

1 **Loss and recovery of carbon and nitrogen after mangrove**
2 **clearing**

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20 **Abstract**

21 Offsetting carbon (C) emissions and reducing nitrogen (N) pollution have been goals of
22 mangrove restoration programs around the world. There is a common, yet dubious
23 expectation that mangrove restoration will result in immediate and perpetual delivery of
24 ecosystem services. There are expected time lags between mangrove clearing and C and N
25 losses, and between restoration and C and N gains. Obtaining accurate rates of losses and
26 gains requires frequent and long-term sampling, which is expensive and time consuming. To
27 address this knowledge gap, we used a chronosequence of mangrove forests in mangroves in
28 Matang Mangrove Forest Reserve (MMFR) in Malaysia, a region with one of the most C
29 dense forests in the world. In this site, we assessed the ecosystem C and N stocks, including
30 soil, downed wood, downed litter, and trees. The objective was to measure C and N changes
31 through time. After mangrove clearing, C and N losses in soil and downed wood were rapid,
32 with stocks halved after just one year. In the first 10 years after replantation, the forest
33 recovered quickly, with rates of C accumulation of $9.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. After ten years, the
34 rate of accumulation decreased to $2.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. However, 40 years after replantation,
35 mangroves were still about 26% lower in C and 15% lower in N compared to our reference
36 forest. The trajectory of recovery of C and N stocks in these forests was different among
37 mangrove components: forest litter recovered rapidly, but downed wood and soil recovered
38 much slower. Programs aimed at reducing C emissions and N pollution should consider that
39 there are temporal lags and ecosystem trade-offs when assessing the effectiveness of
40 mangrove protection and restoration as climate change mitigation strategies.

41

42 **1. Introduction**

43 Mangrove forests are considered key ecosystems in mitigation programs aimed at reductions
44 in carbon (C) emissions (Murdiyarso et al., 2015) and nitrogen (N) pollution (Mitsch &
45 Gosselink, 2015). Mangrove forests sequester more C and N per area than most terrestrial
46 ecosystems (Donato et al., 2011; Adame et al., 2015a). Contrary to terrestrial forests,
47 mangroves store the majority of their C and N not as plant biomass, but in the soil, where
48 stocks can remain stable for centuries (Adame and Fry, 2016). Mangrove deforestation results
49 in changes in C and N fluxes to the coast (Lee, 2016) and the release of large amounts of C
50 (Alongi et al., 1998; Lovelock et al., 2011). Mangrove restoration has the potential to offset
51 these C and N losses (Alongi, 2012; Ouyang & Guo, 2016).

52

53 Throughout the world, numerous mangrove restoration programs are underway,
54 including Mexico (Zaldívar-Jiménez et al., 2010), U.S.A. (Lewis, 2001), East Africa (Kairo
55 et al., 2001), Sri Lanka (Kodikara et al., 2017), and the Philippines (Walton et al., 2007). The
56 expectation of these programs is to restore ecosystem services (Lee et al., 2014; Adame et al.,
57 2015b). Restoration goals include increased coastal protection (Kodikara et al., 2017),
58 pollution reduction (Ouyang & Guo, 2016), and C emission mitigation (Alongi, 2012). The
59 success of restoration programs is usually assessed, if at all, as the establishment of mangrove
60 seedlings after planting (Ellison, 2000; Kodikara et al., 2017). However, even when
61 established, juvenile mangroves might not immediately provide the expected ecosystem
62 services (Koch et al., 2009). In order to assess the success of restoration programs, it is
63 important to consider time lags between perturbation, restoration, and return of ecosystem
64 services.

65

66 Loss of C and N is likely to occur within the first years after perturbation, while
67 sequestration occurs within the scale of decades (Marchand, 2017). To assess loss and
68 recovery rates of C and N, frequent and long-term sampling is required, which is expensive
69 and time consuming. The lack of adequate data obtained within realistic time frames
70 constrains the capacity of mangroves to participate in C and N markets (Alongi, 2011) and
71 creates false expectations that ecosystem services can be immediately and perpetually
72 restored (Koch et al., 2009).

73

74 In this study, we sampled a chronosequence of mangroves in the managed forest of
75 Matang Mangrove Forest Reserve (MMFR), Malaysia. The MMFR is the only mangrove
76 forest in the world with a century-long history of managed forestry (Shaharuddin et al.,
77 2005). The MMFR is managed for timber harvesting and comprises mangrove plots of
78 various ages, from recently cleared plots to those that were never clear-cut and are almost a
79 century-old. We took advantage of this setting to study how C and N in forest litter, downed
80 wood and soil respond to perturbation, in this case clear-cut harvesting. We also collected
81 published information on soil and tree C from previous studies in MMFR. The aim was to
82 quantify the loss of C and N after mangrove clearing, the temporal trajectory of recovery, and
83 the potential pathways of gains and losses. This information will provide a realistic time
84 frame for the assessment of restoration success and the fair valuation of mangrove forests in
85 one of the most C dense regions in the world (Atwood et al. 2017).

86

87 **2. Materials and Methods**

88 **2.1 Study site**

89 The MMFR is located near the town of Kuala Sepatang ($4^{\circ}50'17.7''$ N; $100^{\circ}37'51.7''$
90 E) on the northwest coast of Perak State, Peninsular Malaysia (Fig.1). The MMFR lies on
91 deltaic sediments fed by the three major local rivers: Sepetang, Larut and Terong Rivers. The
92 MMFR has 40,288 ha of mangrove forests, from which 75% are managed for the production
93 of charcoal and poles. The MMFR includes 569 ha of forest that has never been clear-cut,
94 although had some isolated tree harvesting 70 years ago. This forests, hereafter “reference”
95 forest, supports a high tree diversity. The MMFR also has an old-growth forest of 40+ years
96 set aside for education purposes.

97

98 Forests in MMFR are currently managed on a 30-year rotation cycle with 110 defined
99 compartments or management units (Shaharuddin et al., 2005). Approximately 1,000 ha of
100 mangroves are harvested annually. One to two years after tree harvest, the forest is replanted
101 with seedlings of *Rhizophora apiculata*. At 15 years, the forest is thinned, cutting small trees
102 around a radius of 1.2 m and at 20 years, the forest is thinned a second time by cutting trees
103 around a radius of 1.8 m (Shaharuddin et al., 2005). The managed forests are homogeneous
104 and mostly monospecific stands of *R. apiculata*, with a few trees of *R. mucronata*, *Bruguiera*
105 *parviflora*, *B. gymnorhiza* and *B. cylindrica*. The virgin forest is a mixture of the above
106 species plus 22 other mangrove species (Shaharuddin et al., 2005). Mangrove soils at 0-30cm
107 depth are mainly composed of clay (50-56%) and silt (20-30%) with a low pH (3.2-4.2), and
108 high organic content (40-70%; Azani et al., 2005)

109

110 The region containing the MMFR has a wet humid climate, primarily influenced by
111 two monsoons, the southwest monsoon, which usually arrives in May and lasts until
112 September, and the northeast monsoon, which lasts from November to March. The mean

113 rainfall of the region is between 200-400 mm per month, with the months of October and
114 November being the wettest (Malaysian Meteorological Department, 2017). Annual mean
115 water temperature of the Sepetang River is relatively constant at 29°C; pH values of the water
116 range from 6.8 to 7.2, and salinity ranges from 15.1 ± 0.1 upstream to 24.5 ± 0.5 in coastal
117 waters (Ramarn et al., 2012). Tides are semi-diurnal, mesotidal, with mean high levels of
118 2.69 m and 2.06 m for spring and neap tides, respectively (NHCM, 2016).

