# Root biomass allocation in southern temperate forests

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## A R T I C L E   I N F O

## A B S T R A C T

Accurate quantification of total forest biomass requires sound estimates of root biomass. Because roots are challenging to measure *in situ*, data are sparse, and this has limited our understanding of root allocation across a range of forest types. Increased sampling in the oceanic and cool temperate forests of the southern hemisphere means we are now able to better understand biomass allocation in this biome. Here we compile and systematically review root:shoot ratios for these forests and examine the taxonomic, regional, and environmental determinants of variability in biomass allocation to roots. Specifically, we assess whether limited access to resources resulting from low temperatures or low rainfall:temperature ratios increases root allocation. A literature and database search identified 441 root:shoot records from 25 studies and 32 locations around the South Pacific. Records were weighted by excavated area as a measure of sampling effort. Root:shoot ratios for eucalypts in southeast Australia (0.277) and southern beech in South America (0.275) were 6–7% above the global mean of 0.26, while southern beech (0.233) and other dicots (0.234) in New Zealand were consistent with values reported for temperate (mostly northern hemisphere) broadleaved forests. Low root:shoot ratios (of trees $\geq 5$ cm stem diameter) relative to the global mean were noted for South American gymnosperms (0.219), seemingly driven by low values in the Cupressaceae, and New Zealand tree ferns (0.194). Size effects were taxon dependent, with a marked decline in root:shoot ratios with increasing stem size for the southern beech in South America and modest effects for other combinations of taxa and region. A clear signal of increasing root allocation with declining rainfall:temperature ratios was detected, but no major effects of temperature were noted within the range of the data. Our findings support current approaches to biomass and carbon estimation but leave room for refinement, with specific recommendations given for the New Zealand context.

## 1. Introduction

Determining and forecasting the influence of forests on atmospheric $CO_2$ requires reliable measures of total forest carbon. Temperate forests store vast amounts of carbon, but the destructive and laborious nature of measuring forest biomass makes it unfeasible to undertake direct measurements at scale. We rely instead on allometric models that relate harvested samples of trees or stands to non-destructive biometric measurements, such as stem diameter. Allometric models then allow biomass estimation where only biometric measurements are made. This estimation process introduces uncertainty through model error, and integrated assessments of uncertainty sources have found that model error can, in some instances, be a substantial source of overall uncertainty when estimating forest stand biomass (Chave et al., 2004; Holdaway et al., 2014). Reducing model error is thus key to improving biomass estimates, and this can be achieved by ensuring that the samples underpinning allometric models are representative of the context where estimations are to be made, and that environmental, biogeographic, and floristic components are represented adequately, as well as tree size and life-form (Clark and Kellner, 2012; Roxburgh et al., 2015).

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Tree roots comprise a significant fraction of total forest biomass, and can represent a greater-than-expected carbon store (Robinson, 2007). Despite some progress in synthesizing and interpreting root biomass allocation in forests (Karizumi, 1974; Jackson et al., 1996; Cairns et al., 1997; Poorter et al., 2012), the wide variation in measurements of root biomass allocation has hindered reliable estimates of forest carbon stocks (Cairns et al., 1997). In a comprehensive global synthesis, Mokany et al. (2006) expanded on previous data compilations and examined variation in stand-level root:shoot biomass ratios along various environmental gradients (rainfall, temperature, latitude, potential evapotranspiration, soil texture) and forest development gradients (e.g. forest stand age and height). While their study improved the accuracy of existing root:shoot ratios by providing estimates for different forest biomes, data limitations meant that not all forests could be represented equally. For example, root:shoot ratios of temperate forests were obtained largely from northern latitudes.

Although less extensive than their northern counterpart, temperate forests in the southern hemisphere cover large areas and comprise some of the tallest trees and most carbon-dense forests on record (e.g. Keith et al., 2009; Urrutia-Jalabert et al., 2015). These temperate forests also have marked floristic and physiognomic differences from those in the northern hemisphere. The vast southern oceans exert a major influence in moderating land climates, so that a large fraction of forested lands in the higher mid-latitudes of the southern hemisphere have oceanic climates (McGlone et al., 2012). Mild temperatures and wet-to-mesic conditions often favour evergreen canopies (with exceptions in South America), and tall, emergent trees are characteristic, alongside distinctive rainforest elements such as vines, lianas, and tree ferns (Grubb et al., 2013; McGlone et al., 2016). Tree ferns, although individually small, can be locally abundant and often comprise a significant portion of forest biomass, particularly in New Zealand and Tasmania (Garrett, 1996; Brock et al., 2016). Soils have low pH at latitudes of 40–50°S relative to northern equivalents (Pärtel, 2002), with potential significance for root partitioning since low pH limits accessibility to soil nutrients (Härdtle et al., 2004). Geographic and evolutionary isolation have also led to distinctive biotas across the different land masses of the southern hemisphere (e.g. Kelly and Sullivan, 2010), with New Zealand sharing only 28% and 25% of woody genera with southeastern Australia and Chile, respectively, and southeastern Australia sharing an even lower 9% with Chile (McGlone et al., 2016). Notable floristic differences around the southern hemisphere are the radiation and dominance of the eucalypts in Australia and of tall podocarps in New Zealand, with some presence of the latter in South America (Ovington, 1983). The effects of these floristic differences on biomass partitioning have yet to be examined.

Here, we conduct a systematic review of root:shoot ratios for southern hemisphere temperate forests to better understand below-ground allocation and the influence of multiple drivers on variability in root:shoot ratios. Our review primarily seeks to determine whether values of root:shoot allocation given by global and biome-specific studies (e.g., Cairns et al., 1997; Mokany et al., 2006) are adequate for temperate forests in the southern hemisphere, and to inform adjustments where necessary. Further, we also examine how root:shoot ratios vary across broad taxonomic groups and biogeographic areas of the south-temperate zone and then assess their response to environmental variables while accounting for tree-size effects. In testing for environmental influences, we build on the 'functional equilibrium' theory (Brouwer, 1963; Poorter et al., 2012) that biomass allocation to plant organs is influenced by the availability of the most limiting resource. Specifically, we test whether the effects of water limitation (e.g., Mokany et al., 2006; Ledo et al., 2018) and/or low temperatures (Reich et al., 2014), reported to influence root:shoot ratios globally, are manifest within southern temperate forests. We focus on oceanic temperate forests of the southern hemisphere (*sensu* McGlone et al., 2016) and the extension of cooler temperate forests further south (here jointly referred to as 'southern temperate forests'). In doing so, we contribute

towards expanding the range of vegetation types and conditions with below-ground biomass allocation data (Weiskittel et al., 2015).

