

1 **Title**

2 Co-benefits of sustainable forest management in biodiversity conservation and carbon
3 sequestration

4 (Running title: Co-benefits of SFM)

5

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14

15 **Abstract**

16 **Background:**

17 Sustainable forest management (SFM), which has been recently introduced to tropical
18 natural production forests, is beneficial in maintaining timber resources, but information
19 about the co-benefits for biodiversity conservation and carbon sequestration is currently
20 lacking.

21 **Methodology/Principal Findings:**

22 We estimated the diversity of medium to large-bodied forest-dwelling vertebrates using a
23 heat-sensor camera trapping system and the amount of above-ground, fine-roots, and soil

24 organic carbon by a combination of ground surveys and aerial-imagery interpretations.
25 This research was undertaken both in SFM applied as well as conventionally-logged
26 production forests in Sabah, Malaysian Borneo. Our carbon estimation revealed that the
27 application of SFM resulted in a net gain of 54 Mg C ha⁻¹ on a landscape scale. Overall
28 vertebrate diversity was greater in the SFM applied forest than in the conventionally-
29 logged forest. Specially, several vertebrate species (6 out of recorded 35 species) showed
30 higher frequency in the SFM applied forest than in the conventionally-logged forest.

31 **Conclusions/Significance:**

32 The application of SFM to degraded natural production forests could result in greater
33 diversity and abundance of vertebrate species as well as increasing carbon sequestration
34 in the tropical rain forest ecosystems.

35

36 **Introduction**

37 Selective logging of marketable, large trees has been a major mode of commercial timber
38 production in Southeast Asian tropical rain forests. Tropical rain forests, designated to
39 permanently produce timber with the application of such selective logging, are called
40 “production forests” and occupy a large chunk of the tropical landscapes [1]. In case of
41 Borneo, production forests cover approximately 35,000,000 ha, nearly one half of the
42 total land area (K. Kitayama unpublished). Logging intensity by selective logging
43 encompasses the amount of both harvested timber as well as collateral mechanical
44 damages to residual stands. Comprehensive approaches to reducing harvesting intensity
45 of selective logging (both in terms of harvested amount and collateral damages)
46 determine the fate of dynamics of the production forests on a regional scale.

47 Historically, the principle of sustainability dictates that a production forest should
48 be managed to limit as much undesirable damage as possible to the residual stand and
49 overall ecosystem, and the detailed regulations (such as annual allowable cut, improving
50 logging methods, forest zoning) were determined based on the concepts of guiding
51 principles [2]. For example, the annual allowable cut has been determined to regulate the
52 yield and rotation period in relation to expected regrowth based on ecological and
53 silvicultural information and to maintain timber resources at a sustainable level [2,3].
54 However, such regulations could not provide loggers with enough incentives to protect
55 their timber resources and loggers harvested, in a short time, a much greater amount of
56 timber than specified by the regulations. This also caused disproportionately greater
57 collateral damages to the residual stands [4-6]. Consequently, extensive areas of highly
58 degraded tropical rain forests cover large areas of tropical landscapes of Borneo and
59 elsewhere in tropical Asia [1].

60 Recently, sustainable forest management (SFM) combined with reduced-impact
61 logging (RIL) and forest certification has been applied in some production forests in
62 Sabah, Malaysian Borneo [7,8]. RIL consists of careful pre-harvest planning and
63 improved harvesting techniques [9], but also involves reduced harvest and post-harvest
64 silvicultural treatments [7,8]. The higher costs and the reduced timber yields can be
65 compensated by the economic benefits of forest certification, which result in an improved
66 market access and in an increased unit log price [10]. Quantitative criteria and standards
67 used in the auditing of a certification process bring loggers to comply with the
68 regulations. Investigations have revealed that such SFM is beneficial not only in
69 maintaining timber resources but also in conserving the carbon stock in the residual

70 stands [4-6,11]. In this paper, we demonstrate that SFM results in greater diversity and
71 higher densities of forest-dwelling mammal species while also increasing ecosystem
72 carbon sequestration relative to forests, in which unregulated (conventional) logging is
73 applied.

74 **Study sites and contrasting logging histories**

75 Study sites are the production forests of the Deramakot and Tangkulap Forest Reserve in
76 Sabah, Malaysian Borneo (5°14-30'N, 117°11-36'E). In this paper we use the term
77 “reserve” for land, designated for production. Deramakot (551 km²) and Tangkulap (275
78 km²) are located adjacent to each other and are covered by mixed dipterocarp lowland
79 tropical rain forest. Deramakot is a sustainably managed forest with reduced impact
80 logging, while Tangkulap is a forest damaged by conventional logging at the time of our
81 investigation (2001-2007). We demonstrate the effects of SFM (especially RIL) on
82 carbon density in terms of the sum of above-ground, fine roots, and soil organic carbon
83 and the diversity of forest-dwelling medium to large-bodied vertebrate species at a
84 landscape-scale based on a comparison between the two reserves.

