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Structural diversity underpins carbon storage in Australian temperate forests

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Biosketch

The author team is broadly interested in understanding forest dynamics and the impacts of fire, climate and management on forest values now and into the future.

Data Accessibility

Data available from Figshare

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Abstract

Aim: Forest carbon storage is the result of a multitude of interactions among biotic and abiotic factors. Our aim was to use an integrative approach to elucidate mechanistic relationships of carbon storage with biotic and abiotic factors in the natural forests of temperate Australia, a region that has been overlooked in global analyses of carbon-biodiversity relations.

Location: South-eastern Australia

Time period: 2010 – 2015

Major taxa studied: Forest trees in 732 plots

Methods: We used the most comprehensive forest inventory database available for south-eastern Australia and structural equation models to assess carbon-storage relationships with biotic factors (species or functional diversity, community-weighted mean (CWM) trait values, structural diversity) and abiotic factors (climate, soil, fire history). To assess the consistency of relationships at different environmental scales, our analyses involved three levels of data aggregation: six forest types, two forest groups (representing different growth environments), and all forests combined.

Results: Structural diversity was consistently the strongest independent predictor of carbon storage at all levels of data aggregation, whereas relationships with species- and functional-diversity indices were comparatively weak. CWMs of maximum height and wood density were also significant independent predictors of carbon storage in most cases. In comparison, climate, soil, and fire history had only minor and mainly indirect effects via biotic factors on carbon storage.

Main conclusions: Our results indicate that carbon storage in our temperate forests was underpinned by tree structural diversity (representing efficient utilisation of space) and by CWM trait values (representing selection effects) moreso than by tree species richness or functional diversity. Abiotic effects were comparatively weak and mostly indirect via biotic factors irrespective of the environmental range. Our study highlights the importance of managing forests for functionally important species and to maintain and enhance their structural complexity in order to support carbon storage.

Keywords: forest carbon, fire, functional diversity, functional identity, mass-ratio, niche-complementarity, structural diversity, structural equation model, temperate forests.

1. INTRODUCTION

Forests are a critical component of the global carbon cycle as they support 70-90% of terrestrial aboveground and belowground biomass (Houghton, Hall,Goetz, 2009) and are a major carbon sink (Pan et al., 2011). Carbon stored in forest biomass is often estimated as a cumulative function of net primary productivity (Pan, Birdsey, Phillips,Jackson, 2013), which has been positively linked with plant diversity (species, phylogenetic, and/or functional) in a range of forest types (Liang et al., 2016; Paquette,Messier, 2011; Poorter et al., 2017). Similarly, positive relationships have been documented between plant diversity and other forest-ecosystem functions relating to nutrient cycling, regeneration, and resistance to disturbance (Ratcliffe et al., 2017). Nonetheless, much remains unknown about the mechanisms underpinning positive associations between biodiversity and functions like productivity, particularly in natural ecosystems (Tilman, Isbell,Cowles, 2014). In addition, relationships between biodiversity and carbon stocks ('carbon storage'), which are driven not only by productivity but also by mortality (Pan et al., 2013), remain under-examined for many forest types.

Two main non-mutually exclusive mechanisms underpin positive biodiversity-ecosystem functioning (BEF) relationships: the niche complementarity effect, where niche partitioning and facilitation among species allow diverse communities to exploit available resources more efficiently than less diverse communities; and the selection effect, where diverse communities are more likely than species-poor communities to contain highly functional species that contribute strongly to ecosystem productivity and carbon storage (Loreau,Hector, 2001; Tilman et al., 2014). The importance of niche complementarity in forests worldwide has been indicated by multiple examples of greater carbon storage with increasing diversity of plant species (Huang et al., 2018; Poorter et al., 2015; Ratcliffe et al., 2017), and/or functional traits ('functional diversity'; (Ruiz- Benito et al., 2014). Nonetheless, selection effects on forest carbon storage have also been indicated in part through support for the 'mass-ratio' hypothesis (Ruiz- Benito et al., 2014), which suggests that carbon storage will be mainly determined by the functional traits of the dominant species (Mokany, Ash,Roxburgh, 2008). That is, support for the mass-ratio hypothesis has been indicated by close associations of forest biomass or carbon stocks with community-weighted mean (CWM) trait values for a range of forest types (Adair, Hooper, Paquette,Hungate, 2018; Finegan et al., 2015; Fotis et al., 2018). Indeed, the relative importance of complementarity and selection mechanisms can vary between forest types (Ruiz- Benito et al., 2014), highlighting the need for further BEF studies that encompass an extended range of forest conditions.

In addition to plant species/functional diversity and CWM trait values, the structural arrangement of forests provides insights into the mechanisms underpinning relationships between forest carbon storage and biotic factors. In particular, tree 'structural diversity' – represented by measures of tree-size variability (Brassard, Chen, Wang,Duinker, 2008) – has been highlighted in some studies as having a positive association with forest carbon storage (Wang, Lei, Ma, Kneeshaw,Peng, 2011), since high structural complexity of trees can enhance efficient use of resources for growth (Zhang,Chen, 2015). Structural diversity can be related to species or functional diversity since increasing species/functional diversity could lead to the occupation of more spatial niches (Brassard et al., 2008; Zhang,Chen, 2015). However, structural and functional diversity are not always highly correlated since monospecific and species-poor stands can still be structurally diverse through vertical and horizontal differentiation of a limited number of species (Brassard et al., 2008). Similarly, while old-growth forests can be structurally complex (Franklin, 1988), structural diversity might not simply increase with time since disturbance. For example, successional pathways may lead to similar or greater complexity at early- (Donato, Campbell,Franklin, 2012) or mid-seral stages (Brassard et al., 2008). Also, disturbances like non-stand replacing fire may lead to mixed-aged structures comprised of post-fire regeneration and older resprouting cohorts (Bennett et al., 2017).

Abiotic factors influence forest carbon storage both directly through effects on processes like growth and decomposition, and indirectly through influences on biotic factors (Adair et al., 2018). Climate, for example, is closely associated with forest net primary productivity worldwide (Luyssaert et al., 2007), although this is at least partly due to indirect effects of climate on vegetation age (as influenced by time since last disturbance) and biomass (driven by maximum plant size; (Michaletz, Cheng, Kerkhoff,Enquist, 2014). Relationships between climate and forest productivity vary with the environmental range considered (Luyssaert et al., 2007), and climate also influences the relative importance of diversity effects on productivity. For example, tree productivity has been more closely associated with niche complementarity in harsher climates, and with selection effects in more benign climates (Mori, 2018; Paquette,Messier, 2011). However, complementarity effects on forest productivity are not always stronger in more stressful climates (Ruiz- Benito et al., 2014), and selection for particular traits can be important for tree growth in harsh climates (Ratcliffe et al., 2016), although the latter was at least partially attributed to successional shifts in trait variation (see also (Craven, Hall, Berlyn, Ashton,van Breugel, 2018). In terms of forest carbon storage, which is only partly dependent on productivity (Pan et al., 2013), forest biomass (a principal carbon stock) can be closely related to climate variables within geographically-restricted forest types but poorly related at broader continental scales (Stegen et al., 2011). This inconsistency in climate-biomass trends reflects spatially variable relationships among biomass, productivity, and mortality, which are also influenced by the spatial distribution of non-climatic factors including soil, disturbance, and species interactions (Pan et al., 2013).

