

Positive effects of tree diversity on tropical forest restoration in a field-scale experiment

Authors: Ryan Veryard¹, Jinhui Wu², Michael J. O'Brien³, Rosila Anthony⁴, Sabine Both⁵, David F.R.P. Burslem⁶, Bin Chen⁷, Elena Fernandez-Miranda Cagigal⁸, H. Charles J. Godfray⁹, Elia Godoong¹⁰, Shunlin Liang¹¹, Philippe Saner¹², Bernhard Schmid¹³, Yap Sau Wai¹⁴, Jun Xie¹⁵, Glen Reynolds¹⁶, Andy Hector^{1*}

Affiliations:

1 - Department of Biology, University of Oxford; South Parks Road, Oxford, OX1 3RB, UK

2 - China Institute of Geo-Environment Monitoring, China Geological Survey; Beijing,

China.

3 - Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos; Móstoles, Madrid,

Spain

4 - Sabah Forestry Department; 90000 Sandakan, Sabah, Malaysia

5 - School of Environmental and Rural Science, University of New England; Armidale NSW 2351 Australia

6 - School of Biological Sciences, University of Aberdeen; Cruickshank Building, St Machar Drives, Aberdeen AB24 3UU, Scotland, U.K.

7 - Division of Landscape Architecture, Faculty of Architecture, The University of Hong Kong; Hong Kong SAR, China

8 - Dendra Systems; Unit A, Oakfield Industrial Estate, Stanton Harcourt Rd, Eynsham, Witney OX29 4TH

22 9 - Department of Biology, University of Oxford; 11a Mansfield Road, Oxford, OX1 3SZ,
23 U.K.
24 10 - Institute for Tropical Biology & Conservation, University Malaysia Sabah; Jalan UMS,
25 88400 Kota Kinabalu, Sabah, Malaysia
26 11 - Department of Geographical Sciences, University of Maryland College Park; College
27 Park, MD, United States
28 12 - Rhino and Forest Fund e.V.; Auf dem Stein 2, D-77694 Kehl, Germany
29 13 - Department of Geography, University of Zurich; Zürich, Switzerland
30 14 - Conservation & Environmental Management Division, Yayasan Sabah Group; 88817
31 Kota Kinabalu, Sabah, Malaysia.
32 15 - Energy and Environment Institute, University of Hull; Hull, United Kingdom.
33 16 - The Royal Society SEARRP (UK/Malaysia); Danum Valley Field Centre, Lahad Datu,
34 Sabah, Malaysia
35 *Corresponding author. Email: Andrew.hector@biology.ox.ac.uk
36

37
38 **Abstract**
39
40 Experiments under controlled conditions have established that ecosystem functioning is
41 generally positively related to levels of biodiversity, but it is unclear how widespread these
42 effects are in real-world settings and whether they can be harnessed for ecosystem
43 restoration. We used a long-term, field-scale tropical restoration experiment to test how the
44 diversity of planted trees affected recovery measured across a 500 ha area of selectively
45 logged forest using multiple sources of satellite data. Replanting with species rich mixtures

46 of tree seedlings that had higher phylogenetic and functional diversity accelerated
47 restoration rates. Our results are consistent with a positive relationship between biodiversity
48 and ecosystem functioning in the lowland dipterocarp rainforests of SE Asia and
49 demonstrate that using diverse mixtures of species can enhance initial recovery after
50 logging.

51

52 **Main Text**

53 A quarter century of ecological experimentation has demonstrated that when other factors
54 are held constant, ecosystem functions like biomass production are generally positively
55 related to levels of biodiversity (1–4). However, for practical reasons the first generation of
56 biodiversity manipulation experiments were conducted with systems that are relatively
57 quick to respond, particularly communities of grassland plants (5–8). More recent
58 biodiversity experiments suggest that similar diversity function relationships are present in
59 many plantations and some forests (9), although there has been little research in tropical
60 systems, particularly outside of the new world (10–15). It is also not clear to what degree
61 the results of biodiversity experiments will extend to more natural settings, nor whether
62 they can be harnessed as a nature-based solution to forest restoration and carbon capture.
63 Here, we report early results from a field-scale experiment that tests different approaches
64 to the restoration of lowland tropical rainforests in SE Asia, focusing in particular on the
65 role of the diversity of tree species used for replanting. Recent results from our lowland
66 tropical forest study system in Sabah, Malaysian Borneo, show that active restoration,
67 including enrichment tree planting, can accelerate recovery (16)—here we go further in
68 demonstrating that recovery can be enhanced by replanting with ecologically diverse

69 mixtures of tree species.

