1   **TITLE**: Soil-vegetation type, stem density and species richness influence biomass of restored

2   woodland in south-western Australia.

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21 **ABSTRACT**

22 Woody plantings are increasing across the globe to satisfy ecosystem service markets for carbon and

23 ecological restoration. Assessments of these complex woody systems typically use coarse-scale

24 parameters, based on the climate and soil type of a region, and/or remotely assessed vegetation

25 cover, to estimate carbon in their above- and belowground biomass. However it remains poorly

26 known what factors influence their biomass at finer scales. Here, we investigated biomass variability

27 after five years across a 250 ha environmental planting on a former agricultural property in south-

28 western Australia. We aimed to understand which factors may influence observed biomass

29 variability. The dominant canopy tree, *Eucalyptus occidentalis*, was planted as seedlings, and other

30 woody species were direct sown in vegetation associations, according to soil type and landscape

31 position, to reflect historic native assemblages. Results from 42 survey plots stratified across these

32 associations showed variable seedling establishment from the seed mix, and that the amount of

33 above- and belowground biomass varied widely (Coefficient of variation = 60 %). A site mean and

34 standard error were inadequate to capture biomass distribution. Instead, two modes were evident

35 within the distribution at approximately 5 Mg ha^{-1} and 15 Mg ha^{-1} with variation primarily associated

36 with differential seedling establishment and growth across the vegetation associations. Additionally,

37 multiple regression analysis showed that stem density explained a significant amount of biomass

38 variation whilst greater species richness was associated with increased biomass once stem density

39 had been accounted for – models combining soil-vegetation association, number of individuals, and

40 species richness explained between 60 and 80 % of biomass variation depending on the response

41 variable (total or live biomass) and choice of allometric equations to predict biomass. There was

42 some evidence for a role of nitrogen-fixing species in determining biomass variation. There was no

43 evidence for biomass variation being explained by the proportional contribution of the dominant

44 canopy tree (*E. occidentalis*) or eucalypts in general once number of individuals had been accounted

45 for, despite their large contribution to plot biomass. The substantial variation we show across the

46 site has implications for carbon accounting practices and cost-benefit analyses guiding investment

47   and regulation of the sector. Our results add weight to emerging evidence that restoring woody

48   plant diversity can be compatible with efforts to maximize biomass and show the potential for

49   diverse restored woodland assemblages to meet developing market demands for carbon.

50   **KEYWORDS**

51   Biodiverse carbon planting, carbon sequestration, carbon stock, environmental planting, eucalypt

52   woodland, functional diversity.

53   **1. INTRODUCTION**

54   Environmental plantings have been widely proposed for ecological restoration and to sequester

55   carbon to mitigate climate change (Silver *et al.*, 2000; Dwyer *et al.*, 2009; Fensham and Guymer,

56   2009). In response to these proposals, there has been an increase in the number and scale of

57   (woody) environmental plantings, often as part of ecosystem service markets and government

58   programs (Phelps *et al.*, 2012; Bradshaw *et al.*, 2013). The ability to determine carbon sequestration

59   of these multi-purpose and large scale (> 100 ha) environmental plantings is not well studied due to

60   the limited number of complex restoration projects of this type (see e.g. Paul *et al.*, 2013a; Paul *et

61   al.*, 2014; Paul *et al.*, 2015). Methods to quantify standing biomass in mixed species plantings may

62   take several forms, such as process models, empirical models and forest inventory methods.

63   Quantification can be complex to determine through sampling and inventory, and current models

64   are not necessarily suitable for site level carbon accounting given they are often at a coarse-scale

65   (e.g. FullCAM, Reforestation Modelling Tool Paul *et al.*, 2003; Paul *et al.*, 2013a). These coarse scale

66   methods will not account for variation that occurs within complex vegetation systems due to the

67   identity and growth form of species planted (e.g. Firn *et al.*, 2007), differential seedling

68   establishment success (Hallett *et al.*, 2014), and subsequent growth (Erskine *et al.*, 2006; Kanowski

69   and Catterall, 2010). Forest inventory methods require an understanding of the spatial variability

70   that may occur both within and between different vegetation associations. Currently, data to assess

71 this variation and its potential impact on carbon accounting are limited, and so too measurements of

72 the underlying ecological factors that might help explain the variation. These factors could further

73 inform stratification of restored woodland assemblages for the purpose of improving the efficiency

74 of biomass measurements without compromising the accuracy of carbon estimates for a site. Here,

75 we estimated standing biomass of woodland assemblages five years after the establishment of a

76 large-scale revegetation project in an old-field in south-western Australia. We then determined the

77 relationships among soil type, landscape position and seed mix on biomass variation together with

78 other biotic attributes. We asked whether the incorporation of these additional factors significantly

79 and parsimoniously improved the explanatory power of statistical models predicting biomass

80 sequestration. We then discuss how this knowledge can inform the stratification of a restored

81 woodland assemblage for the purpose of obtaining the greatest efficiency of measurement-based

82 biomass carbon estimates across a property as a whole.

83 We hypothesized that there are multiple, hierarchical controls on growth of woody species in

84 environmental plantings as intimated previously (Diaz *et al.*, 2007) and that these controls will lead

85 to standing biomass variation across a site. For instance, and regardless of species, climate and large-

86 scale soil changes will broadly influence the amount of biomass sequestered, as shown for *Acacia*

87 *harpophylla* (brigalow) and *Acacia aneura* (mulga) woodland regrowth in Queensland (Dwyer *et al.*,

88 2010b; Fensham *et al.*, 2012) and pine forests in Catalonia (Vila *et al.*, 2003). Below the level of

89 environmental variation at this coarse-scale, small-scale differences in topography, aspect and soil

90 type may influence establishment and subsequent growth of individuals (Tajchman *et al.*, 1996; Paul

91 *et al.*, 2008; Preece *et al.*, 2012), especially in areas where depth to water table is an important

92 determinant (e.g. Carter *et al.*, 2008). Geometry may also be important; for instance, narrow linear

93 plantings often have greater biomass than block plantings due to higher resource availability at their

94 edges (Paul *et al.*, 2013a). At a given site and topographic location, the diversity of plants, typically

95 measured as species richness, has been shown to also influence above ground biomass (Hooper *et*

96 *al.*, 2005). However, most research supporting this relationship has been conducted in grasslands

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97 and microbial microcosms with fewer investigations of woody species assemblages in field settings

98 (Cardinale *et al.*, 2012). A recent meta-analysis, of the few published experimental studies of woody

99 species growth, indicated that species richness had a positive effect on aboveground biomass, but