In this study, we examine the relative importance of biotic factors (species and functional diversity, CWM trait values, and structural diversity) and abiotic factors to forest carbon storage in temperate south-eastern Australia, a region that has been overlooked in global analyses of carbon-diversity relations (Duffy, Godwin,Cardinale, 2017). Landscapes of south-eastern Australia encompass considerable biotic and abiotic heterogeneity (Kasel, Bennett, Aponte, Fedrigo,Nitschke, 2017), supporting a range of broadleaf evergreen forests of varying productivity, including some considered to be the most carbon-dense forests in the world (Keith, Mackey,Lindenmayer, 2009). These landscapes are frequently disturbed by fire, which has increased in frequency and extent in recent decades (Fairman, Nitschke,Bennett, 2016) raising concerns about the ongoing productivity and carbon stability of even the most fire-tolerant forests (Bennett et al., 2017). Our data include 14,933 trees and 134 species from 732 plots, which we aggregate into six forest types, and two forest groups representing productive and less-productive growth environments. We use structural equation modelling (SEM) as a powerful integrative approach (Grace et al., 2016) to examine the independent effects of multiple biotic factors (species and functional diversity, CWM trait values, structural diversity) on carbon storage, while controlling for relationships among those biotic factors and for both the direct and indirect effects of abiotic factors (climate, soil, fire history). Our hypotheses were: 1. Forest carbon storage increases with species and functional diversity, even when accounting for abiotic factors; 2. CWM trait values and structural diversity have comparable or greater independent effects than species/functional diversity on carbon storage; and 3. That the relative importance of biotic effects on carbon storage varies between growth environments, and, in particular, that species, functional and structural diversity (representing complementarity effects) are more important for carbon storage in the less-productive than productive forest group.

2. METHODS

2.1 Study area and forest plot data

We used data collected from c. 730 forest plots across Victoria, in south-eastern Australia (Figure 1), which we selected to encompass as wide a geographic range as possible, and to meet two key criteria: that they included only forest (i.e. not shrubland or grassland); and that all trees had been assessed in sufficient detail to calculate carbon stocks and biotic-factor variables (as below). Our plots spanned about 750 km east-west (35.95S to 39.11S), 360 km north-south (141.35E to 149.64E), and 1500 m in altitude (45–1600 m a.s.l.). Mean annual temperature ranged from 6.4 to 14.6 °C, and annual precipitation from 540 to 1960 mm predominantly falling in winter (~30%) and spring (~30%). Forest plots encompassed 22 ecological vegetation classes based on classifications by the Victorian State Government Department of Environment, Water, Land and Planning. We grouped those classes into six broad forest types (‘Mist’, ‘Rainforest’, ‘Damp’, ‘Montane woodland’, ‘Foothill’, ‘Lowland’) based on the dominant tree species (mostly Eucalyptus spp.), mapped distributions, and stand structure (Supplementary Table S1), and used climate conditions (precipitation, mean annual temperature) to aggregate these six types into ‘Wet’ (four types) or ‘Dry’ (two types) forests, where Wet forests generally represented a more productive environment than our Dry forests.

Plots were sampled in five different field campaigns from 2010 to 2015 (Supplementary Table S2) and involved a range of plot types from fixed-area plots of 0.1 ha, 0.04 ha to variable radius plots (Basal area factor = 4); Supplementary Table S2). At least two plot types were used in each forest type, with the exception of fixed-area plots only in Montane woodland.

2.2 Estimation of above-ground carbon storage

Carbon storage was estimated as carbon stored in the above-ground biomass of all live trees, which represent the principal carbon stocks in these forests and have the greatest carbon sequestration potential (Bennett, Aponte, Baker,Tolhurst, 2014 ; Bennett et al., 2017). Within each plot, live trees were assessed for species, diameter at breast height (DBH, 1.3 m height) and height (Supplementary Table S2; Online extended methods). We calculated above-ground biomass using DBH-based allometric equations that were specific for most eucalypts or generic for less common eucalypts and non-eucalypt species (Supplementary Table S3). We then multiplied tree biomass by average biomass carbon content (50%, (Aponte, Tolhurst,Bennett, 2014), scaled-up to a hectare and summed across all trees at plot level to estimate above-ground carbon storage (Mg ha^{-1}).

2.3 Predictor variables

We initially characterised each plot using 54 potential predictor variables that described biotic factors (species or functional diversity, CWM trait values, structural diversity) and abiotic factors (climate, soil, fire history; Supplementary Table S4). Potential species-diversity indices were based on the number of tree species (species richness, rarefied species richness) and their relative abundance (Shannon and Simpson species diversity indices; (Magurran, 2013). Functional diversity (FD) indices (dispersion, richness, evenness, divergence; (Laliberté,Legendre, 2010; Villéger, Mason,Mouillot, 2008) and community-weighted mean (CWM) trait values were calculated using five functional traits of tree species: maximum height, maximum DBH, wood density, seed mass, and specific leaf area (SLA). CWM trait values (based on relative species abundance as proportional basal area) were calculated for each individual trait, whereas FD indices (based on presence/ absence data) were calculated for all traits together to capture the multidimensional nature of plant functional space (Villéger et al., 2008). Our trait selection was based on the potential to influence tree reproduction, survival, and growth (Reich, 2014), and on evidence from forest BEF studies of trait importance to forest resource partitioning, productivity, and/or carbon storage; examples include: SLA (Craven et al., 2018), maximum DBH (Craven et al., 2018), and combinations of seed mass, maximum height, and wood density (Adair et al., 2018; Fotis et al., 2018; Ruiz- Benito et al., 2014). While linked through allometry, we included both maximum DBH and maximum height in FD indices as representations of potentially different growth forms and horizontal-vertical spatial niches, and on the basis that any (non-trivial) correlation among traits can be considered ‘a relevant aspect of species distribution in functional trait space’ (Villéger et al., 2008). Trait data were compiled from field measures, databases or published sources (as listed for CHM variables; Supplementary Table S4), and, depending on the trait, covered 60–100% of species, which together contributed >96% of the total basal area; missing trait values were filled using values from the nearest-related species of the same genus. Structural diversity indices were based on variability and evenness of tree height and DBH (Supplementary Table S4). Calculations of species and structural diversity were made using the ‘vegan’ R package (Oksanen et al., 2014), calculations of FD and CWM were made using the ‘FD’ R package (Laliberté, Legendre, Shipley,Laliberté, 2014).

Potential climate, soil, and fire-history variables (Supplementary Table S4) were collated based on the field-recorded location of each plot centre. Climate data of ~1-km^2 resolution were obtained from Worldclim (Hijmans, Cameron, Parra, Jones,Jarvis, 2005) and CGIAR (Zomer, Trabucco, Bossio,Verchot, 2008); soil data (~90-m^2 resolution) were obtained from CSIRO Data Collection (Viscarra Rossel et al., 2014); and fire-history data were obtained from DELWP (DELWP, 2014).