119

120 **2.2 Site selection and sampling**

121 Field sampling was conducted in February 2016. A range of mangrove sites of
122 different ages were sampled to assess changes in C and N stocks through time. The selected
123 sites were close to each other (< 5km apart) and had similar salinity and nutrient inputs
124 (Katsuhisa and Choo, 2000). The six sites ranged in age as follows: (1) one year after
125 harvesting, hereafter “clear-cut” site (Block P-14-24 in compartment 19), (2) five years after
126 replantation (Block P-10-119, compartment 31), (3) 15 years after replantation (Block P-00-
127 107, compartment 44), (4) 30 years after replantation (Block P-15-165, Compartment 19), (5)
128 an old-growth forest of 40 years reserved for educational purposes (43 ha), and finally, (6) a
129 70 year-old reference forest (Fig. 1, Table 1). All forests fringed a main river channel, except
130 the 40 year-old forest, which fringed a smaller creek (Reba River).

131 At each site, a 100m-transect perpendicular to the water edge was established
132 following the methodology of Kauffman & Donato (2012). This sampling design considers
133 that the variation in mangrove structure and biomass is mainly driven by tidal inundation
134 (Lugo and Snedaker 1992). Within each transect, we established six plots of 7m in radius at
135 25 m intervals. In the clear-cut site, the intervals were 10 m because the cleared patch was <

136 100 m in width. At each plot, we collected samples to measure C and N in forest litter,
137 downed wood, and soil as explained below.

138

139 **2.2.1 Forest litter**

140 Forest litter was collected at each plot in duplicates with 40 x 40 cm quadrats established at
141 opposite sides of the transect. The litter from each quadrat was rinsed, air-dried for 48 h, and
142 weighed. A representative subsample of ~10 g was taken to the laboratory, where it was dried
143 at 60°C and reweighed. The amount of biomass was estimated as dry weight per area (ha).
144 Forest litter biomass was converted to C and N stock on the basis of its C and N content,
145 which was measured with an elemental analyser coupled to an isotopic ratio mass
146 spectrometer (EA-IRMS, Sercon System, Griffith University).

147

148 **2.2.2 Downed wood**

149 Downed wood was sampled at each plot with the planar intersect technique (Brown *et al.*
150 1982) adapted for mangroves by Donato & Kauffman (2012). The wood pieces were sorted
151 into three categories: small (<2 cm width), large-sound, and large-rotten. Wood density was
152 measured from 50 pieces of wood collected across sampling sites as dry weight divided by
153 volume measured as water displacement. The C content in the downed wood was estimated
154 by multiplying the mean wood biomass by a factor of 0.5 (Kauffman *et al.* 1995) and by a
155 factor of 0.005 for N (Gong & Ong, 1990; Romero *et al.*, 2005). In the 5 and 15-year old
156 plots, recent downed wood was separated from downed wood from the previous harvest,
157 which was clearly identified because widths of older downed wood were larger than those of
158 standing trees.

159

160 **2.2.3 Soil**

161 In each plot, a soil core of one meter length was taken with a stainless steel open auger of 6.4
162 cm diameter (1,609 cm³) attached to a cross handle. Soil samples of known volumes were
163 collected at each plot ($n = 5$ per site) from at least four depths (0-15, 15-30, 30-50, > 50cm).
164 To assess small scale variability with depth, we collected an extra core at each site and
165 divided it to six depths (0-10, 10-20, 20-30, 30-40, 40-50, > 50 cm). Interstitial salinity was
166 measured from the water within the hole from where the core was retrieved. Salinity was
167 measured with a hand-held refractometer (ATAGO Master-S/Millα). Soil depth was
168 estimated by inserting a 2-meter aluminium rod of 1 cm in diameter in the soil and measuring
169 the depth of the horizon between organic matter and parental bedrock material. The soil
170 samples were air-dried in the field, and then oven-dried in the laboratory at 60°C. Bulk
171 density was calculated by dividing dry weight by volume of the sample. Roots were not
172 removed from the soil samples, thus the soil includes live roots recently produced and dead
173 roots preserved in the soil, which usually comprise most of the soil OC in mangrove forests
174 (Adame et al. 2017). To reduce costs of analysing a large number of soil samples ($n = 163$),
175 two thirds of the samples ($n = 103$; plots 1, 3 and 5 at each site) were analysed for %C and
176 %N (EA-IRMS, Sercon System, Griffith University). Additionally, all the samples were
177 analysed for organic matter (OM) using the loss of ignition method (Heiri et al., 2001). There
178 is a strong correlation between organic carbon (OC), OM and bulk density (e.g. Adame et al.
179 2016, Fig 1S) from which we calculated the rest of the OC values. All soil samples were
180 corrected for inorganic C (Heiri et al., 2001), although in all samples it was low (< 10%).

181

182 **2.2.4 Ecosystem C stocks**

183 To estimate ecosystem C stocks we compiled published data on tree biomass within the
184 MMFR (Table 1S). Mean tree biomass with forest age is quite consistent due the design of
185 the planting and managing of the forest. For example, forest yields between 1980-1989 were
186 177 tonnes ha⁻¹, between 1990-1999 were 175 tonnes ha⁻¹, and between 2000 and 2009 were
187 179 tonnes ha⁻¹. Tree biomass from plots of different ages was obtained from published
188 values of biomass (which were estimated from diameter at breast height and allometric
189 formulas) by Ong et al. (1984), Gong et al. (1984), Putz and Chan (1896), Azahar et al.
190 (2005), Alongi et al. (2004), Goessens et al. (2014), Hazady et al. (2014) (Table 1S). Tree C
191 stocks were obtained by multiplying tree biomass by a factor of 0.48 (Kauffman & Donato,
192 2012). Tree N stock was obtained by multiplying biomass content by 0.005 (Gong & Ong,
193 1990). Tree C and N stock were added to forest litter, downed wood, and soil to estimate
194 changes in ecosystem stocks through time.

195

196 **2.2.5 Origin, stability, and decomposition of soil C**

197 We analysed 103 samples for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which are ratios of light and heavy isotopes,
198 which are useful proxies of C and N origin and soil decomposition (Adame & Fry, 2016).
199 The most likely sources of C and N from mangrove soils are mangrove material (roots, wood
200 and litter) and phytoplankton transported during tidal inundation (Adame & Fry, 2016). We
201 analysed 14 samples of mangrove litter fall from each site. Phytoplankton were sampled
202 along the Sepetang River at 11 locations by filtering water through a 20- μm -mesh plankton
203 net. In the laboratory, phytoplankton was retained by filtration onto pre-combusted Whatman
204 GF/C glass fibre-filters.

205

206 Mangrove soils, litter and phytoplankton were analysed with an elemental analyser
207 coupled to an isotopic ratio mass spectrometer (EA-IRMS, Sercon System, Griffith
208 University, and ANCA-SL -Europa 20-20, Marine Biological Laboratory, Woods Hole,
209 U.S.A). The analytical standard deviation of the standards were < 0.1 ‰ for $\delta^{13}\text{C}$ and < 0.2
210 ‰ for $\delta^{15}\text{N}$. The stability of the soil C and N was determined from the variation of the $\delta^{13}\text{C}$
211 and $\delta^{15}\text{N}$ values within depth of mangrove stands of different ages. We expected that if C and
212 N amounts were stable, their isotopic values will remain constant with depth; if the soil was
213 perturbed after tree harvest, $\delta^{13}\text{C}$ values should become enriched as a result of increased
214 decomposition (Nadelhoffer & Fry, 1988; Adame & Fry, 2016).

