height (c) scaling exponents of angiosperm (filled circles) and gymnosperm (empty circle) trees growing in different biome types arranged according to their aridity index. Error bars denote both the 80% (thick lines) and the 95% confidence intervals (thin lines) of the parameter estimates. Grey horizonal lines indicate scaling exponents predicted by metabolic scaling theory. Biome classification follows that of Olson et al. (2001), while aridity was calculated as the ratio between mean annual precipitation and potential evapotranspiration and therefore ranges from arid at low values of the index to humid at higher values.

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respectively) and was broadly consistent across biomes (Figure 2c). In fact, while we did observe a couple of groups for which *CR–H* scaling exponents match MST predictions (e.g. angiosperm trees in the temperate grassland biome and gymnosperm trees in tropical rain forests), no clear relationship emerged between a biome's *CR–H* scaling exponent and its degree of aridity ($\rho = 0.22$, $p = .38$).

Overall, our analysis indicates that tree crown allometries only conform to MST under certain environmental conditions and tend to do so more for gymnosperms than angiosperms. Moreover, while *CR–D* relationships were found to be consistent with MST across most biomes, they did so despite clear deviations of *CR–H* relationships from which the former are derived (Shenkin et al., 2020). This suggests that while MST may serve as a useful starting point for understanding scaling relationships between different axes of tree size, at least some of its underlying assumptions need to be revisited.

4.2 | Case study 2: Plasticity in height–diameter scaling relationships along aridity gradients

Trees adapt their size and shape to match the environment in which they grow (Jucker et al., 2015; Kafuti et al., 2022; Lines et al., 2012). A classic example is the fact that trees tend to be shorter for a given stem diameter in drier environments (Chave et al., 2014; Hulshof et al., 2015; Jucker et al., 2017; Lines et al., 2012; Vieilledent et al., 2012), as taller trees are generally at greater risk of hydraulic failure due to embolism and this effect is exacerbated when access to water becomes progressively more limiting (Domec et al., 2008; McDowell & Allen, 2015; Olson et al., 2018; Stovall et al., 2019). However, it remains unclear to what extent the negative relationship between tree height and aridity is driven by turnover in species composition along environmental gradients (i.e. species with shallower *H–D* scaling relationships dominating arid environments and vice versa) as opposed to plasticity and local adaptation within species (Lines et al., 2012).

To answer this question, we selected a subset of species in the `Tallo` database that had been sampled at multiple sites spanning a gradient in aridity (defined and quantified in the same way as the previous case study). Specifically, we only included records for species that (i) were found at two or more distinct sites with at least 10 individual trees sampled at each site, (ii) were recorded at locations with at least a 20% difference in aridity index between their most arid and humid site and (iii) spanned a size range of at least 20 cm in stem diameter. This left us with 155,002 trees belonging to 342 species (303 angiosperms and 39 gymnosperms). Using these data, we tested how *H–D* relationships (modelled on a log–log scale) vary along aridity gradients in relation to both species turnover and within-species plasticity by fitting the following linear mixed-effects model in the `lme4` package in R:

$$\text{lmer}(\log(H) \sim \log(D) + AI_{SP} + AI_{GMC} + (\log(D) + AI_{GMC}|\text{Species}))$$

where AI_{SP} is the mean aridity index value of each species and AI_{GMC} is the group-mean centred aridity index value of each tree (calculated as the difference between each tree's aridity index value and AI_{SP}, the mean value of its species). The AI_{SP} term in the model tests whether tree species found in more arid environments tend to be shorter, for a given stem diameter, than those from more humid regions. Instead, AI_{GMC} tests whether individuals within a species growing at the arid-end of at their distribution (where $AI_{GMC} < 0$) are shorter than those at the humid-end (where $AI_{GMC} > 0$). The effects of both `log(D)` and AI_{GMC} on `log(H)` were allowed to vary among species (i.e. random intercept and slopes model) and a permutation approach was used to generate 95% confidence intervals for the random slope terms of the model. This allowed us to determine which tree species exhibited significantly negative or positive shifts in height in response to rising aridity.

