

1 Underproductive agriculture aids connectivity in 2 tropical forests.

3
4 Luke J. Evans^{1,2*}, Benoit Goossens^{2,3,4,5}, Gregory P. Asner¹.
5

6 1 - Department of Global Ecology, Carnegie Institution for Science, 260 Panama Street, Stanford,
7 CA, 94305, USA.

8 2 - Danau Girang Field Centre, c/o Sabah Wildlife Department, Wisma Muis, Block B, 5th Floor,
9 88100 Kota Kinabalu, Sabah, Malaysia.

10 3 - Sabah Wildlife Department, Wisma Muis, Block B, 5th Floor, 88100 Kota Kinabalu, Sabah,
11 Malaysia.

12 4 - Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University, Sir
13 Martin Evans Building, Museum Avenue, Cardiff CF10 3AX, UK.

14 5 - Sustainable Places Research Institute, Cardiff University, 33 Park Place, Cardiff, CF10 3BA, UK.

15 *Corresponding Author

16 Email: levans@carnegiescience.edu

17 Key Words: restoration ecology; elephants; oil palm; wildlife corridors; Borneo; Sabah

18

19 Abstract

20 Establishing connectivity in tropical lowland forests is a major conservation challenge,
21 particularly in areas dominated by agriculture. Replanting schemes have been widely utilized as
22 a method for reconnecting once contiguous forest patches. However, these approaches require
23 funds for both initial planting and subsequent site maintenance. Furthermore, identifying sites
24 for habitat rehabilitation schemes is difficult and may require purchasing of land, sometimes at
25 great expense. Underproductive, often unprofitable, areas of agriculture have the potential to aid
26 in re-establishing forest connectivity via natural forest regeneration. We identified an area of
27 natural forest regrowth, previously cleared for agriculture and abandoned due to high levels of

28 flooding. We assessed the structural regrowth of this forest after a 17-year period, and examined
29 its efficacy as corridor habitat for Bornean elephants. Regrowth areas had re-established tree
30 canopy areas similar to that of adjacent forest, as well as a randomly selected site of uncleared
31 forest. Flooding in the area hampered the regrowth of some sections of the site; however, ~79%
32 of the site exhibited canopy coverage. Aboveground carbon levels have returned to 50% those of
33 uncleared forests, with flooding resulting in areas of reduced vegetation regeneration. Elephants
34 have shown increasing usage of the regenerated forest, suggesting that the area has regenerated
35 its suitability as elephant corridor habitat. We have shown that what would traditionally be
36 thought of as low-quality, flood-prone areas for habitat restoration can be a useful, cost-effective
37 tool for wildlife corridor management. We propose that natural regeneration of reclaimable,
38 underproductive agriculture has the potential to play a key role in lowland tropical forest
39 connectivity, reconnecting now isolated populations of endangered Bornean elephants.

40

41 **1. Introduction**

42 Tropical forests are primary targets for land conversion due to their high agricultural
43 productivity potential (Hansen et al., 2013). South East Asia, in particular Malaysia, is currently
44 experiencing among the highest rates of forest conversion globally (Achard et al., 2014; Hansen
45 et al., 2013; Pfeifer et al., 2016), and this is largely fueled by the rapid expansion of the palm oil
46 (*Elaeis guineensis*) industry (Gaveau et al., 2016). The island of Borneo has experienced some of
47 the heaviest conversion levels in the region (Achard et al., 2002), with some 18.7 million hectares
48 of old-growth forest cleared across the island between 1973 and 2015 (Gaveau et al., 2014). Of
49 these cleared areas, approximately 23-25% were converted to oil palm plantation within five
50 years (Gaveau et al., 2016).

51

52 Oil palm trees produce the highest yields when cultivated in lowland coastal terrain, and require
53 a near-constant water supply (Basri Wahid et al., 2005). However, flooding and standing water
54 within plantations creates a poor growth environment, and areas with periodic flooding may
55 become less productive or even unprofitable, to continue to cultivate (Abram et al., 2014;
56 Sumarga et al., 2016; Woittiez et al., 2017). Lowland forests exhibit higher rates of agricultural

57 conversion (Sodhi et al., 2004), which is particularly important because these areas are
58 associated with high levels of biodiversity (Curran et al., 2004). Therefore, their large-scale
59 conversion to agriculture poses a severe threat to the continued functionality of lowland forest
60 ecosystems, as well as the overall biodiversity of a region (Meijaard and Nijman, 2003; Scriven et
61 al., 2015).