215

216 **2.3 Statistical analyses**

217 Linear regressions were conducted to assess the relation between %C and %N (dependent
218 variables) and bulk density and %OC (explanatory variables) using linear regressions (SPSS
219 v24, IBM, New York, USA). To obtain rates of C and N accumulation, we modelled the
220 stock of C and N as an additive function of time using generalised additive models (Wood
221 2011). We used a Gaussian distribution and thin-plate regression splines for the two predictor
222 variables. We set the k parameter (upper limit on effective degrees of freedom) to 5 for all
223 components. We chose this value of k because it was sufficient to all non-linearities in the
224 splines and this value also ensured the model assumptions were met (Wood 2006). Predicted
225 C and N stock values were given as means for the average plot, with standard errors. We also
226 used the generalised additive models to estimate the change in the tree and soil C stocks over
227 time from values obtained from the literature for the MMFR. C and N sequestration rates
228 were estimated from the changes in time of the mean predicted values.

229

230 To compare isotope values among forests of different ages and among soil depths, we
231 used depth and age as fixed factors and plot as the random factor of the ANOVA model.
232 Normality was assessed with probability plots and the Shapiro-Wilk test. When the variable
233 was not normally distributed (e.g. $\delta^{15}\text{N}$), it was transformed ($\log_{10} x$). When transformations
234 were not enough to achieve normality (e.g. N:C), the samples were analysed with the non-
235 parametric Kruskal Wallis test. Statistical tests were performed with R and SPSS Statistics
236 (v24, IBM, New York, USA). Values reported are means and standard errors, unless
237 specified otherwise.

238

239 **3. Results**

240 **3.1 Forest litter**

241 Forest litter biomass ranged between $1.7 \pm 0.5 \text{ Mg ha}^{-1}$ in the 5 year-old forest to 3.7 ± 0.7
242 Mg ha^{-1} in the 30 year-old forest. The litter accumulated in the floor corresponds to a
243 minimum of $0.78 \pm 0.2 \text{ Mg C ha}^{-1}$ and $0.02 \pm 0.00 \text{ Mg N ha}^{-1}$ and a maximum of 1.7 ± 0.3
244 Mg C ha^{-1} and $0.03 \pm 0.01 \text{ Mg N ha}^{-1}$ (Table 2). The C accumulation of forest litter was
245 highest during the first eight years with $0.01 \pm 0.00 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, then decreased to values \leq
246 $0.005 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ after 42 years (Fig. 2a). Similarly, N accumulated at a rate of $0.004 \pm$
247 $0.000 \text{ Mg N ha}^{-1} \text{ yr}^{-1}$ in the first 15 years, and at rates $\leq 0.001 \pm 0.000 \text{ Mg N ha}^{-1} \text{ yr}^{-1}$ from 34
248 years onwards (Fig. 2d). At seven years, the amount of forest litter was 50% of the original
249 stock in the reference forest. The clear-cut site had no forest litter, thus, one year after tree
250 harvest, $0.93 \pm 0.15 \text{ Mg C ha}^{-1}$ and $0.02 \pm 0.00 \text{ Mg N ha}^{-1}$ of forest litter was lost from the
251 forest, either by decomposition, consumption or tidal exchange.

252

253 **3.2 Downed wood**

254 The density of small pieces of downed wood averaged $1.09 \pm 0.1 \text{ g cm}^{-3}$, the density for
255 large-sound wood averaged $1.24 \pm 0.1 \text{ g cm}^{-3}$, and for large-rotten wood averaged 0.71 ± 0.1
256 g cm^{-3} . Downed wood stocks ranged from 10.4 to $62.7 \text{ Mg C ha}^{-1}$ and from 0.11 to 0.63 Mg N
257 ha^{-1} for the 5 year old and reference forest, respectively (Table 2). Downed wood
258 accumulation increased linearly with age with a constant mean rate of $0.80 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and
259 $0.07 \text{ Mg N ha}^{-1} \text{ yr}^{-1}$ (Figure 2b, e). At 35 years, the amount of downed wood was 50% of the
260 original stock (Figure 2b,e). The clear-cut and the 5 year-old mangrove had 76 and 58 Mg ha^{-1}
261 of downed wood biomass from the previous harvest, respectively, so five years after tree
262 harvest most of the downed wood was still decomposing in the mangrove floor. At 15 years,
263 the downed wood from previous harvest had mostly disappeared.

264

265 **3.3 Soil**

266 Mangrove soil was deeper than 2.5 m at all sampled sites. Soil %OC and %N increased with
267 forest age (Table 3). Lowest values were measured in the surface of the clear-cut stand with
268 $6.3 \pm 0.5 \text{ %OC}$ and $0.35 \pm 0.02 \text{ %N}$; highest %OC values were measured in deep soils (50-
269 100 cm) of the reference forest with $19.4 \pm 0.9\%$ and highest %N was measured in the
270 surface of the 30-year old forest with $0.79 \pm 0.14\%$. Bulk density ranged between 0.26 ± 0.02
271 g cm^{-3} in the 30-year old forest and $0.43 \pm 0.03 \text{ g cm}^{-3}$ in the clear-cut forest (Table 3). In all
272 samples, the inorganic C fraction was < 10% of the total C, but usually < 5%. Soil bulk
273 density was significantly correlated with %OC and %N ($y = -43.3x + 29.6$, $R^2 = 0.62$, $p < 0.001$;
274 and $y = -1.15x + 0.94$, $R^2 = 0.53$, $p < 0.01$, respectively, Fig. S1), so that high %OC
275 and %N was measured in soil with low density. Soil %OC and %N were also correlated with

276 soil %OM, but only when the clear-cut site was excluded ($y = 0.37x - 0.063$, $R^2 = 0.61$,
277 $p < 0.001$; and $y = 0.013x + 0.063$; $R^2 = 0.78$; $p < 0.001$, respectively, Figure 1S).

278

279 The clear-cut mangrove soils had 29.3% less OC and 24.2% less N than the reference
280 mangrove forest, suggesting that after clearing a forest, about a third of soil OC and a fourth
281 of soil N is lost. Additionally, the clear-cut forest had 18.7% less C and 14.4% less N than
282 the forest at 30 years, suggesting that clearing a managed forest causes the loss of about a
283 sixth of the soil C and N. Soil OC and N loss in the clear-cut site was observed throughout
284 the sediment column to depths of up to 1m (Table 3).

285

286 Soil OC and N stocks increased with forest age from $385.2 \pm 72.6 \text{ MgC ha}^{-1}$ and $15.7 \pm 1.80 \text{ MgN ha}^{-1}$ in the clear-cut site to $545.0 \pm 113.4 \text{ MgC ha}^{-1}$ and $20.73 \pm 1.77 \text{ MgN ha}^{-1}$ in
287 the reference forest (Fig 2c, e). The highest soil OC stock was measured in the reference
288 forest ($F_{5,25} = 5.86$, $p = 0.001$). Soil OC accumulation was $5.7 \pm 0.2 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ in the first
289 ten years after replantation, which decreased to $\leq 5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ until 40 years. After 40
290 years, accumulation rates were variable between 0.2 to $7.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, probably due to
291 low C stocks in the 40 years forest (Fig 2c). When analysing our soil C stocks with those
292 estimated from published data (Alongi, 2004) we found accumulation rates of $2.9 \pm 0.0 \text{ Mg C}$
293 $\text{ha}^{-1} \text{ yr}^{-1}$ in the first ten years decreasing to rates $\leq 1.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ after 50 years (Fig.
294 3b). Soil N accumulation followed a linear trajectory, with a constant accumulation rate of
295 $0.07 \text{ Mg N ha}^{-1} \text{ yr}^{-1}$ (Fig. 2f). It took about 50 years for soil OC and about 35 years for soil N
296 to recover half of the losses after clearing (Fig 2c,d, 3b)

298

299 **3.4 Ecosystem C and N stocks**

300 The trajectory of tree C stocks was analysed from published data (Table 1S). Tree C
301 accumulation was $4.4 \pm 0.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in the first 12 years, decreasing to values $\leq 1 \text{ Mg}$
302 $\text{C ha}^{-1} \text{ yr}^{-1}$ after 62 years. It took 24 years, for the forest to reach half of the reference tree C
303 stock (Fig. 3a).