We found that aridity plays a key role in modulating the relationship between tree height and stem diameter, with trees growing in more arid environments generally much stouter than those from more humid climates (Figure 3). For example, a 30 cm diameter tree growing in a location where mean annual rainfall is only half of potential evapotranspiration (aridity index = 0.5) is on average 9.7 m shorter (−42%) than one growing where annual rainfall is double the evaporative demand (aridity index = 2). Standardized model coefficients for AI_{SP} (0.145 ± 0.026) and AI_{GMC} (0.085 ± 0.021) were both significantly positive ($p < .0001$). This indicates that the strong effect of aridity on *H–D* scaling relationships is driven by a combination of both species turnover and intraspecific plasticity across aridity gradients, with the former playing a particularly important role.

While we found that decreasing aridity generally led to trees becoming more slender, this effect varied considerably among species. Most species (n = 241, 70% of the total) tended to be taller at the humid end of their sampled distribution, with 44% exhibiting a significantly positive increase in height with decreasing aridity (i.e. lower bounds of the 95% confidence intervals of the random AI_{GMC} slope > 0; blue arrows in Figure 3). However, we also observed a smaller proportion of species that exhibited the opposite trend (n = 38, 11% of the total; red arrows in Figure 3). In relative terms, these were more likely to be gymnosperms (26% of species) than angiosperms (9% of species). Moreover, we found that species adapted to drier environments were generally more likely to respond positively to increased water availability in terms of investment in height growth compared to those from more humid climates ($\rho = -0.18$, $p = .0006$ when relating a species' random AI_{GMC} slope estimate to its AI_{SP}). Overall, our results confirm the importance of water availability in shaping *H–D* scaling relationships in trees and shed new light on the role that both species turnover and intraspecific plasticity play in driving these patterns.

4.3 | Case study 3: Global maps of potential tree height under current and future climates

Large, tall trees play a disproportionately big role in shaping carbon cycling on land, as they store the vast majority of the aboveground biomass in a given patch of forest (Bastin et al., 2018; Lutz et al., 2018; Slik

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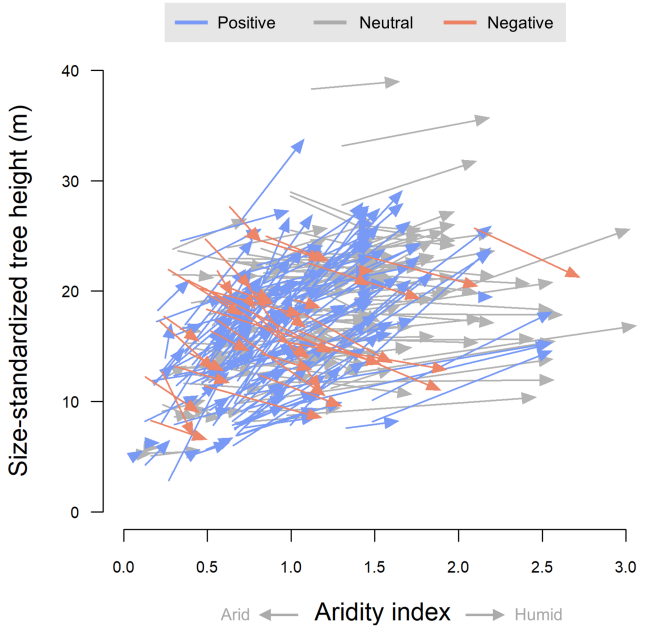


FIGURE 3 Variation in the height of a tree with a stem diameter of 30 cm ($H_{D=30cm}$) across a gradient of aridity. Each arrow corresponds to one of 342 species, with the beginning and end of the arrow indicating the species' predicted $H_{D=30cm}$ at the arid and humid end of its sampled distribution, respectively. Blue arrows denote species for which $H_{D=30cm}$ increased significantly as aridity decreased ($n = 147$), while those in red showed the opposite trend ($n = 37$). Aridity was calculated as the ratio between mean annual precipitation and potential evapotranspiration and ranges from arid at low values of the index to humid at higher values.