62

63 Lack of connectivity caused by high instances of poorly planned land-use change is one of the
64 greatest challenges in modern conservation (Dobson et al., 1997). Reclamation of
65 underproductive agricultural lands represents a major opportunity for restoring once contiguous
66 forest. Complete, or enrichment, replanting schemes generally utilize dozens of native species to
67 quickly establish canopy coverage and encourage faunal repopulation (Bowen et al., 2007;
68 Parotta and Knowles, 1999). These methods are, however, costly both in terms of initial outlay,
69 as well as site maintenance (Brancalion et al., 2012; Zhou et al., 2007). Without enrichment
70 planting, forests are unlikely to reach the level of complexity of old growth forests (Chazdon,
71 2008). Studies such as Aide et al. (2000) in Puerto Rico, have suggested that enrichment planting
72 may be necessary to achieve community composition in line with old growth forests. Despite this
73 finding, small remnant forest fragments can provide natural seed dispersal capabilities to aid in
74 the natural reconnection of forested fragments (Turner and Corlett, 1996).

75

76 Borneo is at the forefront of land conversion for oil palm plantations, with approximately 1.43
77 million ha cultivated in the Malaysian state of Sabah alone (Abram et al., 2014). The
78 Kinabatangan floodplain is among the largest floodplains in Borneo, providing ideal land for the
79 cultivation of oil palm. This has led to large-scale land clearance and planting (Ancrenaz et al.,
80 2004). Clearance for large estates has often led to the removal of forested areas that would
81 subsequently prove unsuitable for later cultivation. Abram et al. (2014) conducted a study
82 throughout the Kinabatangan to identify areas that were currently being cultivated with low, or
83 even unprofitable yields, and found that almost 16,000 ha (oil palm in Kinabatangan floodplain
84 totals ~250,000 ha) were deemed to be commercially redundant and thus represent significant
85 opportunities for reclamation, or natural successional regeneration.

86

87 Reforestation of agriculture, and its potential use in corridor re-establishment, is a crucial
88 recovery tool in sustaining biodiversity levels throughout the tropics. Re-establishing corridor
89 systems and restoring patch connectivity provides the most feasible method of ensuring long-
90 term survival of large mammals in tropical systems, especially for forest-restricted species that
91 range farther and require large home ranges. Bornean orang-utans (*Pongo pygmaeus*) and
92 Bornean elephants (*Elephas maximus borneensis*), for example, have been shown to rely heavily
93 on existing corridor systems, both in terms of population dynamics and genetic diversity (Alfred
94 et al., 2012; Goossens et al., 2005). Bornean elephants in particular range over many kilometers,
95 heavily utilizing highly productive agricultural areas (Alfred et al., 2012). The Kinabatangan
96 floodplain supports a population of ~300 individuals out of an estimated total population of
97 between 1100-3600 individuals (Alfred et al., 2010; Estes et al., 2012). Enhancing connectivity in
98 such an important habitat for this endangered species has become an essential requirement to
99 ensure the continuity of both the elephant population and a burgeoning local ecotourism
100 industry (Hai et al., 2001).

101

102 Herein, we examine whether allowing secondary forests to regenerate naturally on abandoned
103 oil palm plantation could provide a cost-effective method of enhancing habitat connectivity for
104 Bornean elephants. We also explore the efficacy of this particular reclaimed forest area as
105 elephant corridor habitat. The main objectives of the study were to 1) examine natural forest
106 regrowth structure and compare against representative intact forest throughout the study site;
107 2) investigate levels of flooding that initiate oil palm abandonment and its implications for future
108 agricultural reclamations; 3) discuss the value of natural regeneration as a tool for tropical forest
109 connectivity and its use as a corridor by the endangered Bornean elephant.

110

111 **2. Materials and Methods**

112 *2.1 Study Site*

113 The study site (N5.551166, E117.890413) is located in “Lot 5” of the Lower Kinabatangan
114 Wildlife Sanctuary (LKWS). The study region, a large tropical, lowland floodplain, consists of a
115 mosaic of degraded, logged forest and agriculture. Both large- and small-holding agriculture are

116 present in the vicinity; however, both largely focus on oil palm cultivation. Land conversion
117 peaked in the area during the 1970s and 80s, and remnant forest fragments are largely under
118 governmental protection (Goossens et al., 2005), although fragments now exhibit varying levels
119 of connectivity, with complete isolation of several of the LKWS lots. Using data from Gaveau et al.
120 (2014), we determined that the study site had been selectively logged, initially, between the
121 years of 1990 and 1995. Subsequent land clearance for oil palm development was carried out in
122 1999 and the title transferred to the Sabah Forestry Department in 2000 (M. Martin, pers.
123 comm.). The edge of the cleared area was identified by the remnants of a large drainage ditch
124 visible in the digital elevation model. Clearance was carried out in accordance with Sabah state
125 law which requires the maintenance of a riparian buffer zone (Sabah Land Ordinance, 2010).
126 Numerous forest replanting schemes have occurred within the study region, with Davison &
127 Prudente (2001) representing the largest. This project involved planting within several
128 kilometers of the study site.