304

305 Total C and N stocks (including forest litter, downed wood, soil and trees) generally
306 increased with forest age from $385.2 \pm 72.6 \text{ Mg C ha}^{-1}$ and $15.7 \pm 1.8 \text{ Mg N ha}^{-1}$ in the clear-
307 cut forest, to maximum values of $895.8 \pm 113.9 \text{ Mg C ha}^{-1}$ and $24.6 \pm 1.8 \text{ Mg N ha}^{-1}$ in the
308 reference forest. The clear-cut forest had 57% of the C and 37% of the N of the reference
309 forest, suggesting that tree clear-cutting causes the loss of more than half of the total
310 mangrove ecosystem C, and more than a third of the ecosystem N within a year. In the first
311 10 years, rates of C accumulation were $9.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, after which rates decreased to 2.8
312 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$.

313

314 **3.5 Pathways of C accumulation and loss**

315 The mangrove soil had a mean $\delta^{13}\text{C}$ value of $-28.6 \pm 0.04 \text{ ‰}$ (range = -27.6 to -29.9 ‰) and
316 $\delta^{15}\text{N}$ value of $3.1 \pm 0.1 \text{ ‰}$ (0.9 to 8.8 ‰). The $\delta^{13}\text{C}$ values in the soil were close to those of
317 mangrove litter, which were $-29.4 \pm 0.1 \text{ ‰}$, consistent with a mangrove origin for the soil OC
318 (Fig. 4). For $\delta^{15}\text{N}$, relatively large differences between sites were evident for soils (1.3 to 6.2
319 ‰), but they were all well within the values of mangrove litter. Isotope values from
320 phytoplankton were variable, but in general higher in $\delta^{13}\text{C}$ compared to the mangrove soil.

321 Phytoplankton $\delta^{15}\text{N}$ (mean= $-25.5 \pm 0.8 \text{‰}$, 30.4 to -21.1) were similar to those of mangrove
322 litter (mean = $6.1 \pm 0.7\text{‰}$; 1.1 to 9.2 ‰).

323

324 Comparing soils averaged across 0-100 cm depths, the clear-cut forest soils had a
325 significantly higher mean $\delta^{13}\text{C}$ value ($-28.09 \pm 0.02 \text{‰}$) than the observed at rest of the sites
326 ($F_{5, 8.9} = 20.48, p < 0.001$; Fig. 4a). For $\delta^{15}\text{N}$, the clear-cut mangrove soil, and those of the 5-
327 year old and 40-year old forests had significantly higher values ($> 3 \text{‰}$) compared to soils of
328 the 16-year forest, 30-year forest and the reference forest ($F_{8, 9.5} = 6.36, p = 0.007$; Fig. 4). The
329 N:C values were not significantly different among sites ($p = 0.065$) or depths ($p = 0.093$),
330 although the clear cut site and the 40-year old site had notably higher N:C in the first 50 cm
331 of sediment of soil compared to the rest of the sites (Fig. 4c). Among soil depths, $\delta^{13}\text{C}$ was
332 about 0.6 ‰ enriched in the deep sediment compared to the surface ($F_{8, 40.3} = 3.51, p =$
333 0.005). Finally, $\delta^{15}\text{N}$ values were not significantly different within depths ($F_{8, 24.6} = 1.91, p =$
334 0.104; Fig. 4b). The clear cut site was notably different from the rest of the sites, with higher
335 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and N:C values. In general, mangrove soils were depleted in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and
336 decreased in N:C with age, consistent with decreased decomposition (Table 2S).

337

338 **4. Discussion**

339 One year after tree harvest, mangrove ecosystem C and N stocks were halved. In the
340 first ten years, the forest recovered quickly with rates of C accumulation of $9.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$,
341 primarily as a result of rapid tree and root growth in this humid-warm and nutrient-rich
342 environment. After ten years, the rate of accumulation decreased to $2.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. Forty

343 years after replanting, mangroves were still a 26% lower in C and 15% lower in N compared
344 to the reference forest.

345

346 After tree harvest, soil $\delta^{13}\text{C}$ values significantly increased throughout the sediment
347 column, an effect likely due to decomposition (Nadelhoffer & Fry, 1988; Adame & Fry,
348 2016). In the surface, increased $\delta^{13}\text{C}$ values could also partly reflect increased benthic
349 microalgal photosynthesis in the newly open forests (Lovelock, 2008). Mangroves in MMFR
350 have respiration rates of 0.5-1.8 Mg C $\text{ha}^{-1} \text{yr}^{-1}$, and oxidation rates of 3.4-5.2 Mg C $\text{ha}^{-1} \text{yr}^{-1}$
351 (Alongi et al., 2004). Our measured rate of loss of soil C after perturbation of 3.1 Mg C ha^{-1}
352 yr^{-1} is well within these expected ranges.

353

354 Nitrogen dynamics followed a similar pattern to C variations. The N budget in
355 mangrove forests is primarily the sum of outputs (denitrification-nitrification, plant uptake)
356 and inputs (N fixation and sediment burial). MMFR has denitrification rates of 0.04-1.1 Mg
357 N $\text{ha}^{-1} \text{yr}^{-1}$, plant uptake of 0.8-2.3 Mg N $\text{ha}^{-1} \text{yr}^{-1}$, sediment burial of 0.3-0.4 Mg N $\text{ha}^{-1} \text{yr}^{-1}$
358 and low N fixation rates, which ranged from undetectable to 0.3 Mg N $\text{ha}^{-1} \text{yr}^{-1}$, (Alongi et
359 al., 2004). In general, mangrove forests of MMFR are considered sinks of 0.8 to 3.5 Mg N ha^{-1}
360 yr^{-1} (Alongi et al., 2004). Our estimated net ecosystem N uptake rate after restoration is
361 between 0.1 and 0.6 Mg N $\text{ha}^{-1} \text{yr}^{-1}$, values within the lower end of measurements by Alongi
362 et al. (2004).

363

364 The years between tree harvest and replantation are critical for N and C losses. In
365 cleared mangroves, the sediment becomes oxygenated, which causes the rapid decomposition

366 of organic matter, increased respiration, decreased denitrification, and decreased sediment
367 burial, all of which results in C and N loss (Rivera-Monroy & Twilley, 1996; Alongi et al.,
368 1998; Sidik & Lovelock, 2013). After replantation, soil $\delta^{13}\text{C}$ values stabilized around -29‰, a
369 value similar to mangrove litter. It is likely that at after replantation, a gradual shift from
370 aerobic to anaerobic soil conditions occurs, with anaerobic reactions such as sulphate
371 reduction dominating (Alongi et al., 1998) and limiting C loss. Regrowth of roots following
372 tree replantation may account for most of the early (< 5 years) recovery of soil C stocks
373 (Adame and Fry 2016, Adame et al. 2017).

374

375 In the first five years, soil C accumulation rates were between 2.9 and 6.1 Mg C ha^{-1}
376 yr^{-1} , which were twice as large as those in mature forests (> 50 years) that were $\leq 1.2 \text{ Mg C}$
377 $\text{ha}^{-1} \text{ yr}^{-1}$. Our estimates of C accumulation in mature forests were similar to previous
378 assessments of soil OC accumulation of 2-2.5 Mg C $\text{ha}^{-1} \text{ yr}^{-1}$ in planted forests in MMFR
379 estimated with ^{210}Pb (Alongi et al., 2004), 0.7-4.9 MgC $\text{ha}^{-1} \text{ yr}^{-1}$ in mangrove forests in
380 French Guiana (Marchand, 2017) and 0.4-1.8 MgC $\text{ha}^{-1} \text{ yr}^{-1}$ in mangroves in Mexico (Adame
381 et al., 2015a). Mangrove OC and N accumulation followed a logarithmic trajectory for soil,
382 trees and litter, with highest sequestration rates in the early years. Similarly, the increase in
383 the soil layer resulting from mangrove progression followed a logarithmic trajectory in
384 French Guiana for mangroves from 3-48 years old (Marchand, 2017). This result highlights
385 that restoration projects should be valued considering different C uptakes between young and
386 mature forests (Alongi, 2011).