An initial assessment of predictor variables based on correlation analyses and principal component analysis (PCA) among variables in the same biotic or abiotic group was used to identify variables that were redundant (correlated with other predictors in the same group, $r \geq |0.7|$) and/or not significantly related to the response variable, carbon storage. These variables were excluded from subsequent analyses (see Supplementary Table S4). To reduce the number and collinearity of soil variables, the first PCA axis, rather than individual soil variables, was retained for further analysis because it explained 58% of soil data variability (collectively representing a gradient of increasing soil nutrient availability, clay content, and water retention capacity), and was more strongly correlated with carbon storage than any single soil variable. The final selected predictors of carbon storage included: Species richness (S), Functional dispersion (F_{dis}), CWM of maximum height (CWM_{MAXH}), CWM of specific leaf area (CWM_{SLA}), CWM of wood density (CWM_{WD}), Shannon structural diversity index (H'), Mean annual temperature (MAT, ºC), Soil PCA ($SOIL_{PCA}$), and Time-since-last wildfire (TSLWF, years).

2.4 Statistical analyses

We examined relationships of carbon storage (as above-ground carbon stocks in live trees per plot) with plot-level estimates of the nine selected predictor variables using bivariate relationships with each predictor, and structural equation models (SEMs) that integrated multiple predictors. To examine consistency of relationships across growth environments and environmental ranges, we implemented all statistical analyses at three levels of plot aggregation: forest type (n=6), Wet and Dry forests, and Temperate forest (all data pooled). To adhere to assumptions of data normality and homoscedasticity, both carbon storage and S were square-root transformed, and TSLWF was $\log_{10}$+1 transformed, prior to statistical analyses. All non-transformed and transformed predictor variables were standardised (by subtracting the variable's mean and dividing by the standard deviation) prior to bivariate analyses and SEM development.

We examined bivariate linear and non-linear (quadratic) relationships of carbon storage with predictors to elucidate the form of these relationships, and to ensure that they were adequately captured in the SEMs (below). Bivariate relationships were run as mixed models using the 'nmle' R package (Pinheiro, Bates, DebRoy, Sarkar,R-core Team, 2019), with plot type (i.e. large plot, 0.1 ha; small plot, 0.04 ha; and variable radius plot BAF4) as a random effect. The relative strength of a predictor's relationship with carbon storage was assessed using the standardized coefficients (β, the higher the value the stronger the relationship), and the change in the Akaike Information Criteria (ΔAIC). Heterogeneity in plot size can influence estimates of diversity and carbon storage (Rosenzweig, 1995). We found no significant relationships between plot type and diversity metrics and carbon storage. Plot type was included in the mixed models, but it had not influence on the strength of predictor relationships with carbon storage. A separate analysis (data not shown) using boosted tree regression showed negligible influence of plot type on our results (< 1% relative to other predictors) (Zhang,Chen, 2015).

We used SEMs as an integrative approach (Grace et al., 2016) to examine the independent effects of each biotic factor on carbon storage. Our SEM schematic (Figure 2) reflects our main hypotheses; for example, that species or functional diversity would have a significant independent effect on carbon storage even when accounting for the direct and indirect effects of abiotic factors and the direct effects of other biotic factors. Note that while correlations among biotic factors included in SEMs were weak ($r \leq 0.4$, Supplementary Table 5) and their covariance was accounted for in the SEMs they are not considered further because our focus was on comparing the independent effect of each biotic factor on carbon storage (after (Adair et al., 2018; Poorter et al., 2017)). We built on a previous conceptual SEM for biomass stocks in neotropical forests (Poorter et al., 2017) by including H', as a test of the independent effects of structural diversity, rather than basal area, which might have been trivially related to tree-biomass carbon since both were derived from DBH. A separate analysis on the relationships between H', basal area and tree-biomass carbon showed that the three variables tended to covariate (r ~ 0.5) but confirmed the independent effect of structural diversity on tree carbon when accounting for basal area (Online extended methods). At each level of data aggregation, we considered six possible SEMs, which were the result of combining each of two variables representing species or functional diversity (S or F_{dis}), with each of three CWM trait values (CWM_{SLA} or CWM_{MAXH} or CWM_{WD}), and a fixed set of variables to represent structural diversity (H'), and abiotic factors (MAT, $SOIL_{PCA}$, TSLWF). MAT was included as a composite variable ("MAT+MAT^2") to account for its unimodal relationship with carbon storage (as indicated by the above bivariate analyses). All SEMs were developed using the lavaan R package (Rosseel, 2012), with models compared using ΔAIC, AIC weights (normalized model relative likelihoods, which can be directly interpreted as conditional probabilities for each model), and the comparative fit index (CFI), which provides an indication of the relative improvement in fit of a given SEM over an (implausible) baseline model, which assumes all variables are non-correlated (CFI > ~0.9 indicating good fit; (Rosseel, 2012)).

3. RESULTS

3.1 Carbon stocks and forest environment

Mean carbon storage was greater in Wet (178 Mg C ha^{-1}) than Dry (109 Mg C ha^{-1}) forests (Supplementary Table S6), with trends in carbon stores by forest type reflecting those in basal area and tree density (Figure 3). Dry forests were on average 30% drier and two degrees warmer than Wet forests, with Lowland forest being the driest (MAP = 943 mm) and Montane woodland being the coldest (MAT = 8.1 ºC; Figure 3). Species diversity (S) was on average lower in Dry than Wet forests, although mean S was low (2 to 5) irrespective of forest type (overall range 1 to 14; Supplementary Table S6). The two broad forest groups encompassed similar ranges in most other biotic variables (Figure 3; Supplementary Table S6).

3.2 Bivariate relationships

Carbon storage was most strongly related to structural diversity (H') in all cases (as evidenced by greater β and ΔAIC; Table 1; Figure 4). Carbon storage was also consistently related to CWM trait values, although the strength and direction of the CWM relationships varied across forest types and levels of data aggregation. Carbon storage increased with CWM_{MAXH} and decreased with CWM_{WD} for all forest types (except Montane woodland) and all levels of aggregation. However, while carbon storage was positively related to CWM_{SLA} in Wet forests and most component forest types, it was not in Dry forests. In contrast to biotic variables, relationships of carbon storage with abiotic variables (climate, soil, fire history) at the forest-type level were inconsistent and relatively weak, particularly for those forest types with fewer than 50 plots (Rainforest, Montane Woodland; Table 1). Abiotic relationships with carbon storage were stronger at the higher levels of data aggregation (Temperate forests, Wet and Dry forest), but their predictive capacity (as indicated by ΔAIC) was always lower than the best biotic predictors (H', CWM_{MAXH}; Table 1).

3.3 Structural equation models: direct and indirect effects on carbon storage

All models had a better fit than the baseline model (CFI ≥0.9) and explained variation in carbon storage that ranged from $R^2_{carbon} = 0.20$ in the Foothill forest to $R^2_{carbon} = 0.50$ in Montane woodland (Supplementary Table S7). The best models explained close to 40% of the variance in carbon storage in Temperate forests (i.e. all data pooled) and Wet forests, and 22% in Dry forests (Supplementary Table S7).

Forest carbon storage increased with either species or functional diversity in SEMs at the highest level of data aggregation (Temperate Forest, Wet or Dry forests) and for most forest types with the exception of Foothill forest, and the two forests that had fewer than 50 plots (Rainforest, Montane woodland; Figures 5 and 6; Supplementary Table S8). Overall, the strength of species and functional diversity effects on carbon storage in Wet and Dry forests was comparable, if less consistent in Dry forests (no effect of F_{dis}). Among the biotic factors, structural diversity (H') had consistently the greatest independent effect on carbon storage, comparatively stronger than that of species or functional diversity, CWM trait values, and both the direct and indirect effects of abiotic factors (Figures 5 and 6; Supplementary Table S8, S9). CWM_{MAXH} and CWM_{WD} (but not CWM_{SLA}) were also significant predictors of carbon storage at the highest levels of data aggregation and across most forest types (particularly Rainforest), although the CWM-trait effects were mostly weaker (lower β coefficients) than those of structural diversity (Supplementary Table S8, S9).

