

From mallees to mountain ash, specific leaf area is coordinated with eucalypt tree stature, resprouting, stem construction, and fruit size

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ABSTRACT

Context. The radiation of eucalypts into almost every Australian environment offers valuable insights to plant ecological strategies. **Aims.** We aimed to assess the degree to which functional traits across different organs are independent or reflect coordinated strategies in southern eucalypts. **Methods.** We applied ordinary and phylogenetic generalised least squares regressions to 164 southern Australian taxa, examining the network of pairwise relationships between 10 functional traits representing aspects of stature, leaf economics, reproduction and post-fire regeneration. We examined coordination and modularity in this network and estimated how phylogeny affects observed trait correlations. **Results.** Stem and stature traits were generally independent of reproductive traits, with Specific Leaf Area the most connected trait, being correlated with traits from all organs. Resprouting ability was also connected to several traits. Species able to resprout basally, but not epicormically, were on average shorter, stouter, with higher stem sapwood density, thinner bark, smaller leaves and lower Specific Leaf Area than those able to resprout using both methods. Taxa resembled their relatives; phylogenetic signal was significant for all continuous traits except Relative Height, ranging from Pagel's Lambda $\lambda = 0.37$ (Relative Bark Thickness) to $\lambda = 0.82$ (Specific Leaf Area). Phylogenetic analyses showed weakened correlations for most (but not all) trait pairs. However, most moderate relationships on the trait correlation network also displayed correlated evolution. **Conclusions.** Stature, stem, leaf and reproductive traits and fire response of eucalypts are somewhat coordinated, principally through leaf economics. Trait combinations that confer ecological competence on eucalypt taxa in present-day conditions are likely to have been similarly favoured throughout their evolutionary history. **Implications.** This supports theory of coordinated plant strategies.

Keywords: correlated traits, eucalypts, fire response, functional traits, PGLS, phylogenetic signal, plant ecology, plant evolution, plant strategies, southern Australia.

Introduction

Eucalypts comprising the genera *Eucalyptus* L'Hér., *Corymbia* K.D. Hill & L.A.S. Johnson, and *Angophora* Cav. represent a remarkable radiation of approximately 900 species, with *Eucalyptus* dating back to at least the Eocene (~52 Mya) (Gandolfo *et al.* 2011) and the eucalypt group to the Late Cretaceous (Ladiges *et al.* 2003). Dominating most woody vegetation in the Australian landscape, their open forests and woodlands cover much of the land mass excluding only the driest deserts, saline areas, and most closed forests (Williams and Woinarski 1997; Montreal Process Implementation Group for Australia and National Forest Inventory Steering Committee 2018). Studying functional ecology of the eucalypts is important intrinsically, to their conservation, and to the ecosystems and organisms, including people, that depend on them (Keane *et al.* 2000; Werner *et al.* 2008; Bayle 2019). Eucalypts serve as a model clade for understanding ecological radiation, owing to the large and growing knowledge of phylogeny, functional traits and distribution and

function (Cavender-Bares 2019). Relationships between functional traits (*sensu* Westoby and Wright 2006; Violle *et al.* 2007) observed across larger datasets (see Díaz *et al.* 2016; Kleyer *et al.* 2019) may not hold uniformly at more local geographic or taxonomic scales (Messier *et al.* 2017a). The broadly dry, fire-prone, and often nutrient-deficient environment in which the eucalypts have evolved is likely to have influenced ecological strategies that may be reflected in their functional traits and how they have evolved through time (Beadle 1966; Burrows 2013; Dantas and Pausas 2013; Bui *et al.* 2017). More specific hypotheses about the interplay of landscape and evolution for ecological and life history strategies, such as OCBIL theory, also prompt study of functional ecology of eucalypts (OCBIL: ‘old, climatically buffered, infertile landscapes’; Hopper 2009, 2021). Here we aim to characterise patterns of functional traits and their evolutionary patterns in a large subset of eucalypts of southern Australia.

Much work has investigated single, or suites of, traits representing the same organ or function. A number of axes of variation in trait-based trade-offs have since emerged, such as: the leaf economics spectrum relating to leaf carbon assimilation vs leaf longevity (Wright *et al.* 2004); wood economics relating wood density to hydraulic and mechanical stress tolerance vs growth (Chave *et al.* 2009); and the seed mass vs seed output trade-off (Westoby *et al.* 2002; Muller-Landau 2010). In the eucalypts, particular study has also focused on traits related to similar aspects of plant ecology such as stem hydraulics (Pfausch *et al.* 2016; Fernández *et al.* 2019), leaf and photosynthetic characteristics (Asao *et al.* 2020), bark (Lawes *et al.* 2021), and fruit and seed characteristics (Murray and Gill 2001), as well as fire response (Nicolle 2006) and buds (Burrows 2013). Fire responses of plants have received considerable focus (Clarke *et al.* 2013, 2015; Lawes *et al.* 2022) but with rather less attention to their connection to other functional traits (though, see Pausas *et al.* 2016). A notable exception is the finding that plants that resprout are shorter than non-resprouters (Midgley 1996; Kruger *et al.* 1997).

We use the term ‘coordination’ to refer to functional relationships that occur between traits owing to some hypothesised causal process, such as the trade-offs underlying ecological strategies (Westoby *et al.* 2002; Westoby and Wright 2006; Reich 2014). We use the term ‘correlation’ to refer to the observed statistical relationship between two variables. Coordination may be expected within organs, such as the leaf economics spectrum characterising conservative vs acquisitive carbon assimilation strategies (Wright *et al.* 2004). Correlation between traits in a spatially extensive dataset may result from coordinated shifts in two traits responding to an environmental gradient, as observed for specific leaf area and leaf size both declining to low rainfall (Fonseca *et al.* 2000).

However, there is reason to believe that neither traits nor the axes they represent occur independently, but in integrated

combinations within the whole-plant system that are all subject to natural selection simultaneously (Givnish 1988; Messier *et al.* 2017b). Because many plant traits relate to multiple aspects of ecological strategy and physical constraints, their interrelationships likely form complex constellations rather than independent discrete axes (Messier *et al.* 2017b; Kleyer *et al.* 2019; Caminha-Paiva *et al.* 2021). We expect strong coordination among some traits measured on the same organs due to allometric constraints (e.g. large seeds can only be borne by large fruits; Cornelissen 1999) or reflecting allocation trade-offs (e.g. stem sapwood density may be lower among trees capable of greater maximum height in a vertical light gradient; Falster and Westoby 2005). Coordination may also exist between organs. Corner’s rules highlight that larger twigs are needed to bear bigger appendages, whether they are leaves or fruit (Corner 1949). Thin twigs cannot support big leaves nor big fruits, but the relationship between size of those organs – leaves and fruit – may be triangular and not a linear correlation (Cornelissen 1999). Reich (2014) argued that a continuum of fast–slow growth strategies reflecting acquisitive to conservative resource use manifests across all organs (leaf, stems and roots).

Evidence for coordination includes a global analysis of woody plant form and function, which reports moderate, positive correlations ($r > 0.3$) among leaf size, plant height and seed mass and between leaf size and specific leaf area (Díaz *et al.* 2016). Studies utilising trait network analyses demonstrate that traits across organs (leaves, fruits stems and roots) and function (allocation economics, architecture, regeneration) may be coordinated (Messier *et al.* 2017a; Kleyer *et al.* 2019).

To explore the interrelations of different dimensions of ecological strategy, we studied multiple, easily measured allocation traits in eucalypts representing strategies related to stature, stem allocation, leaf size and economics, along with regeneration, through fruit and seed and post-fire resprouting ability. A full list of traits used in this study and their functional significance can be found in Table 1.