85 Deramakot and Tangkulap were originally licensed for logging starting in 1956
86 and 1970s, respectively, and the conventional logging commenced there [12]. In 1989,
87 Deramakot was chosen by the Sabah State Government as a model site to develop a
88 sustainable forest management system and all logging activities were suspended
89 thereafter. A new management system with reduced-impact logging was implemented in
90 1995. Deramakot was certified by Forest Stewardship Council in 1997 for its well
91 management.

92 Deramakot is now divided into 135 compartments of varying size (approx. 500 ha
93 each), and annual harvests are planned on a compartment basis [8]. 17 of these
94 compartments (3,473 ha in area) are reserved for conservation (not to produce logs) [12].
95 About two to four compartments are harvested annually using RIL methods with a
96 planned rotation period of 40 years. Average annual yield in Deramakot during 1995-
97 2004 was about $23 \text{ m}^3 \text{ ha}^{-1}$ for the net harvested area of two to four compartments. Based
98 on the available data, the average timber production in Deramakot was much higher with
99 $109 \text{ m}^3 \text{ ha}^{-1}$ during the pre-RIL era in 1959-1968 [12].

100 By contrast, the Tangkulap forest reserve was repeatedly logged using a
101 conventional logging technique until 2001, when the government suspended all logging
102 activities. As there are no reliable statistics for the log production in Tangkulap, we
103 reconstructed the logging history of Tangkulap in comparison to Deramakot, which
104 served as a reference, using Landsat satellite data.

105 To demonstrate the logging history in terms of forest management system in the
106 two forest reserves, area-disturbance intensity curves were compared across six periods
107 during 1985-2002 in the two reserves (Figure 1). Disturbance intensity is estimated
108 based on the amount of bare soil (opened crown cover) in contrast to vegetation (see
109 Methods). In Deramakot, the volume of harvested log was consistently lower than
110 $15,000 \text{ m}^3 \text{ yr}^{-1}$ with a net harvested area of less than four compartments after 1995 [8].
111 The area-disturbance intensity curves of Deramakot were indeed mutually similar across
112 the four consecutive years from 1999 until 2002 (Figure 1), indicating that the curves
113 could represent logging intensity and area. The curves were generally more convex in
114 Tangkulap than in Deramakot ($P < 0.01$) except for 1991, suggesting that much heavier

115 logging occurred in greater areas in Tangkulap at these periods due to unregulated
116 conventional logging. The curve in Tangkulap became steeper reflecting the
117 governmental suspension of logging activities after 2001. In 1991 when logging was
118 being suspended in Deramakot, the curves of the two reserves did not differ from each
119 other ($P>0.01$), suggesting that the logging intensity and areas in Tangkulap were also
120 restricted.

121 Carbon sequestered in forests was estimated for the year 2001 based on aerial-
122 imagery interpretations and ground-based measurement. As has been demonstrated in
123 Figure 1, logging intensity was most contrasting between the two reserves probably after
124 1995 until 2001. Accordingly, the difference in carbon stock between the two reserves
125 represents a net effect of the application of SFM with RIL. Vertebrate species were
126 investigated in 2008, i.e. seven years after the suspension of logging in Tangkulap.
127 Therefore, any positive effects of RIL on vertebrate species can be a conservative
128 estimate.

129 **Results and Discussion**

130 **Carbon density**

131 Carbon density in terms of the sum of above-ground, fine roots, and soil organic carbon
132 varied greatly among forest stands reflecting the past logging intensity and recovery
133 processes (Figure 2). Carbon density varied from 156 Mg C ha^{-1} in a low-stocked forest
134 to 427 Mg C ha^{-1} in a high-stocked forest, corresponding to a highly degraded forest
135 harvested by conventional logging and to a pristine forest, respectively.

136 Figure 3 demonstrates the distribution of forest stands with four timber stock
137 classes; high stocked (427 Mg C ha^{-1} on average), mid-high stocked (325 Mg C ha^{-1}),

138 mid-low stocked (272 Mg C ha^{-1}) and low stocked (156 Mg C ha^{-1}) based on aerial-
139 imagery interpretations as of 2001. The two areas consist of complex mosaics, reflecting
140 past logging activities as well as vigorous post-logging regrowth. High and mid-high
141 stock classes together covered 34 % of the area in Deramakot, but only 10 % in
142 Tangkulap. Low stock class covered 11 % in Deramakot, while 38 % in Tangkulap.
143 Approximately one half of the area was covered by the mid-low stock class in both areas.
144 In Deramakot, the conservation area covered 8.9%, 7.0%, 6.6%, and 5.8% of the land
145 area of high, mid-high, mid-low, and low stock classes, respectively.