Direct effects of abiotic variables relating to climate (MAT), soil ($SOIL_{PCA}$) and fire history (TSLWF) were weak compared with biotic factors, and were all non-significant in Wet-forests SEMs (Figures 5 and 6). Interestingly, the indirect effects of abiotic variables were more pronounced than direct effects in most SEMs irrespective of the level of data aggregation, although the strength of indirect effects varied markedly among forest types (Figure 6). The indirect effects of $SOIL_{PCA}$ were comparatively stronger (β coefficients >0.3) than MAT or TSLWF effects for the full Temperate forest data (strongest effects on S, F_{dis}, H', and all CWM trait values), and for Dry forests (strongest effects on H', and all CWM trait values), whereas the indirect effects of MAT on all types of biotic variables were similar if not stronger than those of $SOIL_{PCA}$ for Wet forests (Figure 5 and 6, Supplementary Table S8). Indirect effects of TSLWF were comparatively weak or non-significant, and the majority of abiotic effects on biotic variables were positive (with notable exceptions being negative MAT effects on H' and CWM_{MAXH} in Dry forests; Supplementary Table S8).

4. DISCUSSION

4.1 Carbon storage more strongly associated with structural diversity than species or functional diversity

Consistent with forest studies elsewhere (Huang et al., 2018; Ruiz- Benito et al., 2014), we found some support for our first hypothesis that forest carbon storage increased with tree-species diversity and functional diversity. However, while our species- and functional-diversity relationships with forest carbon storage were of comparable strength to those in other SEM-based analyses (β coefficients ~0.2; (Poorter et al., 2015; Poorter et al., 2017)), they were relatively weak at all levels of data aggregation compared to those with our other biotic variables (H', $CWM_{MAXH,}$ CWM_{WD}). We anticipated strong diversity effects on carbon storage in our forests given generally low tree-species numbers (range 1 to 14), since the largest changes in forest carbon storage can occur at low levels of functional diversity (Ruiz- Benito et al., 2014) where each additional species can still influence niche complementarity effects (Poorter et al., 2015). However, diversity effects on carbon storage can be weak in species-poor forests where strong environmental filtering leads to a small number of species (van der Sande et al., 2018), which is consistent with indications in our data of stronger associations of species- and functional-diversity indices with abiotic factors (as indirect effects) than with carbon storage itself.

Between the diversity indices, structural diversity consistently had the strongest relationships with carbon storage irrespective of the level of data aggregation. This is consistent with results for boreal forests (Zhang,Chen, 2015) where a measure of structural diversity, the coefficient of variation of tree DBH, had greater effects on above-ground biomass than species diversity. Structural diversity as measured in our study (H') accounts for the number and evenness of canopy layers and DBH size classes (Staudhammer,LeMay, 2001) and was moderately correlated (r=0.5) with basal area. Greater structural diversity implies a complex canopy structure that optimises canopy packing and aboveground light capture within a site (Parker et al., 2004) thereby increasing the potential for productivity and carbon storage (Wang et al., 2011; Yachi,Loreau, 2007; Zhang,Chen, 2015). This suggests that carbon storage in our temperate forests was underpinned by efficient utilisation of space by a limited number of tree species moreso than by diversity in species or species functional traits. That is, while at least part of the structural-diversity effect on carbon storage in our study could be associated with tree-species diversity – since more efficient space occupation of mixed than mono-specific forests can contribute to greater productivity (Pretzsch et al., 2015) – the strong independent effect of H', as well as relatively weak overall correlations of H' with species diversity (r 0.4) and functional dispersion (r 0.3), indicate that structural diversity in its own right was a principal biotic mechanism of carbon storage. Indeed, that H' effects on carbon storage were relatively strong irrespective of forest type or growth environment suggests that structural diversity would be a robust indicator of carbon storage in the temperate forests of southern Australia.

4.2 Carbon storage also associated with CWM trait values

CWM trait values were also relatively strong predictors of carbon storage in many of our forest types and in both growth environments, suggesting that the identity of the community and the species within (i.e. their trait values and therefore functional strategy) are important determinants of forest carbon stores (Prado- Junior et al., 2016). This finding provides support for the ‘mass-ratio hypothesis’, where the ecosystem processes underpinning above-ground carbon stores are determined by the functional traits of the dominant species. Consistent with other studies across a range of forest types (Adair et al., 2018; Finegan et al., 2015; Ruiz- Benito et al., 2014), the stronger associations of CWM trait values than species- or functional-diversity indices with carbon storage also provides evidence of a stronger role for selection effects than niche complementarity effects in our forests.

We included three functional identity traits that relate to species acquisition strategies in our analyses: a whole-plant trait (maximum height), a foliar trait (SLA), and a stem trait (wood density). CWMs of maximum height and wood density were more strongly related to carbon storage than CWM_{SLA}, which was a non-significant predictor in all SEMs. Species maximum height is often positively related to species productivity and of greatest importance at the extremes of the productivity gradient (Ratcliffe et al., 2016). Similarly, species with lower wood density are also considered fast-growing acquisitive species as they generally have higher stem hydraulic conductivity and photosynthetic carbon gain and lower construction cost per wood volume (Chave et al., 2009). Consistent with the mass-ratio hypothesis, forests dominated by highly productive species have the potential to support the greatest amount of carbon, although this is not a limitless possibility because fast-growing trees with lower wood density might also have higher turnover through mortality (Pan et al., 2013). We might expect CWM_{MAXH} and structural diversity to be related, as higher canopies would allow for a greater number of canopy layers. However, the two variables were only weakly correlated (r 0.3) and both emerged as significant predictors, indicating that their effects on forest carbon storage were somewhat independent.

Bivariate analyses showed some significant relationships between CWM_{SLA} and carbon storage (for Temperate forests and Mist forest) but we found no significant relationships in the multivariate SEM analyses. This suggests that CWM_{SLA} bivariate relationships with carbon storage reflected covariation with other predictor variables, but that the independent effects of SLA on carbon storage were weak. This contrasts with results from cold deciduous to xeric evergreen forests in Spain, where CWM_{SLA} was a better predictor of tree productivity and carbon stores than CWMs of maximum height, wood density, seed mass, and leaf nitrogen content (Ruiz- Benito et al., 2014). Our study included a comparatively small range in CWM_{SLA} values, which was probably due to the dominance of all forest types (except Rainforest) by eucalypt species.

4.3 Abiotic factors indirectly influence above-ground carbon storage

With few exceptions, our SEM analyses indicated that the indirect effects of abiotic factors on carbon storage via biotic factors were greater than their direct effects at all levels of data aggregation. Moreover, while bivariate relationships of carbon storage with abiotic variables were strongest at the broadest environmental range (i.e. all data combined), these relationships were weak compared to those with most biotic factors. Thus, the principal importance of climate and soils to above-ground carbon stocks in other broad-scale forest studies (Adair et al., 2018; Poorter et al., 2015; van der Sande et al., 2018) were not clearly evident in our temperate forests. Similarly, carbon storage in our forests was not clearly related to fire history, despite its prominence as a disturbance in the fire-prone landscapes of south-eastern Australia. This could in part be due to the crudeness of available fire-history variables like time-since-last-wildfire (Kasel et al., 2017), particularly given the diverse range of potential fire effects on tree recovery in eucalypt-dominated forests from full stand replacement to variable mixtures of post-fire seedlings with resprouting established trees (Fairman et al., 2016).