100 noted that the identity and functional traits of the species involved are an important component of

101 how much carbon will likely be sequestered (Hulvey *et al.*, 2013). Furthermore, individual studies

102 can show conflicting results (e.g. Potvin *et al.*, 2011) suggesting context dependency is important. In

103 addition to plant species number and identity, the density of established individuals potentially

104 influences the amount of carbon sequestered by an environmental planting (Dwyer *et al.*, 2010a;

105 Paul *et al.*, 2013a).

106 Surveys of recently established non-experimental environmental plantings (and old growth forest

107 e.g. Jacob *et al.*, 2010; Seidel *et al.*, 2013), as compared to experimental approaches, provide an

108 alternative avenue to investigate potential influences on biomass/productivity, especially if 1) the

109 planting is large enough to capture spatial heterogeneity (e.g. > 100 ha); 2) there are records of

110 establishment practices and site conditions; and, 3) records include accurate identities and

111 measurements of established individuals. The first two allow investigations of biomass relationships

112 among and within soil - vegetation type associations while the latter provides important information

113 so that suitable allometric relationships can be applied to estimate biomass and carbon (e.g. Jonson

114 and Freudenberger, 2011). Peniup, a large-scale environmental planting established in south-

115 western Australia in 2008, meets these criteria and it thus provided us the opportunity to identify

116 *potential* drivers of variation in standing biomass. Although this environmental planting lacked

117 experimental controls, the planting was large enough (250 ha) to explore possible relationships with

118 topography, soil type, seed mix, plant density, species richness and species identity, but small

119 enough to ignore large-scale variation in climate.

120 We therefore asked: What site factors are associated with the variation in total (above- and

121 belowground) biomass across a 250 ha environmental planting? We hypothesized that there would

122 be marked spatial variation among surveyed plots which can be explained, in part, by differences in

123 soil-landscapes that were sown with different seed mixes. Within any one of these soil- landscape-

124 seed mix associations (hereafter "*vegetation associations*"), we hypothesized that greater numbers

125 of established individuals, higher species richness, and the differential proportional presence of

126 particular functional and structural groups (e.g. nitrogen-fixing woody plants) will lead to more

127 biomass accumulation at this early stage of growth. Disentangling the influence of each of these

128 factors separately and attributing causation, given the constraints of the survey design, is not

129 possible; however we can make inferences using the statistical approach adopted. Finally, we also

130 investigated whether biomass relationships with potential drivers varied among the different

131 vegetation associations. All our hypotheses were defined *a priori* and informed by (limited) previous

132 studies of these relationships in smaller-scale environmental plantings elsewhere in Australia (e.g.

133 Erskine *et al.*, 2006; Dwyer *et al.*, 2010b; Kanowski and Catterall, 2010; Paul *et al.*, 2013a) as well as

134 our local ecological knowledge, and observations of seedling establishment at Peniup (Jonson, 2010;

135 Hallett *et al.*, 2014). We researched this with the view that understanding fine-scale variability in

136 woodland restoration plantings could be used to inform a stratified sampling approach for more

137 accurate, and potentially cost-effective, estimates of carbon sequestration.

138 **2. SITE DESCRIPTION, METHODS AND STATISTICAL ANALYSES**

139 **2.1 Site Description**

140 Peniup is a 2406ha former agricultural property that was purchased by the non-governmental

141 organisations Greening Australia and Bush Heritage in July 2007 as part of the Gondwana Link

142 initiative (www.gondwananlink.org). It was one of the first carbon-funded ecological restoration

143 projects in Australia (Jonson, 2010). Peniup is located in the south west of Western Australia (34°

144 5'17.55'' S; 118° 51' 44.47'' E). A Mediterranean climate prevails with most of the 456mm annual

145 average rainfall falling in the cool winter months, while summers are dry and hot (as reported in

146 Hallett *et al.*, 2014). Since its purchase, rotational wheat and sheep farming has ceased and

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147 revegetation of the cleared areas of the property has been undertaken in a staged manner.

148 Revegetation includes spatially discrete environmental plantings based on locally occurring native

149 woody species and sandalwood (*Santalum spicatum*) plantations. There has been no natural woody

150 regeneration even though the site was only cleared about 50 years ago. Restoration has therefore

151 involved direct interventions. Here, we investigate the 250 ha of environmental planting that was

152 seeded between April and September 2008. Different seed mixes were directly sown across the site

153 dependent on soil type (defined by results of a pre-planting soil survey) and landscape position, and

154 with reference to surrounding eucalypt woodland remnants, for economic (voluntary carbon

155 market), ecological and evolutionary reasons outlined and described in detail by Jonson (2010).

156 Seedlings of *Eucalyptus occidentalis* (yate; a native woodland tree with the highest local carbon

157 carrying capacity (Jonson, 2010)) were also planted in some areas of the site where it likely occurred

158 prior to clearing. Evenly spaced seedlings were planted rather than directly sown from seed in order

159 to ensure carbon sequestration outcomes. Planted seedlings (tubestock) provided greater

160 confidence in the stocking density, establishment and survival of this dominant eucalypt species.

161 Further details regarding pre-planting herbicide and pesticide treatments, direct seeding

162 methodologies, and strategies to increase seed germination through pre-treatment can be found in

163 Jonson (2010) and Hallett *et al*. (2014).

164 Seed mixes comprised common woody species from the nearby remnant woodland vegetation most

165 closely associated with the soil types found across the 250 ha revegetation site. Remnant vegetation

166 structural types included tall mallee, mallee heath, open mallee heath, low woodland (Moort) and

167 tall woodland systems (Yate). Taking into account differences in topography, soil texture and

168 corresponding plant species, seed mixes were prepared for seven vegetation associations as termed

169 by Jonson (2010): Light Yate, Sandy Yate, Upland Yate and Gully associations (all including planted *E.*

170 *occidentalis* seedlings), and Sandy Gravel, Duplex and Pallid Clay associations, without planted *E.*

171 *occidentalis* seedlings.

172 Monitoring during the first year after seeding showed that early emergence of seeded individuals

173 was greater in sandy soils, but post-summer survival was higher in soils with greater clay content,

174 leading to overall establishment numbers, at the end of the first summer, roughly equivalent in

175 sandy and clay soils (Hallett *et al.*, 2014). There had been additional establishment and some

176 mortality in the subset of plots investigated by Jonson (2010) and Hallett *et al*. (2014) and in plots

177 located elsewhere at the site over subsequent years. Here we investigate how these longer term

178 dynamics across the site have influenced the amount of total standing (dead and live) and live

179 biomass (both above- and belowground) in the woody vegetation five years after seeding and

180 planting.