70 Sabah Biodiversity Experiment (17–19) is designed to simultaneously test the applied
71 question of whether increasing tree diversity in replanting schemes enhances restoration
72 and the ecological hypothesis of whether there is a positive relationship between tree
73 diversity and ecosystem functioning in tropical forests. There is ongoing debate over the
74 importance of diversity for the functioning of tropical forests with some predictions of no
75 or small ecological differences among tree species in tropical forests, and therefore an
76 absent or weak link between diversity and functioning (20–23).

77 To be relevant to forestry and forest restoration, the Sabah Biodiversity Experiment was
78 designed to be field-scale and covers 500 ha of selectively logged tropical forest in Malua
79 forest reserve. The experimental treatments are applied to 4 ha plots and comprise different
80 restoration approaches including liana removal ('climber cutting') and enrichment line
81 planting where seedlings of the harvested native trees are planted into the resulting selectively
82 logged vegetation (Fig. S1). Over 100,000 seedlings of 16 different species of the dominant
83 dipterocarp trees (Table S1) have been planted along lines cut into the residual background
84 vegetation left after selective logging in the 1980s and monitored periodically for survival
85 and growth since 2002. The treatments include: unplanted controls, single-species plots
86 enrichment planted with seedlings of one of sixteen different species of dipterocarp;
87 polycultures planted with mixtures of 4 or 16 species; sixteen species mixtures with
88 additional liana removal; and manipulations (within the 4-species treatment) of generic
89 diversity and predicted canopy complexity (Table 1). To gain an overview of the effects of
90 the experimental treatments on the whole 500 ha area of the experiment over time we used
91 multiple sources of satellite remote sensing data including RapidEye estimates of vegetation

92 cover, aboveground biomass and Leaf Area Index in 2012 and estimates of cover from
93 Landsat from 1999 (prior to enrichment planting) to 2012 (24).

94 Analysis of estimates of vegetation cover, aboveground biomass and Leaf Area Index derived
95 from RapidEye satellite data in 2012 revealed several differences among the restoration
96 treatments a decade after initial planting (Fig. 1, Table S2). Comparison of unplanted controls
97 with enrichment planted plots revealed that active restoration increased levels of estimated
98 biomass (Mean \pm SE: 182.67 ± 4.27 vs 264.17 ± 3.883 Mg ha $^{-1}$), cover (62.05 ± 2.28 vs 69.31
99 ± 2.23 %) and Leaf Area Index 4.57 ± 0.25 vs 5.64 ± 0.24 m 2 m $^{-2}$) relative to unrestored
100 controls (Fig. 1, Table S3).

101 While enrichment planting had a general positive effect on restoration its effectiveness was
102 positively related to the diversity of species used. The relationship was positive and
103 approximately linear with the logarithm of the number of enrichment-planted species: each
104 doubling in tree species richness increased estimated biomass by 13.2 Mg ha $^{-1}$ (± 1.5 , Fig. 2,
105 top), cover by 1.14 % (± 0.39 ; Fig. S2) and Leaf Area Index by 0.21 m 2 m $^{-2}$ (± 0.04 , Fig. S3).

106 These treatment differences from 2012 were supported by estimates of changes in vegetation
107 cover across three LANDSAT monitoring periods covering the preceding decade which show
108 the absence of treatment differences prior to restoration (1999-2002), the emergence of
109 positive effects of enrichment planting (2003-2008) and the subsequent divergence of
110 treatments (2008-2012) with those planted with a greater diversity of tree species showing
111 stronger recovery of vegetation cover (Fig. 2; Table S4).

112 Our experimental design also contains a factorial manipulation of two other aspects of
113 diversity within the four species treatment level. Half of the four-species plots were enrichment

114 planted with four species from four different genera and half with species from only two
115 genera. This manipulation of generic diversity is crossed orthogonally with a treatment that
116 compares mixtures of four species with a lower or higher diversity of predicted mature tree
117 height that is intended to produce canopies that are thinner and simpler or thicker and more
118 complex (Table S5). Both manipulations produced only slight increases in estimated mean
119 aboveground biomass with enhanced generic diversity and canopy complexity (Fig. 1; Table
120 S6) that were statistically indistinguishable between treatments (cover and leaf area index
121 showed qualitatively similar results: Fig. S4, Table S6).