Analyses of traits, their interrelations, and trait–environment relations across extant species reflect species’ competence in current environments (Westoby and Wright 2006). That is, the observed trait combinations enable a plant species to make a living in the present-day ecological milieu. We have previously demonstrated the use of traits to explain and predict eucalypt species distributions along environmental gradients (Pollock *et al.* 2012, 2018; Vesk *et al.* 2021). However, studying the evolution of traits through phylogeny (i.e. ‘tree-based’ thinking) offers opportunities to gauge the generality of inferences across clades, especially important when studying closely related taxa. In *Eucalyptus*, many traits differ notably between subgenera, for example: traits related to resistance to herbivory and pathogens, hydraulics, nutrient usage, as well as tolerance of flooding and salinity (Noble 1989; Hill *et al.* 2001). In contrast, the structure of epicormic strands is thought to be

Table 1. Summary of how each trait was measured and its ecological significance.

Trait	Method of measurement	Represented strategy dimension
Stature traits		
Maximum height (MH)	Downloaded from EUCLID database (Slee et al. 2015)	Growing tall confers a competitive advantage for light from above. But it incurs costs of investment in support and supply (Givnish 1982; Loehle 2000; Westoby et al. 2002; Falster and Westoby 2003). Greater height growth is associated with site 'productivity' (Moles et al. 2009) and might be expected to coordinate with more 'productive' than 'conservative' strategies. Frequent disturbances causing loss of canopy or stem, limit height.
Relative height (RH)	Height (H, m) of individual trees was first measured via clinometer along with girth (G) at breast height. Relative Height at 100 cm girth was calculated via the allometric equation $RH = H \times (100/G)^{0.55}$ determined from data across all species	Stem growth vs investment in secondary growth or thick bark etc. Tall or lanky vs stout or corky (Dantas and Pausas 2013)
Stem traits		
Stem sapwood density (SD)	Measured as dry mass (g) of an approximately 1 cm diameter \times 10 cm long section of twig divided by fresh volume (mL) measured using the displacement method	Stem growth vs defence, or cavitation resistance (Chave et al. 2009) Resistance to competition (Kunstler et al. 2016)
Relative bark thickness (RBT)	Bark thickness (BT) on individual trees was measured in mm using a bark thickness gauge 5 times at breast height along with girth. Relative Bark Thickness at 100 cm girth was calculated according to the allometric equation: $RBT = BT \times (100/G)^{0.52}$ determined from data across all species	Stem growth vs defence, especially surface fire, likely associated with epicormic sprouting (Lawes et al. 2013) Lanky vs stout (Pausas 2015)
Leaf traits		
Specific leaf area (SLA)	Area of fresh leaf (mm ²) including petiole divided by dry mass (mg) after oven drying at 60–70°C for 72 h	Photosynthetic assimilation vs leaf longevity (i.e. leaf economics spectrum) (Westoby et al. 2002; Wright et al. 2004)
Leaf area (LA)	Area of a single fresh leaf including petiole (cm ²) measured with leaf area meter	Light interception, heat balance (Wright et al. 2017)
Leaf mass (LM)	Mass (g) of a single leaf including petiole after oven drying at 60–70°C for 72 h	Coordination of leaf size and support from twigs (Corner 1949)
Reproductive traits		
Fruit wall width (FWW)	Minimum thickness (mm) of outer layer of fruit below valves	Protection of seeds from heat of fire; seed reproduction prioritised vs vegetative reproduction (Murray and Gill 2001)
Fruit mass (FM)	Mass of single fruit found by averaging mass of five replicate empty fruits (mg) weighed simultaneously	Fruit size scales with and constrains seed size, also seed protection (Lord and Westoby 2006) Coordination with supporting twigs (Corner 1949).
Seed mass (SM)	Average seed mass found by dividing total mass of 10 seeds (mg) weighed simultaneously	Tolerance–fecundity trade-off (Moles and Westoby 2006; Muller-Landau 2010) Persistence of seedlings in adverse conditions vs dispersal to more locations
Fire response	Field observation of individuals of different ages in wild populations found in Nicolle's survey (Nicolle 2006) or other sources (see Table S2.3)	Ability and mode of resprouting in response to fire (Clarke et al. 2013) Lignotuber/basal-only resprouter, Combination resprouter, or Obligate Seeder (Nicolle 2006) Persistence vs investment in future generations (Bellingham and Sparrow 2000)

relatively uniform across the eucalypt genera *Angophora*, *Corymbia* and *Eucalyptus* (Burrows 2013) and yet other traits may vary equally within all clades. Shared ancestry may influence contemporary relationships between traits; if related taxa are similar in multiple traits, they are likely to have inherited their trait combinations rather than

represent independent occasions where trait combinations evolved (Felsenstein 1985; Grafen 1989). Accounting for the varying degrees to which traits show such phylogenetic patterns, termed phylogenetic signal (Münkemüller et al. 2012), allows more accurate estimates of correlated evolution of traits (Rohle 2006). By correlated evolution we mean the

pattern of changes in two traits across divergences throughout a phylogenetic tree being correlated. For instance, across divergences in a phylogeny, where one lineage shifts to lighter seeds, does it also (on average) shift to shorter maximum height? When studying taxa like the eucalypts that include some prolific lineages, functional relationships across the tips of the phylogeny will tend to reflect those prolific lineages. Such patterns may or may not generalise across other taxa. Investigating phylogenetic signal can reveal the extent to which functional relationships observed among extant/contemporary taxa may be driven by small numbers of prolific lineages. Further, the relationships that are estimated when accounting for phylogeny may be expected to have more generality across taxa. To further the understanding of eucalypts, their functioning and the role of phylogenetic signal, we collected and analysed a dataset of southern Australian eucalypts comprising ~20% of all eucalypt taxa to:

1. Examine relationships among 11 functional traits (Table 1) encompassing stature, stem, leaf and regeneration aspects of plant ecological strategy, using pairwise correlations and network analyses.
2. Examine the phylogenetic signal within each of these traits.
3. Determine how the shared ancestry of taxa affects these trait–trait relationships, thus allowing us to identify which traits displayed correlated evolution, providing strong evidence for general functional trade-offs.

Materials and methods

Study taxa and traits

Traits were primarily measured on field surveys and collections by the authors and others over several years associated with distinct campaigns (Pollock *et al.* 2012, 2018; Vesk *et al.* 2021; Vesk *et al.* unpubl. data). For this study, we used a subset of this dataset, including measurements from 1942 trees across 164 eucalypt taxa, following Brooker (2000) and Nicolle (2019), including *Angophora* (2 taxa), *Corymbia* (5 taxa) and *Eucalyptus* (157 taxa), along with two other Myrtaceae tree species important in the south-eastern forests, *Lophostemon confertus* and *Syncarpia glomulifera* subsp. *glomulifera*. These were collected predominantly around the southern Great Dividing Range in south-eastern Australia, but also included smaller collections in the Gariwerd Grampians, Millewa Mallee region, and Koi Kyenunu-ruff Stirling National Park in Western Australia (Fig. 1). This included several regions of high species richness and endemism for the genus *Eucalyptus* and mostly corresponds to the alpine and mainland subregions within the South-east bioregion defined by González-Orozco *et al.* (2014), though some samples also fall into the South-west bioregion.

Sampled traits included those in the Leaf-Height-Seed scheme (Westoby 1998) but extended to associated traits for each of these strategy axes including leaf size, bark thickness, fruit mass and fruit wall width, wood density and stature. Details on trait measurement or extraction can be found in Table 1 and, although this was predominantly consistent across collecting campaigns, fruit wall width data were not available for 14 taxa collected in the Millewa Mallee region. Some fruit and seed masses for the Millewa Mallee also were made from herbarium material (Pollock *et al.* 2018). Relative height, relative bark thickness, stem density and fruit wall width data were also not available for some 11 taxa sampled exclusively in the Millewa Mallee region. The remaining traits were measured in almost all taxa. We added Maximum Height based on values extracted from the EUCLID database (Slee *et al.* 2015).