## 2. Methods

### 2.1. Bioclimatic domain

Our review encompasses oceanic and cool temperate forests around the southern Pacific. A unifying climatic feature of oceanic temperate forests is the weak seasonality owing to the moderating influence of oceanic masses: winters are warm (June–August mean > 5 °C), summers cool (December–February mean < 20 °C), and there is no regular dry season, with precipitation in the driest month often over 35 mm (McGlone et al., 2012, 2016). Cool temperate forests are best recognised by cold winters (mean < 5 °C), but summers are mild (means typically < 15 °C) (McGlone et al., 2012). Combined, these conditions are found from about 26°S in eastern Australia and 38°S in Chile, to 55°S in southern Chile, encompassing much of Tasmania and most of New Zealand (McGlone et al., 2016). Longitudinal boundaries are given by drier conditions towards inland Australia and across the Andes into the Patagonian steppe in South America.

Physiognomically, oceanic temperate forests are characterized by evergreen tree canopies 15–45 m tall, represented commonly by species with microphyllic leaves and by the presence of climbers and epiphytes (McGlone et al., 2016). Floristic differences are more marked. Broadly, oceanic temperate forests largely match definitions of 'warm temperate rainforests' (Grubb et al., 2013) but encompass somewhat broader climatic envelopes and geographic distributions. Towards their southern boundary and montane areas, the mixed-species oceanic temperate forests transition into cool temperate forests largely dominated by nanophyllic Nothofagaceae, and they are characterized by a single canopy layer and with rarer occurrence of lianas, epiphytes, and tree ferns (McGlone et al., 2016). In southeastern Australia, oceanic temperate forests are predominantly wet and dry sclerophyll forests dominated by fire-adapted *Eucalyptus* species, with extensive areas of cool temperate rainforest dominated by *Nothofagus* species in Tasmania (Keith, 2017). Comparable temperate oceanic forests are also found in South Africa, such as the southern Cape Afrotemperate forest, but these are not included in our study as no root harvest data could be identified for trees indigenous to that region.

### 2.2. Literature search

A recent review has comprehensively compiled and examined the below-ground allometries of woody vegetation across ecological regions of Australia (Paul et al., 2019). Our study builds on a component of that work, the oceanic and cool temperate forests of southeastern Australia and Tasmania, and incorporates records from climatically comparable forests from New Zealand and southern South America. We searched the Web of Knowledge for published below-ground biomass records with the terms "forest(s)" and any of the phrases "below-ground biomass", "below-ground carbon", "root biomass" and "root carbon". We then narrowed the outputs to southern regions with oceanic temperate climates (Australia, New Zealand, South Africa, Chile and Argentina). We also narrowed the initial search outputs by genera (*Nothofagus, Lophozonia, Fuscospora, Weinmannia, Dacrydium, Beilschmiedia, Metrosideros, Kunzea*, and *Prumnopitys*) and plant families (Nothofagaceae, Cunoniaceae, Podocarpaceae, Lauraceae and Myrtaceae) for the 10 species that make up the greater part of woody biomass in natural forests of New Zealand (Peltzer and Payton, 2006). In addition to genera shared between New Zealand and Chile (i.e., *Nothofagus, Lophozonia, Fuscospora, Weinmannia*), we also searched for genera that are dominant in Valdivian evergreen forest, either due to high basal area or to high stem numbers (Donoso, 1989): *Drimys, Laurelia, Eucryphia, Aextoxicon, Persea, Saxegothaea, Podocarpus, Amomyrtus*. Given their distinctive architecture and prevalence in New Zealand and Australian

forests, we also searched for the two main tree fern genera, *Cyathea* and *Dicksonia*, the locally abundant New Zealand palm, *Rhopalostylis*, and other monocotyledon trees (e.g. *Cordyline*).

In addition to the above, we searched two large electronic databases of partitioned plant biomass for a broad spectrum of plant/tree taxa (Niklas and Enquist, 2004; Mokany et al., 2006) and identified studies from southern hemisphere temperate forests or comprising taxa that are present or closely related to them. A significant volume of these database records originates from earlier worldwide reviews of forest biomass (Cannell, 1982) and root biomass allocation (Cairns et al., 1997). Finally, we examined the review of Phillips and Watson (1994) and searched for studies citing Cairns et al. (1997), concentrating on studies published within the last 5 years.

### 2.3. Data collation

Data collation methods for the Australian forests are described in Paul et al. (2019). For the remaining regions, we sourced the publications identified by the literature search and checked their extraction and root sampling procedures to validate the integrity of sampling and measurements. We verified that root:shoot values were derived from original measurements (instead of values from other studies), that both root and shoot biomass were given where root:shoot ratios were not directly reported, that excavations were sufficiently deep ($\geq 60$ cm) to capture the largest fraction of coarse roots, and that dry mass was determined from oven-dry samples. Noting that much of the biomass in old-growth natural forests of New Zealand is contained in trees with stem diameter at breast height (DBH) of between 2.5 and 100 cm (and principally those between 10 and 60 cm; Holdaway et al., 2017), we prioritized trees $\geq 2.5$ cm DBH and included saplings $\geq 1.3$ m in height when available; shorter saplings and seedlings are outside scope in this review. Both naturally established and planted trees were included, so long as the species sampled originated from southern temperate forests. Trees were thus sampled from different competitive situations. Evidence that light affects plant biomass partitioning has been equivocal (Poorter et al., 2012), but a meta-analysis of growth experiments from controlled conditions concluded that relative allocation belowground decreases with decreasing light, particularly at low light (Poorter et al., 2012). Effects seem less clear with moderate shading; an extensive assessment with *Nothofagus antarctica* found only negligible effects of tree crown position on biomass partitioning (Gargaglione et al., 2010). As a result, we were inclusive and did not filter data based on canopy position or form of establishment. We also note that only minor gains ($< 2\%$ variation explained) have resulted from accounting for stand management history when modelling below-ground biomass–DBH relationships in Australian trees (Paul et al., 2019) and so we have been inclusive with respect to management history.

Since measurements of coarse root biomass are uncommon, we incorporated data derived either from whole-tree excavation or from soil pits, the two most accurate methods for estimating coarse-root biomass (Addo-Danso et al., 2016). Whole-tree excavation is often aided by machinery (e.g., excavators or hydraulic sluicing), and sampling is limited to roots connected to the focal tree over the extension of the root mat. Soil pits are often excavated manually, tend to sample smaller areas compared to whole-tree excavation, and intersect roots from more than one tree. Soil pits also tend to exclude root crowns and taproots,

potentially underestimating coarse root biomass (Addo-Danso et al., 2016). Therefore, we limited their influence using two analytical approaches: (i) we weighted root:shoot ratios from all sources by the corresponding excavated area (in effect down-weighting records from soil pits and small excavated trees), and (ii) we independently analysed the excavated tree data.