122 A subset of the plots planted with 16-species were also subjected to an additional treatment:
123 reduction of lianas in the tree canopy by stem cutting ('climber cutting'), reflecting typical
124 Bornean forest management practice (17). At the time of the RapidEye data snapshot the liana
125 removal treatment had only been applied to the southern block and the treatment had no
126 statistically detectable effects on the satellite remote sensing estimates of biomass (Fig. 1),
127 cover and Leaf Area Index (Fig. S4, Table S7). Previous analysis of longer-term field data (17)
128 has demonstrated positive effects of liana removal on the growth and survival of trees,
129 particularly seedlings and saplings in the understory, most likely due to increased light
130 availability (although with potential increased seedling mortality if cutting is followed by
131 drought). A more complete test of the liana removal treatment will require a longer series of
132 more detailed field and remote sensing data that can discriminate between vegetation cover
133 comprised of dipterocarp tree canopies versus lianas.

134 To understand why the manipulation of diversity from 1-16 species had detectable impacts on
135 multiple measures of restoration while increasing generic diversity of the 4-species mixtures
136 from 2 to 4 genera did not, we calculated estimates of functional and phylogenetic diversity

137 (FD and PD) for our species mixtures (25). Levels of biomass were positively related to levels
138 of FD and PD across the full species richness gradient from 1 to 16 enrichment planted species
139 but showed only small, statistically indistinguishable increases from the two to four genera
140 treatments and in relation to the manipulation of canopy complexity (Fig. 3). The explanation
141 for the lack of effect of our manipulation of generic diversity probably involves both the small
142 increase in diversity from two to four genera relative to the increase across the whole gradient
143 from 1 to 16 species and the fact that dipterocarp taxonomy when the experiment was designed
144 did not accurately reflect the underlying evolutionary relationships (the genus *Shorea* is now
145 thought to be polyphyletic for example, although dipterocarp taxonomy is still
146 unresolved). The analyses of functional diversity (FD) and phylogenetic diversity (PD) support
147 this interpretation showing much smaller increases in diversity within the subset of treatments
148 applied to the four species mixtures than across the entire gradient from 1 to 16 species (Fig.
149 3). These results suggest that the benefits of low levels of diversification in enrichment
150 planting can be increased by the use of more species rich mixtures (at least up to the 16 species
151 used here).

152 Our results suggest that the positive relationship between biodiversity and ecosystem
153 functioning observed in experiments in other ecosystems, including some forests, also applies
154 to the lowland tropical rainforests of SE Asia. While our remote sensing data has limitations
155 (see supplementary information: *Study limitations*) the results reported here appear robust
156 since the same qualitative patterns are evident in two different sources of satellite data.
157 Comparing these satellite data with field data for a similar period (18) suggests that during the
158 first decade of the experiment, the effects of diversity do not come primarily through higher
159 survival or greater trunk diameter. Instead, we hypothesize that the differences detected by

160 satellite remote sensing are due to the development of different canopy architectures in
161 monospecific and multi-species mixtures that we were unable to monitor in the field.
162 Diversity-dependent growth forms have previously been shown to play a role in generating
163 biodiversity effects in the Wageningen biodiversity experiment (26). Testing this hypothesis,
164 and whether differences in canopy responses subsequently feed back to improve survival and
165 DBH growth in mixtures, will require continued long-term monitoring and, ideally,
166 coordinated combination of field and remote sensing data, including more detailed
167 measurements of canopy growth.

168 A recent analysis of secondary succession and recovery after deforestation at sites in West
169 Africa and Central and South America suggests forests in these areas are resilient, recovering
170 old growth characteristic for some properties in as little as two decades (although >120 years
171 for others) as long as land-use intensity after deforestation was low (27). Our results suggest
172 the recovery of lowland forests in aseasonal SE Asia can be accelerated by active restoration
173 through enrichment planting, especially with diverse mixtures of complementary tree species.
174 Differences between the forests of SE Asia and other parts of the tropics are possible due to
175 characteristics of the dominant dipterocarp species that may slow the recovery of these forests
176 including the absence of a seedbank, intermittent mast fruiting and low dispersal ability of
177 many species (28–30). Our results suggest that conservation of the diversity of tree species in
178 these forests is needed to support the ecosystem functions and services that they provide—a
179 matter of urgency given the recent estimate that 70% of Bornean dipterocarp species are
180 threatened with extinction (31). Our results also suggest that replanting of these secondary
181 forests with diverse mixtures of the native species removed by selective logging may provide
182 a nature-based solution for their accelerated restoration.