387

388 Despite our described progression of C and N accumulation with time, natural factors
389 are likely to contribute to spatial and temporal variations. Mangroves are constantly perturbed

390 by natural factors, such as tropical storms which can cause extensive damage to trees
391 (Sherman et al., 2001; Kauffman & Cole, 2010) and peat collapse (Cahoon et al., 2003).
392 Many mangroves can naturally recover after such perturbations if the conditions are
393 adequate, but some stands may never return to their original condition (Sherman et al., 2000;
394 Baldwin et al., 2001). Additionally, mangrove C accumulation is closely related to sea level
395 (Krauss et al., 2013; Lee et al., 2014), which will increase in the coming decades. Thus, the
396 establishment of a mangrove forests and their rapid rates of C and N sequestration do not
397 guarantee continual delivery of this ecosystem service. Based on our results, planted
398 mangroves can recover relatively quickly, but only if the conditions are adequate.

399

400 Carbon and N stocks typically follow a progression with age. However, we found
401 variability within a few sites. The 40-year old forest supports mixed *Rhizophora* and
402 *Brugueira* species, and has been conserved for educational purposes and is close to the town
403 of Sepatang. This forest at 40 years had lower C stocks than the managed forests at 30 years.
404 Thus, despite differences in age, the spatial variability within sites, such as nutrient inputs,
405 management, and climate will affect C and N sequestration potential for different mangrove
406 forests.

407

408 The differences among sites with age in C and N content can be translated into
409 delivery of ecosystem services. For example, our reference had twice as much downed wood
410 as the rest of the forests. Downed wood could be an important habitat for fauna in mangrove
411 forests (Allen et al., 2000; Feller & Chamberlain, 2007). Thus, restoration of mangroves, as
412 with any other ecosystem, might have resulted in a novel type of forest (Hobbs et al., 2009)
413 with lower habitat diversity.

414

415 Our results provide valuable information on the rates of loss and recovery of C and N
416 after mangrove clearing and replantation in Malaysia. However, the comparison with other
417 mangrove forests needs to be made with caution, because variability within environmental
418 factors and management practices will strongly affect C and N sequestration rates.
419 Mangroves in Asia Pacific are very productive and have the highest soil C stocks on Earth
420 (Atwood et al., 2017). In MMFR conditions for mangroves are ideal, with warm
421 temperatures, high rainfall and high nutrients; factors contributing to high forest productivity
422 (Reef et al., 2010). Additionally, replantation of the mangroves in the MMFR occurs in soil
423 with conditions highly suitable for plant growth. Rates for C and N gains are likely to be
424 lower for other mangrove forests in less productive locations. In some cases, C and N gains
425 could be close to zero if the soil has been strongly perturbed and the conditions for plant
426 growth are inadequate (Kodikara et al., 2017). Nevertheless, in this study we describe the best
427 account to date for long-term C and N loss and sequestration rates in mangrove forests.

428

429 **4.1 Implications for the Matang Mangrove Forest Reserve**

430 The MMFR has been successfully managed for forestry for over a century. At the
431 moment, there are plans for reducing the harvesting cycle from 30 to 20 years to increase
432 charcoal wood supply. However, with concerns of decreased tree productivity and the decline
433 on the price of charcoal, C markets could be an attractive option (Ullman et al., 2013, Ammar
434 et al., 2014).

435

436 The current management program releases 1163 MgCO_{2eq} ha⁻¹ after mangrove
437 clearing. After replanting, the forest recovers relatively quickly in the first ten years, although
438 there is likely to be a small loss of carbon every clearing-planting cycle which results in
439 lower C stocks in the managed versus the reference forest (Fig. 5). If instead of clearing and
440 planting, the forest is protected and left to recover for 70 years, it will sequester 1735
441 MgCO_{2eq} ha⁻¹. The protection of the mangroves compared to the business-as-usual scenario in
442 which the forest is continuously clear cut and planted, will provide reduced carbon emissions
443 of 572 MgCO_{2eq} ha⁻¹ (Fig. 5). The reduced carbon emissions could be worth \$USD 4,574
444 based on the Chinese market in 2017 in which C is valued at \$8 USD per Mg. If 1,000 ha of
445 mangroves were changed protected, the revenue is \$USD 4.6 million in 40 years, or \$USD
446 114,348 per year. In addition to the avoided emissions, the conservation of mangrove forests
447 will provide habitat for birds, improved fisheries, and costal protection, which could also be
448 considered in the future for payments for ecosystem services (PES, Locatelli et al. 2014).

449

450 The sustainable management of the MMFR has allowed for productive mangroves to
451 be maintained in this region for over a century. The rates of loss and gain of C and N
452 estimated in this study could facilitate the inclusion of mangroves in emerging C and N
453 markets. These results could also provide an incentive to the protection, restoration, and
454 sustainable management of mangrove forests in the Indo-Pacific region and in similar
455 mangrove forests throughout the world.

456

457

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466

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- 622
- 623

624 **7. Figure legends**

625 Fig. 1. Sampling locations in the Matang Mangrove Forest Reserve, Peninsular Malaysia.

626 Sampling sites are indicated by numbers corresponding to years after clear cutting; 1 – clear-
627 cut or one year after tree harvest, 5-year old mangroves, 15-year old mangroves, 30-year old
628 mangroves, 40-year old mangroves, and a 70- year old mangrove, which was considered the
629 reference forest.

630

631 Figure 2. Carbon (C) and nitrogen (N) stocks ($Mg\ ha^{-1}$) after mangrove replantation for (a,d)
632 forest litter, (b,e) downed wood, and (c,f) soil in Matang Mangrove Forest Reserve,
633 Peninsular Malaysia. The dotted lines represent standard errors and the shaded area shows the
634 period after which 50% of the original stock has been recovered.

635

636 Figure 3. Carbon (C) stocks ($Mg\ ha^{-1}$) after mangrove replantation for (a) trees and (b) soil in
637 Matang Mangrove Forest Reserve. Tree data was estimated from published biomass values
638 from Ong et al. (1984), Gong et al. (1984), Putz and Chan (1896), Azahar et al. (2005),
639 Alongi et al. (2004), Goessens et al. (2014), and Hazady et al. (2014). Soil data from this
640 study and those estimated from C values in Alongi et al. (2004).

641

642 Figure 4. (a,b) Isotope values ($\delta^{13}C$ and $\delta^{15}N$; ‰) and (c) N:C values of soils in mangrove
643 stands of different ages and depths in Matang Mangrove Forest Reserve, Malaysia. Each
644 value represents the mean \pm standard error of 3 to 5 plots. The shaded area indicates values of
645 mangrove litter (range).

646 Figure 5. Conceptual diagram of avoided emissions resulting from changes in land use
647 practices from clear cutting-planting mangroves to conservation in Matang Mangrove Forest
648 Reserve, Peninsular Malaysia.