Once studies were confirmed as suitable for analysis, we extracted values of dry root and shoot biomass and root:shoot ratios and collated basic information on the study site, vegetation sampled, and sampling methods. The main variables recorded were geographical location, latitude, elevation, sampling procedure (whole-tree excavation or soil pit), number of trees sampled or area and depth of soil pits, species, and age and size of sampled trees. We documented fine-root cut-off diameters as defined by each study and separately compiled biomass of coarse and fine roots where both were reported. In most cases, root:shoot ratios encompassed only medium and coarse roots, but 15% of studies (some soil-pit excavations) sampled fine roots and did not report them separately. Roots were generally sampled down to 2–3 mm diameter, but 7% of studies limited sampling to roots $\geq 5$ mm. Previous research indicates that fine roots ($< 2$ mm) generally comprise $< 14\%$ of the total root biomass in woody plants (e.g., Li et al., 2003; Mokany et al., 2006) and that the fine root fraction rapidly becomes smaller with increasing tree size (e.g., Li et al., 2003; O'Grady et al., 2006). The Australian records had originally been presented so that a stump 10 cm from the ground was included with root biomass. We estimated stump biomass as a proportion of above-ground biomass using a model developed for eucalypt trees (Paul et al. 2014) and recalculated root:shoot ratios so that stumps were considered part of the above-ground biomass. As much as possible, and in line with recent approaches (e.g., Ledo et al., 2018; Paul et al., 2019), we traced back the records for individual excavated trees. However, in a few cases, only mean values for a group of excavated trees (often of similar size) were available. Individual records associated with Paul et al. (2019) were sourced from the AEKOS repository, and those associated with Gargaglione et al. (2010) were drawn from the BAAD global biomass and allometry database (Falster et al., 2015).

The Australian records presented by Paul et al. (2019) encompass below-ground allometry for woody life-forms across six broad ecological regions in Australia. We separated sites with oceanic temperate conditions from the associated biomass library (Paul et al., 2018) by drawing monthly temperature and rainfall data from climate surfaces (WorldClim Version 2, Fick and Hijmans, 2017) and selecting locations with a mean December–February temperature below 20 °C and an annual rainfall over 500 mm, so long as no month received less than 35 mm (McGlone et al., 2016). This excluded records from Mediterranean or semiarid climates from southwest and inland Australia and warmer subtropical and tropical sites from eastern Australia. Two sites from southeast Patagonia (Gargalione et al., 2010) with low rainfall ($< 425$ mm) and marked annual water deficit ($> 750$ mm yr$^{-1}$) were also excluded.

The data assembly process resulted in 441 root:shoot records from 25 studies (Appendices B and C). Some records were mean values for a given species or stand and so the underlying data comprised 285 excavated trees $\geq 5$ cm DBH (including tree ferns) and 186 saplings $\geq 1.3$ m in height and $< 5$ cm DBH (Table 1). Most records were for individual excavated trees but nine were from soil pits with excavated areas $\leq 10$ m$^2$.

**Table 1**
Summary of the number of compiled root biomass records by country/region and tree size category.

| Region | Studies | Sites | Records | Soil pits | Trees | Trees < 5 cm DBH | Trees ≥ 5 cm DBH | Species ≥ 5 cm DBH | Records in Mokany et al. 2006 | Records in Ledo et al. 2018 |
|---|---|---|---|---|---|---|---|---|---|---|
| Australia | 7 | 10 | 114 | 0 | 114 | 26 | 88 | 13 | 0 | 109 |
| New Zealand | 12 | 12 | 240 | 3 | 262 | 153 | 109 | 19 | 1 | 0 |
| South America | 6 | 10 | 87 | 6 | 95 | 7 | 88 | 11 | 1 | 17 |
| Total | 25 | 32 | 441 | 9 | 471 | 186 | 285 | 43 | 2 | 126 |

## 2.4. Data analysis

Plant biomass allocation to roots can be expressed as (i) root:shoot ratio – the dry biomass of roots divided by the combined dry biomass of stem, branches and foliage; or as (ii) root mass fraction (RMF, also root weight ratio or root:plant ratio) – the ratio of root to total plant dry weight (roots, stems, branches and foliage), often expressed as a percentage (Appendix A). We compiled or estimated both variables from the literature but report root:shoot ratios for comparison with key global reviews (e.g., Cairns et al., 1997; Mokany et al., 2006) and for more direct estimation of below-ground biomass in successive applications.

One New Zealand-based study reported below-ground biomass but not above-ground biomass for *Leptospermum scoparium* and *Kunzea* spp. (Watson and O'Loughlin, 1985). In this instance, root:shoot ratios relied on predictions of above-ground biomass (*AG*) from measured stem diameter (*DBH*, in cm) and height (*H*, in m) using a robust allometric model developed for the same species ($AG = 1.961(DBH^2H)^{0.741}$; $df = 43$, $R^2 = 0.88$, $p < 0.0001$).

Variable sampling effort among studies can be a limitation to obtaining reliable estimates of root:shoot ratio, and this has previously led to the exclusion of studies where the sampled area or volume of soil was small (e.g., Mokany et al., 2006). To overcome this situation while maximising the use of data, we computed weighted averages of root:shoot ratios, with the weighting based on the soil area sampled by each study. For soil-pit studies this was simply the total ground area excavated. For whole-tree excavation we relied on measurements of maximum radial root spread where these were available (Watson and O'Loughlin, 1985; Czernin, 2002; Marden et al., 2005; Marden et al., 2018a, 2018b) and estimated excavated area as the corresponding circular area. Otherwise, we conservatively assumed that the area covered by the roots of a tree in closed canopy forest was close to the projected crown area of that tree. Rooting areas were thus estimated from simple linear allometric functions that predict crown width (a surrogate for lateral root spread) as a function of tree stem diameter in four functional groups: canopy angiosperms, conifers, southern beech (Nothofagaceae), and understory trees. These functions had been parameterized with records from 1966 trees in 31 species from various locations in New Zealand (Coomes et al., 2014).

Weighted averages were computed separately for major taxonomic groups: southern beech, eucalypts, other dicot angiosperms, monocot angiosperms, gymnosperms, and tree ferns. Given that root:shoot ratios decrease with plant age/size, particularly in the small range of plant age and size (Peri et al., 2006; Ledo et al., 2018), weighted averages were computed separately for stems < 5 cm DBH and stems ≥ 5 cm DBH. The analytical approach of using weighted averages has the desirable effect of assigning lower weight both to records derived from soil pits and to small excavated trees. Soil pits tend to exclude taproots, root crowns, and lignotubers and thus can underestimate coarse root biomass (Addo-Danso et al., 2016), and they generally involve only small excavated areas. Small excavated trees can have high root:shoot ratios but only account for a small fraction of the biomass in forest stands. Values reported in the original studies were mostly averages and, with a few exceptions, did not report measures of deviation (or individual measurements, to allow estimates of associated measures of deviation). Because of the limited information available from original publications, we could not follow the metanalytical approach of weighting primary records by their inverse variances nor could we report on statistical tests, but note that weighting by excavated area provides an alternative measure of sampling effort (Gurevitch et al. 2018).