183 **References and Notes**

184 1. F. Isbell, A. Gonzalez, M. Loreau, J. Cowles, S. Díaz, A. Hector, G. M. Mace, D. A. Wardle, M. I. O'Connor, J. E. Duffy, L. A. Turnbull, P. L. Thompson, A. Larigauderie, Linking the influence and dependence of people on biodiversity across scales. *Nature*. **546**, 65–72 (2017).

188 2. B. J. Cardinale, J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, S. Naeem, Biodiversity loss and its impact on humanity. *Nature*. **486**, 59–67 (2012).

192 3. J. S. Lefcheck, J. E. K. Byrnes, F. Isbell, L. Gamfeldt, J. N. Griffin, N. Eisenhauer, M. J. S. Hensel, A. Hector, B. J. Cardinale, J. E. Duffy, Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat. Commun.* **6**, 1–7 (2015).

196 4. D. Tilman, F. Isbell, J. M. Cowles, Biodiversity and Ecosystem Functioning. *Annu. Rev. Ecol. Evol. Syst.* **45**, 471–493 (2014).

197 5. A. Hector, B. Schmid, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Giller, J. Good, R. Harris, P. Högberg, K. Huss-Danell, J. Joshi, A. Jumpponen, C. Körner, P. W. Leadley, M. Loreau, A. Minns, C. P. H. Mulder, G. O'Donovan, S. J. Otway, J. S. Pereira, A. Prinz, D. J. Read, M. Scherer-Lorenzen, E. D. Schulze, A. S. D. Siamantziouras, E. M. Spehn, A. C. Terry, A. Y. Troumbis, F. I. Woodward, S. Yachi, J. H. Lawton, Plant diversity and productivity experiments in European grasslands. *Science*. **286**, 1123–1127 (1999).

204 6. D. Tilman, P. B. Reich, J. Knops, D. Wedin, T. Mielke, C. Lehman, Diversity and productivity in a long-term grassland experiment. *Science*. **294**, 843–845 (2001).

206 7. C. Roscher, V. M. Temperton, M. Scherer-Lorenzen, M. Schmitz, J. Schumacher, B.
207 Schmid, N. Buchmann, W. W. Weisser, E. D. Schulze, Overyielding in experimental
208 grassland communities – irrespective of species pool or spatial scale. *Ecol. Lett.* **8**, 419–
209 429 (2005).

210 8. J. van Ruijven, F. Berendse, Diversity–productivity relationships: Initial effects, long-term
211 patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci.* **102**, 695–700 (2005).

212 9. Y. Feng, B. Schmid, M. Loreau, D. I. Forrester, S. Fei, J. Zhu, Z. Tang, J. Zhu, P. Hong,
213 C. Ji, Y. Shi, H. Su, X. Xiong, J. Xiao, S. Wang, J. Fang, Multispecies forest plantations
214 outyield monocultures across a broad range of conditions. *Science*. **376**, 865–868 (2022).

215 10. D. I. Forrester, J. Bauhus, A Review of Processes Behind Diversity—Productivity
216 Relationships in Forests. *Curr. For. Reports.* **2**, 45–61 (2016).

217 11. Y. Huang, Y. Chen, N. Castro-izaguirre, M. Baruffol, M. Brezzi, A. Lang, Y. Li, X. Yang,
218 X. Liu, K. Pei, S. Both, B. Yang, D. Eichenberg, T. Assmann, T. Behrens, X. Chen, D.
219 Chesters, B. Ding, W. Durka, A. Erfmeier, J. Fang, M. Fischer, L. Guo, D. Guo, J. L. M.
220 Gutknecht, J. He, C. He, A. Hector, R. Hu, A. Klein, Y. Liang, S. Li, S. Michalski, M.
221 Scherer-lorenzen, K. Schmidt, T. Scholten, A. Schuldt, X. Shi, M. Tan, Z. Tang, S.
222 Trogisch, Z. Wang, E. Welk, C. Wirth, T. Wubet, W. Xiang, M. Yu, X. Yu, J. Zhang, S.
223 Zhang, N. Zhang, H. Zhou, C. Zhu, L. Zhu, H. Bruelheide, P. A. Niklaus, B. Schmid,
224 Impacts of species richness on productivity in a large-scale subtropical forest experiment.
225 *Science*. **83**, 80–83 (2018).