181   **2.2 Survey methods**

182 Forty-two permanent plots were surveyed in April 2013, five years after the establishment of the

183 environmental planting. Plots were located in a stratified random manner among the different

184 vegetation associations, based on the area coverage of each association and as determined at the

185 outset of the planting (Jonson, 2010). Plots measured 10 m in length and covered 10 soil scalp lines

186 (planting rows at 1.4 m distance apart), leading to each plot having an area of approximately 0.014

187 ha. In each plot, stem diameter measurements of all woody plants were measured at 10cm (D10)

188 above ground level, or where possible at breast height (1.3m; DBH), all to the nearest mm using

189 calipers. Multi-stemmed trees and shrubs were converted to an equivalent stem diameter through

190 the square root of the sum of squares of individual stem diameters.

191 Measurements were converted to above- and belowground biomass of individuals using two sets of

192 allometric equations. Firstly, we used a local set of allometric equations (Jonson and Freudenberger,

193 2011) for the dominant planted and sown tree species (mallee form *Eucalyptus* species and *E.*

194 *occidentalis*), in conjunction with localised equations and shoot-to-root ratios for *Acacia pulchella*

195 (see also Monk *et al.*, 1981; Grove, 1988; Grierson *et al.*, 2000). We also derived an equation for

196 *Allocasuarina huegeliana*, combining data from Jonson and Freudenberger (2011) and Hawkins *et al*.

197 (2010) (see Supplementary Information, Appendix A) to gain accurate estimates of biomass for

198 measured individuals with a small D10 survey range. Generic allometric equations were used for the

199 remaining species (e.g. other *Acacia* sp., *Calothamnus*, *Gastrolobium* and *Melaleuca* genera) (Paul *et*

200 *al.*, 2013a; Paul *et al.*, 2013b; Paul *et al.*, 2014). With this collection of equations (see Tables A1 – A3

201 in Appendix A), we estimated total standing and live plot biomass. This approach is the most robust

202 for testing our hypotheses for two reasons: 1) most equations were calculated from harvested

203 individuals in the immediate locality thereby increasing their accuracy compared with generic

204 equations that include variation in growth due to large scale differences in climate and soil; and, 2)

205 *A. pulchella* was a very common plant measured across the site, which justified a more accurate

206 estimate of biomass using a species-specific allometric equation rather than using a generic equation

207 for *Acacia* shrubs.

208 Species-specific allometric equations are not always available and so we compared biomass

209 estimated from the local allometric equations with another set of equations recently published for

210 species growing in low rainfall, non-arid regions of southern and eastern Australia (Paul *et al.*, 2013a;

211 Paul *et al.*, 2013b; Paul *et al.*, 2014). We tested whether any of our inferences were affected by

212 substituting the locally derived allometric equations, for the tree species and *Acacia pulchella*, with

213 these generic equations, which also include data from this site. For both sets of analyses, we used

214 genus-level allometric relationships if species-specific relationships were not available (Paul *et al.*,

215 2013b; Paul *et al.*, 2014). Total plot biomass was estimated by summing the individual biomass of all

216 live and dead woody plants (using allometric equations for dead biomass where available), and

217 scaled up to a per hectare basis, while 'live biomass only' included data for just the individuals alive

218 in April 2013.

219 The use of a second set of generic allometric equations is of particular interest given that there are

220 many revegetation plantings in Australia (and elsewhere) where locally derived allometric equations

221 are not available and generic equations are readily accessible. In addition, there may be commercial

222 implications around the expense of developing local allometric equations – if conclusions regarding

223 overall amounts of biomass remain unchanged, then the use of generalized allometric equations for

224 accounting purposes can be justified. From a purely scientific perspective, if factors potentially

225 driving biomass variation remain unchanged this suggests our results are robust regardless of

226 whether local or generic equations are used. We present results using the local allometric equations

227 in the figures and main text as these are most relevant for the testing of our hypotheses, and show

228 results for the generic low rainfall allometric equations in Supplementary Information and discuss

229 the comparison.

230 **2.3 Data Analysis**

231 We first investigated whether the different seed mixes had indeed led to the establishment of

232 different assemblages across the soil types using non-metric multi-dimensional scaling (MDS) and

233 PERMANOVA (Anderson, 2001; Anderson and Walsh, 2013) in PRIMER-E (Clarke and Warwick, 2001).

234 This analysis informed subsequent analyses to investigate our main hypotheses, as reported in

235 *Results*. We considered presence-absence and abundance data for all individuals (live and dead) and

236 live individuals only (Supplementary Information, Appendix B). Absences in a given plot were defined

237 as those species that recruited in at least one of the 42 plots, but were absent in the focal plot; i.e.

238 species that were sown but did not recruit in any plot were ignored. Square root and fourth root

239 transformations were performed. The latter transformation potentially increases the importance of

240 rare species in the analysis as does examining presence-absence alone rather than taking into

241 consideration realised abundances (Clarke and Warwick, 2001).

242 To explore biomass variation across the site we calculated a histogram of plot biomass scaled to a

243 per hectare basis. We bootstrapped 95 % confidence intervals of mean scaled plot biomass,

244 sampling with replacement, to check how many plots were required to consistently predict the

245 overall mean. We then tested whether biomass differed among vegetation association (including

246 Gully) using a linear model, confirming model assumptions were met via graphics (e.g. a Q-Q plot)

247 and the Shapiro-Wilks normality test.

248 To explore biotic attributes that may have contributed to differences among and within vegetation

249 associations, we calculated (for each plot) number of individuals and number of species (total and

250 live), as well as the proportional contribution (in terms of numbers of individuals) of nitrogen fixers

251 (e.g. *Acacia* sp., *Gastrolobium* sp.) and different structural components (tree, planted *E. occidentalis*,

252 all *Eucalyptus* sp., other tree, mallee, or shrub form) to total or live plot biomass respectively, scaled

253 to a per hectare basis. Given the negative relationship between proportion of shrubs and mallees

254 (i.e. if there were proportionally more shrubs, mallees were proportionally fewer), and the stronger

255 relationship of proportion of shrubs with plot biomass, we used proportion of shrub as a possible

256 explanatory factor in explaining plot biomass in the first instance and included other potential

257 structural proportional explanatory factors after initial model simplification.