Potential relationships between root:shoot ratios, tree size, and environmental variables were assessed with linear regression models with the original tree-level harvest data, without weighting by sample area. Root:shoot ratio and DBH were $\log_e$ transformed to accommodate for curved relationships and for the typically skewed distribution of root:shoot ratios (e.g. Mokany et al., 2006). This analytical approach was supported by diagnostic checks that showed satisfactory balance and homogeneity of model residuals. Effects of mean temperature and rainfall:temperature ratios were tested using WorldClim monthly data for October to March, the Austral growing season. Both variables had distinctly skewed distributions and were $\log_e$ transformed prior to analysis. Because temperature data were negatively skewed, we multiplied values by −1 to reverse the skew and added a constant to rescale into positive values before $\log_e$ transforming. Taxon-specific relationships were tested for each predictor by means of two-way interaction terms. Model selection was based on Akaike information criteria (AIC) values, with lower AIC values indicating greater support for a model. Differences in AIC (ΔAIC) < 2, between 4 and 7, and > 10, respectively, indicate negligible, moderate, and strong differences in support between alternative models (Burnham and Anderson, 2002).

## 3. Results

Records spanned 32 locations across the southern Pacific (Fig. 1) and included a total of 53 species, with similar numbers of excavated trees for New Zealand, southern South America, and the climatically comparable region in southeastern Australia and Tasmania (88 to 109 excavated trees ≥ 5 cm DBH; Table 1). Much of the compilation is original in that few New Zealand (< 1%) and southern South American records (< 20%) are included in either of two global syntheses of root biomass (Table 1). A summary of climatic conditions across the compiled sample locations is presented in Table 2.

### 3.1. Root:shoot ratio by region

Across all the records compiled for southern temperate forests, root:shoot ratios ranged from 0.035 to an extreme value of 2.42, but 95% of all records ranged from 0.078 to 0.665. The weighted general mean root:shoot ratio for all regions across all seed trees (i.e., excluding



**Fig. 1.** Southern temperate locations where tree root biomass data were collected.

**Table 2**
Range of main climatic descriptors for sites across all southern temperate forest locations.

|  | No. sites | Mean annual temp. (°C) | Mean summer temp. (°C) | Min temp. coldest month (°C) | Mean annual rainfall (mm) | Mean October–March monthly rainfall (mm) |
|---|---|---|---|---|---|---|
| Australia | 10 | 8.0–14.7 | 10.5–17.7 | −2.9–4.1 | 512–1446 | 46–134 |
| New Zealand | 12 | 7.8–15.3 | 11.2–17.7 | −3.9–7.2 | 694–2159 | 55–167 |
| South America | 10 | 3.6–10.7 | 6.2–13.8 | −5.5–1.3 | 519–2140 | 35.5–116 |

tree ferns) was 0.379 for stems < 5 cm DBH and 0.268 for stems ≥ 5 cm DBH. With records grouped by region, weighted mean root:shoot ratios for stems ≥ 5 cm DBH were 0.277, 0.256 and 0.254 for oceanic and cool temperate forests of Australia, New Zealand, and southern South America, respectively.

### 3.2. Root:shoot ratio by taxa

Once records were grouped by taxonomic group and tree size in each region (Fig. 2), weighted means and standard means were generally consistent, except for some departure between the two estimates for monocots in New Zealand and gymnosperms in South America. When considering trees ≥ 5 cm DBH, weighted mean root:shoot ratios for eucalypts (0.277) in oceanic temperate conditions in Australia, southern beech (0.233) and other dicots (0.234) in New Zealand, and

southern beech (0.275) and the dicot *Drimys winteri* (0.233) in South America, were similar (6–10% difference) to the global root:shoot ratio of 0.26 reported by Cairns et al. (1997) (Fig. 2). The remaining taxa showed more marked departures from the global estimate. Mean values greater than the global average were observed for one dicot species in Australia (0.291, all records from *Acacia mearnsii*), and, notably, for the monocot tree *Cordyline australis* in New Zealand (0.437) (Fig. 2). Mean values lower than the global average were observed for tree ferns in New Zealand (0.194) and for gymnosperms in southern South America (0.219) (Fig. 2). Of the taxa shared between regions, only southern beech had sufficient records for comparison, and mean values were relatively consistent, with only a moderately higher root:shoot ratio in South America relative to New Zealand (Fig. 2).

No root biomass data were located for the southern beech or tree ferns in southeastern Australia and Tasmania. Although measurements
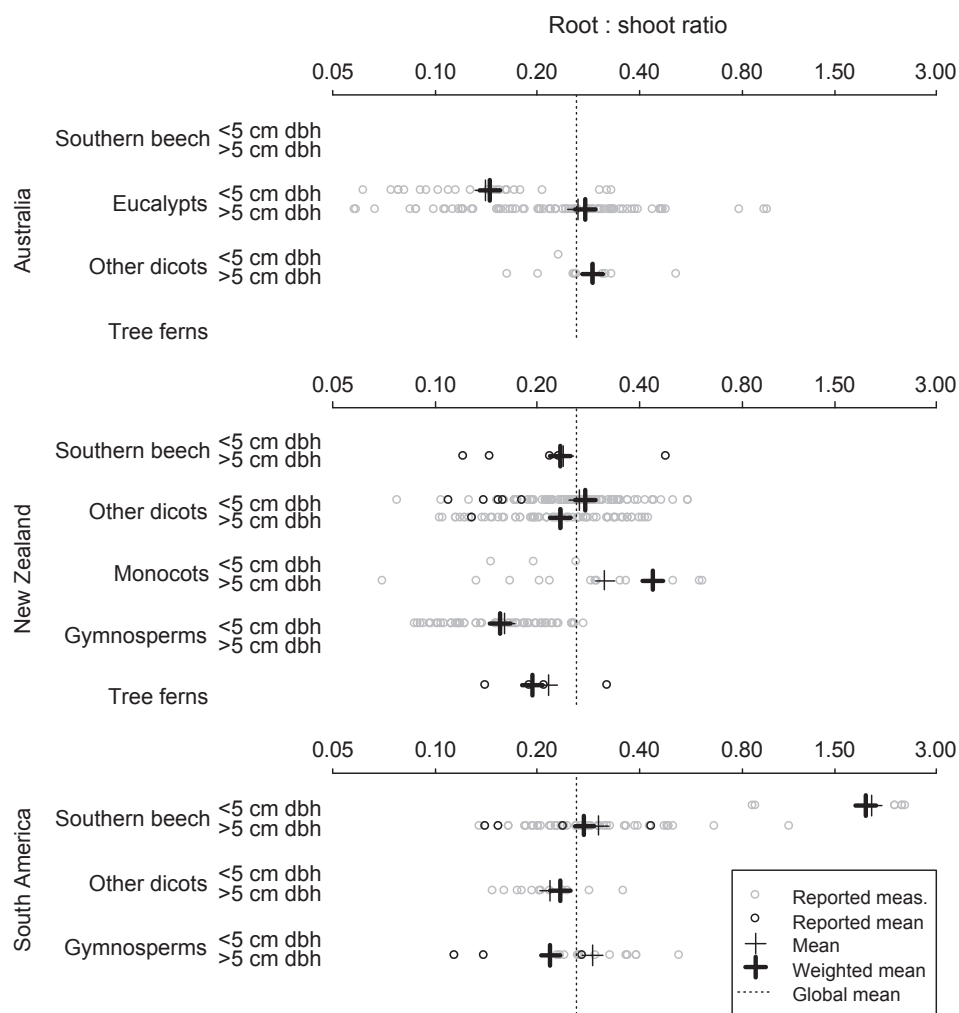