For all continuous traits, we characterised each taxon with trait medians, first taking the median by individual tree and then by taxon. Where taxa in the trait dataset were not resolved to subspecies level, we did so by reference to distribution information (Western Australian Herbarium 1998; VicFlora 2021). We calculated the median maximum height of all subspecies. The remaining six taxa were assigned maximum heights based on that of their closest relatives or other databases such as the current accessible EUCLID website (Slee *et al.* 2015) or local flora databases such as Florabase and VicFlora (Western Australian Herbarium 1998; VicFlora 2021). A list of the taxa for which maximum height was inferred and a more detailed description of how this was done in each case can be found in Supplementary Table S1. To aid in comparison, all trait data were log-transformed, mean-centred and scaled by dividing by one standard deviation prior to analysis.

Fire-response strategies were added for each taxon designating it either an obligate seeder, lignotuber-only (or basal-only) resprouter, stem-only (epicormic only) resprouter, or combination (basal and epicormic) resprouter based upon the definitions and census conducted by Nicolle (2006). Eleven taxa identified by Nicolle to be resprouters of ‘Variable’ type, were included within the combination resprouter category. To include relationships between fire response strategy and other traits in our network analysis, we also defined basal-only resprouting (BOS) behaviour as a binary variable with basal-only resprouters coded as 1 and species known to exhibit other strategies combined and coded as 0. Before scaling to match the variance of the other variables, the mean and standard deviation were 0.25 and 0.43, respectively. We believe this dichotomy was the most useful among fire response strategies due to preliminary data showing that basal-only resprouters had the greatest difference in their traits compared to the remaining categories (see Fig. S2) and our dataset contained enough species exhibiting these strategies to have reasonable statistical power. Further discussion and the full justification of fire-response categorisation is in Supplement 2.



Fig. 1. Collecting locations for samples of 164 eucalypt taxa for which we collected trait data. Regions sampled include alpine, mallee and coastal environments as well as regions of species richness and endemism in South-western WA, Gariwerd Grampians and South-Eastern NSW.

Phylogenetic tree

Calculation of phylogenetic signal requires a phylogenetic tree of all taxa with included trait data to measure genetic distance between them. We constructed a phylogenetic tree from several published phylogenies, supplemented with taxonomic information. We used a recent phylogeny of the eucalypts based on Bayesian analysis of both nuclear (internal and external transcribed spacer, ITS and ETS) and plastid (matK and psbA-trnH) DNA regions, and which included many of the taxa in our trait data set (Thornhill *et al.* 2019). We note that the tree of Thornhill *et al.* (2019) (their fig. 4) was forced by their methodology to be fully resolved and not all nodes would have had character support. We accessed the tree associated with the Thornhill *et al.* (2019) paper from Knerr and Thornhill (2019), pruned this tree to the taxa from our trait dataset or their closest relatives (159 taxa in total), and combined it with a smaller (39 taxa), but well-supported, chloroplast-DNA phylogeny (Bayly *et al.* 2013) in order to confer greater statistical support to deeper divergences. Before the trees were combined, taxon names were verified against the Australian Plant Census (Council

of Heads of Australasian Herbaria 2021) and branch lengths removed to avoid inconsistencies between different sources, as root depths were different. We then merged the two phylogenies using supertree methods (implemented with R package *phangorn*; Schliep 2011; R Core Team 2021) using Matrix Representation Parsimony (Baum 1992; Ragan 1992). To avoid the effects of random resolution of polytomies in the output supertrees (either originating from inherent phylogenetic uncertainty within the input trees or from regions of disagreement between them) we ran the supertree function 100 times and used the strict consensus (with *ape* package; Paradis and Schliep 2019), which was considered the most conservative approach.

We assumed species to be monophyletic for the purposes of positioning taxa, and so, although only 113 taxa in the trait dataset had an exact representative in either input tree, 43 taxa could be positioned on the final tree based on the position of members of the same species or by identifying orthographic variants. When the trait dataset and phylogeny used names that were not both resolved down to subspecies level, we used other subspecies or the species name to position these taxa. We positioned the remaining 13 taxa on the tree

based on the positions of their proposed closest relatives. Although various phylogenetic and taxonomic sources disagreed considerably about which taxa were closest relatives, testing taxa with the most extreme trait values in different potential positions revealed only a marginal effect on phylogenetic signal compared to its uncertainty (see Table S3.1). Hence, even large uncertainty in taxon positions is unlikely to significantly affect results. Where closest relatives were determined using other published phylogenies (Jones *et al.* 2016; Fahey *et al.* 2022), only the sections of those phylogenies that were not yet resolved by previous methods (i.e. the immediate sister taxa to those of interest) were considered. Any disagreements these other phylogenies had regarding the relative positions of other taxa we had already resolved were ignored. More detail on the justification of the position of each such taxon can be found in Table S3.2 along with any other taxa whose position was similarly inferred.

Trait data for four taxa were ultimately excluded from this analysis due to a lack of phylogenetic information to position them on the tree, resulting in a final dataset of 164 taxa (Supplement 4). Finally, to enable computation of phylogenetic distance, we recalculated branch lengths for the resulting tree using the ‘Grafen’ method (Grafen 1989), which allows branch length calculation for purely topological trees. The final version of the tree used in this analysis can be found in Fig. S5.

Statistical analysis

Phylogenetic signal of individual traits

We estimated phylogenetic signal for each continuous trait using Pagel’s Lambda (λ) (Pagel 1999), estimated with maximum likelihood (*caper* package; Orme *et al.* 2018). Lambda is a scaling factor for the off-diagonal elements of the variance–covariance matrix constructed from the genetic distances between each of the taxa on the phylogeny, relative to the root-to-tip distance. It is a measure of the degree to which the actual covariance structure of the residuals in the model match this expected phylogenetic covariance structure. It varies between 0 and 1, where 0 indicates traits are distributed independently of phylogeny and 1 represents trait values distributed across the tree exactly as expected from Brownian evolution along the lineages. Pagel’s Lambda is robust to phylogenetic uncertainty (i.e. polytomies) and incomplete branch length information (Münkemüller *et al.* 2012; Molina-Venegas and Rodríguez 2017) and is therefore suitable for this analysis. We also further tested each lambda value to determine if it was significantly different from zero or one.

Cross-species trait relationships

To quantify the cross-species relationships between traits, we fit Ordinary Least Squares regression models for each combination of pairwise comparisons between each of the 11 traits including the binary BOS variable (‘lm’ function

stats package; R Core Team 2021). This was to ensure our measure of correlation strength remained comparable to subsequent regression-based correlation strength estimates from phylogenetically-informed analyses. We used the square root of the coefficient of determination output by the regression models ($\pm\sqrt{r^2}$) to quantify correlation strength. The difference between the r -values calculated this way for each fitted model compared with the corresponding Pearson’s r were generally negligible, with 40/55 models showing differences of less than 0.05 in magnitude (mean 0.037 and median 0.033). We then visualised the resulting relationships as a network diagram using the R package *qgraph* (Epskamp *et al.* 2012), which uses r -values to construct a force-embedded diagram whereby nodes that are more closely related are placed closer together. We restricted the displays to moderate correlations, with $|r| > 0.3$, to aid visualisation. Note, this is very conservative, equating to $P < 0.0004$ for the sample sizes for each regression model for each pairwise comparison, which ranged from 150 to 163. We also corrected for multiple comparisons using a Holm adjustment (Holm 1979) for P -values of all models shown in the networks. Several models with $P < 0.0004$ had adjusted P -values above this, though they were all below 0.05. Hence, we focus on biologically important relationships, following the guidelines from Cohen (1988) of weak ($|r| < 0.3$), moderate ($0.3 > |r| > 0.7$) and strong ($|r| \geq 0.7$).

To compare traits among fire responses, we used similar regression models. We first compared obligate seeders to all resprouters together, then contrasted obligate seeders to each of the other resprouting categories individually, and finally compared combination resprouters (those that can resprout *both* basally and epicormically) with lignotuber-only/basal-only resprouters to get the most complete picture of the relative positions of each of these three categories on each of the trait spectra. Although stem-only resprouters were present in our dataset, only four species demonstrated this strategy and hence were excluded from this section of the analysis.