146 Estimated mean carbon density in above-ground vegetation was 178 and 126 Mg
147 C ha^{-1} in Deramakot and Tangkulap, respectively. The difference of 52 Mg C ha^{-1} can be
148 considered a net effect of SFM on a landscape level, reflecting the reduced harvest
149 intensities, reduced logged area, and vigorous post-logging regrowth in Deramakot. In
150 contrast, there was little difference in below-ground carbon density in the two forests (91
151 Mg C ha^{-1} in Deramakot and 89 Mg C ha^{-1} in Tangkulap). The application of SFM has
152 resulted in a net gain of 54 Mg C ha^{-1} at a landscape scale during 1989-2001 (between the
153 time when SFM commenced in Deramakot and the time when aerial photographs were
154 taken for carbon estimation).

155 **Wildlife diversity**

156 We investigated the frequency and diversity of medium to large-bodied ($> 1 \text{ kg weigh}$)
157 vertebrates throughout Deramakot and Tangkulap using automatic heat-sensor cameras.
158 We systematically chose 29 plots throughout the two forest reserves (20 and 9 plots in
159 Deramakot and Tangkulap, respectively), and three cameras were randomly installed at
160 each of the 29 plots. Animals which passed an anterior position of each camera were

161 recorded from June 2008 to April 2009, and the data of 480 camera-days during the same
162 period at each plot were used for the consistency across plots.

163 A total of 3,734 photos of 35 species (35 species in Deramakot and 31 species in
164 Tangkulap) were recorded at the entire plots during the above period (i.e., 13,920
165 camera-days). The mean (\pm SD) number of species recorded per plot was significantly
166 greater in Deramakot (17.5 ± 2.8 ; $n=20$) than in Tangkulap (15.2 ± 2.0 ; $n=9$) ($P<0.05$).
167 Among the 35 species recorded, the following six species showed a significantly higher
168 frequency per plot in Deramakot than in Tangkulap ($P<0.05$) (Table 1); Borneo yellow
169 muntjac (*Muntiacus atherodes*), Malay civet (*Viverra zibetha*), Banded palm civet
170 (*Hemigalus derbyanus*), Sun bear (*Helarctos malayanus*), Chestnut-necklaced partridge
171 (*Arborophila charltonii*) and Short-tailed mongoose (*Herpestes brachyurus*). Greater
172 species diversity and abundance in Deramakot than in Tangkulap are considered to be the
173 result of SFM in the former. In particular, beneficial effects for vertebrates may have
174 been derived from reduced intensity of logging per unit area, more localized logging
175 operations (i.e., restricted to 2-4 compartments per year), and more developed vegetation
176 (as shown in Figure 3).

177 **Concluding remarks**

178 Forestry practices have been generally considered destructive and disharmonic with
179 biodiversity conservation. It is true in the sense that they cause negative impacts if
180 applied to pristine forests. However, contemporary landscapes in the tropics and
181 elsewhere are dominated by degraded forests that are legally designated as timber
182 “production forests” [1]. Wildlife including critically endangered species reside in such
183 degraded forests [13]. Given that strictly protected areas are rather limited in area [14], a

184 pragmatic approach to conserve biodiversity including endangered mammals is to
185 sustainably manage such production forests. SFM with reduced-impact logging applied
186 to degraded natural forests can help to mitigate the deleterious logging impacts on the
187 diversity of vertebrate species as well as the amount of above-ground carbon. If we
188 consider “conventional logging” as a business-as-usual scenario common to many
189 tropical countries, the application of SFM can add carbon and biodiversity in a regional
190 context above such a baseline scenario while maintaining log production. Biodiversity
191 and carbon are the two important ecosystem services of global concern [15,16], but
192 neither are yet much internalized into SFM, because SFM is purely a forestry practice
193 based on timber production. If an international mechanism can be developed to promote
194 recognition of carbon and biodiversity in SFM, SFM will be adopted in much larger areas
195 of natural production forests. If the management approach used in Deramakot were
196 applied to all Bornean production forests, additional 1.88×10^9 Mg of carbon could be
197 sequestered and a much richer assemblages of forest dwelling vertebrate species could be
198 conserved.

199

200 **Methods**

201 **Study site**

202 This study was carried out in Deramakot (5°14-28'N, 117°19-36') and Tangkulap (5°17-
203 30'N, 117°11-21') Forest Reserves in Sabah, Malaysia. The climate of this region is
204 humid equatorial. Its mean annual temperature is 27 °C and the mean annual
205 precipitation is about 3,500 mm, with little seasonal variation [7]. Soils in this region are

206 mainly nutrient-poor Acrisols [12]. Altitudes in the reserves range between 20-300 m
207 above sea level, and the entire area is covered with lowland mixed dipterocarp forest.