**Fig. 2.** Summary of root:shoot ratios for broad taxonomic groups indigenous to oceanic and cool temperate forests of Australia, New Zealand, and southern South America. Points represent individual measurements ('Reported meas.'), or site-level means ('Reported mean') extracted from the source studies; crosses represent arithmetic means ('Mean') and means weighted by excavated area ('Weighted mean') for each taxon and size group; dotted lines indicate the global root:shoot biomass mean ('Global mean') of 0.26 reported by Cairns et al. (1997). Blank fields represent combinations with no data. Note the logarithmic axis scale.

are available for saplings of New Zealand gymnosperm trees, no measurements are available for larger trees in this group, which includes over a dozen species of tall-canopy and emergent trees in the Podocarpaceae, Araucariaceae, and Cupressaceae. Other than the Nothofagaceae, only one other dicot species had root biomass data in South America (*Drimys winteri*). Further, the records for New Zealand monocots were limited to *Cordyline australis*, with no biomass data found for the New Zealand palm tree, *Rhopalostylis sapida*.

### 3.3. Root:shoot ratio and environmental factors

Root:shoot ratios exhibit much variability within each broad taxonomic group (eucalypts, other dicots, monocots, gymnosperms), but also within the narrower taxonomic group of southern beech (Fig. 2). When only individual excavated trees were assessed, there were interactions between size and taxonomic group. Size effects were notable for southern beech in South America, driven by very large root:shoot ratios (> 2) in five small saplings, yet manifest even with those records removed (ΔAIC = −59 for a model with taxon-specific tree-size effects relative to a model that only accounted for taxon effects). Other taxa and regions exhibited more moderate size effects (Fig. 3), but these were still statistically manifest (ΔAIC = −41 for taxon-specific tree-size effects relative to taxon-only effects when models were fitted to all taxa except southern beech). Negative relationships were noted for 'other dicots' in New Zealand and a positive relationship for Eucalypts in SE Australia and for the monocot *Cordyline australis* in New Zealand. When larger trees were considered (stems ≥ 10 cm DBH), the size–taxon interaction effect was no longer supported (ΔAIC < 2); South American gymnosperms (two Podocarp species) had a trend for high root:shoot ratios (mean = 0.316, CI = 0.246–0.386) relative to South American southern beech (mean = 0.266, CI = 0.224–0.308), dicots in New Zealand (mean = 0.242, CI = 0.200–0.285), and eucalypts in Australian oceanic temperate forest (mean = 0.265, CI = 0.234–0.296) but differences were not statistically notable (ΔAIC < 2).

We further assessed three taxa and regions with sufficient samples of excavated trees (54 southern beech in South America, 103 eucalypts in Australia, and 154 dicots in New Zealand) and modest to ample spread of sampled environmental ranges (3, 12, and 7 sites, respectively). A model selection process indicated that, once taxon and tree size effects were accounted for, there was clear statistical support for an effect of rainfall:temperature ratios (ΔAIC = −17 relative to a model that accounted for tree size, taxon, and their interaction, Table 3). Inclusion of a term for temperature resulted in a model with comparatively lower support (ΔAIC = −11 relative to a model accounting for tree size, taxon, and their interaction), and the combination of both variables did not improve model fit relative to rainfall:temperature alone (ΔAIC = −1, Table 3). In all three taxonomic groups, higher rainfall:temperature ratios were consistently associated with lower root allocation (Fig. 4), but the variation explained by this effect was minor relative to the simpler model that only accounted for a taxon-dependent size effect (Table 3).

## 4. Discussion

Root allocation patterns are highly variable among forest types. Globally, stand-level estimates of root:shoot ratios encompassing different forest biomes range from 0.05 to 1.16 (Cairns et al., 1997; Mokany et al., 2006), although root:shoot ratios between 0.20 and 0.30 tend to be more common (Cairns et al., 1997; Mokany et al., 2006). Several studies have attempted to explain the drivers of biomass partitioning into roots, but few of the variables tested have been found to have any influence, and root:shoot ratios tend to be insensitive to most environmental conditions (Enquist and Niklas, 2002; Mokany et al., 2006). We briefly summarize what is known in the global context and discuss the implications of our findings for southern oceanic and cool temperate forests.

### 4.1. Size effects

Tree size has been identified as one of two main predictors of root:shoot ratios in a global assessment that combines data across many taxa, tree life-forms, and forest types (Ledo et al., 2018). Our results show that size effects are mainly driven by small trees, reinforcing the results of Ledo et al. (2018). While some taxonomic variation in size effects was noted, with a marked negative effect for the southern beech in South America and moderate effects in other taxa (Fig. 3), root:shoot ratios were statistically invariant to size for stems larger than 10 cm DBH. Over that threshold, ratios were relatively stable, even in the large eucalypts excavated in southeastern Australia and Tasmania. The implication is significant: trees over 10 cm DBH invest proportionally in above- and below-ground biomass, with mean root:shoot ratios typically ranging from c. 0.19 to 0.30, and hence, the pool of below-ground biomass in mature forests is substantial.

A marked negative relationship with size detected in Nothofagaceae in South America was driven by very high ratios (up to ~2) in saplings of *Nothofagus antarctica.* High root allocation and logistic declines with age have been noted in the source studies for this species (Peri et al., 2006), which reproduces vegetatively and sprouts vigorously after disturbance (Veblen et al. 1996). All four deciduous South American *Nothofagus* (*N. alpina*, *N. antarctica*, *N. obliqua, and N. pumilio*) reproduce vegetatively to some degree (Veblen et al., 1996) and lignotubers have been observed for one of these (*N. obliqua*, Montenegro et al., 2003), signalling possible accumulation of belowground reserves in some cases. But generalizations do not seem to hold. Marked declines in root allocation have been documented from small seedlings to tall saplings of *Nothofagus pumilio* excavated at 52°S in southern Chile (Schmidt et al., 2009) but allocation in saplings was moderate (root:shoot ratios of 0.5 for 1.3 m-tall saplings, as estimated from biomass equations). More broadly, some north temperate Fagales are known to invest in deep root systems in early stages, with ratios of 0.8–1.0 reported for 1.7 m tall saplings of *Quercus robur* and *Fagus sylvatica* but, again, ratios can be lower in other species (ratios of 0.5 in 3.2 m tall *Betula pendula*) (van Hees and Clerkx, 2003). It may be that small trees of some Nothofagaceae and related taxa have potential for high root allocation but the generality and drivers of that pattern remain unknown and warrant investigation; with low temperatures and dry conditions potentially playing a role (see Section 4.3).