649

650 **8. Tables**

651 Table 1. Characteristics of mangrove forests in Matang Mangrove Forest Reserve,
 652 Malaysia.

Location	Stand age	Stand description	Interstitial salinity (ppt)
4° 50.714'	0	Harvested	14.8 ± 0.6
100° 35.937'	("clear-cut")		
4° 48.914'	5	Planted	9.3 ± 0.3
100° 37.297'			
4° 49.157'	15	Planted	9.7 ± 0.2
100° 37.531'			
4° 50.651'	30	Planted and thinned	8.7 ± 0.6
100° 37.287'			
4° 50.527'	40	Reserved	7.7 ± 0.8
100° 38.196'			
4° 50.292'	>70	Reserved	7.7 ± 0.5
100° 37.189'	("reference")		

653

654

655 Table 2. Carbon (Mg C ha^{-1}) and nitrogen stock (Mg N ha^{-1}) in forest litter and downed wood
 656 from mangrove forest of different ages in the Matang Mangrove Forest Reserve, Malaysia.
 657 The clear-cut site had no forest litter one year after tree harvest. In the 5 and 15 year-old
 658 forests, natural downed wood was separated from downed wood of previous harvest (width of
 659 wood > DBH of standing trees).

	5 years	15 years	30 years	40 years	70 years
Forest litter					
C stock	0.78 ± 0.22	1.48 ± 0.29	0.93 ± 0.15	1.66 ± 0.30	1.31 ± 0.25
N stock	0.02 ± 0.00	0.03 ± 0.01	0.02 ± 0.00	0.03 ± 0.01	0.03 ± 0.01
Downed wood					
C stock	10.4 ± 2.3	15.3 ± 2.8	35.1 ± 5.9	29.6 ± 12.1	62.7 ± 10.7
N stock	0.11 ± 0.02	0.15 ± 0.03	0.35 ± 0.06	0.30 ± 0.12	0.63 ± 0.11

660

661

662 Table 3. Soil organic carbon (%OC), nitrogen (%N), bulk density (g cm^{-3}), organic carbon
 663 and nitrogen stocks (Mg ha^{-1}) up to 1m and extrapolated to 2.5m for mangrove stands of
 664 different ages in the Matang Mangrove Forest Reserve, Malaysia. BD= bulk density. Values
 665 are means \pm standard error of six plots.

Depth (cm)	%OC	%N	BD (g cm^{-3})	OC stock (Mg C ha^{-1})	N stock (Mg N ha^{-1})
Clear-cut					
0-15	6.3 ± 0.5	0.35 ± 0.02	0.46 ± 0.03	41.3 ± 5.8	2.41 ± 0.26
15-30	6.9 ± 0.7	0.37 ± 0.02	0.48 ± 0.02	51.2 ± 4.1	2.60 ± 0.13
30-50	11.0 ± 0.9	0.42 ± 0.03	0.41 ± 0.02	88.6 ± 6.4	3.50 ± 0.23
50-100	11.5 ± 0.9	0.44 ± 0.02	0.36 ± 0.02	204.2 ± 20.7	7.19 ± 1.72
Total: 0-100				385.2 ± 72.6	15.70 ± 1.80
Total: 0-250				$1,018 \pm 33.0$	33.0 ± 6.05
5 years					
0-15	8.8 ± 1.5	0.39 ± 0.01	0.47 ± 0.03	58.7 ± 9.6	2.58 ± 0.25
15-30	8.8 ± 1.2	0.40 ± 0.01	0.45 ± 0.02	61.3 ± 5.1	2.66 ± 0.32
30-50	11.8 ± 2.1	0.46 ± 0.02	0.42 ± 0.02	96.8 ± 3.5	3.64 ± 0.17
50-100	14.3 ± 1.6	0.47 ± 0.04	0.35 ± 0.01	244.0 ± 6.2	8.66 ± 1.12
Total: 0-100				460.8 ± 14.8	17.50 ± 1.10
Total: 0-250				$1,234 \pm 18.0$	40.1 ± 4.06
15 years					
0-15	16.8 ± 1.7	0.64 ± 0.07	0.30 ± 0.03	69.3 ± 7.0	2.63 ± 0.28
15-30	14.4 ± 1.3	0.58 ± 0.08	0.36 ± 0.02	79.3 ± 3.7	2.87 ± 0.38
30-50	17.0 ± 1.0	0.54 ± 0.06	0.33 ± 0.02	111.5 ± 3.6	3.81 ± 0.03
50-100	16.6 ± 1.1	0.54 ± 0.04	0.27 ± 0.01	223.1 ± 14.3	8.14 ± 0.74
Total: 0-100				483.2 ± 22.1	17.45 ± 0.62
Total: 0-250				$1,169 \pm 68.8$	40.51 ± 3.19
30 years					
0-15	18.1 ± 1.6	0.79 ± 0.14	0.26 ± 0.02	67.8 ± 4.3	2.80 ± 0.32
15-30	18.2 ± 1.7	0.66 ± 0.04	0.29 ± 0.02	77.4 ± 5.1	2.71 ± 0.18
30-50	17.2 ± 1.7	0.67 ± 0.06	0.31 ± 0.02	104.7 ± 7.6	3.97 ± 0.37
50-100	17.6 ± 1.1	0.61 ± 0.06	0.29 ± 0.02	247.6 ± 8.9	8.86 ± 0.32
Total: 0-100				497.5 ± 21.5	18.35 ± 0.75
Total: 0-250				$1,240 \pm 45.2$	44.95 ± 1.72
40 years					

0-15	11.1 ± 1.9	0.47 ± 0.10	0.41 ± 0.06	56.5 ± 5.2	2.95 ± 0.19
15-30	10.5 ± 2.2	0.45 ± 0.11	0.41 ± 0.04	54.9 ± 6.3	2.42 ± 0.12
30-50	10.3 ± 1.9	0.44 ± 0.09	0.47 ± 0.03	79.5 ± 12.3	4.21 ± 0.61
50-100	13.5 ± 2.2	0.53 ± 0.07	0.42 ± 0.02	252.3 ± 25.3	9.69 ± 0.78
Total: 0-100				454.3 ± 21.3	19.26 ± 0.83
Total: 0-250				$1,187 \pm 100$	48.5 ± 4.23

Reference (70 years)

0-15	18.5 ± 1.0	0.72 ± 0.02	0.31 ± 0.01	70.1 ± 14.4	3.45 ± 0.16
15-30	18.3 ± 1.1	0.73 ± 0.03	0.32 ± 0.03	79.8 ± 16.7	3.75 ± 0.36
30-50	17.7 ± 1.0	0.68 ± 0.03	0.31 ± 0.01	91.8 ± 16.8	3.83 ± 0.36
50-100	19.4 ± 0.9	0.66 ± 0.03	0.31 ± 0.03	303.3 ± 77.6	9.69 ± 1.49
Total: 0-100				545.0 ± 113.4	20.73 ± 1.77
Total: 0-250				$1,309 \pm 270$	51.5 ± 5.52

