

1 **Conversion of sub-tropical native vegetation to introduced conifer forest: impacts on**
2 **below-ground and above-ground carbon pools**

3

4 Tom Lewis^{1,2*}, Timothy E. Smith^{1,2}, Bruce Hogg¹, Scott Swift¹, Luke Verstraten², Philippa
5 Bryant², Bernhard J. Wehr³, Neil Tindale², Neal W. Menzies³, Ram C. Dalal^{3,4}.

6

7 ¹*Dept of Agriculture and Fisheries, Queensland Government, University of the Sunshine Coast, Sippy*
8 *Downs, 4556, Australia*

9 ²*Faculty of Science, Health, Education and Engineering, University of the Sunshine Coast, Sippy*
10 *Downs, 4556, Australia*

11 ³*School of Agriculture and Food Sciences, The University of Queensland, St Lucia, 4072, Australia*

12 ⁴*Dept of Science, Information Technology and Innovation (DSITI), Queensland Government,*
13 *Ecosciences Precinct, 41 Boggo Rd, Dutton Park, 4102, Australia*

14

15 * Author for correspondence

16 Email: tom.lewis@daf.qld.gov.au; Phone: +61 7 54565768

17

18

19 **Abstract**

20 Land-use change can have a major influence on soil organic carbon (SOC) and above-ground
21 C pools. We assessed a change from native vegetation to introduced *Pinus* species plantations
22 on C pools using eight paired sites. At each site we determined the impacts on 0–50 cm
23 below-ground (SOC, charcoal C, organic matter C, particulate organic C, humic organic C,

24 resistant organic C) and above-ground (litter, coarse woody debris, standing trees and woody
25 understorey plants) C pools. In an analysis across the different study sites there was no
26 significant difference ($P > 0.05$) in SOC or above-ground tree C stocks between paired native
27 vegetation and pine plantations, although significant differences did exist at specific sites.
28 SOC (calculated based on an equivalent soil mass basis) was higher in the pine plantations at
29 two sites, higher in the native vegetation at two sites and did not differ for the other four sites.
30 The site to site variation in SOC across the landscape was far greater than the variation
31 observed with a change from native vegetation to introduced *Pinus* plantation. Differences
32 between sites were not explained by soil type, although tree basal area was positively
33 correlated with 0–50 cm SOC. In fact, in the native vegetation there was a significant linear
34 relationship between above-ground biomass and SOC that explained 88.8% of the variation
35 in the data. Fine litter C (0–25 mm diameter) tended to be higher in the pine forest than in the
36 adjacent native vegetation and was significantly higher in the pine forest at five of the eight
37 paired sites. Total litter C (0–100 mm diameter) increased significantly with plantation age
38 ($R^2 = 0.64$). Carbon stored in understorey woody plants (2.5–10 cm DBH) was higher in the
39 native vegetation than in the adjacent pine forest. Total site C varied greatly across the study
40 area from 58.8 Mg ha⁻¹ at a native heathland site to 497.8 Mg ha⁻¹ at a native eucalypt forest
41 site. Our findings suggest that the effects of change from native vegetation to introduced
42 *Pinus* sp. forest are highly site-specific and may be positive, negative, or have no influence
43 on various C pools, depending on local site characteristics (e.g. plantation age and type of
44 native vegetation).

45

46 *Keywords:* soil organic carbon, litter, tree biomass, organic matter, plantation forest,
47 ecosystem carbon stocks

48 **1. Introduction**

49 There is global concern that land-use change results in a depletion of soil organic carbon
50 (SOC), terrestrial biomass and consequent increases in atmospheric CO₂ (e.g. Houghton,
51 2003; Strassmann et al., 2008). Conversion of forest to agricultural land-uses usually results
52 in loss of above-ground biomass C and SOC, particularly when conversion is to cultivated
53 land (Brown and Lugo, 1990; Ellert and Gregorich, 1996; Murty et al., 2002; Guo and
54 Gifford, 2002). However, the impacts of change from one forest type to another are less clear
55 and there is a high degree of uncertainty regarding the degree and direction of change
56 (Bashkin and Binkley, 1998; Rhoades et al., 2000) due to factors such as plantation age, type
57 of plantation (native or exotic species), soil type and environmental factors (e.g. climate) and
58 management factors (Kasel and Bennett, 2007).

59

60 The role of different forest compositions on forest C stocks and dynamics is poorly
61 understood (Jandl et al., 2007) and there is a paucity of detailed information on soil C stocks
62 in sub-tropical forests. An international review by Guo and Gifford (2002) reported that, on
63 average, SOC stocks declined by 15% following conversion from native forest to conifer
64 plantation, but there was variability in this change depending on plantation species, rainfall
65 and plantation age. Studies in southern Australia (e.g. Turner and Lambert, 2000, Turner et
66 al., 2005) also reported reductions in SOC stocks following land-use conversion to conifer
67 plantations. Further, in the sub-tropics, Chen et al. (2004) and Richards et al. (2007) reported
68 significant reductions in total SOC following conversion of native vegetation to hoop pine
69 (*Araucaria cunninghamii*, a native species to the region) plantations. The losses in SOC are
70 likely due, at least in part, to site preparation for tree planting, which involves cultivation
71 (e.g. ripping and mounding) that disturbs soil structure and breaks down soil aggregates

72 (Jandl et al., 2007). However, few published studies have reported the impacts of conversion
73 to introduced conifer plantations in the sub-tropics, and few studies have considered the form
74 of soil organic C (i.e. humic, particulate or resistant) which is important when considering the
75 resilience of these C stocks and our ability to model SOC changes.

76

77 Following clearing of native forest there is an initial reduction in above-ground plant
78 biomass. In the case where native forest is replaced with plantation forest, above-ground
79 biomass may be lower (Chen et al. 2005), similar, or reach higher levels than in the previous
80 vegetation (e.g. Lugo, 1992), usually through modification of the site productivity (e.g.
81 addition of fertilizer, Oren et al., 2001). Reports of the amount of above-ground biomass for
82 *Pinus* plantations in the sub-tropics suggest approximately 316 Mg ha⁻¹ (~155 Mg C ha⁻¹) can
83 be sequestered by age 30 (Simpson et al., 2000). Tree C stocks in native vegetation in sub-
84 tropical Australia may vary greatly from site-to-site but range from approximately 40 to 220
85 Mg C ha⁻¹ depending on the soil type and site productivity (Westman and Rogers 1977; Hero
86 et al. 2013; Ngugi et al. 2014; Moroni and Lewis 2015). We are unaware of any studies that
87 consider the impact of conversion of native vegetation to *Pinus* sp. plantation on tree C and
88 litter C stocks in the sub-tropics of Australia.

89

90 In both native vegetation and plantation forest, a significant C stock can be found in the litter
91 layer, which potentially plays an important role in building soil C (Liski et al. 2002). This C
92 pool may be dynamic (Bubb et al., 1998; Birk and Simpson, 1980), but often a steady state
93 between litterfall and decomposition is reached over time (Olson, 1963) and incorporating
94 litter C into total site C stocks can be important when assessing land-use changes (Richter et
95 al., 1999; Paul et al., 2002). *Pinus* sp. forests are known to contain particularly high litter

96 biomass stocks, partly due to slower rates of decomposition relative to native forests (e.g.
97 Paul and Polglase, 2004; Prescott, 2010), however, there are few published comparisons
98 between *Pinus* sp. forests and native vegetation in tropical and sub-tropical regions.

99

100 The commercial plantation forestry estate covers approximately two million hectares in
101 Australia, of which 51% is planted with softwood species (Montreal Process Implementation
102 Group for Australia and National Forest Inventory Steering Committee, 2013) with
103 approximately 18% of this softwood estate occurring in Queensland. This study focusses on
104 the impacts of change from native vegetation to plantation forest, which occurred 28–60
105 years ago, using paired comparison sites in Queensland. We aimed to determine, across a
106 range of sites with varying soil types and plantation ages, whether C pools differed between
107 introduced *Pinus* plantations and adjacent native vegetation. Based on the above-mentioned
108 studies in southern Australia we hypothesised that SOC would be lower in the conifer
109 plantations, but litter C would be higher in these plantations relative to the native vegetation.
110 We also hypothesised that above-ground woody plant C would be lower in the *Pinus*
111 plantations, particularly in young plantations, given the likely relationship between above-
112 ground biomass and plantation age.

113

114 **2. Methods**

115 ***2.1 Site details***

116 Eight paired sites were selected from within the *Pinus* sp. plantation resource in south-eastern
117 Queensland, Australia (Figure 1). *Pinus* sp. plantations in the paired comparisons varied from
118 six to 34 years since planting (mean age of 21 years, Table 1). Plantation plots were either in

119 their first or second rotation (Table 1). Soil types varied between the eight sites (classified
120 using Australian Soil Classification, Isbell, 1996): two sites were on yellow Kandosols, two
121 sites were on brown Kandosols, one site was on a grey Chromosol and three sites were on
122 Podosols (Table 1). Pine plantations were dominated by *Pinus elliotii* var. *elliotii*, *Pinus*
123 *caribaea* var. *hondurensis* and *P. elliotii* × *P. caribaea* hybrids (Table 1). Adjacent native
124 vegetation varied between sites; in most cases (six sites) it was naturally occurring forest
125 dominated by tree species including *Eucalyptus racemosa*, *Corymbia intermedia*, *E.*
126 *acmenoides*, *Lophostemon suaveolens*, *Syncarpia glomulifera* and *Melaleuca quinquenervia*,
127 or open woodland (one site) and heathland (one site) with dominant species such as *E.*
128 *umbra*, *Banksia aemula* and *Melaleuca viridiflora* (Table 1). In all cases the native vegetation
129 was multi-aged remnant vegetation and hence could not be accurately aged. Mean annual
130 rainfall across the study region varied from 1193 to 1611 mm (average = 1408 mm, Table 1),
131 with rainfall being higher in the summer months. Mean minimum temperature ranged from
132 14.7°C to 15.8°C while mean maximum temperature ranged from 25.1°C to 26.6°C. Climatic
133 data for the study area were based on spatially interpolated Bureau of Meteorology
134 observational data from 1889–2013 (Jeffrey et al., 2001).

135

136 **2.2 Plot layout**

137 Paired-comparison sites were chosen on the basis of sufficient area of the target vegetation
138 being on the same soil type, with the same slope position. Plots were 0.5 ha (in most cases
139 100 × 50 m) in both the pine and native vegetation, and were separated by <200 m at each
140 site. Six of the eight paired sites were selected as part of an earlier (unpublished) study in
141 1998 and the authors are currently investigating temporal trends in soil nutrients over this
142 time. Each plot was divided into 50 sub-plots of 10 × 10 m and six sub-plots were randomly

143 selected for sampling (stratified simple random sampling, Figure 1b). Plots and sub-plots
144 were established using tape measures, optical squares and sighting posts to ensure right-
145 angles. Each sub-plot contained 100 1×1 m squares, of which ten were randomly selected
146 for sampling (e.g. Figure 1c). Each selected sub-plot and square was marked with line-
147 marking paint to delineate the sampling positions. The positions of sub-plots and sampling
148 squares were referenced from the plot corner positions to determine their UTM reference
149 points and to allow future sampling within the same locations. Sampling took place between
150 May and November 2013.