The high ratios and positive asymptotic size effect in the New Zealand monocot *Cordyline australis* are atypical, but seem unsurprising given the development of rhizomes in this species (Simpson, 2000; Czernin, 2002), where below-ground allocation tends to level off after an initial period of resource allocation to rhizomes. Exceptional instances can derive from distinct plant adaptations, as exemplified by a root:shoot ratio of 1.73 in the mangrove *Avicennia marina* (Tran et al., 2017).

As a final point, although not directly examined here, tree-size effects can be expected to scale up to stand level. Two global reviews spanning various forests types across tropical, temperate, and boreal biomes have reported declining root:shoot ratios with increasing aboveground biomass density (Cairns et al., 1997; Mokany et al., 2006), with stand age, mean tree height, and mean stem diameter also having an effect (Mokany et al., 2006).

### 4.2. Effects of tree taxa

Globally, species identity has been found to account for a relatively low fraction of variance in root:shoot ratios (Ledo et al., 2018). Broadly, our results from southern hemisphere taxa support this, as there were no major differences in root:shoot ratios across taxonomic groups and regions for trees ≥ 5 cm DBH. With two exceptions (*Cordyline australis* in New Zealand and *Acacia mearnsii* in Australia), our revised estimates show limited departure (≤7%) above the global mean given by Cairns et al. (1997; Fig. 2). Given an evolutionary history of dry conditions and
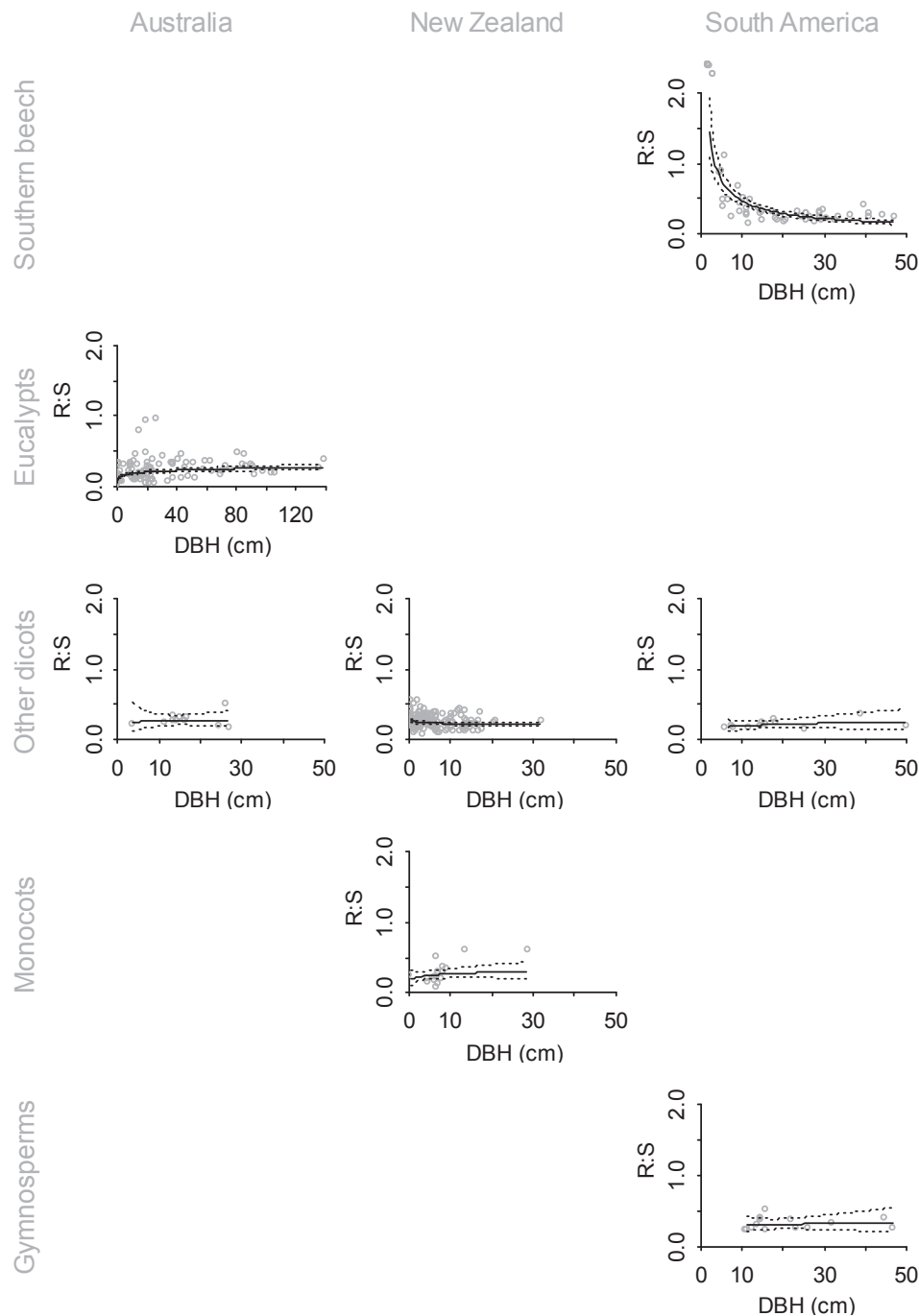
**Fig. 3.** Root:shoot (R:S) biomass partitioning across tree size (diameter at breast height, DBH) for different taxonomic groups and regions. Dotted lines indicate 95% confidence intervals. Note that DBH is presented on a different scale for eucalypts in Australia, and that tree ferns are not considered here.

frequent above-ground disturbance from fire and herbivory typical in Australia (Bowman, 2000), we had expected high root allocation in the eucalypts but our results indicate this is not the case for oceanic and cool temperate conditions in Australia. We found a low root biomass fraction in gymnosperms from South America, but values varied widely across species (Fig. 2). While the low mean was driven by two Cupressaceae, *Fitzroya cupressoides* and *Austrocedrus chilensis,* which had unusually low root:shoot ratios, as noted in one source study (Laclau, 2003), two podocarps, *Podocarpus nubigena* and *Saxegothaea conspicua,* had significantly higher ratios than southern beech, other dicots, and eucalypts of comparable size. Previous reviews have failed to find any statistical difference in root:shoot ratios between angiosperms and gymnosperms (Cairns et al., 1997; Enquist and Niklas, 2002; Mokany

et al., 2006; Poorter et al., 2012), but root:shoot allocation appears to be more variable in angiosperms than in gymnosperms (Cairns et al., 1997). Lower root:shoot ratios were also noted in the tree ferns (0.194), consistent with similar ratios (0.179) reported for *Cyathea hornei* sampled in Fiji (Ash, 1987). These differences may be expected given the distinctive anatomy and growth form of tree ferns, and we suggest it could also be partly attributed to a lack of secondary growth.