258 The small number of plots within any one vegetation association precluded the fitting of all potential

259 explanatory factors and their interactions in a multiple regression model. Instead, we used backward

260 and forward selection to investigate potential explanatory factors within and among vegetation

261 associations and to find the most parsimonious model (Crawley, 2007). First, we fitted all potential

262 explanatory factors in the absence of their interactions and used backward selection to drop non-

263 significant terms ($p > 0.05$) in the order of least significance; we assumed that all explanatory terms

264 acted as fixed effects. Since order matters in fitting such a model (Crawley, 2007), and given the

265 strong relationship between number of individuals and species number (Supplementary Figure D1, r

266 = 0.78 (total biomass)), we fitted vegetation association and the number of individuals in a plot first

267 and then asked whether additional terms (e.g. species number) significantly improved the model fit

268 ($p < 0.05$). In essence, this model asked whether species number (for instance) added explanatory

269 power once variation assigned to different overall numbers of individuals had been accounted for.

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270 Once a candidate model had been identified (all main effects significant), we added in each unused

271 explanatory factor (including proportion of mallees, proportion of eucalypts) in turn, to assess

272 whether it could significantly explain residual variation. We then assessed whether there were

273 significant interactions (p < 0.05) among retained main effects and inspected the residuals of the

274 simplest possible model. Biomass was square root transformed to satisfy test assumptions. In sum,

275 this analysis revealed whether there was an overall effect of explanatory factors on plot biomass,

276 and, if interactions were present with vegetation association for instance, that the slope of

277 relationships differed among vegetation associations. To assess whether the proportion of *E.*

278 *occidentalis* individuals affected biomass accumulation in plots where it was present (Yate Loam and

279 Light Yate; n = 18) we used the same procedure to select the most parsimonious model. Other than

280 the preliminary ordination and PERMANOVA analyses, these data were analysed and presented

281 using R 3.1.1 (R Core Team, 2014).

3. RESULTS

3.1 Species Assemblages

284 Species assemblages varied by vegetation association. Inferences drawn were unchanged by the

285 assumptions or response variable used in the multi-dimensional analysis – in all iterations there was

286 strong evidence for compositional differences among vegetation associations (PERMANOVA p <

287 0.0001 on >9800 permutations; see Supplementary Information Appendix B for individual model

288 results). Pairwise comparisons showed nearly all differences between pairs of associations were at

289 least significant (p < 0.05) and many were highly significant (as also indicated by MDS plots (not

290 shown)). However, for Upland Yate and Sandy Yate associations, there was no evidence for them

291 being compositionally different from each other (p > 0.1 in 4 cases, p > 0.05 in all cases). This was not

292 totally surprising as the same seed mix was used, although landscape position varied slightly. There

293 was also limited support for the Gully association being different to the Sandy Yate association (p >

294 0.05 in all cases). Based on the evidence of no difference in established vegetation associations in

295   Upland and Sandy Yate, and the limited number of plots for the Gully association, we combined

296   Upland and Sandy Yate (and renamed it "Yate Loam") and ignored the Gully association in most

297   statistical analyses examining relationships within vegetation associations. We do however present

298   data for Gully plots on the figures and include the Gully plots in the analysis of biomass variation

299   across the site.

300   In total, fifty species were found across all plots (cf. Jonson, 2010), including a few unidentified

301   *Eucalyptus* and *Melaleuca* individuals. It was not possible to identify these at the time because they

302   had not formed flowers or fruit, which are key diagnostic features for these genera. Individuals

303   unidentified to the species level were predominantly in the Pallid Clay (see Figures D2a-f in

304   Supplementary Information Appendix D), and to a lesser extent in Duplex and Sandy Gravel

305   associations. Although 31 of the 42 plots had unidentified species, all plants were confidently

306   recorded to genus and correct growth form e.g. mallee form *Eucalyptus* or shrub form *Melaleuca*,

307   thus enabling both the robust application of allometric relationships to predict biomass and accurate

308   counts of species richness. Species richness at the site was greater in Light Yate compared with other

309   associations despite similar numbers of species being sown within the majority of associations (Table

310   1). A generalised linear model with Poisson errors showed a significant difference among

311   associations compared to a model that only fits an across association mean (χ^2 p = 0.0019). The

312   estimate for species richness in Light Yate was higher than that for any of the other vegetation

313   associations (Table 1; p = 0.028). There was no evidence of over dispersion – residual deviance in this

314   model was 30.68 on 35 degrees of freedom; null deviance was 51.63 on 41 degrees of freedom.

315 **Table 1:** Mean species number across Peniup by vegetation association in comparison to number of species

316 sown (for further details on vegetation associations see Site Description and Jonson, 2010).

Vegetation Association[a]	Number of plots	Species richness (± 1 standard error)	Sown and planted[b] species richness
Light Yate	9	13.3 (0.8)	31 + 1
Sandy Yate	3	7.3 (2.4)	25 + 1
Upland Yate	6	8.0 (1.4)	25 + 1
Sandy Gravel	9	9.4 (0.75)	25 + 0
Duplex	6	9.3 (0.95)	49 + 0
Pallid Clay	6	7.0 (1.03)	39 + 0
Gully	3	7.7 (1.3)	22 + 1

317 a: For reasons explained in the *Data Analysis* section, Sandy Yate and Upland Yate were combined in analyses

318 presented in the Results, and renamed "Yate Loam". We did not investigate relationships within Gully sites in

319 multiple regression analyses due to the small number of plots and the fact that seed mix and density of *E.*

320 *occidentalis* planting varied by gully position, partly to ensure soil stability.

321 b: *E. occidentalis* was planted as seedlings across Peniup; other species were sown. *E. occidentalis* was also

322 direct seeded in the Sandy and Upland Yate vegetation associations, but as of April 2013 only one individual

323 had recruited.

324 **3.2 Biomass variation across the site**

325 Across the site, there was an average biomass of 11.8 Mg ha^{-1} but this varied considerably among

326 plots and vegetation associations – standard error of the mean was 1.1 Mg ha^{-1} with a co-efficient of

327 variation (standard deviation / mean) equal to 0.6 (dimensionless). An overall site mean does not

328 adequately capture biomass variation across the site (Figure 1a): there were two modes to the

329 distribution, one centred on low biomass (approx. 5 Mg ha^{-1}) and one centred at high biomass

330 (approx. 15 Mg ha^{-1}) with a long tail. One plot had an equivalent total biomass of 28.3 Mg ha^{-1}.

331 Bootstrapped 95 % confidence intervals indicate that the sampling regime captured the overall

332 variability within the sampled plots i.e. intervals tapered at around 30 plots (Figure1b). In addition to

333 this plot scale variation, we observed that biomass was often clumped within a plot and patchily

334 distributed suggesting the potential for biomass variation at finer scales, confirming a pattern

335 suggested earlier (Jonson, 2010). These results were qualitatively unchanged when generic

336 allometric equations were used to estimate biomass (Supplementary Figure D3).