151

152 ***2.3 Litter sampling and above-ground carbon estimates***

153 A steel quadrat (0.5×0.5 m square) was placed in the centre of each 1×1 m sample square,
154 and all dead and detached vegetation (litter) was collected down to the soil surface, being
155 careful to exclude mineral soil. All litter material ≤ 25 mm diameter was defined as fine litter
156 and litter material > 25 mm and < 100 mm diameter was defined as coarse litter. All material
157 collected within each sub-plot was bulked by litter type (i.e. fine and coarse) and fine litter
158 was weighed in the field. A representative sub-sample ($> 25\%$ of the total biomass) of the fine
159 litter from each sub-plot was placed in a paper bag, weighed in the field then oven dried at
160 65°C to constant weight. This provided a moisture correction factor for total field weights of
161 fine litter. All coarse litter was collected and oven dried (65°C) to constant weight. Litter C
162 was determined by multiplying biomass by C concentration. Litter C concentration was
163 determined by dry-combustion with a LECO CNS-2000 analyser (LECO Corporation, MI,
164 USA).

165

166 Material ≥ 100 mm was defined as coarse woody debris (CWD) and was assessed using the
167 line-intersect method (Van Wagner, 1968; McKenzie et al. 2000). This involved running a
168 series of 10 m transects from a random start point and initial transect direction. At each 10 m
169 interval, the transect continued at 90° to the current direction of travel, where direction of
170 travel (left or right) was determined randomly. If the transect intersected with the plot edge,
171 then the direction of travel rebounded 90° at that point back into the plot for the remaining
172 part of the 10 m transect (McKenzie et al. 2000). Each transect was continued for a total
173 distance of 50 m and three 50 m transects were conducted in each plot. Diameters were
174 recorded for any CWD that intersected the transect and an estimation of decay (%) recorded
175 for each piece.

176

177 CWD volume V was calculated using:

178
$$\text{Volume} = (\pi^2 \sum d^2 / 8L)$$

179 where V is volume of wood per unit area ($\text{m}^3 \text{m}^{-2}$), d is piece diameter (m) and L is length of
180 transect line (m) (Van Wagner, 1968). This formula assumes that pieces were cylindrical,
181 horizontal and randomly oriented. For CWD with decay, volume calculations involved
182 subtraction of the decayed proportion of each piece (i.e. missing volume in reference to a
183 simple cylindrical volume). To convert CWD volumes to a mass per unit area, the volumes of
184 intact and decayed CWD were multiplied by their respective wood densities (450 kg m^{-3} for
185 pines and 650 kg m^{-3} for native vegetation, Illic et al., 2000). Carbon concentration of CWD
186 was not measured, but C stocks of CWD were estimated by multiplying CWD mass (Mg ha^{-1})
187 by a default C concentration value of 50% (Coomes et al. 2002; Garrett et al. 1998).

188

189 For each plot the diameter at breast height (DBH) of trees ≥ 10 cm was measured. The DBH
190 was used to calculate the basal area ($\text{m}^2 \text{ha}^{-1}$) of woody vegetation and to provide an
191 estimation of the above-ground biomass. The above-ground biomass was estimated using
192 general allometric relationships for softwood plantations and eucalypt vegetation for the
193 *Pinus* sp. forest and adjacent vegetation, respectively (Paul et al., *in press*). These allometrics
194 were developed based on existing biomass datasets in Australia and were based on 455
195 individuals of softwoods (mostly *Pinus radiata*) and 6004 eucalypt individuals (*Eucalyptus*
196 and closely-related genus of *Corymbia* and *Angophora*). For the *Pinus* sp. plantations and
197 native vegetation we used the following equations, respectively:

198 (1) Above-ground biomass (kg) = $\exp [-2.573 + 2.460 \ln(\text{DBH})] \times 1.018$

199 (2) Above-ground biomass (kg) = $\exp [-2.016 + 2.375 \ln(\text{DBH})] \times 1.067$

200 Tree biomass was converted to carbon using a C concentration of 49% (Gifford 2000). In
201 each sub-plot the diameter of all woody plants with a DBH 2.5–9.9 cm were measured to
202 allow calculation of sub-plot basal area and to estimate C stored in these understory plants.
203 No assessment of biomass was made for grasses, herbs and vines. Biomass of these
204 components is usually $< 3 \text{ Mg ha}^{-1}$ in the ecosystems studied (Moroni and Lewis 2015;
205 Westman and Rogers, 1977).

206

207 ***2.4 Soil sampling***

208 Following litter collection, at each randomly selected sampling location soil samples were
209 collected to a depth of 50 cm using 70 cm long hardened steel cores with two different
210 cutting head sizes. Cutting heads were 42 mm and 44 mm, with all cores having an internal
211 tube diameter of 45 mm. For fine textured soils, the 42 mm cutting heads were used due to

212 expansion of clays within the tube, and for coarse textured sandy soils the 44 mm cutting
213 heads were used, as expansion of sands within the tube is usually minimal. The cores were
214 driven into the ground using a Bosch GSH16 jack-hammer powered by a portable generator
215 (Honda EU20i 240V). A specially designed soil-core lifter was used to remove the core from
216 the ground.

217

218 The soil samples were pushed out of the core onto hemi-cylindrical tubes, then divided into
219 five sampling depths: 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm and 30–50 cm and transferred
220 into labelled, sealable plastic bags. Soil samples collected within each of the ten 10 × 10 m
221 sub-plot were bulked together for each depth. Once collected, soils were kept in a cool dark
222 location until the samples were air dried, processed and sent to the laboratory.

223

224 In addition to the soil C samples, samples for ‘soil core mass’ (oven-dried mass per unit core
225 volume for bulk density) determinations were collected from four randomly selected,
226 previously sampled squares in each plot. Each of these samples was collected using the same
227 core sampler as that used for soil C samples. Soil core mass samples were collected for the
228 same sampling depths as for the standard soil samples, and were placed in individually
229 labelled plastic bags for each depth. These samples were later dried in an oven at 40°C to
230 constant weight, to determine air-dry weights, and then dried at 110°C to constant weight, to
231 determine the oven-dry weight for calculation of core mass and the moisture correction factor
232 between air-dry and oven-dry soil for a plot.

233

234 ***2.5 Soil processing and analysis***

235 All soil samples, except the core mass samples, were weighed after air drying and carefully
236 processed by hand through a 2 mm sieve. During processing, visible organic material (roots,
237 buried debris, fungal hyphae and macro fauna including material <2 mm), charcoal and rocks
238 were separated by hand using long nosed surgical tweezers. While we did separate visible
239 plant roots, it is acknowledged that our sampling did not attempt to sample the 'root ball' and
240 tap roots located immediately below the tree bole and it is unlikely that our sampling
241 intensity (60 cores per 0.5 ha) was adequate to accurately sample total root biomass (Resh et
242 al., 2003). The contribution of this root mass is known to be variable, but significant (e.g.
243 Westman and Rogers, 1977; Resh et al., 2003; Coll et al., 2008) and hence our values of
244 below-ground C are under-estimates of total below-ground C. We did not attempt to sample
245 this below-ground 'root ball' biomass pool due to the destructive nature of such sampling,
246 nor did we estimate this pool as there is little available root biomass data for sub-tropical
247 *Pinus* sp. forests and adjacent native vegetation.

248

249 The components removed during processing were oven-dried at 65°C for 48 hours and
250 weighed. The oven-dried weights of these components were subtracted from the moisture
251 corrected total sample weight, to give the oven-dried weight of the <2 mm fraction of the soil
252 sample. The soil density was calculated for each soil sample using the oven-dried weight of
253 the <2 mm soil sample and the volume of the soil coring tube at the individual samples depth
254 interval. The soil sample was also inspected for the presence of carbonates, but no
255 carbonates were detected in the soils in this study (soil pH 4.5–6). Sub-samples of the <2
256 mm soil were separated from the whole sample by passing repeatedly through a riffle box
257 sample splitter. Total C and nitrogen (N) concentrations were then determined by dry-
258 combustion with a LECO CNS-2000 analyser (LECO Corporation, MI, USA). Soil organic C

259 fractions for particulate (POC), humus (HOC), and resistant (ROC) were estimated using
260 mid-infrared spectroscopy (MIRS) following the methods of Baldock et al. (2013).

261

262 SOC stocks for each depth interval were calculated using:

$$263 \text{ SOC (Mg ha}^{-1}\text{)} = \%C \times \rho \times V \times (1-f)$$

264 where %C is the C concentration (% weight); ρ the soil density (g m^{-3}); and V the volume
265 (m^3) of soil per hectare (depth in $\text{m} \times 10^4 \text{ m}^{-2}$) in the samples depth interval, after the volume
266 fraction (f) of the organic material, charcoal and rocks have been subtracted.

267

268 ***2.6 Data analysis***

269 Analysis of variance (ANOVA) was carried out in GenStat (16th edition, VSN International
270 Ltd.) to determine the effects of vegetation type (pine plantation vs native vegetation) on soil
271 C stocks across the eight sites. As the five different depth levels could not be randomised,
272 and there is likely some correlation between values down the profile, we treated the depth
273 factor as a 'repeated measures' factor, which takes into account levels of correlation and
274 makes appropriate adjustments to tests of significance and least significant difference (LSD)
275 values. Soil response variables analysed included SOC (Mg ha^{-1}), charcoal C (Mg ha^{-1}),
276 visible organic material C (Mg ha^{-1}), below-ground C (SOC plus charcoal C plus visible
277 organic material C, Mg ha^{-1}), MIR POC (Mg ha^{-1}), MIR HOC (Mg ha^{-1}) and MIR ROC (Mg
278 ha^{-1}). These variables were converted to a comparable depth (5 cm) prior to analysis to
279 account for the different volumes of soil in the different depth intervals. Analysis of the soil
280 variables was carried out on a fixed depth interval basis and on an equivalent soil mass basis
281 (Ellert & Bettany, 1995) due to likely modifications in density associated with plantation

282 establishment. Equivalent soil mass for each depth interval was calculated using the cubic
283 spline method of Wendt and Hauser (2013). In addition to the above soil variables, we
284 analysed litter C (fine and coarse, Mg ha^{-1}), CWD C (Mg ha^{-1}), small woody plant C (Mg ha^{-1}),
285 plot above-ground tree C (Mg ha^{-1}) and total ecosystem C (0–50 cm below-ground C plus
286 above-ground woody plant C plus all litter and CWD, Mg ha^{-1}) using a split-plot ANOVA
287 (with variation due to sites accounted for in the ‘Block’ stratum). In addition to analysing soil
288 variables at individual depths, variables were also analysed for the total 0–30 cm and 0–
289 50 cm depths using a split-plot ANOVA, with soil type included as a factor.