et al., 2013). Tree height is also a key axis of habitat structural complexity and plays a major role in determining habitat diversity and the buffering effect that forest canopies exert on local microclimates (Atkins et al., 2022; de Frenne et al., 2021; Jucker, Bongalov, et al., 2018; Jucker, Hardwick, et al., 2018). However, tall trees are predicted to be among the most vulnerable to climate change, as they are particularly prone to hydraulic stress (Bennett et al., 2015; McDowell & Allen, 2015; Olson et al., 2018; Stovall et al., 2019), making it critical to identify the environmental conditions under which tall trees can thrive. Most efforts to tackle this challenge have used global or regional maps of forest canopy height derived from remote sensing as a starting point and then worked backward to infer the environmental drivers that shape the distribution of tall forests (Gorgens et al., 2021; Scheffer et al., 2018; Zhang et al., 2016). But an alternative bottom-up approach to answering this question is to build an allometric model that predicts a tree's potential height anywhere in the world based on current-day and future environmental conditions (Chave et al., 2014).

To trial this approach, we used the entire `Tallo` database to fit a multiple regression model in which we expressed tree height (`log(H)`; log-transformed) as a function of stem diameter (`log(D)`; log-transformed), aridity index (`log[AI]`; log-transformed), precipitation seasonality (P_{SEASON}), mean annual temperature (T_{MEAN}), maximum annual temperature (T_{MAX}), and the interaction between `AI` and T_{MEAN}:

$$\text{lm}(\log(H) \sim \log(D) + \log(AI) + P_{SEASON} + T_{MEAN} + T_{MAX} + \log(AI):T_{MEAN})$$

Climate data were obtained at 30-arc second resolution and assigned to each tree based on their geographical coordinates. `AI` values were taken from the Global Aridity Index and PET Database, while all other climatic predictors were obtained from WorldClim2 (Fick & Hijmans, 2017). As our aim was to provide a proof of concept, climatic predictors were selected based on those identified by previous studies as playing a role in modifying *H–D* scaling relationships (Chave et al., 2014; Hulshof et al., 2015; Lines et al., 2012), rather than through an extensive model selection process.

The fitted model was used to generate spatially explicit predictions of tree height at global scale under both current and future climate scenarios at 5-arc minute spatial resolution (approximately 10 km) obtained from WordClim2. Rather than using a single size threshold for defining 'large trees' across all ecosystem types, predictions were made using the 99th percentile stem diameter value of trees from each biome class in the `Tallo` database. These ranged from 33 cm in drylands to 95 cm in tropical rainforests. To explore how climate change might affect the distribution of tall trees, we used CMIP6 future climate projections for the period of 2061–2080 derived from the CNRM-ESM2-1 global climate model run under the shared socio-economic pathway (SSP) 245 (equivalent to RCP 4.5). To simplify the analysis, stem diameter values used to define 'large trees' for each biome type were kept the same under both current and future climate scenarios. As such, any changes in tree height predicted by the model will result entirely from changes in *H–D* scaling relationships along climatic gradients. Given that in many ecosystems tree size distributions are predicted to shift towards smaller-sized individuals under climate change (McDowell et al., 2020), any predicted declines in tree height may therefore be conservative. However, it is also important to note that our model predictions do not account for the effects of rising atmospheric CO_2 on plant water use efficiency, which may offset some of the impacts of rising aridity on tree hydraulic function under global warming (Rifai et al., 2022).

Maps of potential tree height capture major transitions in ecosystem types (Figure 4a), with projected heights of large trees ranging between 4.7 and 69.4 m. Model predictions also capture several known hotspots of tall forests, such as those of Borneo and Southeast Asia (Banin et al., 2012; Jucker, Bongalov, et al., 2018 as well as temperate rainforests in Australia, New Zealand, the western coast of the United States, Chile and Norway (Scheffer et al., 2018). However, other regional trends in forest height are less well replicated. For instance, the map does not capture known east-to-west gradients in canopy height across the Amazon basin, highlighting how other drivers aside from climate—such as soils, wind, fire and herbivory—can play a key role in shaping geographical variation in forest vertical structure (Gorgens et al., 2021; Jucker, Bongalov, et al., 2018; Moncrieff et al., 2011).