337
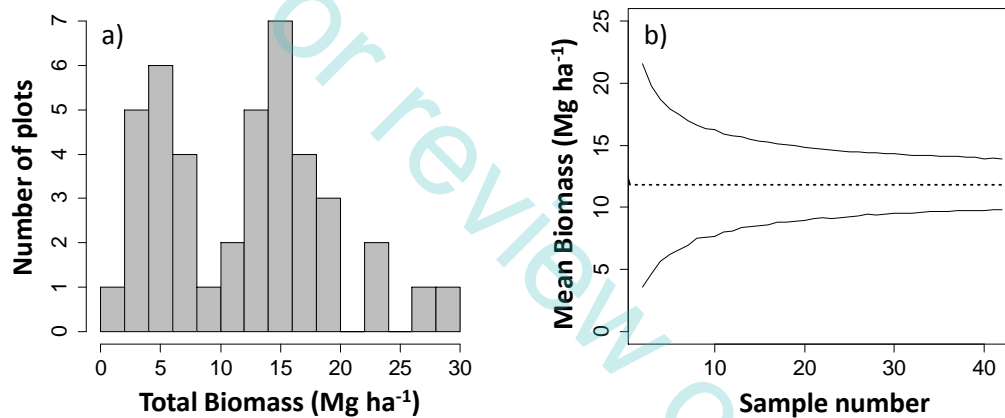
338 **Figure 1: a)** Histogram of biomass (Mg ha^{-1} of dry matter) and **b)** bootstrapped 95% confidence intervals

339 (10000 runs with replacement, solid lines) of mean biomass (dashed line) in forty two 0.014ha plots across

340 Peniup using local allometric relationships.

341 **3.3 Biomass variation explained by vegetation association**

342 Investigating biomass accumulation further, there were differences within and among vegetation

343 associations, with saplings of *E. occidentalis* appearing to contribute to high biomass when present

(Figures 2 and 3, see also Supplementary Figures D4 and D5). However, the Sandy Gravel vegetation

association, which was without these additional planted individuals, also had plots with high biomass

suggesting planted *E. occidentalis* did not necessarily drive biomass accumulation. However,

eucalypts as a whole (i.e. mallee and tree forms) contributed around 80 % (+/- 3 % standard error) of

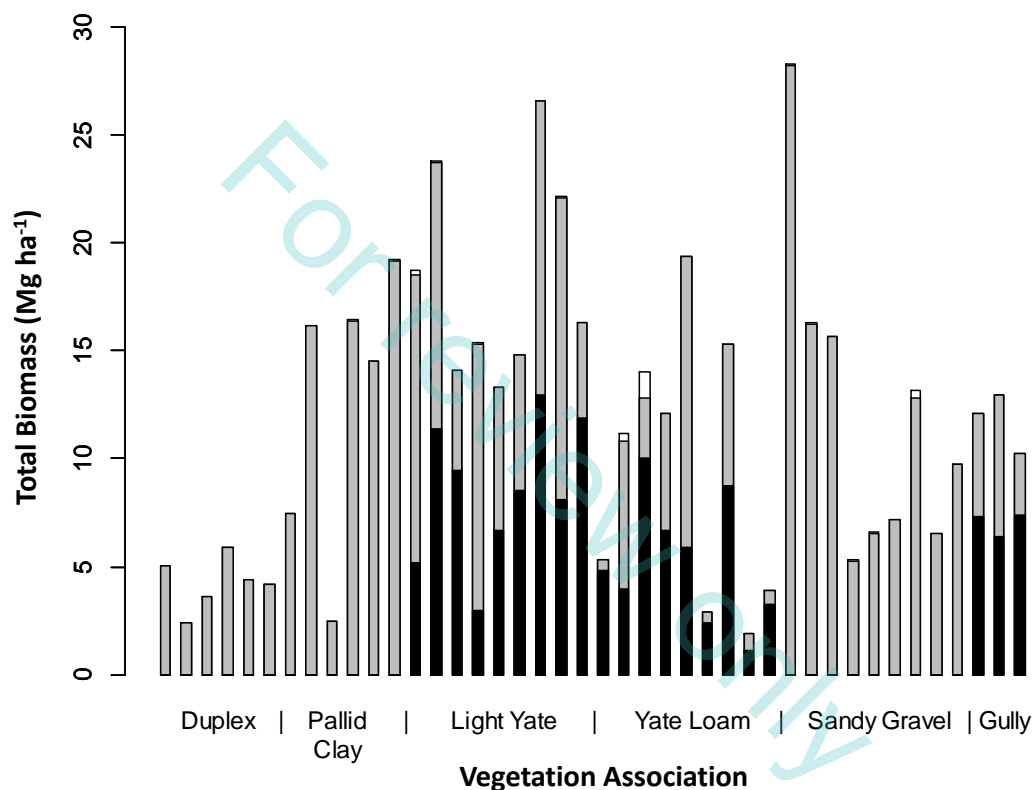total plot biomass despite being around a third of the total number of individuals in any given plot.

Figure 2: Total (above- & belowground) biomass (Mg ha^{-1}) in individual plots across Peniup, stratified

according to vegetation association. The black part of the bar represents live biomass contributed by planted

Eucalyptus occidentalis, the grey portion live biomass from sown species, and the unshaded portion dead

biomass in each plot. Dead biomass makes up a small fraction of total biomass in most plots apart from Plot

111, where there were a few large dead *Alyogyne huegelii*. Elsewhere, dead (standing) biomass was solely that

of sown species; if planted *E. occidentalis* had died, its biomass had disappeared by the time of the survey.