226 12. J. Pelletier, A. Paquette, K. Mbindo, N. Zimba, A. Siampale, B. Chendauka, F.
227 Siangulube, J. W. Roberts, Carbon sink despite large deforestation in African tropical dry

228 forests (miombo woodlands). *Environ. Res. Lett.* **13**, 094017 (2018).

229 13. F. Schnabel, J. A. Schwarz, A. Dănescu, A. Fichtner, C. A. Nock, J. Bauhus, C. Potvin,
230 Drivers of productivity and its temporal stability in a tropical tree diversity experiment.
231 *Glob. Chang. Biol.* **25**, 4257–4272 (2019).

232 14. C. Messier, J. Bauhus, R. Sousa-Silva, H. Auge, L. Baeten, N. Barsoum, H. Bruelheide, B.
233 Caldwell, J. Cavender-Bares, E. Dhiedt, N. Eisenhauer, G. Ganade, D. Gravel, J.
234 Guillemot, J. S. Hall, A. Hector, B. Hérault, H. Jactel, J. Koricheva, H. Kreft, S. Mereu, B.
235 Muys, C. A. Nock, A. Paquette, J. D. Parker, M. P. Perring, Q. Ponette, C. Potvin, P. B.
236 Reich, M. Scherer-Lorenzen, F. Schnabel, K. Verheyen, M. Weih, M. Wollni, D. C.
237 Zemp, For the sake of resilience and multifunctionality, let's diversify planted forests!
238 *Conserv. Lett.* **15**, e12829 (2022).

239 15. E. Warner, S. C. Cook-Patton, O. T. Lewis, N. Brown, J. Koricheva, N. Eisenhauer, O.
240 Ferlian, D. Gravel, J. S. Hall, H. Jactel, C. Mayoral, C. Meredieu, C. Messier, A. Paquette,
241 W. C. Parker, C. Potvin, P. B. Reich, A. Hector, Higher aboveground carbon stocks in
242 mixed-species planted forests than monocultures – a meta-analysis. *bioRxiv*,
243 doi:10.1101/2022.01.17.476441.

244 16. C. D. Philipson, M. E. J. Cutler, P. G. Brodrick, G. P. Asner, D. S. Boyd, P. M. Costa, J.
245 Fiddes, G. M. Foody, G. M. F. Van Der Heijden, A. Ledo, P. R. Lincoln, J. A. Margrove,
246 R. E. Martin, S. Milne, Active restoration accelerates the carbon recovery of human-
247 modified tropical forests. *Science*. **841**, 838–841 (2020).

248 17. M. J. O'Brien, C. D. Philipson, G. Reynolds, D. Dzulkifli, J. L. Snaddon, R. Ong, A.
249 Hector, Positive effects of liana cutting on seedlings are reduced during El Niño-induced

250 drought. *J. Appl. Ecol.* **56**, 891–901 (2019).

251 18. S. L. Tuck, M. J. O. Brien, C. D. Philipson, P. Saner, M. Tanadini, D. Dzulkifli, H. C. J.
252 Godfray, E. Godoong, R. Nilus, R. C. Ong, B. Schmid, W. Sinun, J. L. Snaddon, M.
253 Snoep, H. Tangki, J. Tay, P. Ulok, Y. S. Wai, M. Weilenmann, G. Reynolds, A. Hector,
254 The value of biodiversity for the functioning of tropical forests: insurance effects during
255 the first decade of the Sabah biodiversity experiment. *Proc. R. Soc. B Biol. Sci.* **283**,
256 20161451 (2016).

257 19. A. Hector, C. Philipson, P. Saner, J. Chamagne, D. Dzulkifli, M. O'Brien, J. L. Snaddon,
258 P. Ulok, M. Weilenmann, G. Reynolds, H. C. J. Godfray, The Sabah Biodiversity
259 Experiment: a long-term test of the role of tree diversity in restoring tropical forest
260 structure and functioning. *Philos. Trans. R. Soc. B Biol. Sci.* **366**, 3303–3315 (2011).