129

130 *2.2 Airborne LiDAR*

131 The study area was mapped in April 2016 using discrete-return airborne Light Detection and
132 Ranging (LiDAR) by the Carnegie Airborne Observatory-3 (Asner et al., 2012). Three-dimensional
133 structural information of aboveground vegetation and terrain were acquired through the use of a
134 custom-built LiDAR subsystem, onboard the CAO (Asner et al., 2012). Precision three-
135 dimensional positions and orientations for CAO sensors were captured using the Positioning
136 System-Inertial Measurement Unit (GPS-IMU) subsystem, this allows for precise positioning of
137 ground-based LiDAR observations. Data collected for this study were were taken from an altitude
138 of 3600 m above ground level, with a scan angle of 36° and a side overlap of 30%. Flights were
139 conducted at a velocity of 150 knots and utilized a LiDAR pulse frequency of 150 kHz, which
140 yielded a mean point density of 3.20 laser shots per m². Vertical error was estimated at 7 cm root
141 square mean area (RSME) and horizontal error at 16 cm RMSE.

142

143 A 'cloud' of LiDAR data was produced through a combination of LiDAR laser ranges and
144 embedded GPS-IMU data (Asner et al., 2007), determining 3-D laser return locations. Where
145 elevation is relative to a reference ellipsoid, the LiDAR data cloud consisted of a number of geo-

146 referenced point elevation estimates. The 'lasground' tool packaged in the LAStools software
147 package (Rapidlasso, Gilching, Germany) was used to process LiDAR data points, detecting which
148 laser pulses penetrated the canopy volume and reached the ground. These points were
149 subsequent used to interpolate a raster digital terrain model (DTM). A further digital surface
150 model (DSM) was created using interpolations of all first-return points, which included canopy
151 top and, bare ground where only ground returns were detected. Disparities between DTM and
152 DSM vertical difference yielded a digital canopy model (DCM). Spatial resolutions of 2 m for both
153 ground elevation and woody canopy height models were derived.

154

155 *2.3 Bornean elephant GPS tagging*

156 Data from eight Bornean elephants carrying Global Positioning System (GPS) collars as part of a
157 wider home ranging behavior study, were utilized to assess corridor movement behavior. These
158 were the only individuals that utilized the study area within the entire GPS collaring dataset.
159 Throughout this study individuals were GPS tagged using units produced by Africa Wildlife
160 Tracking (AWT, Pretoria, South Africa). GPS units recorded location points every 2 hours
161 throughout the tracking period. All eight individuals tracked were female and thus their
162 movements were likely indicative of herd movement, compared to often solitary males. The
163 mean tracking period of individuals utilized within this study was 677.63 (± 192.04) days, with a
164 minimum of one and maximum of three individuals being tracked at any given period between
165 2010 and 2016.

166

167 *2.4 Analysis*

168 The LiDAR data were analyzed using both QGIS (Quantum GIS Development Team, 2017) and R
169 statistical software (R Core Team, 2000). Top-of-canopy Height (TCH) was derived from a LiDAR-
170 derived canopy height model (CHM) created by calculating the difference between ground and
171 canopy digital elevation models. Such features as the number of trees per hectare and crown
172 area, were identified using the R package "ForestTools" (Plowright, 2017). A minimum tree
173 height threshold of 4 m was selected to exclude all understory vegetation from the analysis.
174 Quantification of canopy coverage was carried out in QGIS, with gaps identified using crown
175 areas isolated using ForestTools. Digital elevation models (DEM) also produced by the LiDAR

176 mapping were analyzed using the “Raster” package (Hijmans et al., 2016). DEM data were also
177 analyzed using QGIS to identify areas of potential flooding and swamp forest. 1-way Analysis of
178 Variance (ANOVA) tests were performed to assess the variation between regrowth and extant
179 forest fragments. A linear regression was utilized to examine the relationship between the tree
180 counts and site elevation above sea level.

181

182 A randomly-selected forest area of equal size was delineated to provide representative habitat
183 variables for the study region. This site provides an assessment of areas within the study region
184 that are likely to have been selectively logged but not having been previously cleared. Selection of
185 a comparison site involved the creation of a buffer along the northern bank of the Kinabatangan
186 River, and 100 randomly generated locations along the buffered zone. A random number
187 generator was then used to select the location of the comparative site. A site of equal size and
188 shape was selected to provide the truest comparative representation of forest in the area. The
189 site was located six km upriver of the study site. Analysis of the comparative site was performed
190 as above to assess standard habitat traits across degraded, un-cleared forest.