### 4.3. Water deficit and temperature

Functional equilibrium theory proposes that plants allocate proportionally more biomass to the organ that acquires the most limiting resource (Brouwer, 1963; Poorter et al., 2012). The theory derives from

**Table 3**
Summary of models tested for excavated trees in three taxa (eucalypts in Australian oceanic and cool temperate conditions, dicot trees in New Zealand, and southern beech in South America), with some spread in tree sizes and sample locations. Candidate models are sorted according to statistical support, with lower AIC and $\Delta AIC_{i\text{-}null}$ values indicating stronger model support, where $\Delta AIC_{i\text{-}null}$ values are the AIC for the candidate model less the AIC for the null (i.e., intercept only) model. $K$ and $df$ respectively indicate the number of estimated parameters and degrees of freedom.

| Effect tested | Candidate model | $K$ | $df$ | AIC | $\Delta AIC_{i\text{-}null}$ | $R^2$ |
|---|---|---|---|---|---|---|
| Null model | $\log_e(R{:}S) = intercept$ | 1 | 310 | 561 | 0 | 0 |
| taxon | $\log_e(R{:}S) = T \times R$ | 3 | 308 | 521 | −40 | 0.13 |
| taxon × DBH | $\log_e(R{:}S) = T \times R + \log_e(DBH)$ | 6 | 305 | 410 | −151 | 0.39 |
| taxon × DBH + taxon × temp. | $\log_e(R{:}S) = T \times R + \log_e(DBH) + T \times R \times \log_e(DBH) + trTemp + T \times R \times trTemp$ | 9 | 302 | 399 | −162 | 0.42 |
| taxon × DBH + taxon × rain.:temp. | $\log_e(R{:}S) = T \times R + \log_e(DBH) + T \times R \times \log_e(DBH) + trRain{:}Temp + T \times R \times trRain{:}Temp$ | 9 | 302 | 393 | −168 | 0.43 |
| taxon × DBH + taxon × rain.:temp. + taxon × temp. | $\log_e(R{:}S) = T \times R + \log_e(DBH) + T \times R \times \log_e(DBH) + trRain{:}Temp + trTemp + T \times R \times trRain{:}Temp + T \times R \times trTemp$ | 12 | 299 | 392 | −169 | 0.44 |

Abbreviations: R:S: root:shoot ratio; T × R: taxon by region; DBH: diameter at breast height; trRain:Temp: log_e-transformed rainfall:temperature ratio; trTemp: log_e-transformed temperature.

observations that most plant species are plastic in their biomass allocation according to growth conditions. These plastic responses have repeatedly been noted for seedlings grown under alternative nutrient or moisture treatments (e.g. Kramer-Walter and Laughlin, 2017) but are also in agreement with surveys of larger-sized trees sampled along environmental gradients (Gargaglione et al., 2010). On that basis, relatively greater root biomass may be expected with increasingly dry conditions or in cold climates, where soil nutrients are less mobile and in limited supply (Reich et al., 2014). Our analysis detected a consistent effect of 'water balance' on root allocation in three combinations of plant taxonomy and region, confirming reports that low rainfall (Mokany et al., 2006) and water deficit (Ledo et al., 2018) are main drivers of increased root allocation in forests. Interestingly, while the global assessments spanned wide environmental gradients that extended well into arid conditions, we found that the effect was still present and consistent across mesic to moist conditions (> 500 mm per year). It has been suggested that increasing root:shoot ratios from fine to coarse soil textures may be a result of the lower capacity of coarse, sandy soils to retain moisture and nutrients (Mokany et al., 2006), which raises the possibility that interactions between water balance and soil texture may have greater effects than any of those variables individually. Future improvements will likely be made once we are better able to characterize soil structure and chemistry at scale and to test and include their effects in allometric models.

When accounting for effects of tree size and water balance, we found no support for an effect of temperature. This is despite experimental evidence that shows low temperatures can increase root allocation in small plants (Poorter et al., 2012), and contradicts independent findings that biomass partitioning into roots is better predicted by temperature than by moisture availability (Reich et al., 2014). We suggest that soil temperatures under oceanic conditions do not fall low enough to limit nutrient mineralization and water access in the higher middle latitudes of the southern hemisphere, but we also note that the number of sites sampled for each taxon and region was modest, limiting the statistical power to detect multiple site effects.

### 4.4. Implications for biomass and carbon estimation

Root biomass allometries are essential for carbon estimation, both for carbon sequestration and trading initiatives and as part of national plot-based inventories and international reporting. The implications of reviewed root:shoot ratios may differ according to monitoring system and region. We illustrate this by drawing on the New Zealand carbon accounting system, where natural forests are monitored by a grid-based national network of forest plots that are measured following standard protocols that include small trees and deadwood (Payton et al., 2004). The network is used to calculate forest biomass stocks and stock changes, and to assess their principal drivers (Holdaway et al., 2017) while accounting for measurement and model uncertainty (Holdaway et al., 2014). Current calculation methods in the New Zealand network rely on a constant root:shoot ratio of 0.25 for all taxa and environmental conditions (e.g. Coomes et al., 2002; Holdaway et al., 2017), guided by global estimates that overall mean root:shoot ratios are approximately 0.26, independent of latitude, soil texture or tree type (Cairns et al., 1997). It thus becomes clear that improved, taxon-specific, estimates of below-ground allocation would contribute to more accurate estimation of forest carbon stock and reduced uncertainty (Holdaway et al., 2014).