290

291 To account for variations in plantation age, tree basal area (all plants with a DBH >2.5 cm)
292 was included as a covariate in the analyses, where significant. Where necessary, variables
293 were log transformed ($\log_{10} + 1$) to meet the assumptions of ANOVA. ANOVA was also
294 used to determine significant vegetation type effects and vegetation type \times depth effects at an
295 individual site level. Regression analysis was used to investigate relationships between
296 response variables and potential predictors (e.g. plantation age, tree basal area, mean annual
297 rainfall). Predicted means and LSDs (5% level) from ANOVA analyses and adjusted R^2 from
298 regression analysis are reported.

299

300 **3. Results**

301 ***3.1 Soil and below-ground C pools***

302 Soil charcoal C stocks were significantly higher in the pine forest at three of the eight sites
303 and significantly higher in the native vegetation at two of the eight sites while the remaining
304 three sites did not differ significantly in charcoal stocks (Table 2). Across all sites, soil
305 charcoal C stocks did not differ between the native and non-native vegetation types ($F_{1,7} =$

306 1.04, $P = 0.34$, Table 3), the vegetation type \times depth interaction was not significant ($F_{4,56} =$
307 0.34, $P = 0.75$) and tree basal area had no significant influence. Soil charcoal C stocks did
308 vary with depth ($F_{4,56} = 15.71$, $P < 0.001$); with greater stocks in the upper soil layers
309 (predicted means of 0.25, 0.26, 0.15, 0.07 and 0.03 $\log+1$ Mg ha⁻¹ per 5 cm depth, for the 0–
310 5, 5–10, 10–20, 20–30 and 30–50 cm depths, respectively, LSD = 0.13). Mean charcoal C
311 stocks for 0–30 cm depth were 2.9 Mg ha⁻¹ for the native vegetation and 4.6 Mg ha⁻¹ for the
312 pine forest (LSD = 2.7).

313

314 Visible organic matter was significantly higher in the native vegetation than in the pine forest
315 at two of the eight sites, was significantly higher in the pine forest at one site and did not
316 differ significantly at the remaining sites (Table 2). Across all sites, only depth of sample had
317 a significant influence on visible organic matter C stocks ($F_{4,56} = 49.1$, $P < 0.001$). Visible
318 organic matter C stocks were higher at the surface depths (predicted means of 0.69, 0.60,
319 0.50, 0.37, 0.22 $\log+1$ Mg ha⁻¹ per 5 cm depth, for the 0–5, 5–10, 10–20, 20–30 and 30–
320 50 cm depths, respectively, LSD = 0.10). Across all sites, tree basal area had no influence on
321 the visible organic matter pool, but had a significantly positive association at two individual
322 sites (Table 2). Mean visible organic matter carbon stocks for 0–30 cm depth were
323 16.0 Mg ha⁻¹ for the native vegetation and 15.2 Mg ha⁻¹ for the pine forest (LSD = 8.8).

324

325 SOC (equivalent mass) was significantly higher in the pine forest at two of the eight sites,
326 was significantly higher in the native vegetation at two sites and did not differ between native
327 and non-native vegetation types at four sites (Table 2). Across all sites, SOC stocks did not
328 differ between native and non-native vegetation types ($F_{1,6} = 0.48$, $P = 0.51$, Table 3) and the
329 vegetation type \times depth interaction was not significant ($F_{4,56} = 0.47$, $P = 0.64$). However,

330 SOC stocks did differ among depths ($F_{4,56} = 23.0$, $P < 0.001$). SOC stocks decreased with
331 depth; predicted means were 8.27, 7.45, 5.90, 4.20, 2.89 Mg ha⁻¹ per 5 cm depth, for the 0–5,
332 5–10, 10–20, 20–30 and 30–50 cm depths, respectively (LSD = 1.49). Mean SOC stocks for
333 0–30 cm depth were 33.7 Mg ha⁻¹ for the native vegetation and 36.7 Mg ha⁻¹ for the pine
334 forest (LSD = 10.6). Tree basal area was positively associated with SOC at one site (Table 2)
335 and had an overall positive association with 0–50 cm SOC stock ($F_{1,6} = 25.83$, $P = 0.002$, $\beta =$
336 5.09). However, based on the limited number of data points for the plantation sites (eight
337 points, ages 6–34 years), the relationship between SOC and current rotation age was not
338 significant ($F_{1,7} = 2.60$, $P = 0.16$).

339

340 Below-ground C was significantly higher in the pine forest at three of eight sites,
341 significantly higher in the native vegetation at three of the eight sites and did not differ
342 between native and non-native vegetation types at two sites (Table 2). Across all sites, below-
343 ground C (SOC plus charcoal C plus visible organic material C) only differed significantly
344 between depths ($F_{4,56} = 35.21$, $P = < 0.001$). Predicted means were 14.1, 13.5, 10.0, 6.7,
345 4.4 Mg ha⁻¹ per 5 cm depth, for the 0–5, 5–10, 10–20, 20–30 and 30–50 cm depths,
346 respectively (LSD = 2.36). The effects of vegetation type ($F_{1,6} = 0.08$, $P = 0.79$, Table 3) and
347 the vegetation type \times depth interaction were not significant ($F_{4,56} = 0.51$, $P = 0.57$). Tree basal
348 area was positively associated with the below-ground C pool ($F_{1,6} = 10.37$, $P = 0.018$, $\beta =$
349 3.22) across all sites, and at one of the eight individual sites (Table 2). Mean below-ground C
350 stocks for 0–30 cm depth were 59.7 Mg ha⁻¹ for the native vegetation and 62.5 Mg ha⁻¹ for
351 the pine forest (LSD = 21.0).

352

353 Humic organic carbon (HOC) was significantly higher in the pine forest at two of the eight
354 sites, significantly higher also in the native vegetation at two of the eight sites and did not
355 differ between native and non-native vegetation types at four sites (Table 2). Across all sites,
356 the effect of vegetation type ($F_{1,7} = 0.25$, $P = 0.63$) on HOC and the vegetation type \times depth
357 interaction were again not significant ($F_{4,56} = 0.05$, $P = 0.95$). HOC did vary significantly
358 between depths ($F_{4,56} = 25.40$, $P < 0.001$). Predicted means were 3.13, 3.12, 2.70, 2.10,
359 1.63 Mg ha⁻¹ per 5 cm depth, for the 0–5, 5–10, 10–20, 20–30 and 30–50 cm depths,
360 respectively (LSD = 0.42). Mean HOC stocks for 0–30 cm depth were 15.5 Mg ha⁻¹ for the
361 native vegetation and 16.2 Mg ha⁻¹ for the pine forest (LSD = 3.4). Tree basal area was not
362 associated with HOC across all sites and had a negative association with HOC at one
363 individual site (Table 2).

364

365 Particulate organic carbon (POC) was significantly higher in the pine forest at two of eight
366 sites, significantly higher in the native vegetation at three of the eight sites and did not differ
367 between native and non-native vegetation types at three sites (Table 2). Across all sites, only
368 sampling depth had an influence on POC ($F_{4,56} = 24.39$, $P < 0.001$). Predicted means were
369 2.04, 1.39, 0.88, 0.45 and 0.62 Mg ha⁻¹ per 5 cm depth, for the 0–5, 5–10, 10–20, 20–30 and
370 30–50 cm depths, respectively (LSD = 0.44). The vegetation type effect ($F_{1,6} = 0.08$, $P =$
371 0.79, Table 3) and the vegetation type \times depth interaction were again not significant ($F_{4,56} =$
372 0.21, $P = 0.76$). Mean POC stocks for 0–30 cm depth were 6.3 Mg ha⁻¹ for the native
373 vegetation and 5.9 Mg ha⁻¹ for the pine forest (LSD = 1.6). Tree basal area was positively
374 associated with POC across all sites ($F_{1,6} = 11.21$, $P = 0.015$, $\beta = 3.35$) and had a positive
375 influence on POC at two individual sites (Table 2). POC varied significantly with soil type
376 ($F_{3,4} = 7.13$, $P = 0.044$); the Podosol sites had higher POC values than the grey Chromosol
377 site (predicted means of 11.7 and 2.3 Mg ha⁻¹, LSD = 5.91).

378

379 Resistant organic carbon (ROC) was significantly higher in the pine forest at two of eight
380 sites, significantly higher in the native vegetation at one of the eight sites and did not differ
381 between native and non-native vegetation types at five sites (Table 2). Across all sites,
382 sampling depth had a significant influence on ROC stocks ($F_{4,56} = 28.99$, $P < 0.001$);
383 predicted means were 2.39, 2.29, 1.76, 1.03, 0.57 Mg ha⁻¹ per 5 cm depth, for the 0–5, 5–10,
384 10–20, 20–30 and 30–50 cm depths, respectively (LSD = 0.46). The vegetation type effect
385 ($F_{1,6} = 1.14$, $P = 0.33$) and the vegetation type × depth interaction were again not significant
386 ($F_{4,56} = 0.09$, $P = 0.94$). Mean ROC stocks for 0–30 cm depth were 9.7 Mg ha⁻¹ for the native
387 vegetation and 10.8 Mg ha⁻¹ for the pine forest (LSD = 3.5). Tree basal area had a significant
388 positive association with ROC across all sites ($F_{1,6} = 9.04$, $P = 0.024$, $\beta = 2.99$), had a
389 positive association with ROC at one individual site, and a negative association at one site
390 (Table 2).

391

392 **3.2 Above-ground C pools**

393 Fine litter C was significantly higher in the pine forest at five sites and higher in the native
394 vegetation at one site (Table 3). Across all paired sites fine litter C varied marginally between
395 the pine forest and native vegetation ($F_{1,7} = 3.92$, $P = 0.088$). Fine litter C tended to be higher
396 in the pine forest than in the adjacent native vegetation (predicted means of 15.5 and
397 10.7 Mg ha⁻¹, LSD = 5.8, Table 3). Across all sites there was no significant difference in
398 coarse litter C stocks between the pine forest and native vegetation ($F_{1,7} = 3.19$, $P = 0.12$,
399 Table 3), although pine forest had greater coarse litter C than native vegetation at four
400 individual sites (Table 3). Predicted mean coarse litter stocks across all sites were 1.0 Mg ha⁻¹
401 ¹ in the native vegetation and 1.9 Mg ha⁻¹ in the pine forests (standard error = 0.35 Mg ha⁻¹).