208 **Logging history**

209 Several Landsat MSS, TM and ETM+ scenes of the study area were analyzed for
210 describing the disturbance history of the two reserves with different management over a
211 period of 18 years from 1985 until 2002. Taking into account that the land cover type of
212 the study area is lowland dipterocarp forest, the concept of this analysis is based on the
213 fact that reflectance values in the red band can be interpreted as recent disturbances in the
214 crown cover as bare soil is characterized by high reflectance values in the red spectrum,
215 while the undisturbed crown cover of pristine forests shows low reflectance values [17].
216 High reflectance values of the red band represent two different types of disturbances: 1)
217 Selective logging activities, which occurred within a short period (generally less than one
218 year) prior to the acquisition time of the satellite image. Older logging activities (from
219 former years) cannot be detected due to the fast regrowth of understory. 2) Permanent
220 infrastructures such as major logging roads, which transected both forest reserves and
221 existed during the whole study period. Natural landslides can give rise to a false signal of
222 disturbance, but they are rare in both reserves.

223 Due to different spatial resolutions of the single Landsat sensors (MSS in
224 comparison to TM and ETM+) all Landsat images were resampled to 80 m pixel size for
225 better inter-sensor comparison. Masks were derived for each of the 6 Landsat scenes
226 (1985, 1991, 1999, 2000, 2001 and 2002), covering cloud and cloud-shadow
227 contaminations. All masks were combined and finally applied to all Landsat imageries in
228 order to retain only those pixels, which showed no cloud or cloud-shadow contamination

229 in any of the 6 scenes. However, when analyzing the time series of Landsat scenes, we
230 experienced the problem that the spectral signal of the red band was influenced by
231 atmospheric effects. Though clouds and cloud shadows were masked, several Landsat
232 scenes were affected by haze, influencing the reflectance values in the red band.
233 However, as haze shows gradual smooth changes over larger areas, it does not influence
234 the relative relationships of the reflectance values among the neighboring pixels and the
235 abruptness in the spatial change of the reflectance among the neighboring pixels is
236 consistent irrespective of haze. In order to separate and finally eliminate these
237 atmospheric influences from real land cover changes on the ground, the slopes of the
238 corresponding red band values were used to estimate the disturbance impact (in Figure 1
239 referred as ‘Index of disturbance intensity’) instead of directly measuring the reflectance
240 values. The slopes of the reflectance values of the red band of each Landsat imagery
241 were derived using a 3×3 kernel moving window. In Deramakot 12,584 cloud-free
242 pixels were analyzed, while the sample size in Tangkulap was slightly larger with 16,510
243 sample pixels. Finally, the percent relative area was plotted on the y-axis against the
244 disturbance intensity on the x-axis double logarithmically. On such a plot, the shape of
245 the curves represents the intensity of the disturbance impact, with convex curves
246 indicating higher disturbance impact than concave curves. Comparison of shape of the
247 curves between Deramakot and Tangkulap was conducted using a Two-sample
248 Kolmogorov-Smirnov test on a 1% significance level.

249

250 **Carbon density**

251 Above- and below-ground carbon density and their spatial variation were estimated using
252 the stratum map of the entire Deramakot and Tangkulap Forest Reserves. The stratum
253 map was originally produced to indicate the spatial variation of stock volume for canopy
254 trees (≥ 60 cm diameter at breast height (dbh)) using aerial imagery. Panchromatic
255 aerial photographs at a scale of 1:17,500 taken in 2001 were used for Deramakot, and
256 panchromatic SPOT images of 5m resolution taken in 2003 were used for Tangkulap.
257 Both materials were visually interpreted to estimate the density of canopy trees based on
258 crown diameter. Although the imagery for Tangkulap was actually taken in 2003, we
259 assumed that the SPOT images reflected the canopy condition of 2001 because the
260 recruitment of canopy trees was negligible during 2001-2003 due to their highly degraded
261 status. The map depicts five classes (i.e., strata) of timber stock: high, mid-high, mid-low,
262 low stratum, and non-forest correspond to densities with ≥ 16 , 9-15, 5-8, 0-4 and 0 trees
263 ≥ 60 cm dbh per hectare, respectively. The high-stocked forest can be considered as
264 pristine forest, because such a high density of large trees (≥ 16 trees greater than 60 cm
265 dbh per hectare) appeared only in the forests with minimal levels of anthropogenic
266 disturbance in this region (Imai et al. unpublished).

267 We established two to four 0.2 ha rectangular [18] or 0.12 ha circular plots (J.
268 Titin unpublished) in each stratum, as well as one 2 ha plot in each of the mid-high, mid-
269 low, and low density strata during 2005-2008. All trees ≥ 10 cm dbh were measured in
270 each plot. Aboveground biomass was estimated according to Brown's allometric
271 equation [19].