261 20. S. P. Hubbell, A unified theory of biogeography and relative species abundance and its
262 application to tropical rain forests and coral reefs. *Coral Reefs.* **16**, S9–S21 (1997).

263 21. S. P. Hubbell, Neutral Theory and the Evolution of Ecological Equivalence. *Ecology*. **87**,
264 1387–1398 (2006).

265 22. S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton
266 University Press, Princeton, NJ, 2001).

267 23. P. B. Adler, J. HilleRisLambers, J. M. Levine, A niche for neutrality. *Ecol. Lett.* **10**, 95–
268 104 (2007).

269 24. J. Wu, B. Chen, G. Reynolds, J. Xie, M. J. O'Brien, S. Liang, A. Hector, Monitoring
270 tropical forest degradation and restoration with satellite remote sensing: A test using
271 Sabah Biodiversity Experiment. *Adv. Ecol. Res.* **62**, 117–146 (2020).

272 25. Materials and methods are available as supplementary materials.

273 26. J. Van Ruijven, F. Berendse, Diversity-productivity relationships: Initial effects, long-term
274 patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 695–700 (2005).

275 27. L. Poorter, D. Craven, C. C. Jakovac, M. T. van der Sande, L. Amissah, F. Bongers, R. L.
276 Chazdon, C. E. Farrior, S. Kambach, J. A. Meave, R. Muñoz, N. Norden, N. Rüger, M.
277 van Breugel, A. M. A. Zambrano, B. Amani, J. L. Andrade, P. H. S. Brancalion, E. N.
278 Broadbent, H. de Foresta, D. H. Dent, G. Derroire, S. J. DeWalt, J. M. Dupuy, S. M.
279 Durán, A. C. Fantini, B. Finegan, A. Hernández-Jaramillo, J. L. Hernández-Stefanoni, P.
280 Hietz, A. B. Junqueira, J. K. N'dja, S. G. Letcher, M. Lohbeck, R. López-Camacho, M.
281 Martínez-Ramos, F. P. L. Melo, F. Mora, S. C. Müller, A. E. N'Guessan, F. Oberleitner,
282 E. Ortiz-Malavassi, E. A. Pérez-García, B. X. Pinho, D. Piotto, J. S. Powers, S.
283 Rodríguez-Buriticá, D. M. A. Rozendaal, J. Ruíz, M. Tabarelli, H. M. Teixeira, E. V. de S.
284 B. Sampaio, H. van der Wal, P. M. Villa, G. W. Fernandes, B. A. Santos, J. Aguilar-Cano,
285 J. S. de Almeida-Cortez, E. Alvarez-Davila, F. Arreola-Villa, P. Balvanera, J. M.
286 Becknell, G. A. L. Cabral, C. Castellanos-Castro, B. H. J. de Jong, J. E. Nieto, M. M.
287 Espírito-Santo, M. C. Fandino, H. García, D. García-Villalobos, J. S. Hall, A. Idárraga, J.
288 Jiménez-Montoya, D. Kennard, E. Marín-Spiotta, R. Mesquita, Y. R. F. Nunes, S. Ochoa-
289 Gaona, M. Peña-Claros, N. Pérez-Cárdenas, J. Rodríguez-Velázquez, L. S. Villanueva, N.
290 B. Schwartz, M. K. Steininger, M. D. M. Veloso, H. F. M. Vester, I. C. G. Vieira, G. B.
291 Williamson, K. Zanini, B. Hérault, Multidimensional tropical forest recovery. *Science*.
292 **374**, 1370–1376 (2021).

293 28. J. Ghazoul, *Dipterocarp biology, ecology, and conservation* (Oxford University Press,
294 2016).

295 29. L. F. Banin, E. H. Raine, L. M. Rowland, R. L. Chazdon, S. W. Smith, N. E. B. Rahman,
296 A. Butler, C. Philipson, G. G. Applegate, P. Axelsson, S. S. Budiharta, S. C. Chua, M. E.
297 Cutler, S. Elliott, E. Gemita, E. Godoong, L. L. Graham, R. M. Hayward, A. A. Hector, U.
298 Ilstedt, J. Jensen, S. Kasinathan, C. J. Kettle, D. Lussetti, B. Manohan, C. Maycock, K. M.
299 Ngo, M. J. O'Brien, A. Osuri, G. Reynolds, Y. Sauwai, S. Scheu, M. Silalahi, E. M. Slade,
300 T. Swinfield, D. A. Wardle, C. Wheeler, K. L. Yeong, D. F. Burslem, *Philos. Trans. R.*
301 *Soc. B Biol. Sci.*, in press.

