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Carbon stocks in temperate forests of south-eastern Australia reflect large tree distribution and edaphic conditions ☆

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ABSTRACT

Reducing uncertainty in forest carbon estimates at local and regional scales has become increasingly important due to the centrality of the terrestrial carbon cycle in issues of climate change. Despite relatively limited geographical extent, temperate forests are among the most carbon dense forests in the world. Estimates of carbon in key understorey life forms and belowground components of these forests have often been excluded from previous studies in south-eastern Australia. We estimated above- and belowground carbon stocks (including soil to 0.3 m depth) in stands of cool temperate rainforest ('rainforest'), wet sclerophyll forest ('eucalypt forest'), and mixed rainforest–wet sclerophyll stands ('ecotone forest') across a wide range of environmental conditions and forest structures. We examined relationships among component carbon stocks and a range of environmental variables (edaphic, climatic, spatial) and present the first allometric equations and carbon stock estimates for south-eastern Australian tree ferns. Component carbon stocks were within the range of published values for these stand types. Using multivariate analyses of all component stocks, we detected significantly more carbon in total above- and belowground components in ecotone (697 Mg ha^{-1}, 95% confidence interval 575–819 Mg ha^{-1}) and eucalypt forests (689 Mg ha^{-1}, 605–773 Mg ha^{-1}) than rainforest (550 Mg ha^{-1}, 453–647 Mg ha^{-1}). However, we found no significant differences among the stand types in the proportional distribution of carbon among components despite significant differences in structural composition as indicated by size class distributions of the main genera. Of total carbon, ~48% was stored in trees (>2 cm over-bark diameter), and ~72% of tree carbon was stored in the largest 10% of all trees. The most important environmental variables associated with carbon stocks irrespective of stand type were edaphic variables, most commonly total and available soil nitrogen. Tree fern carbon was the only component stock more strongly associated with climatic and spatial than edaphic variables. Our findings indicate that disturbance mediated changes in stand dynamics could significantly alter total carbon stocks, particularly if more frequent fires limit tree recruitment and increase large tree mortality. Monitoring of these forests for carbon could place greater emphasis on key structural elements associated with the largest proportion of total carbon, the largest trees. By reducing uncertainties associated with estimates of carbon in key stocks, we can better understand potential future changes to the carbon cycle from altered stand dynamics under climate change.

1. Introduction

Temperate forests cover 767 million hectares and store 14% of global forest carbon (Pan et al., 2011). Some temperate forests are amongst the world's densest and tallest forests and on average contain more carbon per unit area than tropical rainforests (Pan et al., 2013). The temperate forests in south-eastern Australia have recently been suggested as the most carbon dense forests in the world (Keith et al., 2009), however, current estimates of forest carbon may only be accurate to ±30% (Mackey, 2014). Uncertainty arises from the varying spatial and temporal patterns associated

☆ Nomenclature follows Walsh, N.G., and Stajsic, V., 2007. A Census of the Vascular Plants of Victoria [electronic resource]. Royal Botanic Gardens Melbourne. Ed. 8. with the exception of *Lophozonia cunninhamii* from Heenan, P.B., and Smissen, R.D., 2013. Revised circumscription of Nothofagus and recognition of the segregate genera Fuscospora, Lophozonia, and Trisyngyne (Nothofagaceae). *Phytotaxa*, *146*(1), 1–31.

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with processes affecting sequestration and respiration rates, heterogeneous distribution, and increasingly complex anthropogenic land use and management practices (Reich, 2011; Seidl et al., 2011; Mackey, 2014). In the temperate forests of south-eastern Australia, tall-open wet sclerophyll forests (Patton, 1930; Specht, 1970) dominated by *Eucalyptus* spp. coexist with closed canopy cool temperate rainforests (Diels, 1906; Specht, 1970). This pattern of spatial coexistence creates a stand type that can be defined as ecotonal mixed (Lynch and Neldner, 2000; Wood et al., 2010; Tng et al., 2012). The classification of stands into different types is typically a product of differences in horizontal and vertical structure characterised by the number of life forms, species composition, and tree size and densities (McElhinny et al., 2005). As such, the wide range of published carbon estimates among and within forests may be driven by structural definition rather than environmental variability.

Few studies have reported carbon stocks for cool temperate rainforest in south-eastern Australia with only one generalised estimate for the state of Victoria (209 Mg ha^{-1}; Norris et al., 2010). Of the studies that include cool temperate rainforest, few have measured coarse woody debris (CWD) and litter (Woldendorp and Keenan, 2005) while those reporting above- and belowground carbon (209–590 Mg ha^{-1}; Dean et al., 2004, 2012; Keith et al., 2000; Norris et al., 2010; May et al., 2012) typically exclude values for some or all of the understorey life forms. Published values for carbon stocks in wet sclerophyll forest are limited and span a considerable range (233–1867 Mg ha^{-1}; Feller, 1980; Mackey et al., 2008; Keith et al., 2009; Norris et al., 2010). The largest carbon estimates have so far been reported for ecotonal mixed forests in Tasmania and in the Central Highlands region of Victoria (1246–1867 Mg ha^{-1}; Keith et al., 2009; Dean et al., 2012).