Our study suggests that structural diversity and, to a lesser degree, CWM trait values were relevant to carbon storage in all of our forests irrespective of their growth environments. That is, the consistent relative influences of biotic factors (strongest for H' and CWM trait values, minimal for species and functional diversity) on carbon storage across our Wet and Dry forests provided little support for our third hypothesis that biotic-factor effects would vary between growth environments. Indeed, indirect effects of climate on biotic factors were strongest in our more benign growth environment (Wet forests), which seems at odds with general understanding of increasing modulation of biotic effects on forest functioning with increasing climatic harshness (Ratcliffe et al., 2017). Nonetheless, environmental filtering was still suggested for our Dry forests both in significant (albeit weaker) effects of MAT and often stronger effects of $Soil_{PCA}$ on multiple biotic variables particularly H' and CWM trait values. In the absence of clear bivariate relationships, our study highlights the importance of using an integrative approach like structural equation modelling (Grace et al., 2016) to disentangle the many ways that abiotic and biotic factors can influence carbon storage in forests.

5. **CONCLUSIONS**

Our study highlights complex relationships of above-ground carbon storage with biotic and abiotic factors in Australia’s temperate forests. Consistent with our first hypothesis, carbon storage increased with species and functional diversity, even when accounting for abiotic factors. Nonetheless, in relation to our second hypothesis, diversity effects on carbon storage were weaker than those of structural diversity (in particular) and CWM trait values for all forest types and at all levels of data aggregation. In addition, contrary to our third hypothesis, biotic-factor effects were relatively consistent among forest types and levels of data aggregation and were not more important for carbon storage in the less-productive than productive growth environment. Direct relationships of carbon storage with abiotic factors were comparatively weaker than biotic factors, but stronger indirect effects indicated influence of climate and soil on carbon storage via effects on multiple biotic variables.

Our study had various limitations that might have influenced the strength of our carbon-storage relationships including fewer plots (<50) in two forest types, and imprecise climate, soil, and fire variables. Nonetheless, it is the first study to comprehensively assess BEF relationships across a range of forest types in temperate Australia. Our study's relevance extends beyond the testing of ecological theory to implications for forest management. Our results indicate that maintaining and increasing structural diversity as well as maintaining functionally important species would enhance forest above-ground carbon storage. They also highlight indirect effects of abiotic factors on carbon storage via biotic pathways, raising the importance of understanding biotic-abiotic interactions in temperate forests under changing climate and disturbance regimes (Millar,Stephenson, 2015). Fostering the natural structural complexity and composition of these forests would maintain and enhance their carbon storage capacity.

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Tables

Table 1. Bivariate relationships of above-ground carbon storage with selected abiotic and biotic predictor variables at three levels of plot aggregation (plot numbers indicated in brackets). Relationships were modeled using linear or quadratic mixed models with plot size included as a random variable. Variables were centered and scaled prior to analysis. Values are standardized coefficients (β) and AIC differences to the null model (ΔAIC). Standardized coefficients can directly be compared; the higher the value, the stronger the relationship (strongest relationships in bold). Greater ΔAIC indicates greater predictive capacity. Significance level refers to β coefficients (as indicated by mixed models): *** P <0.001, ** P <0.01, * P <0.05, • P <0.1. For the MAT quadratic model (indicated by Q), maximum p-value between linear and quadratic coefficient is presented. Acronyms as per Figure 3 caption.

							Wet forest types								Dry forest types			
	Temperate forests (732)		Wet forests (280)		Dry forests (452)		Mist forest (102)		Rainforest (40)		Damp forest (90)		Montane woodland (48)		Foothill forest (228)		Lowland forest (224)	
Predictor	β	ΔAIC	β	ΔAIC	β	ΔAIC	β	ΔAIC	β	ΔAIC	β	ΔAIC	β	ΔAIC	β	ΔAIC	β	ΔAIC
Abiotic																		
MAT (Q)	-0.9 ***	90	-1.3 ***	54	0.2	25	-0.9 **	8	0.1	-3	-1.4 ***	8	-0.7	9	-0	-1	0.3	11
MAP	1.2 ***	82	0.7	3	0.5 **	3	-0.1	-1	0.2	1	1.3 **	6	-1.5	4	-0.4 •	0	1.2 ***	12
$SOIL_{PCA}$	-1.3 ***	97	-0.9 **	7	-0.7 ***	11	-0.3	-1	**-2.4**	**3**	1.4 **	7	-2.1 **	9	-0.1	-3	1.2 ***	13
TSLWF	0.4 ***	7	1.3 ***	18	0.4 ***	9	1.1	4	1.1	2	0.4	-1	1.4 •	3	0.7 ***	27	0.1	-3
Biotic																		
S	1.4 ***	129	1.4 ***	49	0.6 ***	15	1.7 ***	21	0.1	-1	0.4	-1	2.7 ***	19	0.3 •	0	0.8 ***	9
F_{dis}	1.4 ***	120	1.6 ***	46	0.4 **	5	1.2 **	6	-1.4 •	2	1.4 ***	12	1.7 **	7	0.1	-3	0.6	3
CWM_{MAXH}	1.7 ***	165	1.6 ***	56	1.1 ***	48	1.5 ***	18	1.8 ***	14	**1.7** ***	**19**	1.4	5	**0.9** ***	**8**	**1.2** ***	**24**
CWM_{SLA}	1.3 ***	76	1.2 ***	32	0.3 •	-1	0.7 **	0	-0.1	-3	0.8 *	3	1.6 *	4	0.2	-3	0.1	-3

CWM_{WD}	-1.1 ***	-67	-0.9 ***	12	-0.8 ***	23	-1.5 ***	18	-0.5 ***	11	-0.9 *	3	2.1 **	6	-0.7 *	1	-0.6 ***	9
H'	**2.1 *** **	**281**	**2.5 *** **	**132**	**1.2 *** **	**79**	**2.4 *** **	**49**	**2.4 *** **	**8**	**1.7 *** **	**24**	**2.8 *** **	**32**	**0.9 *** **	**26**	**1.4 *** **	**41**

Figure legends

Figure 1. Location of forest plots in the state of Victoria, south-eastern Australia.

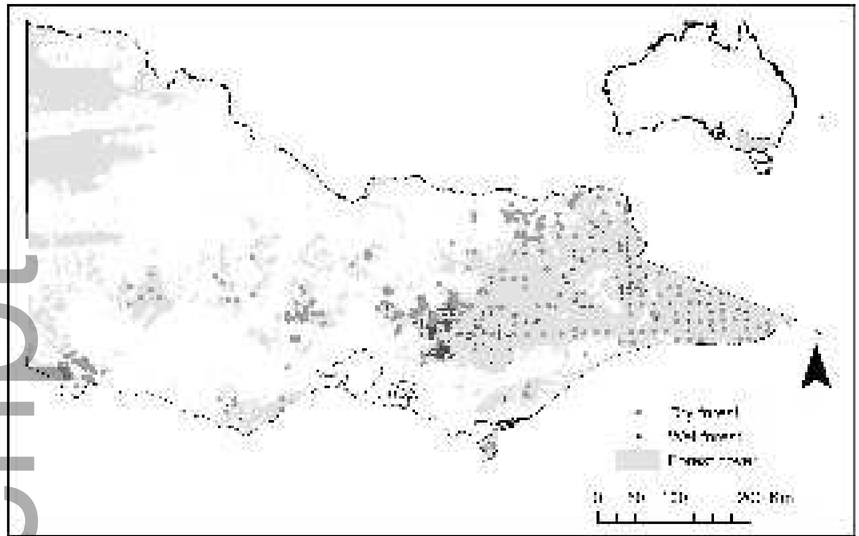
Figure 2. Conceptual diagram of hypothesised relationships of above-ground carbon storage with biotic factors (species or functional diversity, CWM traits, structural diversity), and abiotic factors (climate, soil, fire history). Black lines indicate direct effects whereas dotted lines indicate indirect effect of abiotic factors on carbon storage via influence on biotic factors.