Over a third of the biomass variation could be explained by the vegetation association: the simplest

possible linear model explained 35 % of the variation in biomass ($F_{(2,39)}$=12.11; p < 0.0001), with the

Light Yate association having a significantly higher biomass (18.4 ± 1.6 Mg ha^{-1} (mean ± standard

error)) than Gully, Pallid Clay, Sandy Gravel, and Yate Loam associations (11.4 ± 1.2 Mg ha^{-1}) which in

turn had much greater biomass than the Duplex vegetation association (4.2 ± 0.5 Mg ha^{-1}). There

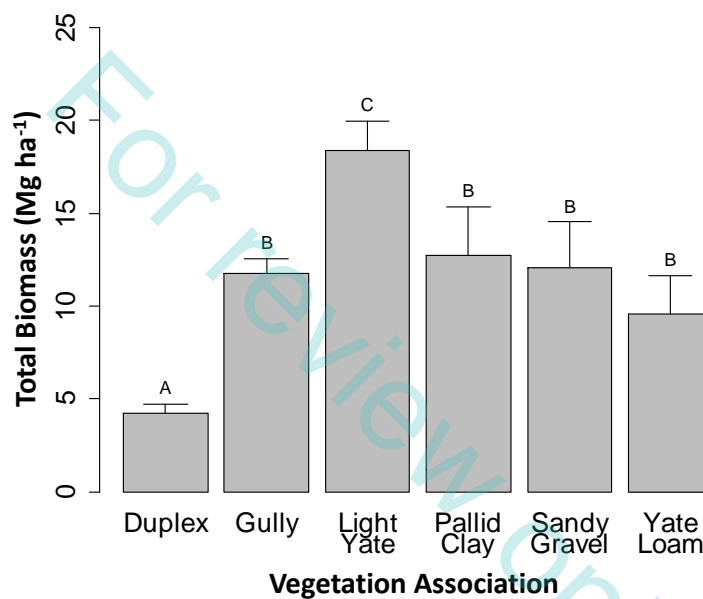was no evidence to suggest residuals were not normally distributed: Shapiro-Wilks W = 0.97, p =

0.31.

Figure 3: Mean (+ 1 s.e.) total biomass by vegetation association across Peniup. Letters indicate significant

differences following model simplification (see Crawley, 2007).

Qualitative conclusions from the statistical model remained unchanged when generic low rainfall

allometric relationships were used (see Supplementary Figure D5 and Appendix C) although in this

case nearly half of the variation in total biomass could be explained by vegetation association.

Utilizing generic low rainfall relationships decreases the estimated amount of biomass in Pallid Clay

and Sandy Gravel associations while it increases that found in associations with *Eucalyptus*

occidentalis. This is because local equations increased the biomass assigned to mallee forms, which

372   were common across vegetation associations. In contrast, the local form of *E. occidentalis* is

373   predicted to have lower biomass for a given DBH than that estimated using the generic low rainfall

374   allometric equations.

375   **3.4 Do number of individuals, species richness, and functional and structural groups explain**

376   **biomass variation *among* and *within* vegetation associations?**

377   When using local allometric equations and in the simplest possible model, total biomass varied

378   according to vegetation association ($F_{(4,26)}$ = 17.5, p < 0.0001), number of individuals in a plot ($F_{(1,26)}$ =

379   27.8, p < 0.0001) and species richness ($F_{(1,26)}$ = 14.8, p < 0.0007). In addition to these significant

380   factors, an increased proportion of nitrogen fixers was associated with greater biomass ($F_{(1,26)}$ = 7.21,

381   p = 0.01) and interactions among factors were also calculated (see Supplementary Information

382   Appendix C). The Shapiro-Wilk normality test suggested that residuals were normally distributed (W

383   = 0.96, p = 0.16), as did inspection of the Q-Q plots. Similar qualitative conclusions were reached if

384   live biomass was used as the response variable, although the interaction between vegetation

385   association and number of individuals (see also Supplementary Figure D6a) was non-significant.

386   In the simplest possible model for total biomass, 77 % of variation in biomass was explained, with

387   the form:

388   (Total biomass)$^{1/2}$ ~ Vegetation association + 0.036 (Number of individuals) + 0.045 (Number of

389   species) + 1.55 (Proportion of nitrogen fixers) + Vegetation Association : Number of individuals –

390   0.114 (Number of individuals : Proportion of N fixers) where ":" means interaction between.

391   In associations with *E. occidentalis* (Yate Loam and Light Yate), number of individuals and identity of

392   vegetation associations were again significant in explaining a high proportion of variation in total or

393   live biomass (see Appendix C for all model results). There was also no evidence for interactions

394   among main effects or a contribution of nitrogen fixers or shrubs to explaining biomass variation in

395   plots with planted Yates. There was no evidence for proportional contribution of *E. occidentalis*, or

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396 eucalypts as a whole, adding explanatory power in any model once overall numbers of individuals

397 had been accounted for.

398 Multiple regressions examining variation in total and live plot biomass derived from generic low

399 rainfall allometric equations also indicated that vegetation association, number of individuals in a

400 plot and species richness, once numbers of individuals had been accounted for, were significant

401 explanatory factors (Supplementary Appendix C). In contrast to models derived from local allometric

402 equations, there was no evidence of a proportional contribution of nitrogen fixers explaining

403 biomass variation, nor any evidence of interactions among potential explanatory factors. Additional

404 analyses, using number of individuals of *Eucalyptus* as an explanatory variable, given their

405 contribution to plot biomass, rather than overall numbers, indicated that *Eucalyptus* individuals and

406 vegetation association were still highly significant at explaining biomass variation, whereas species

407 richness was only marginally significant ($p < 0.1$) whether local or generic allometric equations were

408 used (Supplementary Appendix C). However, when using the local allometric, there was a significant

409 interaction between species number and number of individuals of eucalypts – as the number of

410 *Eucalyptus* individuals in a plot increases, the more positive the relationship between species

411 richness and biomass (Supplementary Figure D7).

412 **4. DISCUSSION**

413 The large scale of the Peniup environmental planting (250 ha) provided an ideal platform to

414 investigate what may be potential drivers of spatial variation in biomass accumulation. To

415 summarize, total (above- and belowground) biomass varied widely across the site, both within and

416 between vegetation associations. Much of this variation was expected because restoration species

417 mixes had been tailored to the landscape position and soil type. Through multiple regression

418 analyses, we showed that vegetation association was the primary correlate, explaining between a

419 third and half of all variation in biomass. Across associations, the number of individuals within a plot

420 also contributed to explaining plot biomass. As we initially hypothesized, species richness added

421 significant explanatory power to the most parsimonious models, which ultimately explained at least

422 two-thirds of biomass variation. There was limited evidence for interactions among these effects -

423 we only found a different relationship between number of individuals and biomass accrual

424 depending on vegetation association in one model. We also hypothesized that the proportional

425 contribution (based on numbers of individuals) of certain functional and structural groups would

426 provide explanatory power to understanding biomass accumulation. We found the contribution of

427 nitrogen fixers was important when biomass was calculated with local allometric equations and not

428 when generic low-rainfall allometric equations were used to calculate biomass. Contrary to our

429 hypotheses, structural identity (e.g., proportion of shrubs, proportion of *Eucalyptus occidentalis*, and

430 proportion of all eucalypts) failed to explain a significant amount of biomass variation in the most

431 parsimonious models once numbers of individuals had been accounted for.