402 Total litter C (fine plus coarse) increased significantly with plantation age in the pine forest
403 ($F_{1,6} = 13.35$, $P = 0.011$, $R^2 = 0.64$; Figure 2a) and with tree basal area across both vegetation
404 types ($F_{1,14} = 8.48$, $P = 0.011$, $R^2 = 0.33$). The variation in litter C stocks among the native
405 forest sites was almost as high as that among the pine plantation sites of varying age (Table
406 3), reflecting the variation in vegetation and soil types across the different native forest sites.
407 There was no difference in coarse woody debris stocks between the pine forest and native
408 vegetation ($F_{1,7} = 0.55$, $P = 0.48$). Mean coarse woody debris stocks were 5.4 Mg ha^{-1} in the
409 native vegetation and 3.2 Mg ha^{-1} in the pine forests (standard error = 2.2 Mg ha^{-1}).

410

411 Pine trees nearing the end of the commercial rotation had sequestered up to 128 Mg C ha^{-1} .
412 Carbon stored in pine plantation trees increased with plantation age (Figure 2b, $F_{1,6} = 30.1$, P
413 = 0.002) and plantation age explained 80.6% of the variation in above-ground tree C. The
414 unexplained variation in this relationship is likely due to local site productivity factors, such
415 as soil fertility and rainfall. Carbon stored in the trees ($\geq 10 \text{ cm DBH}$) in native vegetation
416 adjacent to pine plantations varied from 2.3 Mg ha^{-1} in a heathland site to 183.0 Mg ha^{-1} in a
417 eucalypt forest. Carbon stored in understorey woody plants (2.5–9.9 cm DBH) was a small
418 pool, but was significantly higher in the native vegetation than in the pine forest ($F_{1,7} = 15.3$,
419 $P = 0.006$, Table 3). There was a significant linear relationship between total 0–50 cm SOC
420 and above-ground tree biomass for the native vegetation sites that explained 88.8% of the
421 variation in the data ($F_{1,6} = 56.7$, $P < 0.001$, standard error of estimate = 11.5; Figure 3). There
422 was also a significant linear relationship between total 0–50 cm SOC in the native vegetation
423 sites and mean annual rainfall ($F_{1,6} = 7.78$, $P = 0.032$, standard error of estimate = 16.2; $R^2 =$
424 0.33) which is to be expected given known the relationship between above-ground biomass
425 and rainfall.

426

427 Above-ground C stocks varied greatly between individual sites (Figure 4). Total ecosystem C
428 (0–50 cm below-ground C plus above-ground woody plant C plus all litter and CWD) varied
429 from 58.7 Mg ha⁻¹ on the native heathland grey Chromosol site to 497.8 Mg ha⁻¹ on a native
430 eucalypt forest brown Kandosol site. Across all sites, there was no significant difference in
431 total ecosystem C between the native vegetation and pine forests ($F_{1,7} = 0.00$, $P = 0.98$, Table
432 3).

433

434 **4. Discussion**

435 ***4.1 Below-ground C estimates***

436 Our hypothesis, based on studies in southern Australia (Turner and Lambert, 2000, Turner et
437 al., 2005) and meta-analyses (Guo and Gifford, 2002; Don et al., 2011), that SOC would be
438 lower in *Pinus* plantations than adjacent native vegetation, was not supported across all sites.
439 In fact, at two of eight sites SOC was higher in the plantation forests and this was driven by
440 higher POC and ROC at both sites. Changes in POC are not surprising given these pools are
441 known to respond to land-use changes (e.g. Chan, 2001; John et al., 2005). The differences
442 in ROC between sites were unexpected as the resistant fractions are thought to be relatively
443 inert and turn-over in longer time frames than those associated with vegetation type
444 conversion in the current study (von Lützow et al., 2007). However, it is possible the ROC is
445 higher in some pine plantations due to pyrogenic C, which may not be considered inert
446 (Singh et al., 2012), as these plantations are frequently burnt with low intensity fire to reduce
447 wildfire risk (Hunt and Simpson, 1985) and occurrence of fire to burn debris is common
448 immediately following clearing of native vegetation. In fact at one site, both soil ROC and

449 soil charcoal C that was separated during soil processing, was higher in the pine plantations
450 than the adjacent native vegetation. At the two sites where SOC was greater in the plantation
451 forest, the difference tended to be in the 0–20 cm depth. In fact, a further plantation site had
452 higher SOC in the 0–5 cm depth horizon than in the native vegetation (i.e. significant
453 vegetation type \times depth interaction). This is contrary to the findings of a meta-analysis by
454 Don et al. (2011) who reported higher SOC in the surface horizons of primary forest. This
455 suggests that introduced *Pinus* plantations in the sub-tropics may have higher SOC and
456 visible organic matter in the surface horizons than certain native vegetation communities,
457 perhaps due to shallow and dense root systems (e.g. Mou et al., 1995) and associated
458 mycorrhizae in these plantings.

459

460 Several studies report significant losses in SOC associated with forest type change from
461 native forest to plantation forest (Guo and Gifford, 2002; Chen et al., 2004; Richards et al.,
462 2007) although changes in SOC may be influenced by the species planted (Guo and Gifford,
463 2002; Don et al., 2011). In the current study, of the two sites where SOC was higher in the
464 native vegetation relative to two 26 year old *Pinus* plantations, this difference was restricted
465 to the 0–10 cm depths at one site, and was driven by higher POC. The native vegetation at
466 this particular site was open woodland with dense clusters of proteoid roots near the soil
467 surface (associated with *Banksia aemula*); which play an important role in the acquisition of
468 phosphorus and other mineral nutrients in infertile soils (Dinkelaker et al., 1995; Lamont,
469 2003). At the other site where SOC was higher in the native vegetation the difference was
470 attributed to higher POC, ROC and charcoal C.

471

472 Reviews by Paul et al. (2002) and Guo and Gifford (2002) suggest it may take more than 30
473 or 40 years for SOC to be restored to its original levels following plantation establishment.
474 Similarly, Turner and Lambert (2000) reported initial losses in SOC and suggested that at
475 least 10 to 20 years is needed before net accumulation of SOC occurs after planting. Based on
476 our chronosequence of different plantation ages, total SOC was not related to plantation age,
477 and hence time since the most recent soil disturbance, although we acknowledge that
478 additional data points or time-series data are needed to test this relationship properly. The
479 findings reported here are corroborated by a concurrent study that re-visited six paired sites
480 (native vegetation and *Pinus* sp. plantation) that were initially sampled in 1998 and then
481 again 15 years later (unpublished data). Further, Gholz and Fisher (1982) reported relatively
482 minor changes in SOC with increasing age in *Pinus elliottii* plantations in Florida. It appears
483 that SOC varies greatly from site to site across the landscape, and that this variation is much
484 greater than the variation observed with a change from native vegetation to introduced *Pinus*
485 plantation. Thus changes in SOC associated with vegetation type change really need to be
486 assessed at a site-level. The local site related factors that influence SOC stocks are currently
487 not well understood although we speculate that the variable responses are at least partly due
488 to variations in fine root biomass distribution and turnover in the different vegetation
489 communities (Coleman et al., 2000; Rasse et al., 2005). At a landscape scale, certain
490 environmental factors (e.g. rainfall, temperature, elevation, pH, soil texture, bulk density and
491 vegetation type) and management factors (e.g. fertiliser additions) are known to be drivers of
492 variation in SOC (Paul et al., 2002; Kasel and Bennett, 2007; Rabbi et al., 2014) and
493 influence the site-to-site variation. The fact that our findings differ from some studies of
494 *Pinus radiata* plantations in southern Australia might reflect the different *Pinus* species
495 planted in the sub-tropics, the different environmental drivers (e.g. rainfall) and the high
496 degree of variability between sites in our study (e.g. different plantation ages, site preparation

497 and management methods, soil types, native vegetation types etc). Our findings are, however,
498 supported by those of Kasel and Bennett (2007) who reported variable land-use change
499 responses within different *Pinus radiata* plantations.

500

501 Our study was comprehensive in that it accounted for different below-ground C pools
502 (organic material, charcoal, POC, HOC, ROC) in addition to SOC. However, separation into
503 these pools had no major influence when testing for changes associated with vegetation type
504 across all sites. Visible organic matter C, charcoal C and SOC all decreased with increasing
505 depth down the profile, as expected based on previous studies (Gill et al., 1999; Jobbágy and
506 Jackson 2000; Guo and Gifford, 2002).

507

508 ***4.2 Above-ground and total ecosystem C estimates***

509 Carbon stored in above-ground tree biomass was the largest C pool for most sites in this
510 study (~35% of the total ecosystem C). Our estimates of tree biomass C are in the range of
511 those reported for similar forest types in the region (Westman and Rogers, 1977; Simpson et
512 al., 2000). Few studies have estimated total ecosystem C stocks, including SOC, for the study
513 region. Our findings support those from elsewhere, that the greatest potential for C
514 sequestration in plantation forests is through above- and below-ground tree biomass
515 sequestration (Paul et al., 2002; Peichl and Arain, 2006). Our hypothesis that above-ground
516 woody plant C would be lower in the *Pinus* plantations was only partially supported. At
517 plantation sites that were nearing the end of the commercial rotation, tree C stocks were not
518 always higher in the native vegetation (Figure 4); in fact two such sites had higher tree C

519 stocks in the plantation forest. Nevertheless, across all sites, C stored in trees was similar
520 between the two vegetation types (Table 3).

521

522 A significant finding of the current study was the relatively strong relationship between SOC
523 and above-ground biomass in the native vegetation. Similar relationships have been found in
524 other ecosystems (e.g. Laurance et al., 1999) but are not commonly reported for the sub-
525 tropics. Unfortunately it is uncertain as to whether: (i) the initial high SOC levels support the
526 potential for greater biomass accumulation; or (ii) whether the greater biomass stocks and
527 associated higher site productivity (e.g. due to rainfall) have contributed to SOC
528 accumulation over a long period of time. Nevertheless, it appears that SOC levels in native
529 vegetation could be a useful predictor (along with other confounding site productivity
530 variables) of potential tree plantation growth in an adjacent area. This is to be expected given
531 the importance of soil organic matter, particularly on sandy soils, in influencing soil
532 productivity variables like cation exchange capacity, microbial biomass and physical
533 properties that can increase soil moisture retention (Reeves, 1997; Oorts et al., 2003; Jia et
534 al., 2005; Lal, 2006; Kimetu et al. 2008).