272 In two out of three large plots, we collected wood samples of canopy dominant
273 species, which were defined as species with $\geq 3\%$ of the relative basal area to estimate

274 aboveground carbon stocks. Three trees were sampled from each of the canopy dominant
275 species. Wood samples were extracted from the outer sapwood area 1 m from the ground
276 using an increment borer. We collected at least two wood samples per individual tree,
277 and combined the samples by individual tree.

278 To estimate the stock of soil organic carbon in the upper 1 m, we excavated
279 triplicate soil pits in each of three topographic positions (flat ridge (1.8-10°), gentle (10-
280 30°) and steep slopes (30-43.7°)) in each of the three 2 ha plots (i.e., 9 soil pits per plot).
281 The O horizon comprising fresh litter and humus was sampled at three random points
282 around each pit using a circular frame (23 cm diameter). At the same sampling point
283 below the O horizon, A horizon (0-5 cm deep) was sampled using a 5 cm-deep core
284 sampler. Deeper samples were collected from the walls of soil pits using the same
285 sampler. In nine out of the 11 small plots, we set four 40 m line transects per plot,
286 sampled O and A horizons by the same methods at 10 m intervals on each line transect,
287 combined samples of each transect, and made four composite samples for each plot. We
288 sampled only O and A horizons in small plots, because carbon storage at AB and B
289 horizon did not significantly differ between the three 2 ha plots. Samples of A, AB and B
290 horizons were sorted into soils and living fine roots < 2 mm diameter. O horizon was
291 sorted into living fine roots, leaves and twigs < 2 cm girth. Our estimation of carbon
292 density does not include coarse roots (≥ 2 mm diameter), coarse woody debris (≥ 2 cm
293 girth), trees < 10 cm dbh, herbs and lianas.

294 All vegetative and soil samples were dried, weighed, finely ground, and analyzed
295 for carbon concentration by the dry combustion method with an N-C analyzer
296 (JM1000CN, J-Science Lab, Kyoto). Total carbon density, the sum of above-vegetation,

297 fine roots, and soil organic carbon on an area basis was obtained by multiplying the mass
298 of each component by its corresponding weight-basis concentration. Subsequently, we
299 multiplied the land area of each stratum by the corresponding mean carbon density to
300 obtain the total ecosystem carbon storage of the Deramakot and Tangkulap Forest
301 Reserves. Comparison of carbon density in above- and below-ground system among the
302 four strata were tested by analysis of variance (ANOVA), and the Tukey-Kramer *post-*
303 *hoc* test was performed to determine which pairs of means differ significantly when the
304 ANOVA *p* value was < 0.05 . In this analysis, we omitted the non-forest stratum because
305 it covered $< 2\%$ of each area.

306 We estimated the amount of additionally sequestered carbon if sustainable forest
307 management (SFM) were applied to all production forests in entire Borneo. In this
308 analysis, we assumed that all production forests were as degraded as Tangkulap. The
309 mean difference of carbon density between Tangkulap and Deramakot (54 t C ha^{-1} , see
310 the text) was then multiplied by the area of production forests in Borneo (i.e. 35,000,000
311 ha; K. Kitayama unpublished). This estimate of the difference in carbon density between
312 Tangkulap and Deramakot is conservative because the majority of the contemporary
313 landscape may be much more degraded than Tangkulap.

314 **Frequency and diversity of medium to large-bodied forest-dwelling vertebrates**

315 We estimated the distribution and diversity of medium to large-bodied forest-dwelling
316 vertebrates throughout Deramakot and Tangkulap. In June 2008, we systematically
317 selected 29 circular plots each with 500 m radius at approximately 5 km intervals in the
318 two forest reserves. At each plot, three passive heat-sensor cameras (Filed Note II,
319 Marifu, Iwakuni, Japan) were placed along the animal track closest to a randomly

320 selected point (generally < 20 m). A camera was attached to an appropriate standing
321 tree at about 1 m height and automatically photographed all animals passing at an anterior
322 position of the camera in all hours. Films and batteries were replaced monthly, and the
323 location of the three cameras was shifted to other random points every three to four
324 months for a total of three times per plot, i.e. nine camera points per plot. We conducted
325 the census from June 2008 to April 2009 and obtained data of 480 camera-days per
326 circular plot despite some mechanical failures of some cameras. The frequency with
327 which each species was photographed was calculated for each plot. Differences in the
328 mean number of species and observed frequency of each species per plot between
329 Deramakot and Tangkulap were tested by Welch Two Sample t-test. We counted only
330 forest-dwelling vertebrate species > 1 kg weight, which included 32 mammals, three
331 terrestrial birds, and one reptile. There is no local settlement within the two reserves and
332 hunting activity is prohibited and strictly monitored by Forestry Department. Therefore,
333 hunting pressure is minimal in both reserves.

334

335 **Acknowledgement**

336 Permission to work in Deramakot and Tangkulap Forest Reserves was granted by the
337 Sabah Forestry Department. We are grateful to Datuk Sam Mannan, the Director of SFD,
338 for his constant support.