Figure 3. Notched boxplots of key attributes of the study's six forest types. Medians are significantly different where notches (95% CI of the median) do not overlap. Acronyms: MAT: Mean annual temperature, MAP: Mean annual precipitation, TSLWF: time since last wildfire, S: species richness, H': structural diversity, F_{dis}: functional dispersion, CWM_{MAXH}: community weighted mean of maximum height, CWM_{SLA}: community weighted mean of specific leaf area, CWM_{WD}: community weighted mean of wood density. Light shading represents Dry forest types and darker shading represents Wet forest types.

Figure 4. Relationships of above-ground carbon storage with abiotic and biotic predictor variables for Dry forests (light grey circles, dotted line) and Wet forests (dark grey triangles, dashed line). Acronyms as per Figure 3. The relative strength of the relationships is summarised in Table 1.

Figure 5. Example SEMs for Temperate forest (all pooled data), Wet forests and Dry forests. Numbers indicate standardized β coefficients. Line width is proportional to the coefficient. Solid lines indicate direct effects whereas dotted lines indicate indirect effects of abiotic variables (MAT^2 + MAT, $Soil_{PCA}$, TSLWF) on carbon storage via influence on biotic variables ($F_{dis,}$ H', CWM_{MAXH}). Grey lines indicate coefficients that were not significant (ns). Acronyms as per Figure 3.

Figure 6. Direct (dark grey) and indirect (light grey) effects of predictor variables on above-ground carbon storage in the SEM. Variables were scaled and centred prior to analysis. Direct effects are model standardized coefficients (i.e. are directly comparable, the higher the value the stronger the effect). Indirect effects are calculated by multiplying the standardized coefficients of all paths on one route between the variable and carbon storage. Bars show model-weighted averaged (using AICw) standardized coefficients with error bars showing standard errors. Only significant coefficients ($P<0.05$) are shown. Acronyms as per Fig. 3.



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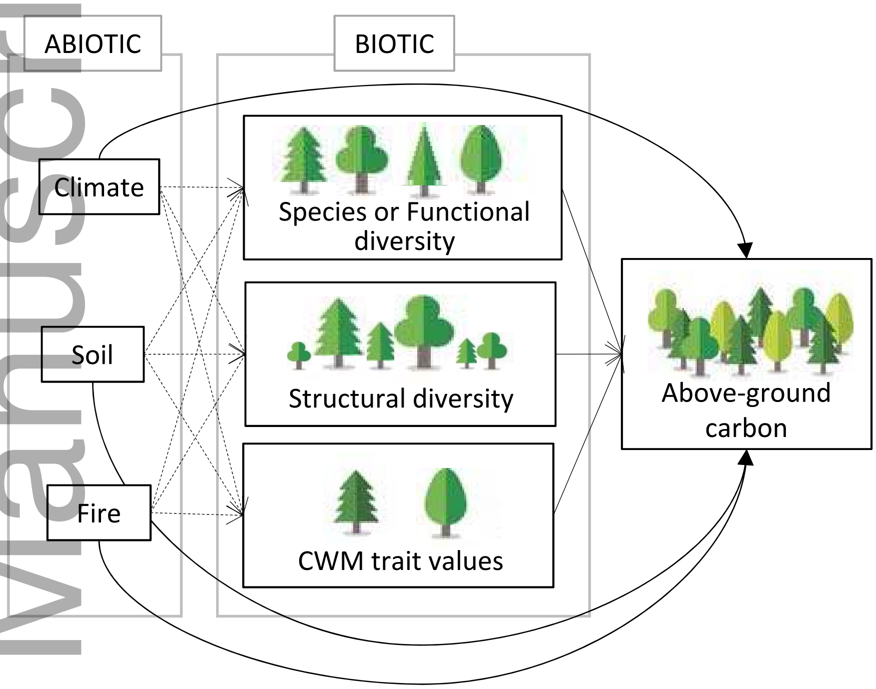

Figure 2. Conceptual diagram of hypothesised relationships of above-ground carbon storage with biotic factors (species or functional diversity, structural diversity, CWM trait values), and abiotic factors (climate, soil, fire history). Black lines indicate direct effects whereas dotted lines indicate indirect effect of abiotic factors on carbon storage via influence on biotic factors.