191

192 Aboveground carbon density (ACD) was calculated for the entire state of Sabah by combining
193 LiDAR TCH models and satellite imaging data (Asner et al. *under review*). These data were
194 calibrated using field plots ranging in size from 0.28 ha to 1.0 ha throughout Sabah (Coomes et al.
195 2017). These ACD estimates were examined across 0.5 m elevations throughout the study site. A
196 linear regression was performed to ascertain the relationship between ACD and site elevation-
197 linked flooding potential.

198

199 Due to fluctuations in occurrences in elephant presence between years, data for both regrowth
200 and riparian habitats uses were converted to proportions of overall elephant presence per year.
201 A linear regression was subsequently performed to assess whether a significant trend in habitat
202 use occurred throughout the sample period.

203

204 **3. Results**

205 The area of regrowth forest (N5.41476; E118.02571) totaled 65.44 ha, bordered by an additional
206 25.49 ha of remnant intact riparian vegetation. There was approximately a 17-year interval
207 between the clearance of forest (1999) and the LiDAR mapping of the study site (2016). The
208 regrowth area was abandoned after clearance due to high flooding probabilities, as well as
209 presence of standing water (M. Martin, pers. comm.). A total of 16.5 ha (25.21%) of the regrowth
210 forest were deemed to be at risk of flooding through the use of elevation data, being located at
211 below riverbank elevation (Fig. 1). We checked these flood risk areas in the field to examine the
212 efficacy of our flood modelling.

213
214
215 Figure 1. Study region DEM fitted with contours depicting meters above sea level. Differences in
216 elevation resulting from historic irrigation ditches become apparent. Areas less than riverbank
217 elevation were deemed to be susceptible to flooding and permanent swamp.
218

219
220 Over the 17-year regrowth period, cleared forest regenerated total canopy coverage of 51.68 ha
221 (79.0%), whilst remnant, riparian vegetation had an overall canopy cover of 22.24 ha (87.4%).
222 Mean total crown areas across habitat types were similar. However, the slightly higher mean
223 crown areas displayed by regrowth forest tended towards significance ($p=0.06$) (Fig. 2).
224 Differences in tree height significantly differed between habitat types ($p<0.001$), with new
225 growth trees being significantly shorter than the riparian corridor.

226
227
228 Figure 2. Comparisons of a) crown area (m^2) and b) tree canopy height (m) between forest types.
229

230
231 Tree numbers per hectare in the regrowth area were statistically lower than those in the extant
232 forest ($p<0.001$) (Fig. 3a). There was a positive correlation between site elevation and number of
233 trees present in 25 m grids ($p=0.013$) (Fig. 3). This suggests that flooding had a negative impact
234 on tree regrowth and accounts for the lower numbers of trees per hectare found within the
235 regrowth site.

236
237 Figure 3a. Tree numbers by 25 m grid across the study site b. Terrain ruggedness analysis,
238 clearly displaying irrigation network dug for agriculture c. Tree height with clear demarcation
239 between cleared and un-cleared sites d. DEM of site showing areas of potential flooding.
240

241
242 Mean ACD values for the regrowth and riparian sites were $23.37 \text{ Mg C ha}^{-1}$ and $45.30 \text{ Mg C ha}^{-1}$,
243 respectively. This equates to an approximated ACD of 51.59% over the 17-year period, since

244 clearance. The riparian site is likely to have been selectively logged in the past; however, this ACD
 245 value is unlikely to represent true historical carbon stocks of the area. A positive correlation
 246 ($p < 0.01$) between increasing elevation and ACD showed that flooding hampered the re-
 247 establishment of those areas of regrowth site that were at lowest elevations (Fig. 4).

248
 249
 250 Figure 4. Aboveground Carbon Density (ACD) of the study site against elevations above sea level
 251 in 0.5 m increments.
 252

253 The comparative site (N5.40860; E118.00016) covered the same number of hectares, and was
 254 orientated across similar distances from the riverbank, whilst ensuring random selection of
 255 overall location. The random site exhibited higher levels of canopy coverage for both the
 256 “cleared” and riparian corridor comparative sites (92.47% and 94.98%, respectively). There
 257 were also fewer areas considered as potential swamp forest, 9.71 ha (14.83%) for regrowth zone
 258 and 1.99 ha (7.8%) for the riparian habitat.

259

260 **Table 1.** Habitat summary statistics for both the study site and comparative site.
 261

	Trees Per ha	Mean Canopy Area (m ²)	Canopy Coverage (%)	Swamp forest (%)
Study Site				
<i>Regrowth area</i>	227.43	34.72	78.97	25.21
<i>Riparian area</i>	291.95	34.26	87.25	16.37
Comparative Site				
<i>“Regrowth area”</i>	263.17	35.91	92.47	14.84
<i>“Riparian area”</i>	220.52	40.29	94.98	7.81

262

263

264 This indicates that the original study site is broadly speaking wetter than a random location
 265 within the study region. This could partially account for the lower number of trees per hectare, as
 266 well as the lower canopy coverage, present in the regrowth forest.