The large variability in present carbon estimates for temperate rainforests limits our ability to model the response of these systems to future scenarios of climate and/or changes in disturbance regimes (Aber et al., 2001; Canadell and Raupach, 2008; Jackson et al., 2008; Canadell et al., 2010; Anderson et al., 2011). Specifically, there is a lack of regional, species-specific allometric equations that are applicable to wide diameter ranges of trees and other life forms, particularly for trees with diameters >200 cm (Feldpausch et al., 2011; Pan et al., 2011). Methodological inconsistencies and the sampling intensities required to measure stocks other than the dominant trees often results in their exclusion, leading to insufficient observations and greater uncertainty (Pan et al., 2011). Reducing epistemic uncertainties in current carbon stock estimates and identifying key variables associated with forest growth, mortality, and biomass will be critical for improving predictive models of how the global carbon cycle might by affected by future climate change (Malhi et al., 1999; Aber et al., 2001; Anderson et al., 2011; Keenan et al., 2013; Pan et al., 2013).

Topographic, edaphic, and microclimate conditions exert strong controls on forest distribution and mortality (Allen et al., 2010) with disturbance contributing to variability in forest composition and structure (Canadell and Raupach, 2008; Swanson et al., 2011; Pan et al., 2013). In the absence of stand-replacing disturbances, a complex structure can develop over time as shade-tolerant species thrive under closed canopy cover (Baker et al., 2004; Tng et al., 2012; Pan et al., 2013; Lindenmayer et al., 2013). Fire regimes in ecotonal forests of temperate Australia vary from once or twice every 100 years to once every ~250 years, with the shorter fire intervals favouring dominance by wet sclerophyll species and the longer intervals favouring rainforest species (Gilbert, 1959; Howard, 1973; Ashton, 1976). This temporal variability of fire drives stand dynamics by increasing the spatial complexity of forest structure due to altered presence and density of large trees and changes in species composition, with the potential to influence stand carbon distributions at local and regional scales. Specifically, increased fire frequency should benefit wet sclerophyll species over rainforest species within these forests, which in turn would reduce spatial and temporal complexity at the landscape-level. In addition, predictions of more frequent and severe wildfires for temperate Australia under climate change will likely shorten the intervals between fires, facilitating changes in species composition and structure (Lindenmayer et al., 2011; Mok et al., 2012; Bowman et al., 2014; Smith et al., 2014), thereby contributing further uncertainties to forest carbon estimates in these landscapes.

The distribution of carbon across forest components is typically a function of structural variability, which arises due to competition for and the cycling of environmental resources with the influence of disturbance, topography, climate, and edaphic constraints on regional forest carbon carrying capacity (Franklin et al., 2002; Keith et al., 2010; Townsend et al., 2011; Li and Elderfield, 2013). We explore the role of structural and environmental variability on forest carbon stocks in the Central Highlands region of south-eastern Australia, an area characterised by high carbon stocks (Keith et al., 2009), variable fire regimes (50–250 years), and a high degree of topographic variation. We anticipated that the environmental/topographic gradients and observed structural differences among stands of cool temperate rainforest, wet sclerophyll forest, and their ecotone would contribute to marked differences in total carbon stocks and in the distribution of those stocks among above- and belowground components.

By addressing key knowledge gaps about carbon stocks in temperate forests of south-eastern Australia, we aimed to:

(1) Assess if total forest carbon and the distribution of carbon among structural components differs among stand types of varying structure.
(2) Identify those environmental variables most strongly associated with carbon in different forest components, and whether these variables differ for above- and belowground components.

2. Materials and methods

2.1. Study area

The Central Highlands region of south-eastern Australia is located approximately 100 km north-east of Melbourne, Victoria (Fig. 1). Annual rainfall ranges from 600 to 2000 mm, falling mainly in winter (June–August), with mean annual temperatures from 5.4 to 14.2 °C (1950–2000, BIOCLIM data; Hijmans et al., 2005). Potential sites were initially identified from GIS data in two vegetation types known locally as 'Cool Temperate Rainforest' and 'Wet Forest' (Cheal, 2010). Cool temperate rainforest is described as closed forest to 25 m height, dominated in all strata by obligate rainforest species (e.g. *Lophozonia cunninghamii* formally *Nothofagus cunninghamii*; *Atherosperma moschatum*; *Pittosporum bicolor*), with occasional emergent *Eucalyptus* spp. trees, an understorey characterised by tree ferns *Cyathea australis* and *Dicksonia antarctica*, and a ground layer dominated by a diversity of ground ferns (Cheal, 2010). Wet Forest is defined by a tall overstorey stratum to 30–80 m dominated by *Eucalyptus regnans*, above an understorey (20–40 m) of trees and tall broad-leaved shrubs (*Acacia* spp., *Pomaderris aspera*, *Cassinia trinerva*, *Prostanthaera lasianthos*, *Zieria arborescens*, *Lomatia fraseri*, *Persoonia arborea*). Candidate cool temperate rainforest sites were visited in the field and selected as 'rainforest' if all woody strata were dominated by obligate rainforest species; a nearby (within 1–5 km upslope) wet forest site was then selected as 'eucalypt' based on an overstorey dominated by *E. regnans*, and an understorey absent of rainforest species. Where the rainforest and eucalypt forest converge, a third 'ecotone' stand type was selected based on an overstorey stratum of