339

340 **Funding**

341 This work was supported by the Global Environment Research Fund (F-071) of the
342 Ministry of the Environment, Japan, to KK and in part by the JSPS AA Science Platform

343 Program to KK. The funders had no role in study design, data collection and analysis,
344 decision to publish, or preparation of the manuscript.

345

346 **Competing Interests**

347 The authors have declared that no competing interests exist.

348

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396

397 **Figure Legends**

398 **Figure 1. Disturbance history of the two forest reserves between 1985 and 2002.**

399 Area - disturbance intensity curves of Deramakot and Tangkulap from 1985 until 2002,
400 based on the slope values of the red band reflectances of the Landsat MSS, TM and
401 ETM+ imagery data. The percent relative area (y-axis) is plotted against the
402 disturbance intensity (x-axis) double logarithmically. The shape of the curves
403 indicates the impact of disturbance, with convex curves indicating higher disturbance
404 impact than concave curves. Comparison of shape of the curves between the two
405 reserves: **, $p < 0.01$; ns, not significant.

406

407 **Figure 2. Carbon density in four timber stock classes.**

408 Carbon density is the sum of above-ground, fine roots, and soil organic carbon.
409 Above-ground carbon density was shown by four dbh (diameter at breast height)
410 classes (i.e., 10-30, 30-60, and 60-90 cm dbh), and soil organic carbon density was

411 shown by three soil depth classes (i.e., 0-5 cm (O and A horizons), 5-15 cm (AB
 412 horizon), and 15-100 cm deep (B horizon)). Timber stock class sharing the same
 413 letters did not significantly differ in carbon density at $p < 0.05$.

414

415 **Figure 3. Benefit of sustainable forest management on carbon sequestration at a**
 416 **landscape level.**

417 Map of Deramakot (right side) and Tangkulap Forest Reserve (left side), showing the
 418 distribution of forest stands with four timber stock classes. Lower circular graphs
 419 indicate the proportion of land area of each timber stock class by the reserve.

420

421 Tables

422 **Table 1. Recorded frequency of the 36 vertebrate species per plot in the two forest**
 423 **reserves.**

424 Frequency is given as the number of photographs during 100 days in each plot.

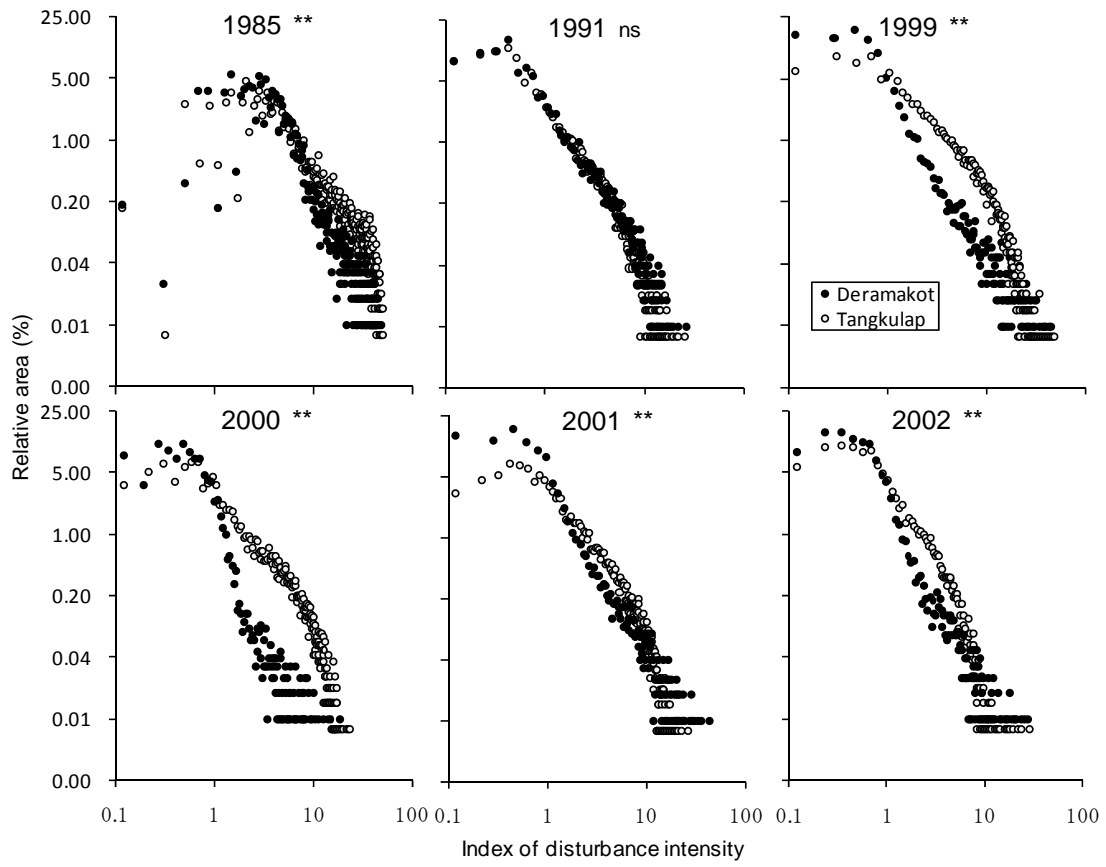
425 Comparison of means between the two reserves:*, $p < 0.05$; **, $p < 0.01$; ns, not
 426 significant.