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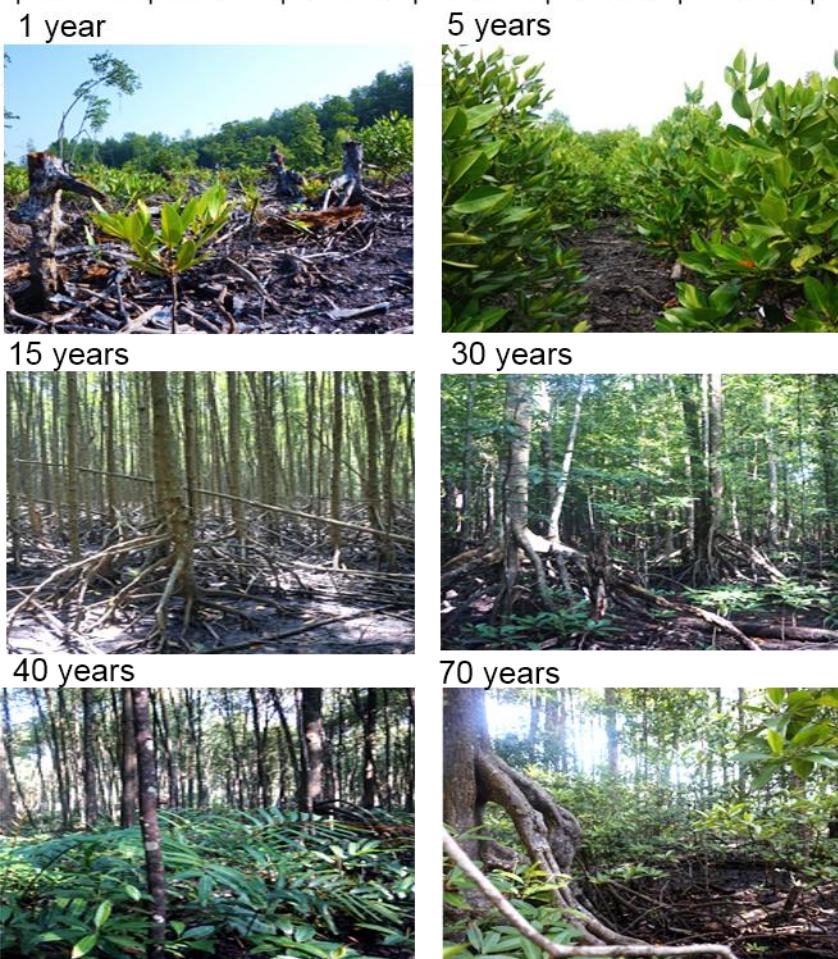
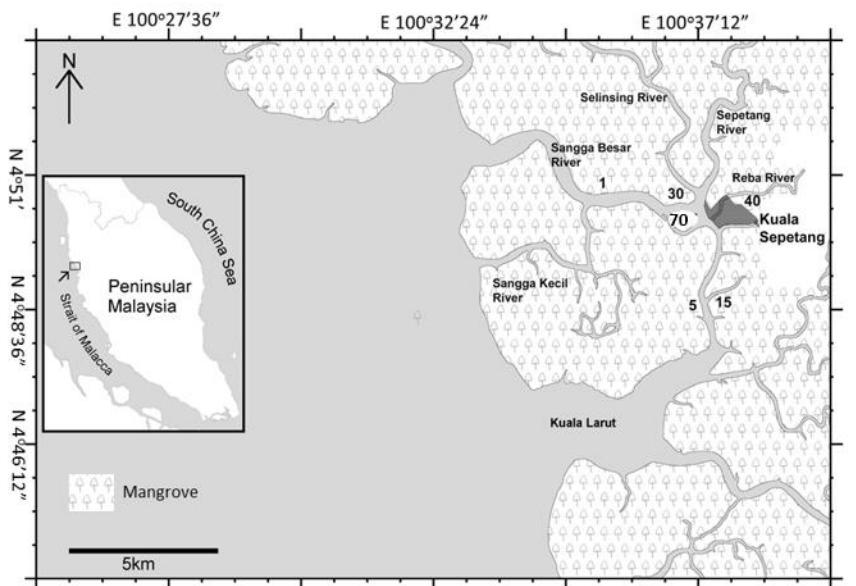
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668 Table 4. Ecosystem carbon and nitrogen stocks (soil up to 1m in depth; MgC ha⁻¹) of
669 mangrove forests of different ages in Matang Mangrove Forest Reserve, Peninsular Malaysia.
670 Tree C stocks were obtained from Alongi et al. (2004), Goessens et al, (2014), and Hamid et
671 al. (2015).

	Clear-cut	5 yrs.	15 yrs*	30 yrs.**	40 yrs.	70 yrs.
C stock	385.2 ± 72.6	472.0 ± 15.0	679.5 ± 22.2	703.0 ± 22.3	630.3 ± 24.5	895.8 ± 113.9
N stock	15.7 ± 1.8	17.6 ± 1.1	19.6 ± 0.6	20.6 ± 0.8	21.2 ± 0.8	24.6 ± 1.8

672 *After one round of thinning; ** after two rounds of thinning

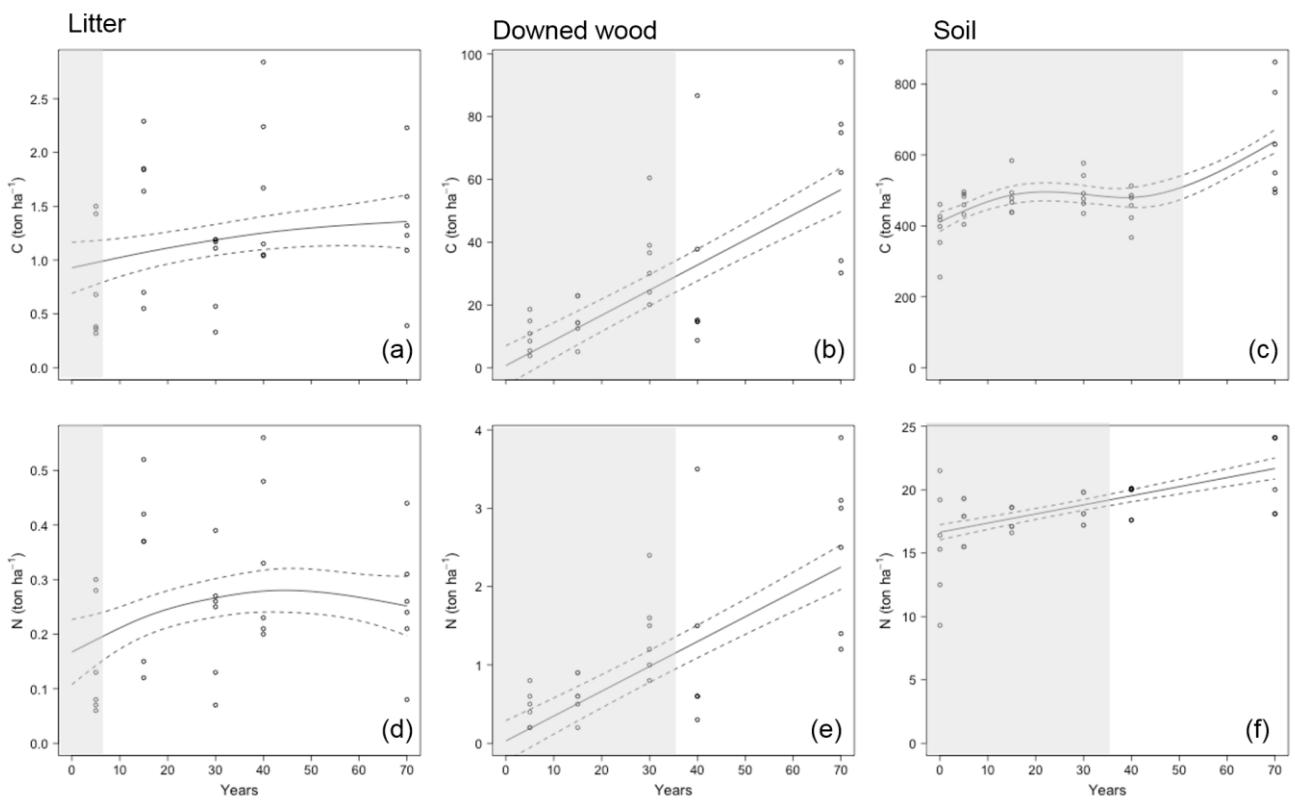
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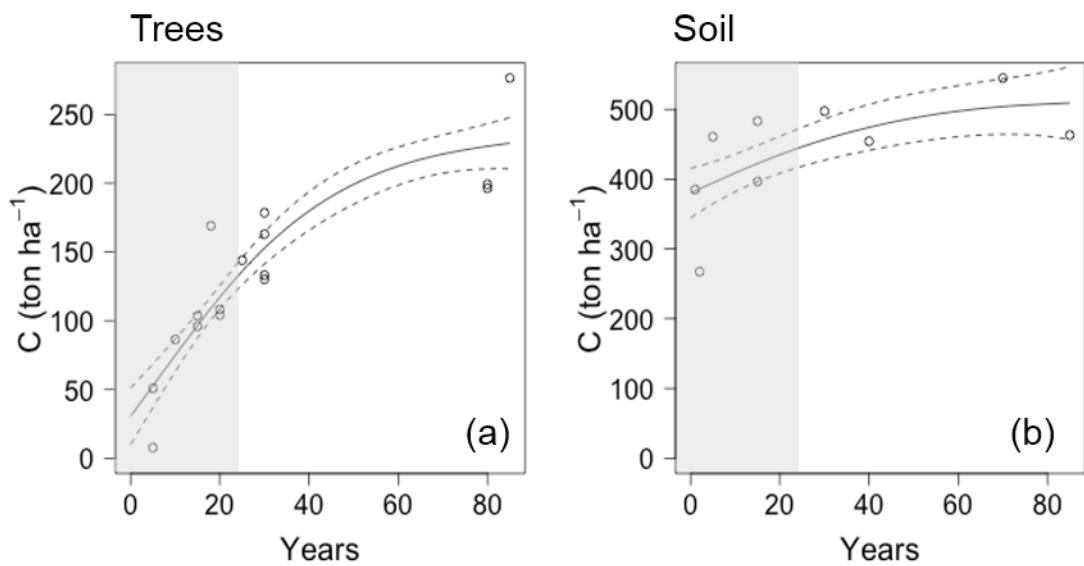