535

536 Litter C, although a relatively small pool (~4.9% of the total ecosystem C in the native and
537 7.4% in the pine forest) responded significantly to plantation age, with a C sequestration rate
538 of 0.67 Mg ha⁻¹ year⁻¹. The relationship between litter C and tree basal area for all sites
539 (plantation and native vegetation), although significant, was not strong and hence caution is
540 needed in predicting litter C from basal area measures alone. Further work is needed to
541 determine the best model and combination of variables for litter C prediction, particularly in
542 multi-aged native vegetation. Based on previous studies (Cuevas et al., 1991; Prescott, 2010)

543 we expected the litter C pool to be higher in the *Pinus* plantations than the adjacent native
544 vegetation. Across all sites this hypothesis was partially supported, at least for the fine litter C
545 pool, reflecting the slower decomposition rates of pine needles (Paul and Polglase, 2004;
546 Prescott, 2010). However, this was not the case at all sites, as at one site, fine litter C was
547 higher in the native vegetation than the pine plantation. At this site, the plantation was
548 relatively young (9.7 years since planting) and hence above-ground biomass had not reached
549 levels similar to those in the native vegetation, presumably resulting in lower litter-fall rates.
550 There is a high degree of variation in litter biomass stocks in both plantation and native
551 vegetation, not only in relation to plantation age and basal area, but also to recent site
552 management, such as fire. The finding that understorey woody plant C stocks were higher in
553 the native vegetation than in the pine forest might reflect the inhibitory effect of pine needle
554 litter on native understorey plants (Baker and Murray 2012), and may also be related to the
555 occurrence of frequent low-intensity fire in the pine forest understories.

556

557 ***4.3 Conclusions***

558 There is regional and global concern regarding the clearing or conversion of native
559 vegetation. While we do not advocate clearing of remnant native vegetation, our findings
560 suggest that historic conversion from native vegetation to commercial plantation has had little
561 influence on ecosystem C stocks across multiple sites in our study region. The two main C
562 pools were above-ground tree C and SOC and neither of these pools was significantly
563 influenced by vegetation type change across all sites. Losses of C from the plantation forests
564 associated with harvesting and plantation management (e.g. site preparation) are offset by
565 increases in live tree biomass and debris pools over time. A key finding of this study is that
566 site-to-site variation in SOC, even within a relatively small geographic area, is much greater

567 than that associated with a change from native vegetation to *Pinus* plantation forest. Another
568 key finding was the significant positive relationship between 0–50 cm SOC and above-
569 ground biomass in the native vegetation areas. Further studies are needed to determine if this
570 relationship holds for other ecosystems and regions.

571

572 **5. Acknowledgements**

573 Bob Meyer (DAF) provided statistical guidance. Keryn Paul (CSIRO) provided allometrics
574 for estimating tree biomass. Student volunteers (Lisa Hunt, Joe McNeal, Corrine Duncan,
575 Dotty Timms, Edward Howell and Ben Francis) assisted with field data collection and soil
576 processing. Brigid McKenna (University of Queensland) assisted with laboratory work.
577 HQPlantations provided access and site information for the pine plantation sites sampled in
578 this study. This work was made possible with funding from the Australian Government,
579 Department of Agriculture, Filling the Research Gap Round 1 National Soil Carbon Program
580 (PN01203.074).

581

582 **6. References**

583 Baker, A. C., Murray, B. R. 2012. Seasonal intrusion of litterfall from non-native pine
584 plantations into surrounding native woodland: Implications for management of an
585 invasive plantation species. *Forest Ecology and Management* 277, 25–37.

586 Baldock, J. A., Hawke, B., Sanderman, J., Macdonald, L. M. 2013. Predicting contents of
587 carbon and its component fractions in Australian soils from diffuse reflectance mid-
588 infrared spectra. *Soil Research* 51, 577–595.

- 589 Bashkin, M. A., Binkley, D. 1998. Changes in soil carbon following afforestation in Hawaii.
590 Ecology 79, 828–833.
- 591 Birk, E. M., Simpson, R. W. 1980. Steady state and the continuous input model of litter
592 accumulation and decomposition in Australian eucalypt forests. Ecology 61, 481–485.
- 593 Brown, S., Lugo, A. 1990. Effects of forest clearing and succession on the carbon and
594 nitrogen content of soils in Puerto Rico and US virgin islands. Plant and Soil 124, 53–
595 64.
- 596 Bubb, K. A., Xu, Z. H., Simpson, J. A., Saffigna, P. G. 1998. Some nutrient dynamics
597 associated with litterfall and litter decomposition in hoop pine plantations in southeast
598 Queensland, Australia. Forest Ecology and Management 110, 343–352.
- 599 Chan, K. Y. 2001. Soil particulate organic carbon under different land use and management.
600 Soil Use and Management 17, 217–221.
- 601 Chen, C. R., Xu, Z. H., Mathers, N. J. 2004. Soil carbon pools in adjacent natural and
602 plantation forests of subtropical Australia. Soil Science Society of America Journal
603 68, 282–291.
- 604 Coleman, M. D., Dickson, R. E., Isebrands, J. G. 2000. Contrasting fine-root production,
605 survival and soil co₂ efflux in pine and poplar plantations. Plant and Soil 225, 129–
606 139.
- 607 Coll, L., Potvin, C., Messier, C., Delagrange, S. 2008. Root architecture and allocation
608 patterns of eight native tropical species with different successional status used in
609 open-grown mixed plantations in Panama. Trees 22, 585–596.
- 610 Coomes, D. A., Allen, R. B., Scott, N. A., Goulding, C., Beets, P. 2002. Designing systems to
611 monitor carbon stocks in forests and shrublands. Forest Ecology and Management
612 164, 89–108.

- 613 Cuevas, E., Brown, S., Lugo, A. 1991. Above- and belowground organic matter storage and
614 production in a tropical pine plantation and a paired broadleaf secondary forest. *Plant
615 and Soil* 135, 257–268.
- 616 Dinkelaker, B., Hengeler, C., Marschner, H. 1995. Distribution and function of proteoid roots
617 and other root clusters. *Botanica Acta* 108, 183–200.
- 618 Don, A., Schumacher, J., Freibauer, A. 2011. Impact of tropical land-use change on soil
619 organic carbon stocks - a meta-analysis. *Global Change Biology* 17, 1658–1670.
- 620 Ellert, B. H., Bettany, J. R. 1995. Calculation of organic matter and nutrients stored in soils
621 under contrasting management regimes. *Canadian Journal of Soil Science* 75, 529–
622 538.
- 623 Ellert, B. H., Gregorich, E. G. 1996. Storage of carbon, nitrogen and phosphorus in cultivated
624 and adjacent forested soils of Ontario. *Soil Science* 161, 587–603.
- 625 Garrett, L. G., Oliver, G. R., Pearce, S. H., Davis, M. R. 2008. Decomposition of *Pinus*
626 *radiata* coarse woody debris in New Zealand. *Forest Ecology and Management* 255,
627 3839–3845.
- 628 Gholz, H. L., Fisher, R. F. 1982. Organic matter production and distribution in slash pine
629 (*Pinus elliottii*) plantations. *Ecology* 63, 1827–1839.
- 630 Gifford, R. M. 2000. Carbon contents of above-ground tissues of forest and woodland trees.
631 National Carbon Accounting System, Technical Report No. 22. Australian
632 Greenhouse Office, Canberra.
- 633 Gill, R., Burke, I. C., Milchunas, D. G., Lauenroth, W. K. 1999. Relationship between root
634 biomass and soil organic matter pools in the shortgrass steppe of eastern Colorado.
635 *Ecosystems* 2, 226–236.
- 636 Guo, L. B., Gifford, R. M. 2002. Soil carbon stocks and land use change: A meta analysis.
637 *Global Change Biology* 8, 345–360.

- 638 Hero, J. M., Castley, J. G., Butler, S. A., Lollback, G. W. 2013. Biomass estimation within an
639 Australian eucalypt forest: Meso-scale spatial arrangement and the influence of
640 sampling intensity. *Forest Ecology and Management* 310, 547–554.
- 641 Houghton, R. A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere
642 from changes in land use and land management 1850–2000. *Tellus B* 55, 378–390.
- 643 Hunt, S. M., Simpson, J. A. 1985. Effects of low intensity prescribed fire on the growth and
644 nutrition of a slash pine plantation. *Australian Forest Research* 15, 67–77.
- 645 Ilic, J., Boland, D., McDonald, M., Downes, G., Blakemore, P. 2000. Wood density phase 1–
646 state of knowledge. National carbon accounting system technical report no. 18.
647 Australian Greenhouse Office, Canberra.
- 648 Isbell, R. F. 1996. *The Australian Soil Classification*. CSIRO publishing, Collingwood,
649 Victoria.
- 650 Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D. W.,
651 Minkinen, K., Byrne, K. A. 2007. How strongly can forest management influence
652 soil carbon sequestration? *Geoderma* 137, 253–268.
- 653 Jeffrey, S. J., Carter, J. O., Moodie, K. B., Beswick, A. R. 2001. Using spatial interpolation to
654 construct a comprehensive archive of Australian climate data. *Environmental*
655 *Modelling & Software* 16, 309–330.
- 656 Jia, G.-m., Cao, J., Wang, C., Wang, G. 2005. Microbial biomass and nutrients in soil at the
657 different stages of secondary forest succession in Ziwulin, northwest China. *Forest*
658 *Ecology and Management* 217, 117–125.
- 659 Jobbágy, E. G., Jackson, R. B. 2000. The vertical distribution of soil organic carbon and its
660 relation to climate and vegetation. *Ecological Applications* 10, 423–436.

- 661 John, B., Yamashita, T., Ludwig, B., Flessa, H. 2005. Storage of organic carbon in aggregate
662 and density fractions of silty soils under different types of land use. *Geoderma* 128,
663 63–79.
- 664 Kasel, S., Bennett, L. T. 2007. Land-use history, forest conversion, and soil organic carbon in
665 pine plantations and native forests of south eastern Australia. *Geoderma* 137, 401–
666 413.
- 667 Kimetu, J., Lehmann, J., Ngoze, S., Mugendi, D., Kinyangi, J., Riha, S., Verchot, L., Recha,
668 J., Pell, A. 2008. Reversibility of soil productivity decline with organic matter of
669 differing quality along a degradation gradient. *Ecosystems* 11, 726–739.
- 670 Lal, R. 2006. Enhancing crop yields in the developing countries through restoration of the
671 soil organic carbon pool in agricultural lands. *Land Degradation & Development* 17,
672 197–209.
- 673 Lamont, B. 2003. Structure, ecology and physiology of root clusters – a review. *Plant and*
674 *Soil* 248, 1–19.
- 675 Laurance, W. F., Fearnside, P. M., Laurance, S. G., Delamonica, P., Lovejoy, T. E., Rankin-
676 de Merona, J. M., Chambers, J. Q., Gascon, C. 1999. Relationship between soils and
677 amazon forest biomass: A landscape-scale study. *Forest Ecology and Management*
678 118, 127–138.
- 679 Liski, J., Perruchoud, D., Karjalainen, T. 2002. Increasing carbon stocks in the forest soils of
680 western Europe. *Forest Ecology and Management* 169, 159–175.
- 681 Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar
682 age. *Ecological Monographs* 62, 1–41.
- 683 McKenzie, N., Ryan, P., Fogarty, P., Wood, J. 2000. Sampling, measurement and analytical
684 protocols for carbon estimation in soil, litter and coarse woody debris. *National*

685 Carbon Accounting System, Technical Report No. 14. Australian Greenhouse Office,
686 Canberra.

687 Montreal Process Implementation Group for Australia and National Forest Inventory Steering
688 Committee, 2013. Australia's State of the Forests Report 2013, ABARES, Canberra,
689 December. Accessed from: daff.gov.au/abares/publications (12 November 2015).