267

268 The study area forms part of the corridor actively utilized by Bornean elephants and links LKWS
 269 lots 5 and 7. The regeneration of the regrowth plot has enhanced the width of this corridor
 270 providing additional habitat for these elephants (Fig. 5). Analysis of elephants traversing this
 271 corridor over a six-year period provided evidence of an increasing trend in elephant usage of the
 272 regrowth site ($p = 0.017$). This suggests that, as the area recovered, and canopy cover was

273 restored, elephants used this additional habitat more frequently (Fig.5). The increasing use of the
274 site by elephants suggests that despite low-ACD and significantly shorter trees, the site can be
275 used for corridor purposes, even for a large mammal.

276
277
278
279
280
281

Figure. 5. Bornean elephant movements across both the regrowth and riparian study sites over a six-year period, with each point denoting an elephant location.

282 **4. Discussion**

283

284 We found that under-productive oil palm can be reclaimed and, without restoration, provide
285 suitable corridor habitat for endangered Bornean elephants. We also found that largely flooded
286 forest, once restored, can provide important connectivity habitat; this is of increased importance
287 when considering reconnecting once contiguous lowland dipterocarp forests. Our findings have
288 implications throughout the tropics, where productive lowland forests are being converted for
289 agriculture at an increasing rate, as well as for the creation of plantations, of which, portions are
290 producing unprofitable crop yields. The findings also examine reclamation of these areas as
291 increased connectivity for elephants in a habitat crucial to the population's survival.

292

293 The LKWS, consisting of degraded forest with varying connectivity, is a prime example of how an
294 increasing number of tropical, lowland floodplains will look in the future. With extremely high
295 levels of ecosystem productivity, paired with agricultural desirability, those floodplains that are
296 yet to experience widespread conversion will come under encroachment pressure over the next
297 decade. The LKWS thus provides a model ecosystem for tropical lowlands across the globe, with
298 it retaining high levels of biodiversity, despite the sanctuary containing only ~ 28,000 ha of
299 forest, across 10 lots (Abram et al., 2014). Abram et al. (2014) determined that 15,810 ha of oil
300 palm plantation throughout the sanctuary were, at that time, commercially redundant, providing
301 a strong case for reclamation and the potential for assisted habitat restoration. This provides a
302 financial incentive for existing plantations to engage in forest regeneration. Despite the fact that
303 flood-prone forest, once regenerated, produce lower ACD than surrounding areas (Fig. 4), over a
304 relatively short time frame (17 years), we have found that naturally regenerating canopy
305 coverage is equivalent to those areas that were not cleared (Fig. 2). In addition, we have

306 demonstrated that corridor habitat suitability is obtainable without enrichment restoration. This
307 has wide-reaching fiscal prioritization implications for future replanting and management
308 schemes.

309

310 The study site, at the time of clearing, retained a narrow riparian corridor (~100 m) that would
311 have likely aided the diversity of saplings during the initial recovery phase. During this study we
312 do not, however, examine the species composition of the regrowth forest, rather its broader
313 structural characteristics and suitability for wildlife use. No intervention forest regeneration of
314 agricultural land has been explored as a means of regeneration, for example in Africa (Chapman
315 & Chapman, 1999), and the Caribbean (Aide et al., 2000). Chapman and Chapman (1999) showed
316 that naturally regenerating forests were more frequently utilized by birds, but that these areas
317 seemed less suitable for large mammals. In this study, we suggest that in instances where fiscal
318 constraints exist or the habitat is, broadly speaking, wetter, that a hands-off approach to
319 restoration can have acceptable results, leading to active corridor utilization.

320

321 In this case study, we identified that a flooding potential of 25.1% of total land area of the
322 regrowth site was cause for abandonment of the study site (Fig. 1). Whilst this by no means
323 represents the upper, nor the lower bounds, of potential abandonment thresholds, it does
324 provide an insight into the drivers of decision making by plantation managers. This figure could
325 be used as a starting point to identify areas for potential reclamation, based on agricultural
326 productivity levels. Whilst these flooded areas, having undergone 17 years of natural
327 regeneration, provide incomplete canopy coverage of ~78%, this is enough to encourage the
328 increased use by large herbivores (Fig. 5).