In terms of projected changes in tree height in response to climate change, the height of large-diameter trees is expected

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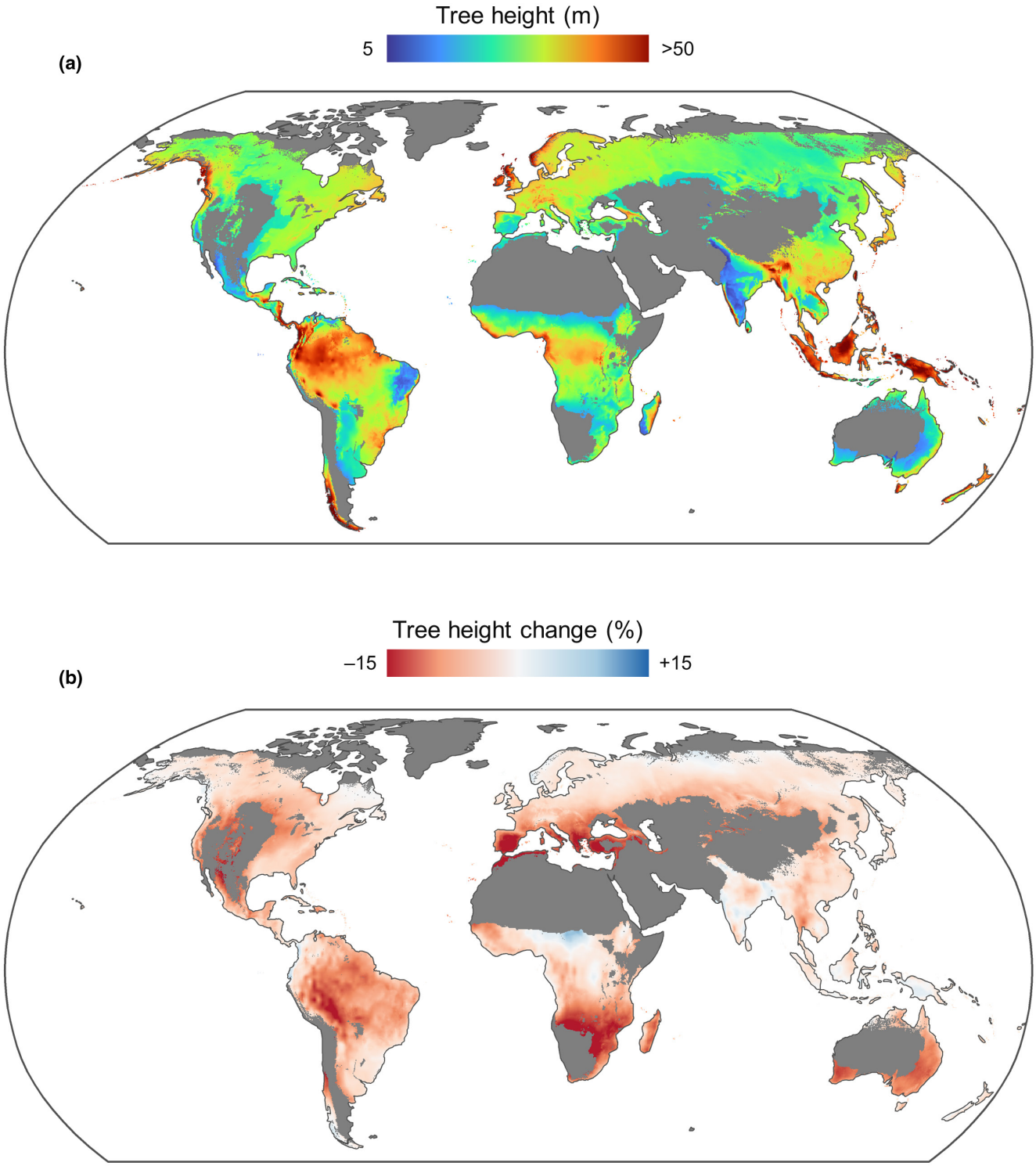