690 Moroni, M. T., Lewis, T. 2015. Comparing measured and modelled eucalypt forest carbon
691 stocks. Forest Management Services Branch, Technical Report 01/2015, Forestry
692 Tasmania, Hobart.

693 Mou, P., Jones, R. H., Mitchell, R. J., Zutter, B. 1995. Spatial distribution of roots in
694 sweetgum and loblolly pine monocultures and relations with above-ground biomass
695 and soil nutrients. *Functional Ecology* 9, 689–699.

696 Murty, D., Kirschbaum, M. U. F., McMurtrie, R. E., McGilvray, H. 2002. Does conversion of
697 forest to agricultural land change soil carbon and nitrogen? A review of the literature.
698 *Global Change Biology* 8, 105–123.

699 Ngugi, M. R., Doley, D., Botkin, D. B., Cant, M., Neldner, V. J., Kelley, J. 2014. Long-term
700 estimates of live above-ground tree carbon stocks and net change in managed uneven-
701 aged mixed species forests of sub-tropical Queensland, Australia. *Australian Forestry*
702 77, 189–202.

703 Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in
704 ecological systems. *Ecology* 44, 322–331.

705 Oorts, K., Vanlauwe, B., Merckx, R. 2003. Cation exchange capacities of soil organic matter
706 fractions in a ferric lixisol with different organic matter inputs. *Agriculture,
707 Ecosystems & Environment* 100, 161–171.

708 Oren, R., Ellsworth, D. S., Johnsen, K. H., Phillips, N., Ewers, B. E., Maier, C., Schafer, K.
709 V. R., McCarthy, H., Hendrey, G., McNulty, S. G., Katul, G. G. 2001. Soil fertility

710 limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere.
711 Nature 411, 469–472.

712 Paul, K. I., Polglase, P. J. 2004. Prediction of decomposition of litter under eucalypts and
713 pines using the FullCAM model. Forest Ecology and Management 191, 73–92.

714 Paul, K. I., Polglase, P. J., Nyakuengama, J. G., Khanna, P. K. 2002. Change in soil carbon
715 following afforestation. Forest Ecology and Management 168, 241–257.

716 Paul, K. I., Roxburgh, S. H., Chave, J., England, J. R., Zerihun, A., Specht, A., . . . Sinclair, J.
717 2015. Testing the generality of above-ground biomass allometry across plant
718 functional types at the continent scale. Global Change Biology, n/a-n/a. doi:
719 10.1111/gcb.13201

720 Peichl, M., Arain, M. A. 2006. Above- and belowground ecosystem biomass and carbon
721 pools in an age-sequence of temperate pine plantation forests. Agricultural and Forest
722 Meteorology 140, 51–63.

723 Prescott, C. 2010. Litter decomposition: What controls it and how can we alter it to sequester
724 more carbon in forest soils? Biogeochemistry 101, 133–149.

725 Rabbi, S. M. F., Tighe, M., Cowie, A., Wilson, B. R., Schwenke, G., McLeod, M., Badgery,
726 W., Baldock, J. 2014. The relationships between land uses, soil management
727 practices, and soil carbon fractions in south eastern Australia. Agriculture,
728 Ecosystems & Environment 197, 41–52.

729 Rasse, D., Rumpel, C., Dignac, M.-F. 2005. Is soil carbon mostly root carbon? Mechanisms
730 for a specific stabilisation. Plant and Soil 269, 341–356.

731 Reeves, D. W. 1997. The role of soil organic matter in maintaining soil quality in continuous
732 cropping systems. Soil and Tillage Research 43, 131–167.

- 733 Resh, S., Battaglia, M., Worledge, D., Ladiges, S. 2003. Coarse root biomass for eucalypt
734 plantations in Tasmania, Australia: Sources of variation and methods for assessment.
735 *Trees* 17, 389–399.
- 736 Rhoades, C. C., Eckert, G. E., Coleman, D. C. 2000. Soil carbon differences among forest,
737 agriculture, and secondary vegetation in lower montane Ecuador. *Ecological*
738 *Applications* 10, 497–505.
- 739 Richards, A. E., Dalal, R. C., Schmidt, S. 2007. Soil carbon turnover and sequestration in
740 native subtropical tree plantations. *Soil Biology and Biochemistry* 39, 2078–2090.
- 741 Richter, D. D., Markewitz, D., Trumbore, S. E., Wells, C. G. 1999. Rapid accumulation and
742 turnover of soil carbon in a re-establishing forest. *Nature* 400, 56–58.
- 743 Simpson, J. A., Xu, Z. H., Smith, T., Keay, P., Osborne, D. O., Podberscek, M. 2000. Effects
744 of site management in pine plantations on the coastal lowlands of subtropical
745 Queensland, Australia. Pages 73–81. Center for International Forestry Research,
746 Jakarta.
- 747 Singh, N., Abiven, S., Torn, M. S., Schmidt, M. W. I. 2012. Fire-derived organic carbon in
748 soil turns over on a centennial scale. *Biogeosciences* 9, 2847–2857.
- 749 Strassmann, K. M., Joos, F., Fischer, G. 2008. Simulating effects of land use changes on
750 carbon fluxes: Past contributions to atmospheric CO₂ increases and future
751 commitments due to losses of terrestrial sink capacity. *Tellus B* 60, 583–603.
- 752 Turner, J., Lambert, M. 2000. Change in organic carbon in forest plantation soils in eastern
753 Australia. *Forest Ecology and Management* 133, 231–247.
- 754 Turner, J., Lambert, M. J., Johnson, D. W. 2005. Experience with patterns of change in soil
755 carbon resulting from forest plantation establishment in eastern Australia. *Forest*
756 *Ecology and Management* 220, 259–269.

- 757 Van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. *Forest Science*
758 14, 20–26.
- 759 von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner,
760 E., Marschner, B. 2007. SOM fractionation methods: Relevance to functional pools
761 and to stabilization mechanisms. *Soil Biology and Biochemistry* 39, 2183–2207.
- 762 Wendt, J. W., Hauser, S. 2013. An equivalent soil mass procedure for monitoring soil organic
763 carbon in multiple soil layers. *European Journal of Soil Science* 64, 58–65.
- 764 Westman, W., Rogers, R. 1977. Biomass and structure of a subtropical eucalypt forest, North
765 Stradbroke Island. *Australian Journal of Botany* 25, 171–191.

766 **List of Figures**

767 **Figure 1.** Locations of paired sampling sites (pine forest and adjacent native vegetation)
768 within the pine plantation estate of southern Queensland, Australia (inset A). Examples are
769 shown of: the plot sampling layout (inset B), where darker shaded cells represent those
770 randomly selected for sampling; and inset C, showing locations of 10 sampling points
771 randomised within a 10 × 10 m sub-plot.

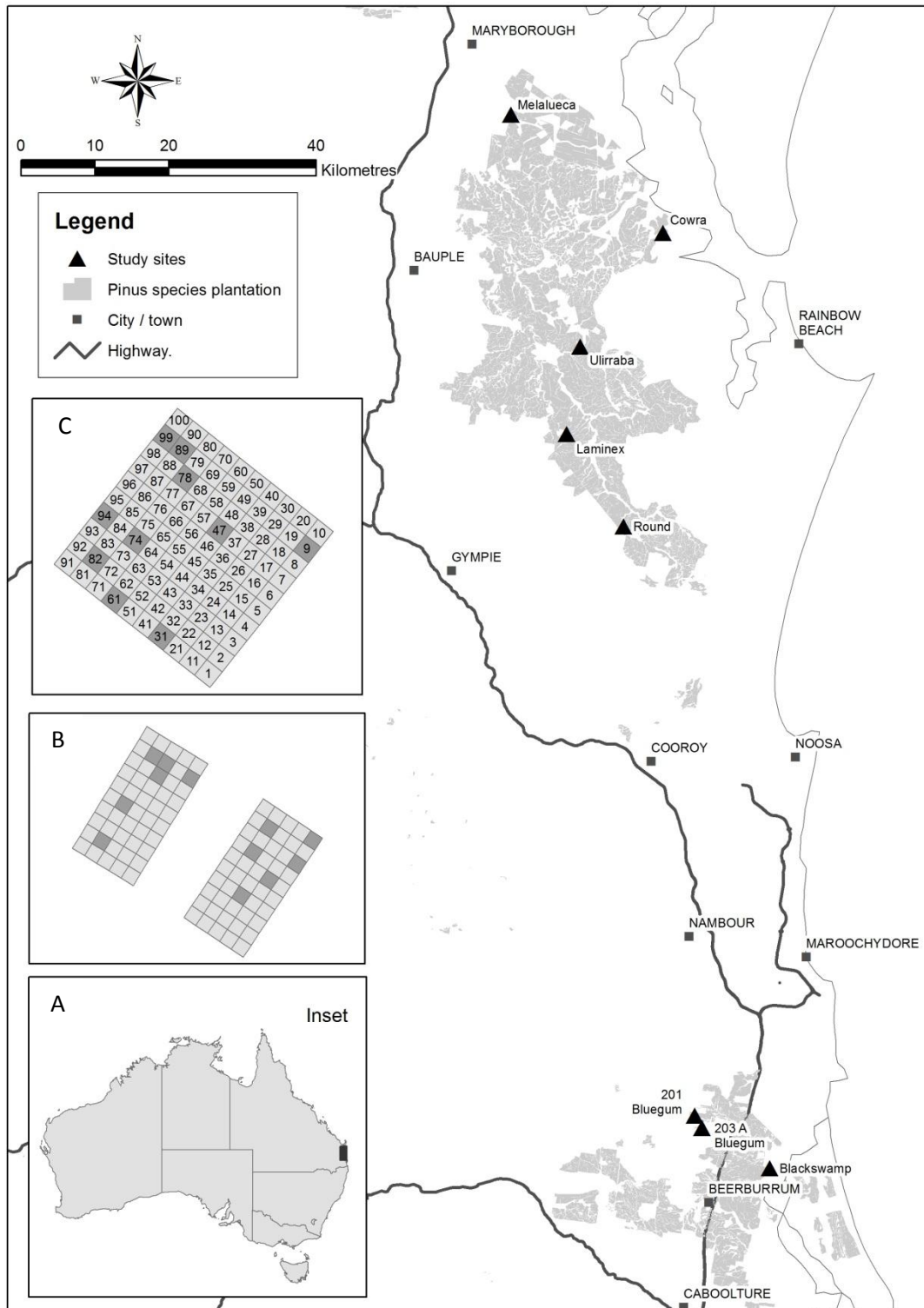
772 **Figure 2.** Significant relationships between total litter C (fine and coarse litter) and pine
773 plantation age (a, significant linear relationship, adjusted $R^2 = 0.64$) and between above-
774 ground tree C and plantation age (b, significant exponential curve, adjusted $R^2 = 0.81$).