4.1 Characterizing biomass across the restoration site

433 Mean biomass was low at the site (11.8 Mg ha^{-1}) which reflected the young age of the restoration

434 planting (i.e. 5 years). However, despite this low biomass the co-efficient of variation (CV) was large

435 (60 %), especially in comparison to more mature eucalypt woodlands with much higher mean

436 biomass (e.g. 22 % CV in *E. regnans* forest in Victoria (Tajchman *et al.*, 1996); 26 % CV in a peri-urban

437 reserve in south east Queensland (Hero *et al.*, 2013)). In contrast to the work of Hero et al. (2013) a

438 single mean value and standard deviation was inadequate to characterize biomass variation in our

439 study. Instead, biomass varied among plots with two distinct modes at approximately 5 Mg ha^{-1} and

440 15 Mg ha^{-1}, regardless of the allometric equations used (Figure 1, Supplementary Figure D3).

441 Further, we showed that standing biomass reflected the vegetation associations. Overall amounts of

442 biomass was largely contributed by *Eucalyptus* species – on average 80 % of biomass in a plot was

443 derived from *Eucalyptus* spp. despite constituting only 33 % of the stems. Different seed mixes,

444 tailored to the soil type and landscape position at the site (Jonson, 2010), have resulted in plant

445 assemblages that differ in species composition (Supplementary Figures D2a-f) and species richness

446 (Table 1), and which have yielded greater than four-fold differences in mean biomass among

447 associations (Figure 3). As Jonson (2010) predicted, the Light Yate association with mixed mallee

448 eucalypts and the dominant canopy tree, *E. occidentalis*, has sequestered more carbon than the

449 other associations.

450 Soil type could not be investigated because it was confounded, in a statistical sense, with the species

451 mix and landscape position of the vegetation associations. However, duplex soils supported

452 relatively low biomass (approximately 4 Mg ha^{-1}) compared to the other associations. This result

453 possibly reflects the nature of these soils with their semi-impermeable clay layer below the soil

454 surface which may limit soil water storage, have reduced plant establishment, impeded root

455 development, increased evaporative stress, and/or caused seasonal waterlogging (Bond, 2010). The

456 lack of an 'inverse texture effect' (Fensham *et al.*, 2012) may also prevent biomass gain in spring and

457 summer due to water limitation. Clearly, these suppositions need testing in field experiments. For

458 example the low biomass may also be related to the delayed emergence and establishment of some

459 measured individuals or a reduction in leaf area index due to early stunted growth.

460 **4.2 Hierarchical controls on biomass accrual: The importance of biotic attributes**

461 We hypothesized that multiple, hierarchical abiotic and biotic attributes would determine plant

462 growth in this restoration planting (Diaz *et al.*, 2007). We expected a hierarchy of abiotic

463 environmental factors (soil and topography, reflected in vegetation associations), and then biotic

464 attributes such as numbers of individuals, species richness, functional composition and finally

465 species identity would influence biomass. We found that individuals and species richness (having

466 controlled for individuals) contributed to explaining biomass variation across the site. The apparent

467 positive influence of number of individuals on biomass in young plantings is consistent with results

468 for other environmental plantings in Australia (Paul *et al.*, 2013a). However, this positive influence

469 may not hold as the plants mature if results for dense natural regrowth elsewhere in Australia can

470 be used as a guide (Dwyer *et al.*, 2010b). Thinning of dense stands may then be required if biomass

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471   accumulation is to be maximized (Dwyer *et al.*, 2010a). Such thinning may have potential biodiversity

472   benefits in a restoration planting (Pichancourt *et al.*, 2014). Initial planning of stocking density

473   attempted to reduce the need for thinning at this particular site (Jonson, 2010). Time will tell if this

474   planning results in the desired target densities in some or all of the vegetation associations.

475   The influence of species richness on biomass, and mechanisms behind responses, remains

476   unresolved and a sometime controversial topic (Adler *et al.*, 2011; Cardinale *et al.*, 2012), especially

477   for native assemblages of woody species as opposed to synthetic herbaceous communities (Firn *et*

478   *al.*, 2007). Field surveys offer an opportunity to explore these relationships (as also noted by Vila *et*

479   *al.*, 2003). Here, we attributed variation in biomass to species richness rather than the alternative

480   way around because of the relatively young age of the plantings and the absence of resident

481   competitors. We contend that there has not been the opportunity for biomass (or more specifically

482   productivity) to influence species richness. We do not know whether there is a mechanistic basis

483   behind the species richness association with biomass at this time, and experimental testing would be

484   required to ascertain any mechanism, especially as complementarity effects, or the effects of

485   sampling (sensu Loreau and Hector, 2001) or facilitation, may only be realised over time in woody

486   plantings.

487   The fact that species richness contributes positively to explaining biomass variation after controlling

488   for soil-vegetation association and numbers of individuals provides evidence, at least at this site, for

489   the suggestion that incorporating more biodiversity in restoration plantings may not compromise

490   carbon sequestration goals (Hulvey *et al.*, 2013). Incorporating species richness should not be

491   perceived as merely a "side-benefit" (Diaz *et al.*, 2009) to carbon sequestration but could be an

492   important strategy to maximise sequestration at the early stage of growth. Indeed, there was no

493   evidence in our survey to suggest that biomass was depressed by having more species in the

494   restored assemblages. However, such contentions require more rigorous testing in field experiments

495   (e.g. Scherer-Lorenzen *et al.*, 2007; Perring *et al.*, 2012). In addition, and as recently cautioned, the

496   magnitude and direction of this relationship may alter due to the ecological context, particularly

497   landscape and climate, of any given restoration site (Pichancourt *et al.*, 2014), the vegetation type

498   planted, as well as through time.

499   There was limited evidence for proportion of nitrogen fixing individuals per plot affecting the

500   amount of biomass in the different assemblages, although local allometric equations suggested that

501   a greater proportion of nitrogen fixers led to higher biomass accrual. The high available nutrients in

502   former agricultural land (McLauchlan, 2006) together with small individuals (because of their young

503   age) may preclude a larger influence of nitrogen fixation at this early stage, despite the proportional

504   range across plots (0 – 0.8 with a mean proportion of 0.4), and this may lead to the conflicting model

505   inferences. There was evidence of an interaction between stem density and nitrogen fixation: at

506   higher stem densities, there were only ever high proportions of nitrogen fixers while plots with low

507   stem density could have high or low proportions of nitrogen fixers. Nitrogen-fixers' contribution to

508   biomass may build through time as they grow, in line with the 'mass-ratio' hypothesis (Diaz *et al.*,

509   2007). However, investigations in more mature tropical restoration plantings in Queensland also

510   failed to find a significant contribution of nitrogen fixers to biomass accrual (Erskine *et al.*, 2006).