427

Speceis	Common names	Deramakot	Tangkulap	P
<i>Tragulus napu</i> &	Greater mouse-deer &	7.08 ±5.23	5.72 ±1.56	ns
<i>Tragulus javanicus</i>	Lesser mouse-deer			
<i>Macaca nemestrina</i>	Pig-tailed macaque	2.36 ±1.67	2.66 ±1.91	ns
<i>Sus barbatus</i>	Bearded pig	2.01 ±1.30	2.75 ±2.32	ns

<i>Trichys fasciculata</i>	Long-tailed porcupine	2.08 ±2.00	1.94 ±1.68	ns
<i>Muntiacus atherodes</i>	Bornean yellow muntjac	3.20 ±2.31	0.39 ±0.49	**
<i>Argusianus argus grayi</i>	Great argus	2.33 ±1.88	1.13 ±1.36	ns
<i>Echinosorex gymnurus</i>	Moonrat	1.34 ±1.34	1.34 ±2.45	ns
<i>Lophura ignita nobilis</i>	Crested fireback	1.42 ±3.60	0.51 ±0.47	ns
<i>Viverra tangalunga</i>	Malay civet	1.58 ±1.83	0.25 ±0.25	**
<i>Cervus unicolor</i>	Samber deer	0.92 ±0.75	0.86 ±0.65	ns
<i>Hemigalus derbyanus</i>	Banded palm civet	1.25 ±0.90	0.46 ±0.89	*
<i>Hystrix brachyuran</i>	Common porcupine	0.61 ±0.95	0.90 ±0.90	ns
<i>Mydaus javanensis</i>	Malay badger	0.67 ±0.73	0.60 ±0.70	ns
<i>Helarctos malayanus</i>	Sun bear	0.41 ±0.38	0.16 ±0.20	*
<i>Pongo pygmaeus</i>	Orangutan	0.21 ±0.28	0.21 ±0.28	ns
<i>Tarsius bancanus</i>	Western tarsier	0.09 ±0.21	0.25 ±0.27	ns
<i>Arborophila charltonii</i>	Chestnut-necklaced partridge	0.34 ±0.52	0.00	**
<i>Paradoxurus hermaphroditus</i>	Common palm civet	0.29 ±0.55	0.02 ±0.07	ns
<i>Herpestes brachyurus</i>	Short-tailed mongoose	0.24 ±0.19	0.07 ±0.10	**
<i>Thecurus crassispinus</i>	Thick-spined porcupine	0.20 ±0.45	0.09 ±0.15	ns
<i>Varanus salvator</i>	Water monitor	0.18 ±0.35	0.09 ±0.11	ns