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675 Fig. 1

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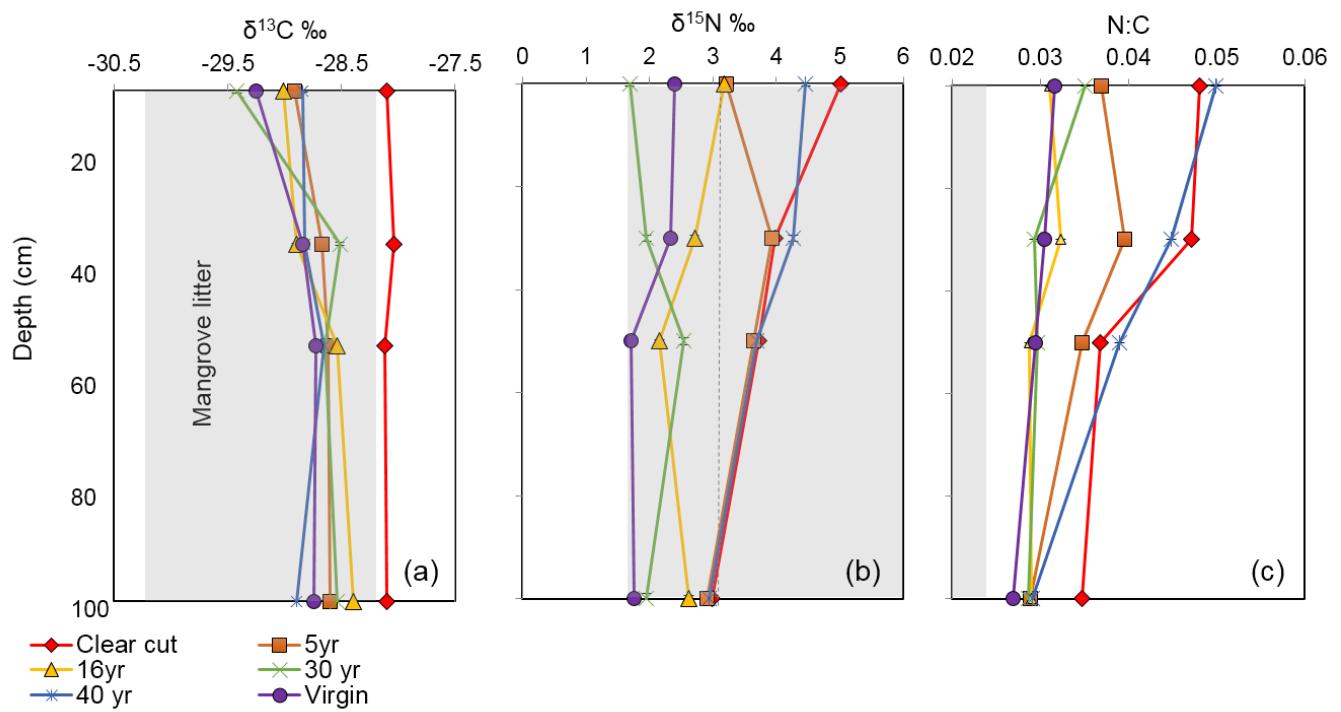




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681 Fig. 3

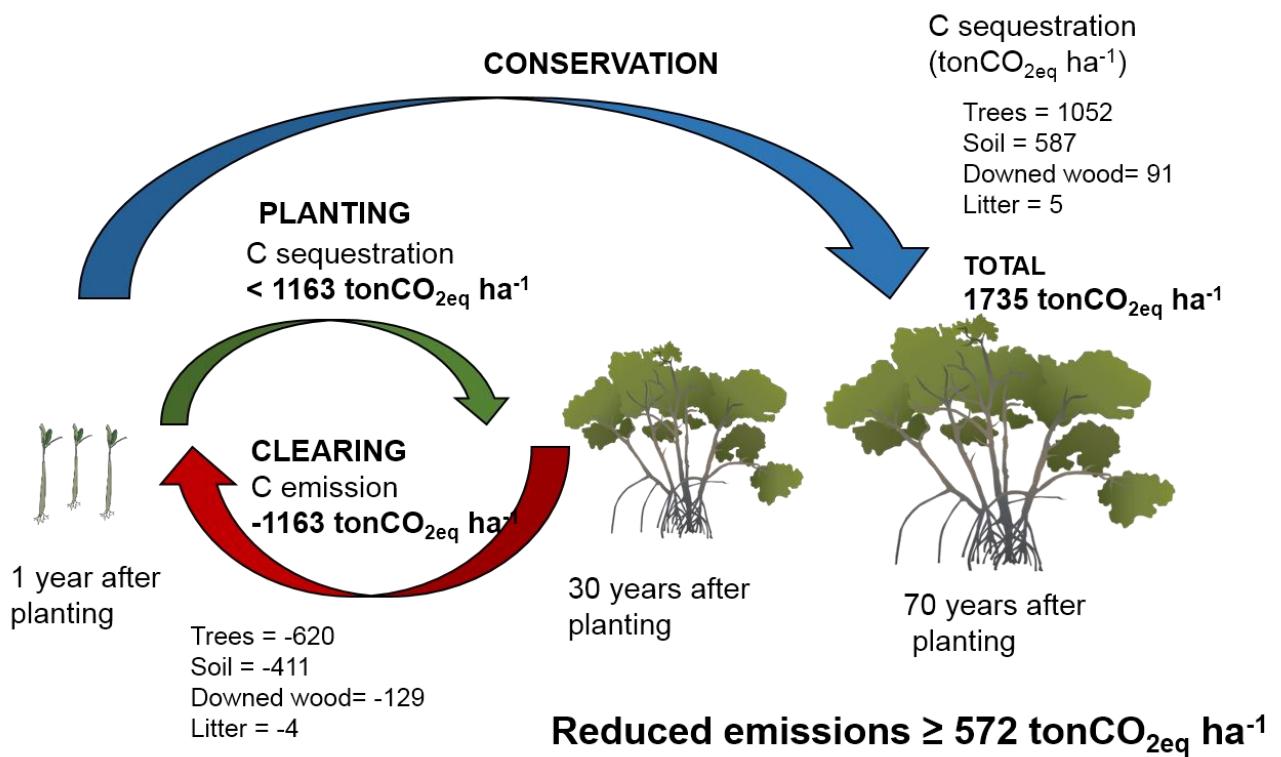
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684 Fig. 4

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687 Fig. 5