329

330 The major value of the study site, despite being a relatively small area for wildlife, is through its
331 ability to expand narrow corridors and to provide validation for future planning where even a
332 narrow corridor, such as was present at this site, may no longer exist. We demonstrated
333 increasing tendencies of elephants to pass through the regrowth area as regeneration progressed
334 (Fig. 5). As all of the individuals tracked were females, these points are, in fact, likely to be
335 indicative of the movement of several family groups, rather than sole individuals. This

336 compounds these movement trends, and places increased importance on its regeneration. Figure
337 5 also suggest that at no point do the herds cut through oil palm, over a six-year period. The lack
338 of movement through agriculture demonstrates the value of even “low quality”, low ACD, habitat
339 restoration. This could provide further impetus for plantation managers to reforest
340 underproductive areas, providing additional corridor habitat and thus mitigating human-
341 elephant conflict. Identifying forested areas as key elephant habitat can provide a mandate for
342 current policy reinforcement or reform, given the species charismatic nature.

343

344 Whilst this study examined only one site, this sites ability to enhance existing corridors within a
345 highly fragmented, vulnerable ecosystem, represents a valuable gain in forest connectivity.
346 Covering just over 65 ha, the restricted nature of the study site means that future studies need to
347 identify additional areas of natural regrowth. Furthermore, these LiDAR data represent just one
348 temporal insight into how regrowth is occurring within the site. Further studies should aim to
349 identify more sites and chart regrowth throughout the regrowth process, using this methodology.
350 This has the potential to provide additional evidence of the value of natural regrowth forests for
351 connectivity. In order to restore connectivity to once contiguous forest, working with
352 increasingly small areas of forest, such as the study site, is going to prove increasingly important
353 in restoring patch connectivity.

354

355 To conclude, we suggest that natural regeneration can be a productive connectivity tool in
356 instances where financial, or habitat traits prevent enrichment planting schemes from occurring.
357 Furthermore, these areas can, within a short timeframe provide corridors usable by even the
358 largest of forest dwelling animals.

359

360 **Acknowledgements**

361

362 Mapping, processing and analysis was funded by the UN Development Programme, Avatar
363 Alliance Foundation, Roundtable on Sustainable Palm Oil, World Wildlife Fund, Morgan Family
364 Foundation, and the Rainforest Trust. We thank J. Heckler, N. Vaughn, R. Martin, P. Broderick,
365 and D. Knapp for LiDAR data acquisition and processing support. The Carnegie Airborne

366 Observatory has been made possible by grants and donations to G.P. Asner from the Avatar
367 Alliance Foundation, Margaret A. Cargill Foundation, David and Lucile Packard Foundation,
368 Gordon and Betty Moore Foundation, Grantham Foundation for the Protection of the
369 Environment, W. M. Keck Foundation, John D. and Catherine T. MacArthur Foundation, Andrew
370 Mellon Foundation, Mary Anne Nyburg Baker and G. Leonard Baker Jr, and William R. Hearst III.
371 We thank the Sabah Wildlife Department and Wildlife Rescue Unit for assistance in darting and
372 collaring of elephants. The purchase of elephant collars was made possible through grants from
373 Columbus Zoo and Aquarium, Houston Zoo, Elephant Family, Mohamed bin Zayed Species
374 Conservation Fund, The Asian Elephant Foundation, US Fish and Wildlife Service Asian Elephant
375 Conservation Fund. We also thank Andrew Davies for proof reading a draft of the manuscript.

376
377

6. References

- 378 Abram, N. K., Xofis, P., Tzanopoulos, J., MacMillan, D. C., Ancrenaz, M., Chung, R., ... & Ambu, L.,
379 2014. Synergies for Improving Oil palm production and forest conservation in floodplain
380 landscapes. *PLoS ONE*, 9, e95388. Available at:
381 <http://www.ncbi.nlm.nih.gov/pubmed/24887555> [Accessed June 3, 2014].
- 382 Achard, F., Eva, H. D., Stibig, H., Mayaux, P., Gallego, J., Richards, T., Malingreau, J., 2002.
383 Determination of deforestation rates of the world's humid tropical forests. *Science*, 297,
384 999–1002.
- 385 Achard, F., Beuchle, R., Mayaux, P., Stibig, H. J., Bodart, C., Brink, A., ... & Lupi, A., 2014.
386 Determination of tropical deforestation rates and related carbon losses from 1990 to 2010.
387 *Global Change Biology*, 20, 2540–2554.
- 388 Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., & Marciano-Vega, H., 2000. Forest
389 regeneration in a chronosequence of tropical abandoned pastures: implications for
390 restoration ecology. *Restoration Ecology*, 8, 328-338.
- 391 Alfred, R., Ahmad, A. H., Payne, J., Williams, C., & Ambu, L., 2010. Density and population
392 estimation of the Bornean elephants (*Elephas maximus borneensis*) in Sabah. *Online Journal*
393 *of Biological Sciences*, 10, 92-102.
- 394 Alfred, R., Ahmad, A. H., Payne, J., Williams, C., Ambu, L. N., How, P. M., & Goossens, B., 2012. home
395 range and ranging behaviour of bornean elephant (*Elephas maximus borneensis*) females.
396 *PloS ONE*, 7, e31400.
- 397 Ancrenaz, M., Goossens, B., Gimenez, O., Sawang, A., & Lackman-Ancrenaz, I., 2004. Determination
398 of ape distribution and population size using ground and aerial surveys: a case study with
399 orang-utans in lower Kinabatangan, Sabah, Malaysia. *Animal Conservation*, 7, 375–385.
400 Available at: <http://doi.wiley.com/10.1017/S136794300400157X> [Accessed June 26,
401 2011].
- 402 Asner, G. P., Knapp, D. E., Boardman, J., Green, R. O., Kennedy-Bowdoin, T., Eastwood, M., ... &
403 Field, C. B., 2012. Carnegie Airborne Observatory-2: Increasing science data dimensionality
404 via high-fidelity multi-sensor fusion. *Remote Sensing of Environment*, 124, 454-465.