775 **Figure 3.** Significant linear relationship between SOC and above-ground biomass (AGB) for
776 the native vegetation plots that were paired with pine plantations (adjusted $R^2 = 0.89$).

777 **Figure 4.** Mean above-ground C pools for individual paired sites (NV, native vegetation and
778 PF, pine forest), showing litter C (fine plus coarse litter), coarse woody debris C (CWD),
779 small woody plant C (DBH 2.5–9.9 cm) and tree C (DBH ≥ 10 cm). Site codes are: BSW,
780 Blackswamp; BG03, Bluegum 203; BG01, Bluegum 201; ULI, Ulirraba; LAM, Laminex;
781 COW, Cowra; MEL, Melaleuca; RND, Round.

782

783 **Figure 1.**



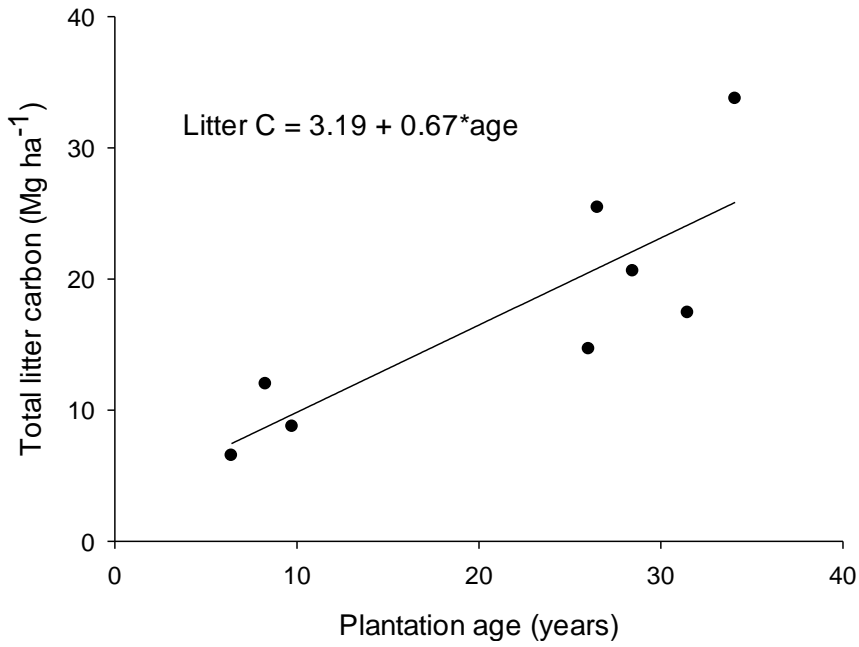
784

785

786

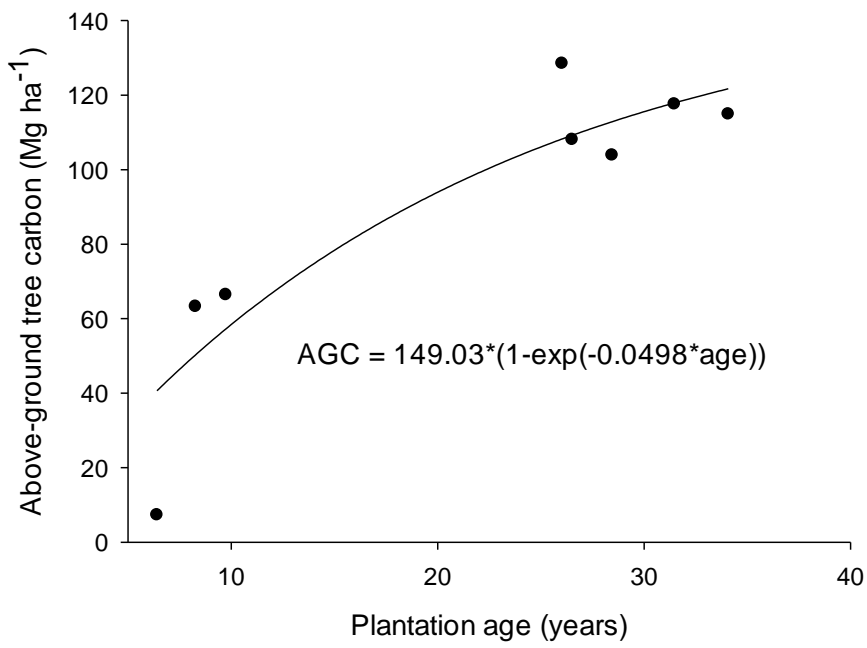
787 **Figure 2.**

788 (a)



789

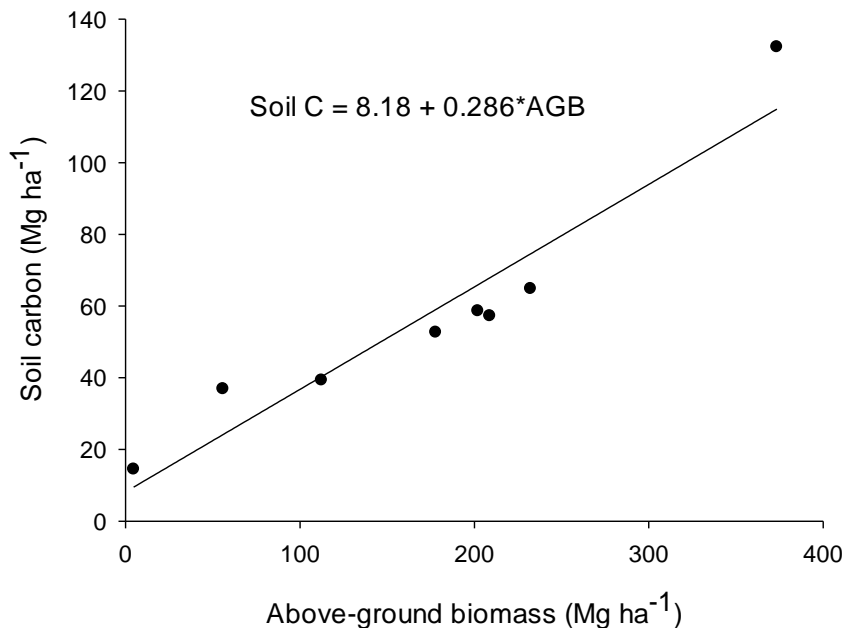
790 (b)



791

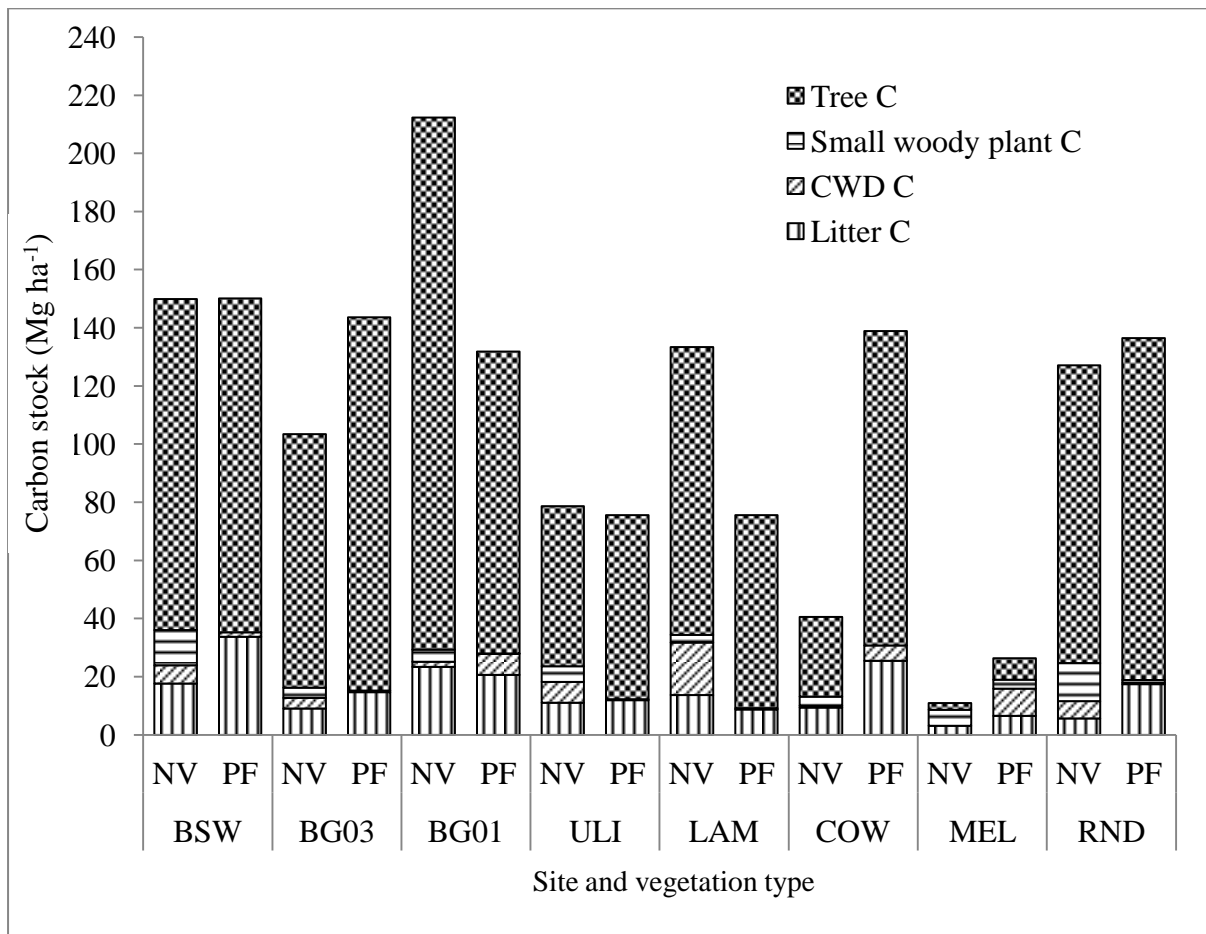
792

793 **Figure 3.**



794

795 **Figure 4.**



796

797 **Tables**

798 **Table 1.** Details of the study sites in south-eastern Queensland Australia. Rotation refers to
 799 whether the plantation is in its first or second *Pinus* sp. rotation following conversion from
 800 native vegetation. Plantation age is based on the number of years since planting in the current
 801 rotation. Soil type is based on Isbell (1996). Tree basal area (BA) was calculated for all live
 802 trees (DBH trees ≥ 10 cm) within a 0.5 ha plot. Mean annual rainfall (MAR, mm) is provided
 803 for each site.