Effect of phylogeny on trait relationships

For our phylogenetic analyses, we used Phylogenetic Generalised Least Squares models (Grafen 1989), a variation of generalised linear models that uses phylogenetic distance between taxa to determine the expected error structure of the data and produce phylogenetically-informed estimates of correlation. We fit pairwise Phylogenetic Generalised Least Squares models (with *caper* package; Orme *et al.* 2018) for each of the relationships between pairs of traits to determine relationships and compare with the cross-species regression models.

For each model, a Pagel’s lambda value for the covariance matrix of the residuals was estimated via maximum likelihood along with the remaining regression parameters.

We then visualised these relationships using the same force-embedded network diagram described for the cross-species

analysis. The lambda value calculated for and used in the model varied significantly depending on which trait was treated as the dependent or independent variable, so we used the model with the highest phylogenetic signal of the two in the network. Being a subset of generalised least squares models and as such having no way to calculate a comparable coefficient of determination to those of ordinary least squares models, a 'pseudo r -squared' value was estimated by comparing the model to a null intercept-only model with the same covariance matrix (i.e. given the same lambda value and covariance matrix calculated for the bivariate model instead of what it would be for a true intercept-only model).

Phylogenetic models were also then used to examine the differences in trait values between the different fire-response categories to compare the results to the similar cross-species analysis. Obligate seeders were again compared to resprouters as a whole and then separately to each resprouter category, after which the combination sprouters were then also compared to lignotuber/basal-only resprouters.

All data manipulation and analyses were conducted within the R statistical computing environment (R Core Team 2021). All the code to reproduce our analyses and results can be found on GitHub at http://www.github.com/EucTraitEcology/euc_phylo_traits.

Results

Traits varied considerably in their ranges across eucalypt species (Fig. 2). The most variable traits included Seed Mass (500-fold) and Fruit Mass (200-fold), Leaf Area and Relative Bark Thickness (nearly 40-fold), and Seed Mass, Leaf Mass, and Maximum Height (30-fold). The least variable trait was Stem Density, which varied roughly 1.5-fold. Specific Leaf Area showed five-fold variation, similar to Relative Height.

Effect of phylogeny on individual traits

A summary of the scaled trait values for continuous traits and fire-response categories and how they are distributed across the phylogeny is presented in Fig. 2. Being a primarily molecular phylogeny, many taxonomic groups delineated within well-known classifications were not preserved. Yet, many groups such as genera *Angophora* and *Corymbia*, all subgenera of *Eucalyptus*, and various sections within subgenus *Symphyomyrtus* (Brooker 2000) could still be recognised. The genera *Corymbia* and *Angophora* could be seen with characteristically large, heavy fruits and seeds along with our single eudesmid (*E. subgenus Eudesmia* Brooker 2000), *Eucalyptus pleurocarpa*, and the other basal monocalypts (*Eucalyptus* subgenus *Eucalyptus* Brooker 2000). Early diverging monocalypts (mainly *Eucalyptus* Sect. *Longistylus* Brooker 2000) generally had lower values for Maximum Height, Specific Leaf Area, Relative Bark Thickness,

Relative Height, Leaf Area and Leaf Mass along with greater values of Stem Sapwood Density. A similar phenomenon was noted within the symphyomyrtes (*E. subgenus Symphyomyrtus*), where section *Dumaria* (Brooker 2000) and section *Bisectae* (Brooker 2000) had similar clustering of basal-only resprouting coupled with lower values of Maximum Height, Specific Leaf Area, Leaf Area, Relative Bark Thickness and Relative Height, and higher values of Stem Density. There were only five obligate seeders in our dataset, all of which are monocalypts, not resolved as closely related in the phylogeny, and also classified in different sections. Most taxa were combination resprouters, with basal-resprouting taxa nested within the same clades.

Closely related eucalypt taxa tended to have similar trait values, but to varying degrees. Phylogenetic signal for each of the ten continuous traits (i.e. excluding fire response) ranged from weak in the case of Relative Bark Thickness ($\lambda = 0.37$), Leaf Mass ($\lambda = 0.41$) and Relative Height ($\lambda = 0.45$) to moderately strong for Specific Leaf Area ($\lambda = 0.82$) and Maximum Height ($\lambda = 0.80$) (Fig. 3). An entirely Brownian model of trait evolution, whereby present-day trait values could be correlated perfectly to ancestry, was rejected for all traits ($\lambda < 1$, $P < 0.0001$). For all traits except Relative Height, we could reject an absence of phylogenetic signal ($H_0: \lambda = 0$, $P < 0.05$).

Trait relationships

Overall, we found evidence for considerable coordination among traits. No traits were entirely independent – all traits correlated with at least one other trait with at least moderate strength $|r| > 0.3$ in both cross-species and phylogenetic analyses. Strengths of relationships varied widely (r^2 : <0.001 – 0.82) and effect sizes (slope magnitudes) ranged from 0.04 to 0.908 for cross-species analyses and from 0.009 to 1.03 for phylogenetic analyses respectively. Stronger relationships had larger effect sizes (slopes closer to one). Phylogenetic signal in trait relationships varied considerably ($\lambda = 0.000001$ – 0.864) even between models with the same dependent variable. A full summary of all regression coefficients for all trait relationships along with a matrix plot of correlation strength is available in Supplement 7.

Correlation networks (Fig. 4) displayed the number and strength of correlations between traits of at least moderate strength with thicker lines for stronger relationships and the position of the trait reflecting the overall strength of all correlations. Correlation networks showed several similarities in the trait relationships found using cross-species analyses (Fig. 4a) and those using phylogenetic analyses (Fig. 4b). Specific Leaf Area was consistently a hub in the networks, being the most, or among the most, connected traits, showing eight (of 10 possible) moderate correlations in the cross-species analyses (Fig. 4a). Resprouting mode was coordinated