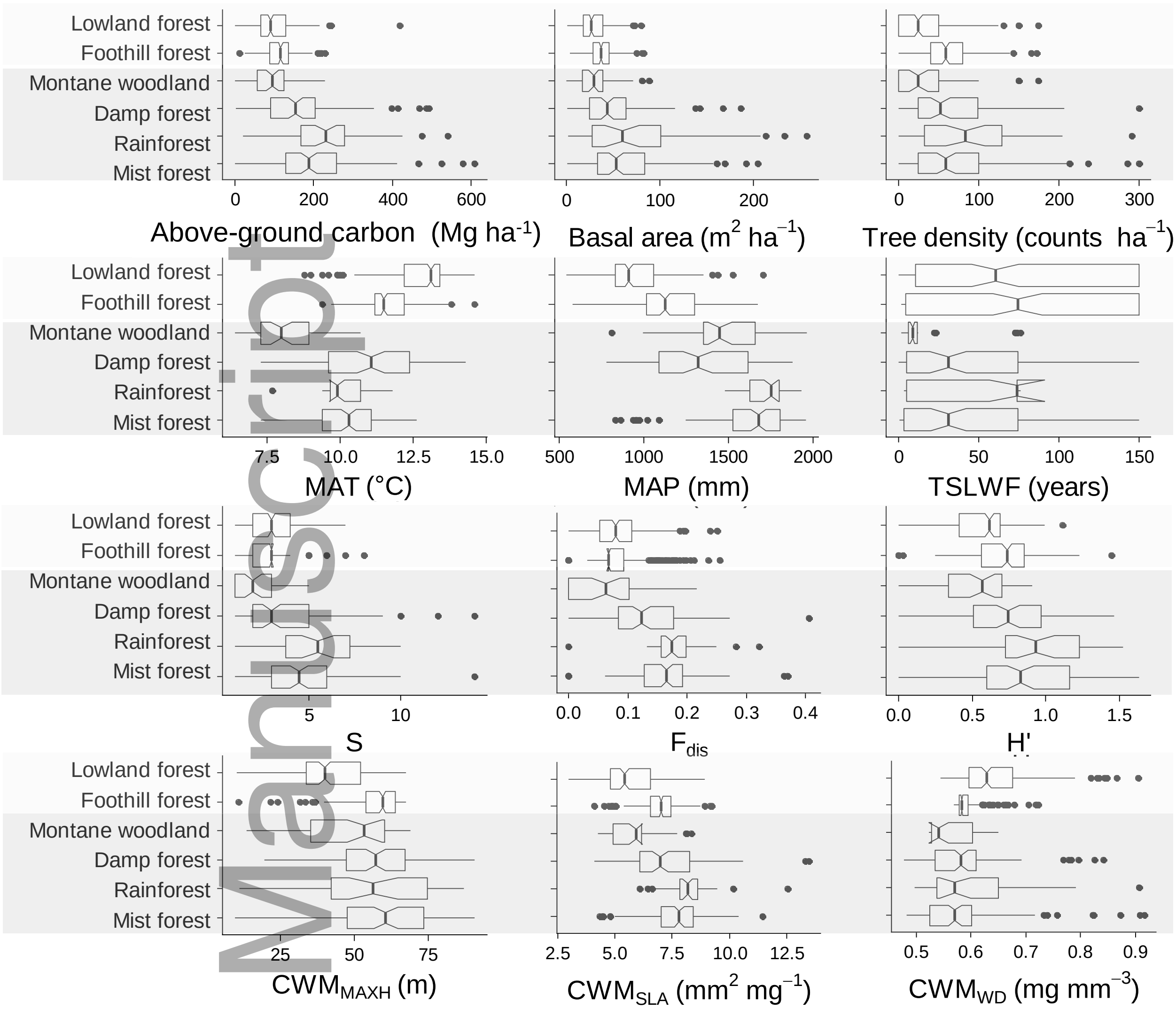

Figure 3. Notched boxplots of key attributes of the study's six forest types. Medians are significantly different where notches (95% CI of the median) do not overlap. Acronyms: MAT: Mean annual temperature, MAP: Mean annual precipitation, TSLWF: time since last wildfire, S: species richness, H': structural diversity, F_{dis}: functional dispersion, CWM_{MAXH}: community weighted mean of maximum height, CWM_{SLA}: community weighted mean of specific leaf area, CWM_{WD}: community weighted mean of wood density. Light shading represents dry forest types and darker shading represents wet forest types.

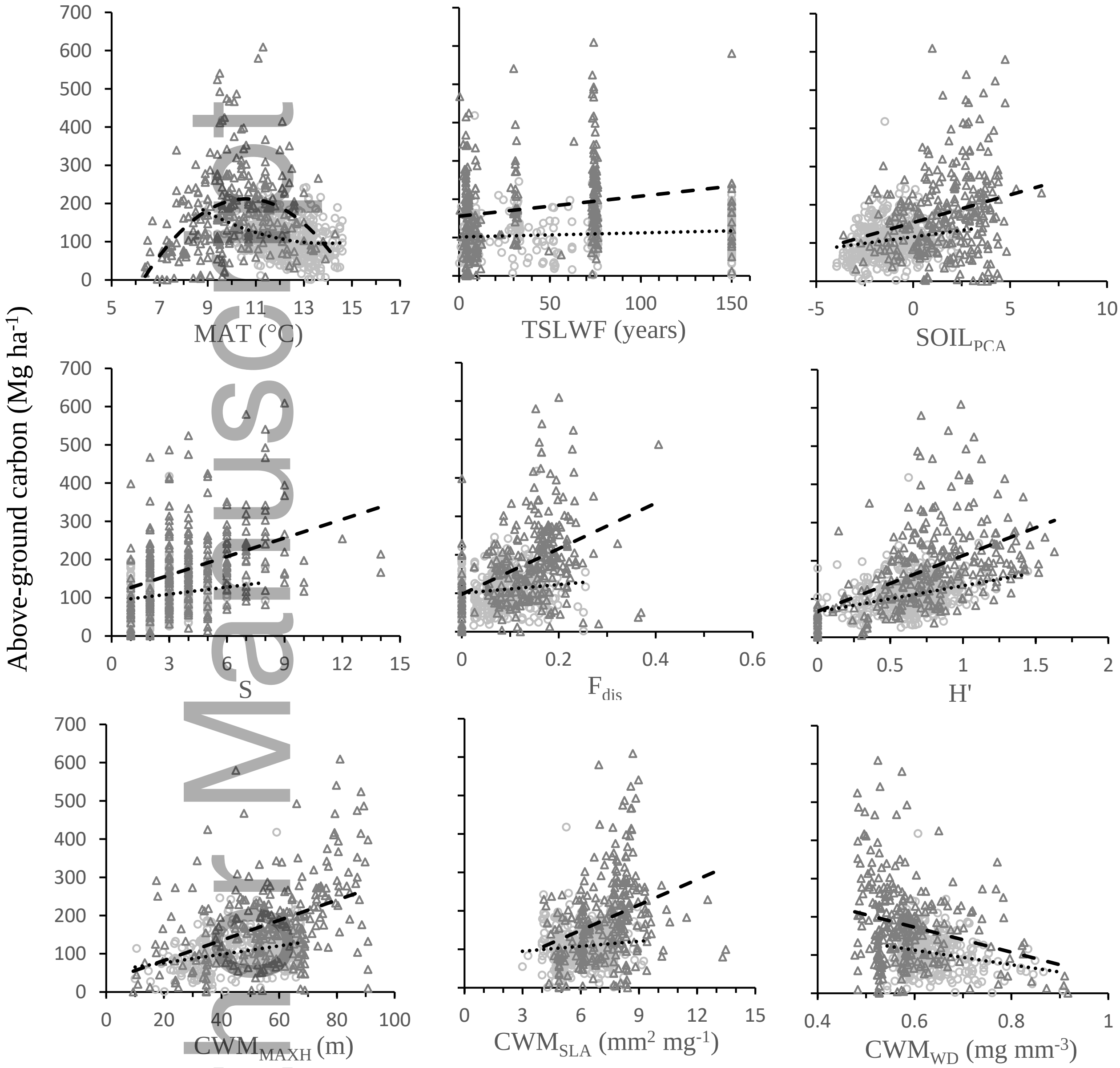

Figure 4. Relationships between above-ground carbon storage and environmental, diversity and identity predictor variables for Dry forests (light grey circles, dotted line) and Wet forests (dark grey triangles, dashed line). Acronyms as per Figure 3.