We found that the main taxonomic groups in southern temperate forests have root:shoot ratios that are generally close to those from previous, independent estimates. This supports current carbon estimation approaches but leaves room for refinement, with specific recommendations given for the New Zealand context (Appendix D). Although New Zealand angiosperms fall within 10% of the global root:shoot ratio of 0.26 (Cairns et al., 1997), the deterministic application of these ratios means that small changes in values can markedly
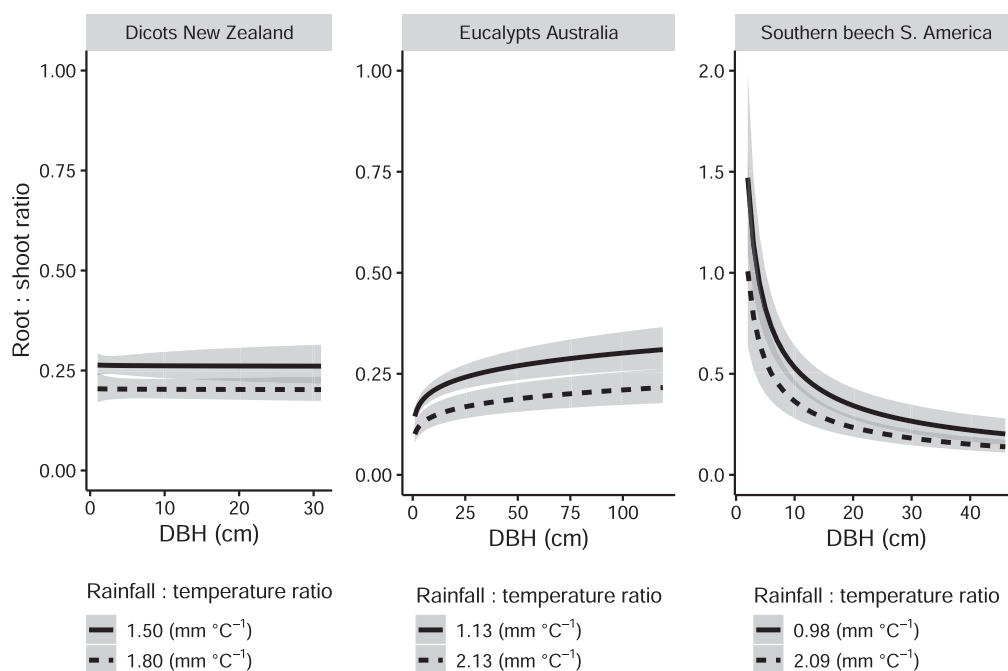
Fig. 4. Most parsimonious log-log model of root:shoot ratios for the three taxonomic groups with wider environmental sampling of individual trees. Mean responses and associated confidence intervals (shaded) are presented for the range of tree sizes for the 10th and 90th percentile of rainfall:temperature ratios sampled for each combination of taxonomic group and region.

affect broad-scale and long-term biomass predictions. A relevant adjustment is that for the widespread and dominant group of New Zealand dicot trees that had a ratio of 0.234. The value is remarkably consistent with ratios of 0.23 and 0.24 given by Mokany et al. (2006) for 'other broadleaf forests' with above-ground biomass of 75–150 and > 150 tonnes ha$^{-1}$, respectively. The lower value relative to a global mean of 0.26 aligns with (i) consistent evidence of lower root allocation where water balance is more favourable (Fig. 4; Mokany et al., 2006; Ledo et al., 2018), and (ii) the mesic to humid conditions characteristic of extant New Zealand forests. Adjustments are also necessary for the monocot *Cordyline australis* (weighted mean of 0.437) and for tree ferns (weighted mean of 0.19). With the tree ferns *Cyathea smithii* and *Dicksonia squarrosa* ranked as 15th and 19th most dominant species in New Zealand forests (Peltzer and Payton, 2006), these species can significantly influence forest biomass estimates.

### 4.5. Data gaps, sampling considerations, and future research directions

Our meta-analytical approach allowed us to retain all information by weighting records so that smaller samples (mostly soil pits and small trees) had a smaller influence on the weighted mean. This approach, however, could not overcome bias in terms of the species or locations sampled. Data restrictions meant we could not quantitatively downweight species with disproportionate representation relative to their typical contribution to forest biomass (e.g., species of *Leptospermum*, *Kunzea* and *Pittosporum* among New Zealand angiosperms) and to balance that influence on the general mean.

Although most sampled genera are common and significant in terms of forest biomass, some important genera in terms of biomass are missing from or poorly represented in existing root studies. In New Zealand this is particularly so for dicot species such as *Beilschmiedia tawa*, *Metrosideros umbellata* and *Weinmannia racemosa*, and the podocarps *Dacrydium cupressinum* and *Prumnopitys ferruginea*, which are all among the 10 species with the largest share of biomass in natural forests (Peltzer and Payton, 2006). For Valdivian rainforest, main canopy angiosperms such as *Laurelia*, *Eucryphia* and *Aextoxicon* are missing root biomass data. In Australia, data are lacking for genera such as *Nothofagus*, *Eucriphya*, *Phyllocladus*, and *Atherosperma*, all of which are important in the cool temperate rainforests covering c. 10% of Tasmania and containing significant biomass stocks. Given their large share of

above-ground biomass in New Zealand forests (Peltzer and Payton, 2006), addressing root data deficiencies for large gymnosperm trees is important but also, in particular, resolving the high variability among conifer lineages that is apparent from differences in the South American Cupressaceae and Podocarpaceae would be useful for improving estimates. Moreover, comparisons of shared lineages across the continents of the southern hemisphere would be useful for testing generalities of size-effects and for disentangling location from taxonomic effects.

A similar problem arises in terms of sampled locations and can be exemplified by 89% of the New Zealand records corresponding to elevations below 500 m asl. A phenomenon of increased fine root allocation in forests at high elevation has been emerging for different montane zones including southern Patagonia (Hertel et al., 2008) and root:shoot ratios for *Fuscospora cliffortioides* (Nothofagaceae) have been noted to increase from 0.135 at 1000 m asl to 0.231 at 1200 m asl in New Zealand (Benecke and Nordmeyer, 1983). Given extensive areas of montane forests in New Zealand and South America, it would thus be relevant to examine the representativity of the compiled means for high-elevation forests and assess if these merit adjustments in carbon estimation procedures.

Below-ground biomass is often predicted as the fraction of above-ground biomass given by root:shoot ratios (Somogyi et al., 2007). Although simple to implement, this approach is subject to the compounded prediction errors associated with both estimation of above-ground biomass and variability associated with root:shoot ratios (Appendix E). Preference is thus leaning towards modelling below-ground biomass as a non-linear function of stem diameter, with good examples of progress in this regard (Milla-Araneda et al., 2013; Marden et al., 2018a, 2018b; Paul et al., 2019). The data gaps above imply that, beyond Australia, we are not yet in a position to fit curves for a sufficiently wide range of species or taxa from southern oceanic or cool temperate forests, but this nonetheless marks the path ahead. Overall, this is the first synthesis of root biomass allocation for southern temperate forests, with some clear patterns of variation and environmental signals being noted despite the mixed nature of the data sources. Beyond Australia, root:shoot estimates for dicot trees are generally closer to values reported for north temperate forests than to the global mean, whilst divergences in root allocation patterns or information gaps are noted for some other taxonomic groups that call either for ensuing adjustments in biomass estimation or further investigation.

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## Appendices A-E. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117542.

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