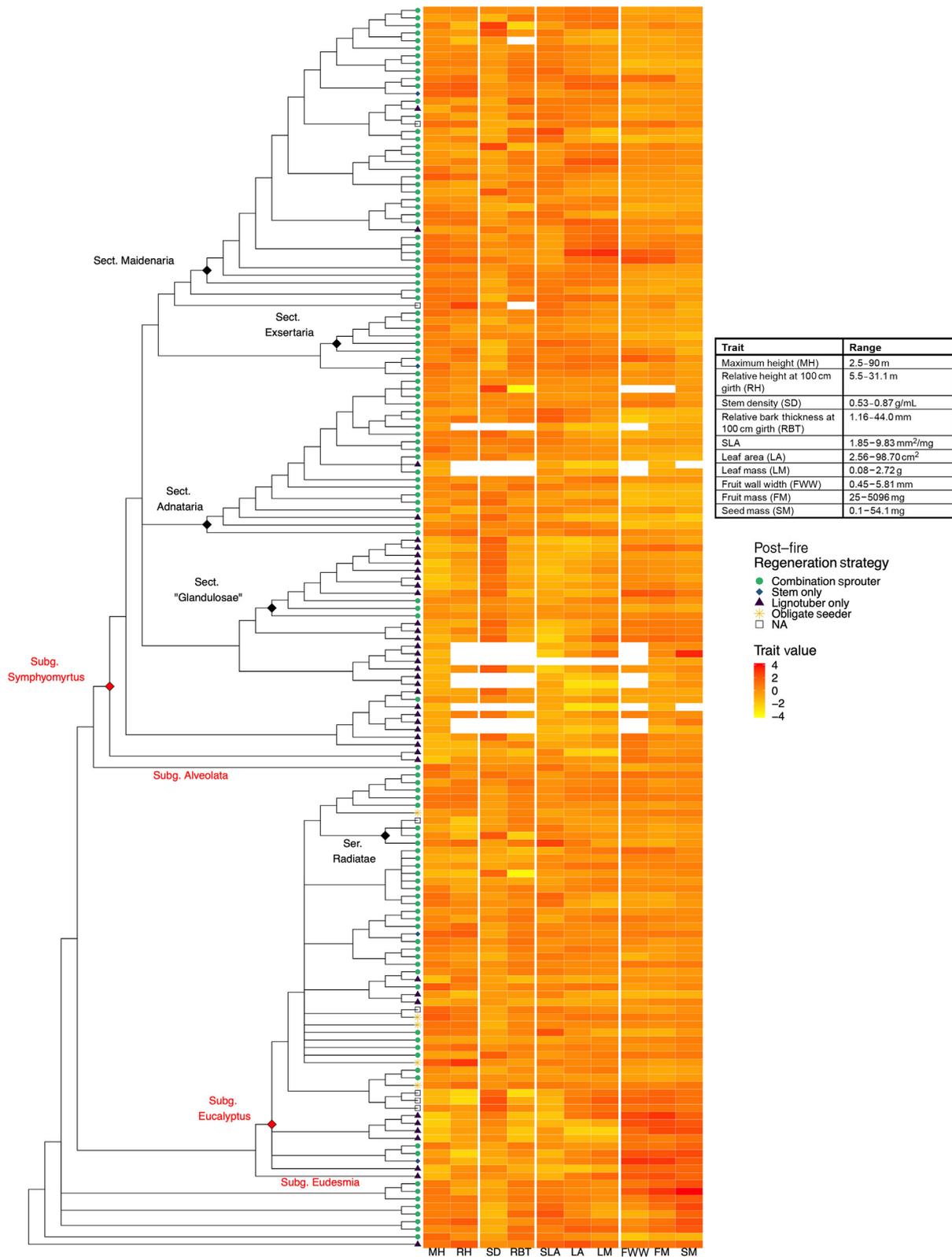


Fig. 2. Distribution of 10 continuous traits and fire-response category across a phylogeny of 164 eucalypt taxa. Abbreviations follow Table 1. Trait values have been log-transformed and scaled for comparison in the heatmap and the Table displays untransformed trait ranges. For inclusion of taxon labels see Fig. S6. Some subgenera, following Nicolle (2019), are indicated in red font and diamonds, and some lower taxonomic levels in black font and diamonds.

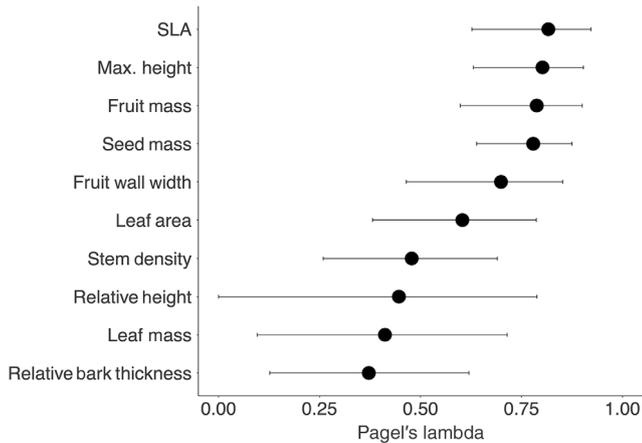


Fig. 3. Phylogenetic signal measured by Pagel's lambda ($\pm 95\%$ confidence interval) for each continuous trait.

with each of leaf, stem and stature traits, indicating the importance of fire response to ecological strategies of eucalypts.

Both networks displayed a general pattern of stem and stature traits (Maximum Height, Relative Height, Stem Density mostly) being positioned on the opposite side of the network to the reproductive traits (Fruit Wall Width, Fruit Mass and Seed Mass) with leaf traits linking the two. This opposition reflects that not only are the stem and stature traits not correlated with reproductive traits, but the patterns of correlation that they each show with the leaf traits differ between those two trait groups. The reproductive traits, Fruit Wall Width, Fruit Mass and Seed Mass showed the greatest correlations ($0.7 < r < 0.9$) among traits reflecting physical constraints: to make big seeds or to have thick fruit walls, requires larger fruits. Unsurprisingly, Leaf Area and Leaf Mass were also consistently strongly correlated ($r > 0.85$), being two measures of leaf size. Being connected to the fewest traits, Seed Mass was at the outside in the cross-species networks, and Relative Height and Stem Density were least correlated with other traits in the phylogenetic network. However, all three traits consistently appeared in relatively peripheral positions on both networks, regardless of their number of connections. Full network diagrams for both analyses, showing either all relationships or only those statistically significant, are in Fig. S8.

Although networks of trait relationships were generally consistent between cross-species and phylogenetic methods, they differed in detail. The network based on phylogenetic analyses generally had fewer connections (Fig. 4) and weaker pairwise trait correlations (based on effect size and correlation strength) than the cross-species network (Fig. 5). Relationships between stem, stature and leaf traits, reflecting taller trees being lanky with thick bark and big leaves but low stem density, were particularly weakened in phylogenetic analyses, resulting in a less pronounced trait cluster. The

connectedness of Specific Leaf Area became even more apparent in the phylogenetic network as other trait relationships weakened.

Although stronger and more numerous moderate relationships ($|r| > 0.3$) emerged in the cross-species analysis, the relationships between leaf traits (Specific Leaf Area, Leaf Area, and Leaf Mass) and reproductive traits (Fruit Wall Width, Fruit Mass, and Seed Mass) had stronger effects when measured using phylogenetic analyses (Fig. 5). Five (of all possible 55) trait–trait correlations were no longer significant ($P > 0.05$) with phylogenetic analyses, whereas three became significant with phylogenetic analyses. This can also be seen in the networks (Fig. 4) where the stem, stature and leaf traits became farther apart and more sparsely correlated, whereas leaf size traits appear much closer to the reproductive trait cluster and positive correlations between Leaf Mass and Seed Mass as well as Leaf Area and Fruit Mass exceeded $r = 0.3$.

Post-fire regeneration strategies overlapped in trait values, although some notable differences were found especially in stem and leaf traits (Fig. 6) and most of these results were similar between the cross-species and phylogenetic analyses. Obligate seeders tended to fall within the trait ranges of the combination resprouters and were few, so we focus on the resprouters here. Supplementary results and discussion relating to obligate seeders and their traits can be found in Supplement 9. On average, basal-only resprouters differed significantly from combination resprouters; they were shorter (Maximum Height -1.62 ± 0.12 (cross-species effect size \pm s.e.); -1.52 ± 0.16 (phylogenetic effect size \pm s.e.)), more stout (Relative Height -0.38 ± 0.18 ; -0.38 ± 0.18), with denser wood (Stem Density 0.89 ± 0.18 ; 0.65 ± 0.21), thinner bark (Relative Bark Thickness -1.12 ± 0.18 ; -1.12 ± 0.18), smaller leaves (Leaf Area -1.40 ± 0.15 ; -1.15 ± 0.19), which were thicker and denser (Specific Leaf Area -1.41 ± 0.15 ; -0.91 ± 0.19), and lighter (Leaf Mass -0.74 ± 0.18 ; -0.71 ± 0.21), with thicker fruit walls (Fruit Wall Width 0.76 ± 0.19 ; 0.54 ± 0.23) in both analyses. The greatest differences between basal-only resprouters and combination resprouters and those where fire response explained the most trait variation, were that basal-only resprouters were shorter (Maximum Height: cross-species $r^2 = 0.56$; phylogenetic $r^2 = 0.40$), had lower Specific Leaf Area (0.37; 0.14), had smaller leaves (Leaf Area: 0.36; 0.20), and thicker bark (Relative Bark Thickness: 0.23; 0.22) (Fig. 6).

Most trait differences between post-fire regeneration strategies weakened when phylogenetic analysis was used, though without crossing the threshold of $P = 0.05$. Only in the cross-species analysis did basal-resprouters also have significantly, though weakly, heavier seeds (0.42 ± 0.19) than combination resprouters. This difference was found to be non-significant in the phylogenetic analysis. The full summary of plots showing the distribution of each trait within each fire-response category can be found in Fig. S2.