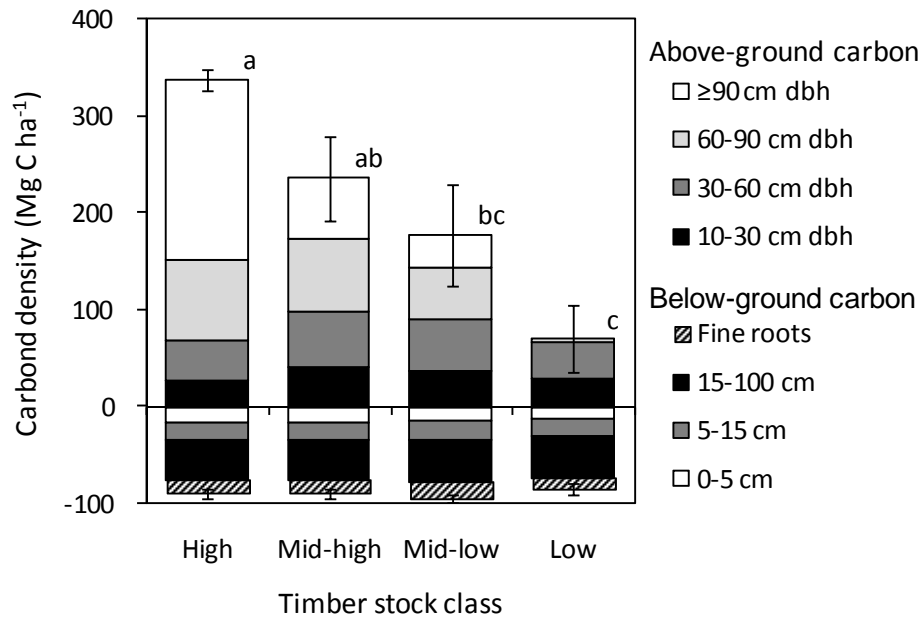
<i>Aonyx cinerea</i>	Oriental small-clawded otter	0.03	±0.10	0.12	±0.18	ns
<i>Elephas maximus</i>	Asian elephant	0.11	±0.29	0.02	±0.07	ns
<i>Macaca fascicularis</i>	Long-tailed Macaque	0.06	±0.14	0.07	±0.21	ns
<i>Martes flavigula</i>	Yellow-throated marten	0.08	±0.14	0.05	±0.09	ns
<i>Manis javanica</i>	Pangolin	0.08	±0.10	0.05	±0.09	ns
<i>Bos javanicus</i>	Tembadau	0.06	±0.20	0.05	±0.14	ns
<i>Prionodon linsang</i>	Banded linsang	0.06	±0.17	0.05	±0.09	ns
<i>Prionailurus bengalensis</i>	Leopard cat	0.03	±0.08	0.05	±0.09	ns
<i>Arctictis binturong</i>	Binturong	0.03	±0.08	0.02	±0.07	ns
<i>Neofelis nebulosa</i>	Clouded leopard	0.03	±0.08	0.02	±0.07	ns
<i>Felis marmorata</i>	Marbled cat	0.02	±0.06	0.02	±0.07	ns
<i>Felis badis</i>	Bay cat	0.01	±0.05	0.00		ns
<i>Herpestes semitorquatus</i>	Collared mongoose	0.01	±0.05	0.00		ns
<i>Arctogalidia trivirgata</i>	Small-toothed palm civet	0.01	±0.05	0.00		ns
Total number of species		17.5	±2.8	15.2	±2.0	*



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430

431 Figure 1

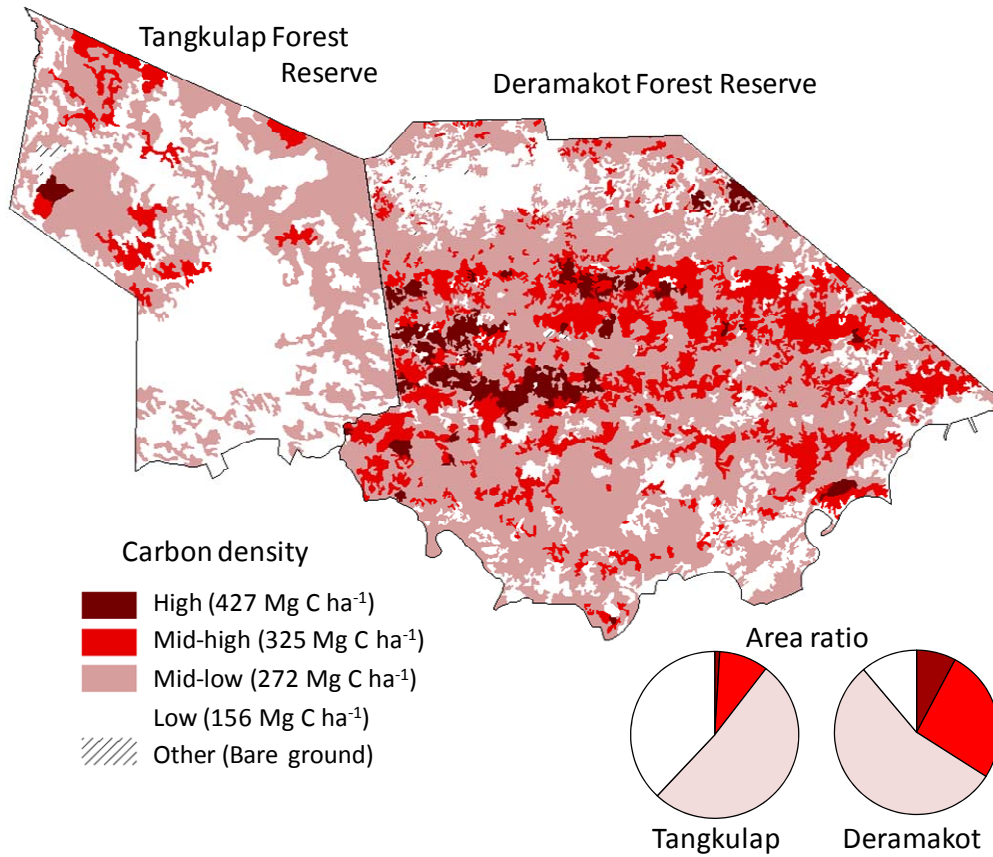


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433 Figure 2

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437 Figure 3