Site name	Dominant species	Plantation		Soil type	Tree BA (m ² ha ⁻¹)	MAR (mm)
		age (years)	Rotation			
	<i>Pinus elliotii</i> var. <i>elliottii</i>	34.1	1st	Podosol	43.4	
Blackswamp	<i>Eucalyptus racemosa</i> , <i>Corymbia intermedia</i> , <i>Melaleuca</i> <i>quinquenervia</i>	na	na	Podosol	30.2	1495
	<i>Pinus caribaea</i> var. <i>hondurensis</i>	28.5	2nd	Brown Kandosol	41.3	
Bluegum 201	<i>Syncarpia</i> <i>glomulifera</i> , <i>C.</i> <i>intermedia</i> , <i>Lophostemon</i> <i>suaveolens</i> , <i>Eucalyptus cloeziana</i>	na	na	Brown Kandosol	60.2	1611

Bluegum 203	<i>P. elliotii</i> × <i>P.</i> <i>caribaea</i>	26.0	2nd	Yellow Kandosol	54.6	1611	
	<i>E. racemosa</i> , <i>Eucalyptus</i> <i>acmenoides</i> , <i>C.</i> <i>intermedia</i> , <i>L.</i> <i>suaveolens</i>	na	na	Yellow Kandosol	22.1		
	<i>Pinus caribaea</i> var. <i>hondurensis</i>	26.5	1st	Podosol	41.7		1358
	<i>Eucalyptus umbra</i> , <i>Banksia aemula</i>	na	na	Podosol	10.0		
Laminex	<i>P. elliotii</i> × <i>P.</i> <i>caribaea</i>	9.7	2nd	Brown Kandosol	31.9	1228	
	<i>E. racemosa</i> , <i>E.</i> <i>acmenoides</i> , <i>C.</i> <i>intermedia</i>	na	na	Brown Kandosol	22.7		
	<i>P. elliotii</i> × <i>P.</i> <i>caribaea</i>	6.4	2nd	Grey Chromosol	5.2		1193
<i>Eucalyptus umbra</i> , <i>Melaleuca viridiflora</i>	na	na	Grey Chromosol	3.4			
Round	<i>Pinus elliotii</i> var. <i>elliottii</i>	31.5	1st	Podosol	47.5	1520	
	<i>Eucalyptus</i> <i>tereticornis</i> , <i>C.</i> <i>intermedia</i> , <i>Melaleuca</i>	na	na	Podosol	37.0		

	<i>quinquenervia, L.</i>					
	<i>suaveolens</i>					
	<i>P. elliotii</i> × <i>P.</i>	8.3	2nd	Yellow	30.9	
	<i>caribaea</i>			Kandosol		
Ulirraba	<i>E. acmenoides, C.</i>					1251
	<i>intermedia, S.</i>	na	na	Yellow	13.2	
	<i>glomulifera, E.</i>			Kandosol		
	<i>racemosa</i>					

804

805

806 **Table 2.** Summary of ANOVA results for individual paired sites (*Pinus* forest, PF vs native vegetation, NV) for below-ground C pools (0–
807 50 cm). Sites at which significant differences ($P < 0.05$) occurred for the main effects of vegetation type (pine and native vegetation) are
808 identified with an *. Sites at which significant differences occurred for depth (0–5, 5–10, 10–20, 20–30 and 30–50 cm) and the vegetation type
809 by depth interaction are listed. Predicted means (Mg ha^{-1}) are presented and where analyses were run on log transformed data means were back-
810 transformed. ‘Site’ refers to site code (BSW, Blackswamp; BG03, Bluegum 203; BG01, Bluegum 201; ULI, Ulirra; LAM, Laminex; COW,
811 Cowra; MEL, Melaleuca; RND, Round); ‘Trend’ refers to the overall trend with depth from the surface to 50 cm. The number of individual sites
812 with significant positive or negative associations with tree basal area are listed under the ‘Covariate’ column.

813

Carbon pool	Vegetation type			Depth			Significant Vegetation type × Depth interactions			Covariate
	Site	NV mean	PF mean	Sites at which differences exist	at	Trend	Site and depths at which differences exist	NV mean	PF mean	(tree BA)
Soil organic C (ESM)	BSW	7.5	8.6	BSW		All ↓	BG01, 0–5 cm	4.2	11.3	1+ve
	BG03*	6.3	5.0	BG03			30–50 cm	10.3	4.3	(BSW)

Vegetation type		Depth		Significant Vegetation type × Depth interactions				Covariate (tree BA)	
BG01	8.7	7.7	ULI	ULI, 0–20 cm	15.5	26.6			
ULI	2.8	4.1	LAM	COW, 0–10 cm	15.3	7.6			
LAM*	5.5	5.2	COW	30–50 cm	1.2	2.8			
COW	4.8	3.2	MEL	MEL, 0–10 cm	4.8	6.4			
MEL*	1.3	1.5	RND						
RND	5.8	6.1							
Humic organic C	BSW*	2.5	3.9	BG03	All ↓	ULI, 20–50 cm	1.9	1.1	1–ve (RND)
	BG03	2.7	2.6	BG01					
	BG01*	1.8	1.4	ULI					
	ULI*	1.7	1.5	LAM					
	LAM	3.1	3.2	COW					
	COW*	0.8	0.9	MEL					
	MEL	1.5	1.6	RND					
	RND	3.6	3.9						

	Vegetation type			Depth		Significant Vegetation type × Depth interactions			Covariate (tree BA)
Particulate organic C	BSW	1.3	1.3	All sites	All ↓	ULI, 10–50 cm	1.1	2.2	2+ve
	BG03*	1.0	0.7			COW, 0–20 cm	4.1	0.7	(BSW,
	BG01	1.1	1.3			MEL, 0–10 cm	0.6	1.4	BG03)
	ULI*	0.8	1.0			RND, 0–20 cm	5.7	4.3	
	LAM	1.0	0.8						
	COW*	0.9	0.2						
	MEL*	0.2	0.4						
	RND*	1.4	1.1						
Resistant organic C	BSW	2.7	3.4	BSW	All ↓	MEL, 0–20 cm	0.4	1.2	1+ve
	BG03*	1.4	1.2	BG03					(BSW)
	BG01	2.5	2.2	BG01					1–ve (RND)
	ULI*	1.2	1.7	ULI					
	LAM	1.2	1.1	LAM					

	Vegetation type			Depth	Significant Vegetation type × Depth interactions				Covariate (tree BA)
	COW	0.3	0.5	MEL					
	MEL*	0.1	0.3	RND					
	RND	1.3	1.7						
Charcoal C	BSW*	0.78	0.37	BG03	All ↓				1+ve
	BG03*	0.44	0.37	BG01					(BG03)
	BG01	0.98	0.75	ULI					1-ve
	ULI*	0.58	1.05	LAM					(COW)
	LAM	0.28	0.27	COW					
	COW*	0.00	0.48	MEL					
	MEL	0.05	0.03	RND					
	RND*	0.02	0.07						
Visible organic matter C	BSW*	1.3	1.6	All sites	All ↓	BSW, 0–10 cm	4.4	8.0	3+ve
	BG03*	1.2	1.3			ULI, 0–10 cm	2.9	9.5	(LAM,
	BG01	0.8	1.0			30–50 cm	0.3	0.1	MEL,

Vegetation type		Depth		Significant Vegetation type × Depth interactions			Covariate (tree BA)		
ULI*	0.9	1.5			BG01, 0–10 cm	2.5	4.4	RND)	
LAM	2.6	2.4			COW, 0–20 cm	24.8	11.2		
COW*	3.8	2.2			RND, 0–5 cm	1.4	3.2		
MEL*	1.9	1.4			20–30 cm	1.2	0.8		
RND	1.3	1.3							
Total below-ground C	BSW*	5.1	6.0	All sites	All ↓	ULI, 0–30 cm	25.9	46.7	2+ve
	BG03	9.1	8.5			BG01, 0–5 cm	8.7	17.2	(BSW,
	BG01*	5.5	5.4			20–50 cm	6.3	4.0	MEL)
	ULI*	3.9	5.9			COW, 0–20 cm	41.4	22.5	
	LAM	10.1	9.3			RND, 0–5 cm	12.3	16.1	
	COW*	5.7	4.2						
	MEL*	2.9	2.7						
	RND*	4.6	4.9						

815 **Table 3.** Summary of observed mean \pm standard error (range) 0–50 cm below-ground C pools
 816 and above-ground C pools (Mg ha^{-1}) for pine plantations and adjacent native vegetation.
 817 Differences based on ANOVA analyses (sometimes on log transformed data) across all sites
 818 were non-significant in all cases except for small woody plant C ($P = 0.006$) and fine litter C,
 819 which was only marginally significant ($P = 0.09$).

Carbon pool (Mg ha^{-1})	Pine plantation	Native vegetation
Soil organic C (ESM)	55.9 \pm 8.2 (17.4–86.8)	57.0 \pm 12.2 (14.5–132.3)
Humic organic C	23.0 \pm 3.5 (13.2–38.4)	21.7 \pm 2.5 (9.5–32.2)
Particulate organic C	7.7 \pm 1.2 (3.1–12.9)	9.4 \pm 1.9 (1.5–18.2)
Resistant organic C	13.4 \pm 2.8 (1.8–27.5)	11.6 \pm 2.6 (0.7–20.8)
Charcoal C	4.3 \pm 1.5 (0.2–13.4)	3.1 \pm 1.1 (0.1–8.7)
Visible organic matter C	17.4 \pm 1.7 (10.7–27.7)	19.7 \pm 5.4 (9.5–55.8)
Total below-ground C	77.6 \pm 8.4 (33.9–107.9)	79.8 \pm 12.5 (33.3–153.2)
Fine litter C	15.5 \pm 2.8 (5.5–30.6)	10.7 \pm 2.0 (3.1–21.0)
Coarse litter C	1.9 \pm 0.4 (0.6–4.0)	1.0 \pm 0.3 (0.0–2.4)
Coarse woody debris C	3.2 \pm 1.3 (0.3–9.4)	5.4 \pm 2.0 (0.0–18.1)
Small woody plant C	0.5 \pm 0.4 (0.0–3.1)	6.2 \pm 1.5 (2.6–13.2)
Above-ground tree C	88.7 \pm 14.3 (7.3–128.5)	83.7 \pm 19.8 (2.3–183.0)
Total ecosystem C	243.3 \pm 28.8 (77.6–344.8)	243.9 \pm 45.1 (58.8–497.8)

820