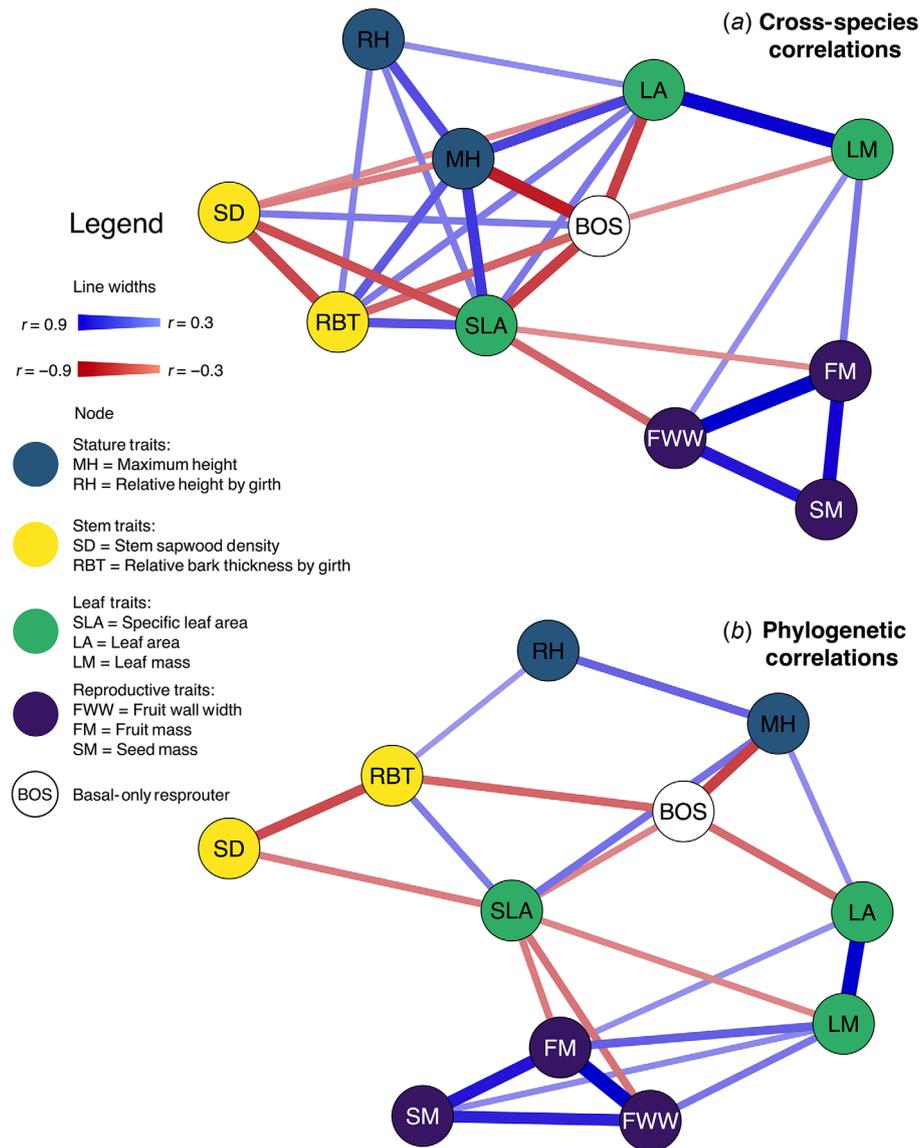


Fig. 4. Trait network diagrams of bivariate correlations among eucalypts summarising (a) cross-species correlations and (b) phylogenetic correlations. Network diagrams represent traits as nodes in a network connected by lines (or arcs) of correlations. Stronger correlations appear as thicker lines and shorter distances between traits. The pattern in the network reflects the overall strength of correlations among all traits. So traits with more, stronger correlations with other traits appear connected by more lines and close to other traits. Hence traits that may be considered ‘hubs’, appear near the centre of the network, connected by lines to multiple traits, e.g. specific leaf area. Traits with weaker and/or fewer correlations appear at the edges of the network. Here, line thickness = $\pm\sqrt{r^2}$ from regression models, henceforth referred to as r . To aid visualisation, only correlations with $|r| > 0.3$ are displayed in the network (adjusted $P < 0.05$), though position of traits is preserved. Abbreviations follow Table 1. Sample sizes for each regression model for each pairwise comparison ranged from 136 to 159. Note that $|r|$ is not comparable across networks, only within a given network.

Discussion

This study examined integrated functional relationships within eucalypts, predominantly genus *Eucalyptus* in southern Australia, demonstrating the usefulness of network methods

that include trait–trait relationships across multiple organs and functions. Our results suggest reproductive traits (Fruit Wall Width, Fruit Mass, and Seed Mass) are strongly correlated with each other, with leaf traits (Specific Leaf Area, Leaf Area) linking them to a loose cluster of stem and stature

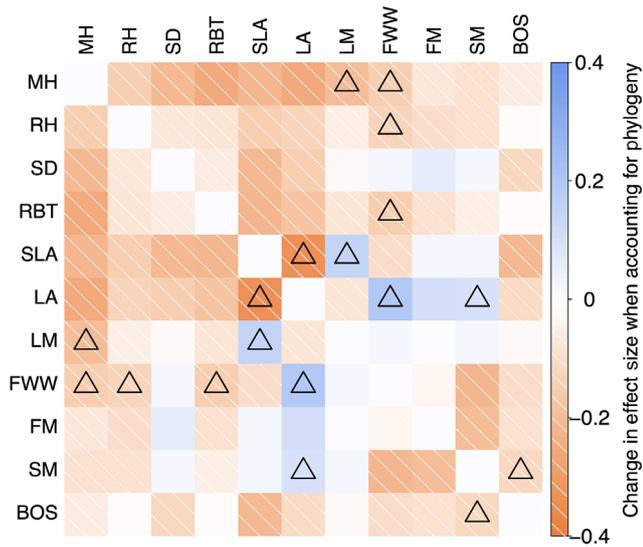


Fig. 5. Difference in effect strength (indicated by the colour scale) between the cross-species and phylogenetic regressions ($|\text{phylogenetic slope}| - |\text{cross-species slope}|$) for each model testing a possible trait pair. The triangle icon on a model indicates a change in effect size that accompanied a change in statistical significance ($P > \text{or} < 0.05$). Note, the phylogenetic models used here for each pair of traits were those that generated the highest lambda value of the two options of assigning dependent and independent variables (see Table S7.2). Trait abbreviations follow Table 1.

traits (Stem Density, Relative Bark Thickness, Maximum Height and Relative Height respectively). Many relationships (e.g. Maximum Height–Leaf Area, Leaf Area–Specific Leaf Area, Specific Leaf Area–Stem Density, Leaf Area–Stem Density), though not all (e.g. Seed Mass–Maximum Height, Seed Mass–Specific Leaf Area), were consistent with those measured elsewhere in global datasets (Díaz et al. 2016; Kleyer et al. 2019). Fire response strategies also were correlated with stem and fruit traits. Most traits differed

considerably (often >1.5 fold) between basal-only and combination resprouters. Phylogenetic signal was variable across traits and shared ancestry generally resulted in amplified trait relationships among extant taxa, especially between stem and leaf traits. However, these phylogenetic effects were not uniform and rarely altered statistical significance of trait correlations. Despite strong phylogenetic signal on several individual traits and some trait–trait relationships bearing phylogenetic signal, the broad patterns of correlation among stem, leaf and reproductive traits were robust to phylogeny. Hence, traits strongly correlated among extant taxa likely represent correlated evolution throughout the eucalypts.