FIGURE 4 Global variation in the predicted height of large trees under current-day climate (a) and projected relative changes in height under a future climate scenario (b). For each biome, the size threshold for 'large trees' was defined as the 99th percentile stem diameter value of trees in the `Tallo` database. Both current-day and future climate data were obtained from the WorldClim2 database at 5-minute resolution (Fick & Hijmans, 2017). CMIP6 future climate projections are for the period of 2061–2080 and were derived from the CNRM-ESM2-1 global climate model run under the shared socio-economic pathway (SSP) 245. A map of potential forest cover (https://data.globalforestwatch.org/documents/potential-forest-coverage) was used to mask out areas deemed climatically unsuitable to support forests and woodlands, which are shown in dark grey.

to decrease by an average of 5.4% globally when CO_2 fertilization is not taken into account. However, projected changes varied substantially among biomes and biogeographical regions (Figure 4b), ranging anywhere between −20.1% and +18.8%. Trees in Mediterranean woodlands are predicted to show the strongest decreases in height, with an average projected height

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loss of 12.5%. Tropical rain forest trees are also expected to decrease in height by 5.6% on average, but this trend is much more pronounced across Amazonia and the Neotropics (−7.9%) and Africa (−4.9%) compared to Southeast Asia (−3.0%) and Australasia (−0.8%). By contrast, high-latitude forests in the northern hemisphere are predicted to increase in height as the climate warms (Figure 4b). Overall, the Tallo database provides a new way to explore how global patterns of forest canopy structure can be reconciled with the processes that constrain the allometry of individual trees. For instance, model predictions could be compared to canopy height maps derived from remote sensing to identify areas of agreement and discrepancy between the two, providing new clues on the processes that shape variation in tree height across the world's forests. Moreover, spatially explicit maps of potential tree height generated in this way could also be used to benchmark the outputs of dynamic global vegetation models.

5 | FUTURE DEVELOPMENTS

Looking ahead, we intend to continue curating and expanding the scope and scale of the Tallo database. In addition to increasing the geographical and taxonomic coverage of the database, we also plan to source new data capturing additional axes of crown size. In particular, we aim to incorporate data on crown depth for as many trees as possible. In addition to being interesting in its own right (Shenkin et al., 2020; Vermeulen, 2014), information on crown depth would allow users to calculate more realistic estimates of crown surface area and volume (Jucker et al., 2015; Loubota Panzou et al., 2021; Shenkin et al., 2020). Additionally, we also plan to augment the database by adding information on local competitive environment (e.g. stand basal area, tree density or cover), as it is well known that tree crown architecture is strongly influenced by competition for light with neighbouring trees (Jucker et al., 2015; Lines et al., 2012; Purves et al., 2007). As part of these efforts, we will also look to expand Tallo beyond its initial focus on seed plants with a single self-supporting dominant stem that undergoes secondary growth—better capturing multi-stemmed trees, as well as other life forms such as shrubs, tree ferns, palms and climbers.

Finally, as the database expands, we also plan to begin incorporating more data on crown dimensions and tree height derived from remote sensing platforms such as airborne and terrestrial laser scanning and structure-from-motion UAV photogrammetry. These emerging technologies allow for much more accurate and comprehensive measurements of different crown attributes (Disney, 2019), as well as capturing data on the crown dimensions of large, canopy dominant trees which tend to be disproportionately underrepresented in traditional field-based surveys (Fischer et al., 2019; Marconi et al., 2021). To this end, we strongly encourage users to help us improve the Tallo database by not only reporting any errors they may come across, but also contributing their own data to future releases.

AUTHORS' CONTRIBUTIONS

T.J. conceived the idea for the Tallo database and led the aggregation of the data with the assistance of J.Ch., D.A.C., J.Ca., A.A., G.J.L.P., T.R.F., D.F. and V.A.U. and all co-authors contributed to the data. T.J. performed the analyses with the assistance of F.J.F. T.J. wrote the first draft of the manuscript, with all authors providing editorial input.

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DATA AVAILABILITY STATEMENT

The version of the `Tallo` database described in this paper is permanently archived on Zenodo (https://doi.org/10.5281/zenodo.6637599) and an updated version of `Tallo` is also maintained on GitHub (https://github.com/selva-lab-repo/TALLO). Both repositories contain a metadata file describing each field of the `Tallo` database and a look-up table with the full list of bibliographical sources from which records were obtained. R code and ancillary data needed to replicate the three case studies presented in this paper can be found on the GitHub repository.

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