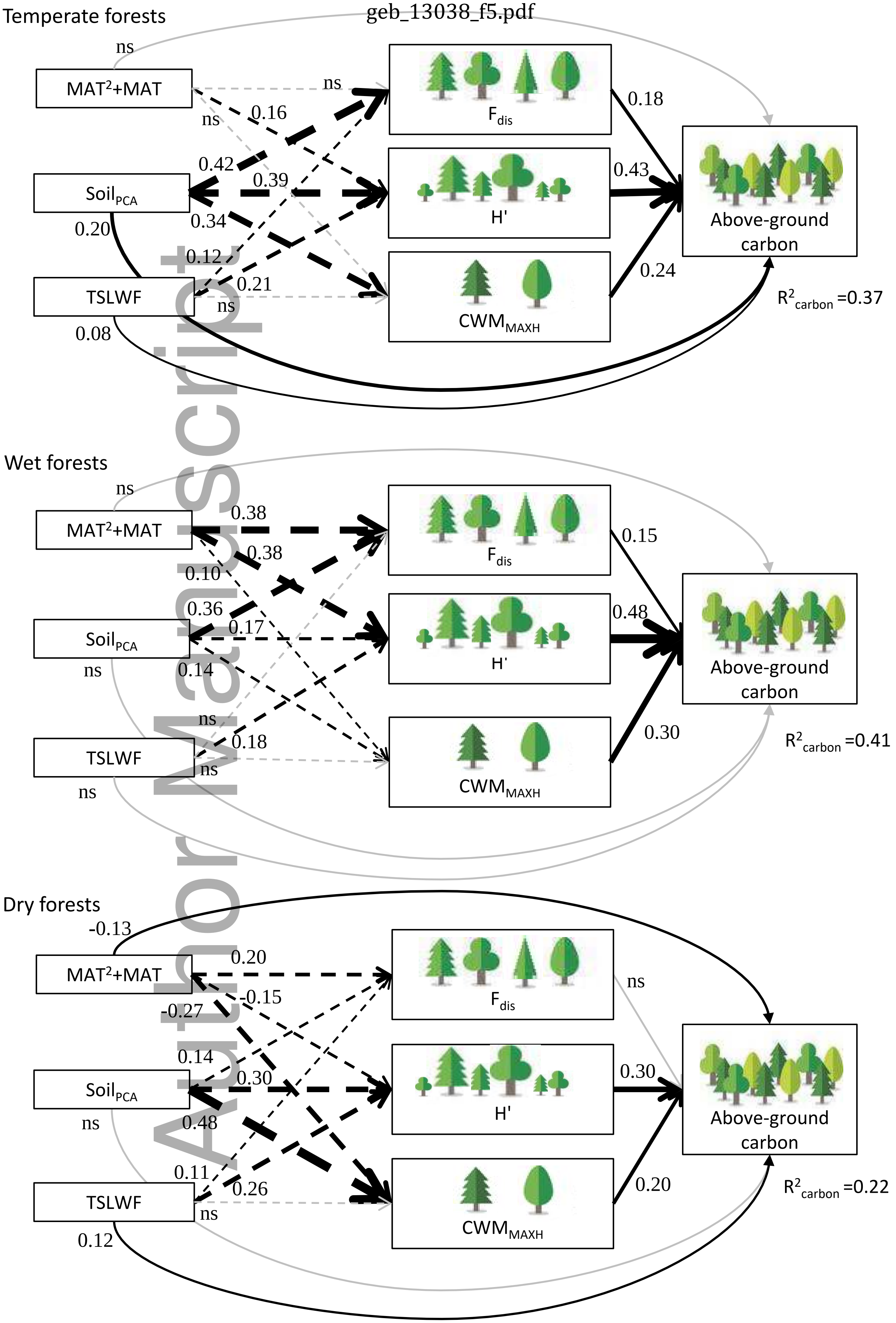

Figure 5. Results of a subset of the SEM for Temperate forest (all pooled data), Wet forest and Dry forest. Numbers indicate standardized β coefficients. Line width is proportional to the coefficient. Solid lines indicate direct effects whereas dotted lines indicate indirect effects of environmental variables on aboveground carbon storage via influence on diversity and identity. Acronyms as per Figure 3.

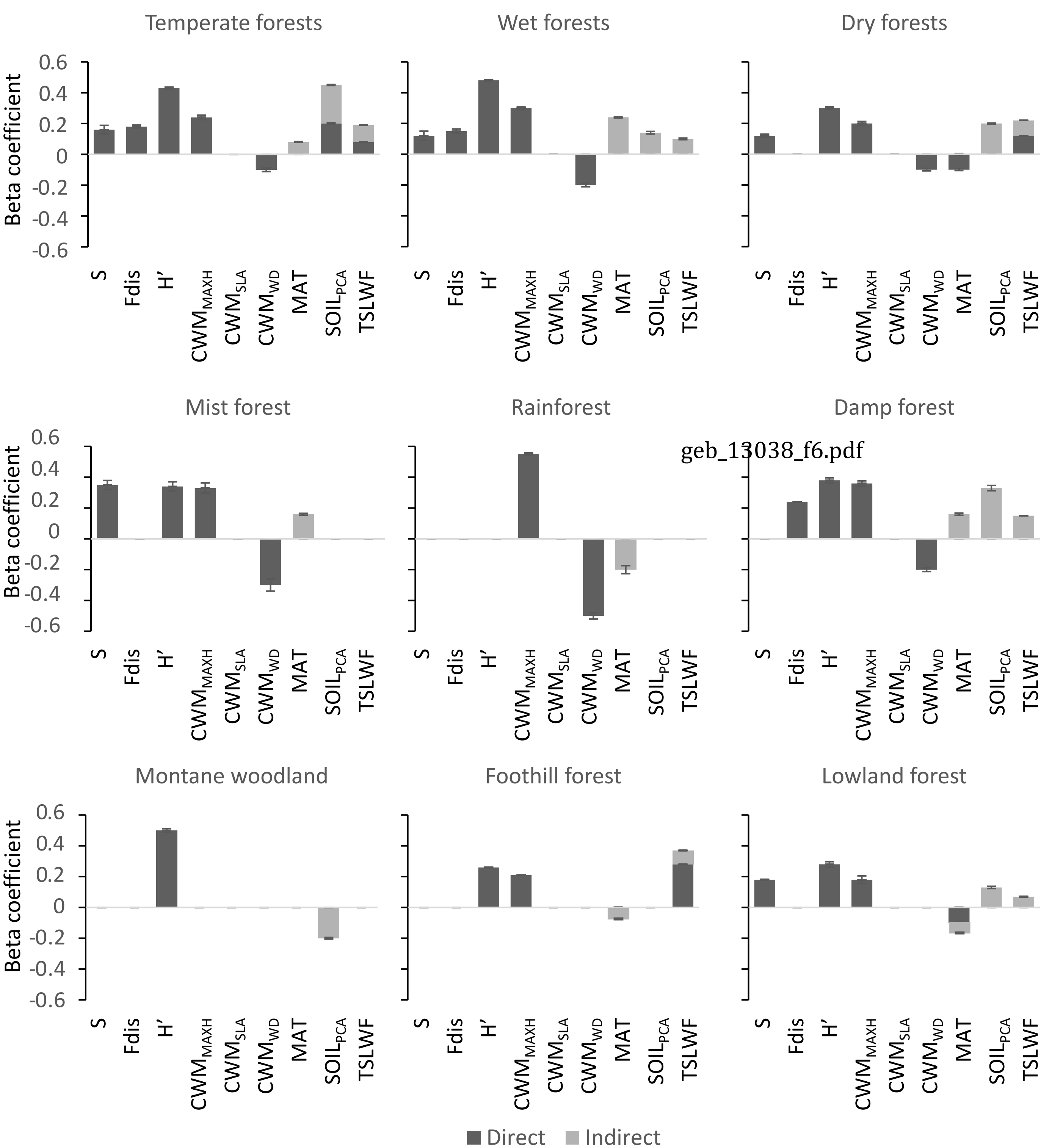

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Figure 6. Direct (dark grey) and indirect (light grey) effects of predictor variables on above-ground carbon storage in the SEM. Variables were scaled and centred prior to analysis. Direct effects are model standardized coefficients. Indirect effects are calculated by multiplying the standardized coefficients of all paths on one route between the variable and carbon storage. Bars show model-weighted averaged (using AICw) standardized coefficients with error bars showing standard errors. Only significant coefficients ($P<0.05$) are shown. Acronyms as per Fig. 3.