Broad trait relationships that were robust to phylogeny

Our results suggest that different dimensions of plant ecological strategy relate to one another and the whole plant does represent an integrated phenotype. Here we discuss those relationships that were detectable by both cross-species and phylogenetic analyses, indicating they are robust to phylogeny. We found strong coordination among reproductive structures, as expected considering that accessory costs of reproduction are known to scale proportionally with seed size (Henery and Westoby 2001; Lord and Westoby 2006). We also found strong coordination between both measures of leaf size and all fruit and seed traits. These associations support ‘Corner’s Rules’ in eucalypts (Corner 1949; Wright et al. 2007), suggesting taxa with twigs capable of bearing large, heavy leaves would also be able to have larger and more elaborate fruits. The robust position of Specific Leaf Area as a hub, highly connected to other traits throughout the phylogeny or across its tips, indicates the important role that the leaf economics spectrum (Wright et al. 2004) plays in multiple dimensions of variation within extant eucalypt taxa studied here and through their evolution.

We find that, compared to other analyses, Specific Leaf Area is a highly connected trait acting as a hub in our

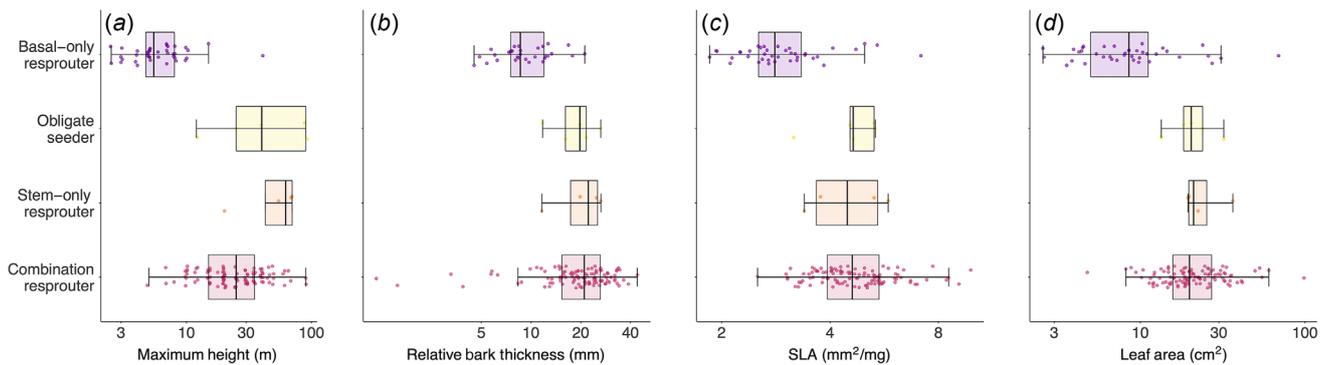


Fig. 6. Boxplots with data plotted traits showing greatest differences between basal-only and combination resprouters. Distribution shown of (a) Maximum Height, (b) Relative Bark Thickness, (c) Specific Leaf Area, and (d) Fruit Wall Width within obligate seeders, basal-only resprouters, and combination resprouters for 151 eucalypt taxa for which fire-response data was available. Note, though scaled data was used for analysis, the x-axis labels are on the original scale. Whiskers extend from interquartile range (IQR) to the largest value no further than 1.5 times the IQR.

networks as well as relatively strongly correlated with other traits. Notably, Specific Leaf Area was positively correlated with Maximum Height and negatively with Stem Sapwood Density; these effects remained when considering evolutionary divergences. Compared to several studies in the Neotropics (Wright *et al.* 2007; Baraloto *et al.* 2010; Fortunel *et al.* 2012) and globally (Díaz *et al.* 2016; Flores-Moreno *et al.* 2019), we found stronger evidence that species of taller trees supported flimsier leaves and that species with more robust leaves had more dense stems. Why might this be? Two aspects of environment may contribute. Compared to the global climates, our sites do not experience strong seasonality, nor very low temperatures, where deciduousness becomes a profitable strategy. Neither is rainfall sufficiently seasonal to justify seasonal drought deciduousness, as is found in wet-dry tropics (Williams *et al.* 1997; Eamus *et al.* 1999). On the other hand, rainfall ranges widely across our sites (e.g. 325 mm mean annual rainfall at Murrayville in northwestern Victoria, to 1368 mm at Falls Creek in the Bogong High Plains of Victoria, data from <http://www.bom.gov.au/climate/data/index.shtml>). Possibly lower water availability drives a coordinated shift in each of lower Specific Leaf Area, higher Stem Density and shorter Maximum Height.

The commonly reported positive relationship between Maximum Height and Seed Mass (Moles *et al.* 2005; Wright *et al.* 2007; Díaz *et al.* 2016) did not appear in either the cross-species or phylogenetically-informed analysis in the eucalypts we studied. Murray and Gill (2001) found a negative correlation between height and fruit size, in a dataset primarily comprising southwestern WA eucalypts. It is possible that a complex interplay of aridity, nutrient poverty, fire frequency, fire severity, plant height, and recruitment dynamics has affected trait expression in the eucalypts (Murray and Gill 2001; Hopper 2021). Further investigation should help clarify what is driving this difference between eucalypts and other plant groups. Notably, this study is biased in sampling to south-eastern Australia. This bias is present in both the environments sampled, but also phylogeny. We have very few *Corymbia*, which are predominantly a northern Australian clade. Further work should endeavour to cover more species from northern and western Australia. We also note that our sampling of mallee growth form eucalypts strongly represents subgenus *Symphyomyrtus* section *Bisectae* (Brooker 2000) and *Eucalyptus* sect. *Dumaria* (L.D.Pryor & L.A.S.Johnson ex Brooker 2000), characteristic of dry regions, whereas those from subgenus *Eucalyptus* section *Eucalyptus* (Brooker 2000) characteristic of wetter regions, were less sampled.

Fire response strongly associated with traits and trait shifts through the phylogeny

Our results reveal that post-fire regeneration strategies and the functional traits of eucalypts are strongly intertwined. We focus on combination resprouters and basal-only resprouters

and their traits and differences, with discussion of the few obligate seeders in Supplement 9. All patterns of traits differing between fire responses were robust to phylogeny, except the differences in fruit and seed mass of basal-only and combination resprouters. This suggests that differentiation between these fire-response categories in extant taxa is underlain by repeated correlated shifts in fire response and almost all traits.

Several traits were particularly strongly associated with fire responses. Aside from the few obligate seeding species (Supplement 9), our results support an interpretation that tall maximum height is benefitted by epicormic resprouting, distinctive among the eucalypts (Burrows 2013), whereas basal-only resprouting is associated with shorter maximum heights. This is likely because, at greater heights, the time difference to re-establish a canopy after fire by resprouting directly from an already-elevated trunk, compared with having to regrow the entire trunk from the ground, is much greater (Burrows 2013; Pausas and Keeley 2017). The multi-stemmed habit (mallee) common amongst basal-only resprouters also means that for the same investment in woody tissue, the maximum height of the whole plant must be shorter (Midgley 1996; Kruger *et al.* 1997). Basal-only resprouting needs no thick bark as the stems are regrown following fire, whereas epicormic resprouters (and obligate seeders) benefit from protective bark (Burrows 2002; Vesik and Westoby 2004a; Lawes *et al.* 2011, 2013; Clarke *et al.* 2013; Pausas 2015). This also provides a potential explanation for the tallest eucalypts, surprisingly, having the thickest bark overall, especially given the resource-intensive nature of maintaining thick bark as protection (Lawes *et al.* 2011, 2021; Pausas 2015). It is possible that such tall taxa compromise in other areas such as lower wood density. However, the link between tall species and thick bark may also be artefactual, given that bark thickness was only measured at a single height and many tall taxa (e.g. *Eucalyptus regnans*, *Eucalyptus pilularis*) have a 'skirt' of thick, rough bark at the base with much thinner bark above. This results in such tall species driving a positive correlation between Maximum Height and thick bark. How representative the thickness of the bark of the skirt is of bark on higher branches is unclear and would be valuable information.