- 405 Asner, G. P., Knapp, D. E., Kennedy-Bowdoin, T., Jones, M. O., Martin, R. E., Boardman, J., & Field, C.
406 B., 2007. Carnegie airborne observatory: in-flight fusion of hyperspectral imaging and
407 waveform light detection and ranging for three-dimensional studies of ecosystems. *Journal*
408 *of Applied Remote Sensing*, 1, e013536.
- 409 Basri Wahid, M., Abdullah, S.N.A. & Henson, I.E., 2005. Oil palm-achievements and potential. *Plant*
410 *Production Science*, 8, 288–297. Available at:
411 <http://joi.jlc.iist.go.jp/IST.ISTAGE/ppp/8.288?from=CrossRef>.
- 412 Bowen, M. E., McAlpine, C. A., House, A. P., & Smith, G. C., 2007. Regrowth forests on abandoned
413 agricultural land: a review of their habitat values for recovering forest fauna. *Biological*
414 *Conservation*, 140, 273-296.
- 415 Brancalion, P. H. S., Viani, R. A. G., Strassburg, B. B. N., & Rodrigues, R. R., 2012. Finding the money
416 for tropical forest restoration. *Unasylva*, 63, 239.
- 417 Chapman, C. A., & Chapman, L. J., 1999. Forest restoration in abandoned agricultural land: a case
418 study from East Africa. *Conservation Biology*, 13, 1301-1311.
- 419 Coomes, D.A., Dalponte, M., Jucker, T., Asner, G.P., Banin, L.F., Burslem, D.F.R.P., Lewis, S.L., Nilus,
420 R., Phillips, O.L., Phua, M.-H., 2017. Area-based vs tree-centric approaches to mapping forest
421 carbon in Southeast Asian forests from airborne laser scanning data. *Remote Sensing of*
422 *Environment*, 194, 77-88.
- 423 Curran, L. M., Trigg, S. N., McDonald, A. K., Astiani, D., Hardiono, Y. M., Siregar, P., ... Kasischke, E.,
424 2004. Lowland Forest Loss in Protected Areas of Indonesian Borneo. *Science*, 303, 1000 LP-
425 1003. Available from <http://science.sciencemag.org/content/303/5660/1000.abstract>
- 426 Davison, G. W. H., & Prudente, J. C., 2001. Rehabilitation and restoration of habitat near the
427 Kinabatangan Wildlife Sanctuary, Sabah. *In International Conference on In-situ and Ex-situ*
428 *Biodiversity Conservation in the New Millennium*, Kota Kinabalu, Sabah (Malaysia), 20-22
429 Jun 2000.
- 430 Dobson, A. P., Bradshaw, A. D., & Baker, A. Á., 1997. Hopes for the future: restoration ecology and
431 conservation biology. *Science*, 277, 515-522.
- 432 Estes, J. G., Othman, N., Ismail, S., Ancrenaz, M., Goossens, B., Ambu, L. N., ... & Palmiotto, P. A.,
433 2012. Quantity and configuration of available elephant habitat and related conservation
434 concerns in the Lower Kinabatangan floodplain of Sabah, Malaysia. *PLoS ONE*, 7, e44601.
- 435 Gaveau, D. L., Sheil, D., Husnayaen, M. A. S., Arjasakusuma, S., Ancrenaz, M., Pacheco, P., &
436 Meijaard, E., 2016. Rapid conversions and avoided deforestation: examining four decades of
437 industrial plantation expansion in Borneo. *Scientific Reports*, 6, e32017. Available at:
438 <http://www.nature.com/articles/srep32017>.
- 439 Gaveau, D. L., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., ... & Meijaard, E., 2014. four
440 decades of forest persistence, clearance and logging on Borneo. *PLoS ONE*, 9, e101654.
441 Available at: <http://dx.plos.org/10.1371/journal.pone.0101654> [Accessed July 16, 2014].
- 442 Goossens, B., Chikhi, L., Jalil, M. F., Ancrenaz, M., Lackman-Ancrenaz, I., Mohamed, M., ... & Bruford,
443 M. W., 2005. Patterns of genetic diversity and migration in increasingly fragmented and
444 declining orang-utan (*Pongo pygmaeus*) populations from Sabah, Malaysia. *Molecular*
445 *Ecology*, 14, 441–56. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/15660936>
- 446 Hai, T. C., Ng, A., Prudente, C., Pang, C., & Yee, J. T. C., 2001. Balancing the need for sustainable oil
447 palm development and conservation: The Lower Kinabatangan floodplains experience.
448 *In ISP National Seminar*.