511   More data are required to ascertain the potential contribution of nitrogen fixers to biomass

512   sequestration in environmental plantings.

513   There was no evidence for the proportion of shrubs contributing to biomass variation perhaps

514   because there was limited variation in their proportional contribution to plot biomass (50 % of plot

515   values were between 0.5 and 0.7; range = 0 – 0.93 and mean = 0.59). At this early stage, the

516   contribution of shrubs is likely overshadowed by the contribution of trees to plot biomass. As the

517   planting matures, this result may become more pronounced whereby plots with a greater

518   proportion of shrubs may have lower biomass accrual compared with plots dominated by trees. At a

519   later, more mature stage, we would predict the proportion of shrubs to be a significant explanatory

520   variable in models seeking to explain biomass variation. Additionally, shrubs with different rooting

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521   strategies (e.g. Canadell *et al.*, 1996) may differ with respect to their longer term contributions to

522   plot biomass. We plan to test these predictions by ongoing annual monitoring. Efforts to improve

523   the precision and accuracy of allometric equations for shrub species (e.g. Paul *et al.*, 2013b) will

524   improve our ability to test these predictions.

525   A multiple regression model explaining 77 % of biomass variation in an environmental planting is

526   unusually high compared with other similar investigations, and suggests that the importance of plot

527   scale variation linked to stem density and biotic composition may have been overlooked in

528   investigations that do not consider this scale and/or consider only abiotic factors. The work of Hero

529   *et al*. (2013) attributed just 15 % of biomass variation in an urban reserve to measured attributes

530   (with no soil chemistry variables being related but topography being important), while investigations

531   of the contribution of soil properties in mature tropical forest explained up to a third of biomass

532   variation (Laurance *et al.*, 1999; although note Clark and Clark, 2000); we are unaware of data

533   related to similar environmental plantings. Coomes *et al.* (2002) found few environmental variables

534   were related to shrub or forest carbon stocks in New Zealand, although satellite measures of

535   normalized difference vegetation index (NDVI) were related to shrub carbon. Factors such as time

536   since fire or fire intensity can be important variables in influencing structure and biomass in

537   Australian native communities (Keith *et al.*, 2002; Gosper *et al.*, 2011) but could be ignored here

538   given the absence of fire at Peniup since the revegetation. Rigorous efforts to stratify the site into

539   vegetation associations based on soil type and landscape position for restoration likely also

540   contributed to the high percentage of explained variation with our model.

541   **4.3 Implications for carbon accounting**

542   Accurate carbon accounting requires a strong understanding of the biomass variability that may

543   occur both within and between different vegetation associations. Practitioners usually attempt to

544   stratify vegetation based on expected growth patterns, and in so doing minimize bias and improve

545   accuracy of results derived through modelling or field sampling (Rombouts, 2006; Golinkoff *et al.*,

546   2011). Unlike existing forests, where remote sensing may be used to determine an appropriate

547   approach to stratification (Global Forests Observation Initiative, 2013), accurate prediction of

548   biomass variability in new restoration plantings on old-fields requires information on soils, water

549   availability and other physical factors that influence the growth of the species being established

550   (Paul *et al.*, 2013a). In this project, this information, together with data from surrounding eucalypt

551   woodland remnants, formed the *a priori* stratified vegetation associations (Jonson, 2010) that we

552   investigated. Although these vegetation associations explained a substantial amount of variability in

553   biomass (giving confidence in the *a priori* stratification that would likely be used for carbon

554   estimation areas), variables related to the finer scale biotic community (i.e. number of individuals,

555   species richness), explained a significant amount of additional variation. The lack of interactions

556   between vegetation association and these other variables though shows a consistent relationship

557   across associations which, in this case, would simplify accounting procedures. In other words,

558   individuals and species richness affect biomass accrual in a similar manner across vegetation

559   associations. More research is needed to describe these relationships for other vegetation types and

560   other places. For now, our results suggest that factors such as stem density and species richness

561   potentially need to be considered when accounting for carbon in environmental plantings.

562   Taking these additional variables into account though may have considerable cost implications given

563   that the complexity of the required monitoring, data management, auditing, and reporting

564   necessarily increases. For instance, we utilized 26 allometric equations across the two analyses to

565   cover the species diversity at the site. Such allometric equations require continued verification and

566   validation over time to comply with somewhat complex and evolving regulatory requirements (see

567   e.g. van Oosterzee, 2012; van Oosterzee *et al.*, 2014) and also note

568   www.environment.gov.au/climatechange/emissions-reduction-fund/cfi/publications/ [checked 28th

569   January 2015]. Although robust local (site-specific) equations are undoubtedly best practice (Paul *et*

570   *al.*, 2013a), our Supplementary Results show that overall carbon credits would be little altered in a

571   five year old planting through the use of generic low rainfall allometric equations derived for

572   southern and eastern Australia. For an investor, the use of these generic equations would, in this

573   case, appear justified and would cut additional costs associated with ongoing development and

574   verification of local allometric equations. However, there may be instances where generic equations

575   are not appropriate, especially when dealing with young environmental plantings where

576   measurements may be outside the ranges of equations (Chaturvedi and Raghubanshi, 2013). This

577   conversation is not just relevant to temperate areas, and further research is required to ascertain

578   the most appropriate equations to use, particularly for sites with high environmental variation.

579   Ultimately, simplifying the accounting process at this and other junctures, such as the provision of

580   clear guidelines on the appropriate use of different methods of carbon accounting including the

581   potential utility of remote sensing data, will assist the development of the industry with obvious

582   potential benefits for the restoration of degraded agricultural landscapes in Australia and elsewhere.

583   **5.   CONCLUSION**

584   Our study highlights the opportunity to meet both carbon sequestration and restoration goals with

585   the large scale restoration of woodland assemblages. The ecological factors influencing variation in

586   biomass of environmental plantings is understudied yet critical information for the inclusion of these

587   plantings in the carbon market. We found that biomass varied widely within and among vegetation

588   associations at our site. Despite the high variation in biomass, we found evidence of a significant

589   association between biomass and species richness once number of individuals had been accounted

590   for. Surprisingly, at least at this early stage of growth, there was limited evidence for a plant

591   functional (nitrogen fixing) effect, and no evidence for a proportional contribution of structural

592   groups (i.e. *E. occidentalis*, shrubs) on biomass once numbers of individuals had been accounted for.

593   This research provides additional evidence that restoring woody plant diversity is compatible with

594   emerging market demands for carbon sequestration.

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