It is worth noting that many of the traits most related to fire response are also known to vary along environmental gradients (Wright *et al.* 2005; Liu *et al.* 2019; Lawes *et al.* 2021) and many of our basal-only resprouters were sampled in more arid environments. This would reduce both Specific Leaf Area and Maximum Height and could account for some of the observed associations between these traits and fire responses. Although numerous studies relate traits to environment (e.g. Wright *et al.* 2005; Pollock *et al.* 2012; 2018) and other studies relate traits to fire-response (e.g. Pausas 2015; Lawes *et al.* 2021), we are not aware of work that does both simultaneously. Further work should aim to

clarify the relative effects of fire response and environment on traits.

Traits displayed phylogenetic signal but with varied strength

Our results show that some traits are strongly related to patterns of heredity, but others are less so. The distributions of continuous traits across the phylogeny were also neither purely Brownian nor absent of any phylogenetic influence. Hence, although the evolution of these functional traits is most certainly affected by some form of selection pressure, ancestry remains an important factor driving many aspects of the functional ecology of extant *Eucalyptus* species.

Although phylogenetic signal for the categorical trait of resprouting could not be calculated, the uniformity of basal-only resprouting within certain lineages is notable, as broad studies across plant phylogeny have found that resprouting in the broad sense is an ancient trait and is labile across broader phylogenies (Vesk and Westoby 2004b; Pausas and Keeley 2014; Lawes et al. 2022). Epicormic resprouting in the eucalypts appears to have evolved from ancestors unable to resprout epicormically (see Crisp et al. 2011). One possible explanation is that the evolution of epicormic resprouting within the eucalypts and relatives presented by Crisp et al. (2011) refers to combination (i.e. epicormic and basal) resprouters, not epicormic resprouting only. Then, basal-only resprouting has repeatedly emerged after subsequent loss of epicormic resprouting ability while retaining basal-resprouting ability.

Highly conserved traits (Maximum Height, Specific Leaf Area, Seed Mass and Fruit Mass) indicated that the eucalypt taxa we studied had most similar maximum height, leaf economics strategies, and fruits and seeds to that of their ancestors and close relatives. Hence, related species are also more likely to have similar tendencies within 'height growth' strategies (Moles et al. 2009), leaf economics strategies (Wright et al. 2004), and seed and seedling provisioning strategies (Muller-Landau 2010). Although this does not necessarily indicate slow evolutionary rates for these traits (Ackerly 2009), it may indicate greater phylogenetic inertia (Felsenstein 1985) within these traits.

The associations of traits such as Maximum Height, Specific Leaf Area, and Seed Mass with environmental gradients have been the focus of numerous studies (in eucalypts see e.g. Schulze et al. 2006; Pollock et al. 2012, 2018; Liu et al. 2019). They reveal varied, and apparently scale-dependent patterns of association, with the climatic associations of height being the clearest (Moles 2018). If environment does influence the relative performance of different trait values, then we might expect strong environmental driving forces to overcome phylogenetic inertia more readily, resulting in relatively a weak phylogenetic signal. Yet, we observed strong phylogenetic signals in these traits (see also Ackerly 2004; Pollock et al. 2015). This may indicate that environmental trait

optima themselves have phylogenetic signal (Hansen et al. 2008). Alternatively, adaptation may be overridden by community assembly via dispersal, abiotic and biotic filtering of taxa from a wider species pool (Keddy 1992), as has been shown to influence traits of co-occurring *Eucalyptus* taxa in Gariwerd Grampians (Pollock et al. 2015).

Furthermore, Leaf Mass and Relative Height, which had among the lowest phylogenetic signal, have not been especially associated with environmental gradients, relating more to allometry (Corner 1949) and perhaps light availability and adaptation to herbivory (Dantas and Pausas 2013) respectively. Bark thickness has been shown to be quite labile within species, likely related to fire regime (Lawes and Neumann 2022), which would accord with low phylogenetic signal. Variance partitioning analysis on a large subset of the taxa studied also suggests that Relative Height varied more within than between species (data not shown). Also, stature is well known to be plastic as the form of trees growing in open paddocks compared to dense plantings readily demonstrate. Hence, Relative Height may not be particularly stable for a given species and its use in cross-species studies may require greater intra-specific replication.

We also noted that traits with high phylogenetic signal were not necessarily correlated and the clades in which taxa had most similar trait values were sometimes different. This indicates that any phylogenetic inertia or lag on trait evolution imposed by phylogeny (Felsenstein 1985) was not specific to any one lineage and trait shifts likely occurred at different divergences in the tree.

Phylogenetic signal depends upon both the scale and accuracy of the phylogeny. Depending on the traits of other genera and families, our findings regarding relative degrees of phylogenetic signal of different traits may not apply at higher levels (Cornwell et al. 2014). Hence, the phylogenetic signal discussed here should be interpreted in the context of the eucalypt clade, and predominantly within *Eucalyptus* and its main subgenera and sections. All assessments of phylogenetic signal (and adjusted correlations depending on it) are also subject to phylogenetic uncertainty. The method by which the phylogeny was built assumed monophyly of species to place the most taxa on the tree. Monophyly may not be reasonable, especially given that different samples of the same eucalypt taxon collected at different locations can form a paraphyletic or even polyphyletic group (Jones et al. 2016). We also assumed bifurcating speciation and divergence, which does not consider the well-established ability of eucalypts to hybridise and undergo more reticulate modes of evolution (Griffin et al. 1988; Jackson et al. 1999; Pollock et al. 2013). We also combined two phylogenies (Bayly et al. 2013, Thornhill et al. 2019) to resolve deep divergences and only used a single tree from Thornhill et al.'s (2019) study and many of the relationships of sections and series within subg. *Eucalyptus* (Monocalypts), e.g. series *Pachyphloia* (stringybarks) appear spurious in light of longstanding morphological classification (Brooker 2000) and remain uncertain. We suggest that similar

analyses using alternative phylogenies would be a fruitful avenue for future work.

Pattern of correlated evolution generally weaker when accounting for phylogeny, but not always

The strengths of most (but not all) relationships were found to weaken upon accounting for shared ancestry. This was most notably observed in the relationships between Specific Leaf Area, Stem Density, Maximum Height, Relative Bark Thickness and Leaf Area (Fig. 4). Within this subset of traits, a consistent pattern of correlated evolution of shifts to shorter trees were accompanied by shifts to thinner bark, lower Specific Leaf Area and smaller leaves, likely associated with the overall safety vs height dimension, allometry, or environmental affinities (Wright *et al.* 2005; Liu *et al.* 2019; Lawes *et al.* 2021). However, several of the correlations among leaf and stem traits weakened or became negligible among phylogenetically independent divergences on the tree. Thus, many of those associations occurred in more closely related taxa rather than in many independent lineages and are less likely to be generalisable to other clades.

Interestingly, the positive relationships between leaf and fruit (also seed) size strengthened upon accounting for phylogeny (Fig. 5). This suggests coordinated evolution of these traits throughout the evolution of the eucalypts, more than would be suggested by the prevalence of this trait combination within extant taxa. In addition to not being uniform in its amplification, shared ancestry can also obscure certain trait correlations.

Together these results suggest that although details of relationships within trait networks were more vulnerable to effects of shared ancestry, especially if they were weak, changes in statistically significant relationships were observed in only a minority of cases. Only one trait relationship with $|r| > 0.3$ became non-significant ($P > 0.05$) after accounting for phylogeny – that between Specific Leaf Area and Leaf Area. This suggests that for eucalypts we can have reasonable confidence that the broad evolutionary relationships between these traits with moderate strength in extant taxa are likely to generalise to other clades and do represent correlated evolution. However, we caution interpreting marginal results or those from small studies (see also Wright *et al.* 2005).

We hope that this study inspires further work to clarify the evolution of the eucalypt clade and provides a basis for systematic investigation of trait–environment relationships in trees at a subcontinental scale.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The authors have archived the data in the Zenodo Digital Repository (<https://doi.org/10.5281/zenodo.8313641>). Observation-level data have also been uploaded to AusTraits (Falster et al. 2021): <https://doi.org/10.5281/zenodo.7583087>.

Conflicts of interest. The authors declare that they have no conflicts of interest.

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