- 449 Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... &
450 Kommareddy, A., 2013. High-resolution global maps of 21st-century forest cover change.
451 *Science*, 342, 850–3. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/24233722>
452 [Accessed May 23, 2014].
- 453 Hijmans R. J., van Etten J., Cheng J., Mattiuzzi M., Sumner M., Greenberg J. A., Lamigueiro O. P.,
454 Bevan A., Racine E. B., Shortridge A., Hijmans M. R., 2016. Package ‘raster’. R package.
455 <https://cran.r-project.org/web/packages/raster/index.html> (accessed 1 October 2016).
- 456 Meijaard, E. & Nijman, V., 2003. Primate hotspots on Borneo: Predictive value for general
457 biodiversity and the effects of taxonomy. *Conservation Biology*, 17, 725–732.
- 458 Parrotta, J. A., & Knowles, O. H., 1999. restoration of tropical moist forests on bauxite - mined
459 lands in the Brazilian Amazon. *Restoration ecology*, 7, 103-116.
- 460 Pfeifer, M., Kor, L., Nilus, R., Turner, E., Cusack, J., Lysenko, I., ... & Ewers, R. M., 2016. Remote
461 sensing of environment mapping the structure of Borneo’ s tropical forests across a
462 degradation gradient. *Remote Sensing of Environment*, 176, 84–97. Available at:
463 <http://dx.doi.org/10.1016/j.rse.2016.01.014>.
- 464 Plowright, A., 2017. Package “ForestTools”. R package. [https://cran.r-](https://cran.r-project.org/web/packages/ForestTools/index.html)
465 [project.org/web/packages/ForestTools/index.html](https://cran.r-project.org/web/packages/ForestTools/index.html) (accessed 20 March 2017)
- 466 Quantum GIS Development Team, 2017. Quantum GIS Geographic Information System. Open
467 Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- 468 R Core Team, 2000. R language definition. Vienna, Austria: *R foundation for statistical computing*.
- 469 Sabah Land Ordinance, 2010. State of Sabah Land Ordinance (Sabah Cap.68). *Land Ordinance*.
- 470 Scriven, S. A., Hodgson, J. A., McClean, C. J., & Hill, J. K., 2015. Protected areas in Borneo may fail to
471 conserve tropical forest biodiversity under climate change. *Biological Conservation*, 184,
472 414–423. Available at: <http://linkinghub.elsevier.com/retrieve/pii/S0006320715000889>.
- 473 Sodhi, N. S., Koh, L. P., Brook, B. W., & Ng, P. K., 2004. Southeast Asian biodiversity: an impending
474 disaster. *Trends in Ecology & Evolution*, 19, 654–60. Available at:
475 <http://www.ncbi.nlm.nih.gov/pubmed/16701328> [Accessed July 13, 2012].
- 476 Sumarga, E., Hein, L., Hooijer, A., & Vernimmen, R., 2016. Hydrological and economic effects of oil
477 palm cultivation in Indonesian peatlands. *Ecology and Society*, 21, 52.
- 478 Turner, I.M. & Corlett, R.T., 1996. The conservation value of small, isolated fragments of lowland
479 tropical rain forest. *Trends in Ecology and Evolution*, 5347, 38–41.
- 480 Woittiez, L. S., van Wijk, M. T., Slingerland, M., van Noordwijk, M., & Giller, K. E., 2017. Yield gaps
481 in oil palm : A quantitative review of contributing factors. *European Journal of Agronomy*,
482 83, 57–77. Available at: <http://dx.doi.org/10.1016/j.eja.2016.11.002>.
- 483 Zhou, S., Yin, Y., Xu, W., Ji, Z., Caldwell, I., & Ren, J., 2007. The costs and benefits of reforestation in
484 Liping County, Guizhou Province, China. *Journal of Environmental Management*, 85, 722-
485 735.

486

487 7. Appendices

488

489

490 Appendix A. Above ground carbon (AGC) map of the study site. Displaying substantially higher
491 carbon densities in the regrowth forest than in regrowth forest.

492

493