302 30. L. Banin, S. L. Lewis, G. Lopez-Gonzalez, T. R. Baker, C. A. Quesada, K. J. Chao, D. F.
303 R. P. Burslem, R. Nilus, K. Abu Salim, H. C. Keeling, S. Tan, S. J. Davies, A.
304 Monteagudo Mendoza, R. Vásquez, J. Lloyd, D. A. Neill, N. Pitman, O. L. Phillips,
305 Tropical forest wood production: a cross-continental comparison. *J. Ecol.* **102**, 1025–1037
306 (2014).

307 31. Botanic Gardens Conservation International, “State of the World’s Trees” (Botanic
308 Gardens Conservation International, Richmond, UK, 2021).

309 32. D. Lussetti, E. P. Axelsson, U. Ilstedt, J. Falck, A. Karlsson, Supervised logging and
310 climber cutting improves stand development: 18 years of post-logging data in a tropical
311 rain forest in Borneo. *For. Ecol. Manage.* **381**, 335–346 (2016).

312 33. C. W. Marsh, A. G. Greer, Forest land-use in Sabah, Malaysia: an introduction to Danum
313 Valley. *Philos. Trans. - R. Soc. London, B.* **335**, 331–339 (1992).

314 34. P. Saner, thesis, University of Zurich, Zurich, Switzerland (2009).

315 35. T. C. Whitmore, *Tropical rain forests of the far east* (Clarendon Press, Oxford, ed. 2nd,
316 1984).

317 36. F. Q. Brearley, L. F. Banin, P. Saner, The ecology of the Asian dipterocarps. *Plant Ecol.*
318 *Divers.* **9**, 429–436 (2016).

319 37. S. Numata, M. Yasuda, R. O. Suzuki, T. Hosaka, N. S. M. Noor, C. D. Fletcher, M.
320 Hashim, Geographical Pattern and Environmental Correlates of Regional-Scale General
321 Flowering in Peninsular Malaysia. *PLoS One.* **8**, e79095 (2013).

322 38. Y. Hautier, P. Saner, C. Philipson, R. Bagchi, R. C. Ong, A. Hector, Effects of Seed
323 Predators of Different Body Size on Seed Mortality in Bornean Logged Forest. *PLoS One.*
324 **5**, e11651 (2010).

325 39. M. J. O'Brien, D. F. R. P. Burslem, A. Caduff, J. Tay, A. Hector, Contrasting
326 nonstructural carbohydrate dynamics of tropical tree seedlings under water deficit and
327 variability. *New Phytol.* **205**, 1083–1094 (2015).

328 40. P. S. Ashton, in *Flora Malesiana* (1982), pp. 237–552.

329 41. P. Saner, Y. Y. Loh, R. C. Ong, A. Hector, Carbon Stocks and Fluxes in Tropical Lowland
330 Dipterocarp Rainforests in Sabah, Malaysian Borneo. *PLoS One.* **7**, e29642 (2012).

331 42. J. O. Sexton, X. P. Song, M. Feng, P. Noojipady, A. Anand, C. Huang, D. H. Kim, K. M.
332 Collins, S. Channan, C. DiMiceli, J. R. Townshend, Global, 30-m resolution continuous
333 fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with
334 lidar-based estimates of error. *Int. J. Digit. Earth.* **6**, 427–448 (2013).

335 43. P. W. Miller, A. Kumar, T. L. Mote, F. D. S. Moraes, D. R. Mishra, Persistent
336 Hydrological Consequences of Hurricane Maria in Puerto Rico. *Geophys. Res. Lett.* **46**,
337 1413–1422 (2019).

338 44. C. Li, H. Wulf, B. Schmid, J. S. He, M. E. Schaepman, Estimating plant traits of alpine

339 grasslands on the qinghai-tibetan plateau using remote sensing. *IEEE J. Sel. Top. Appl.*
340 *Earth Obs. Remote Sens.* **11**, 2263–2275 (2018).

341 45. B. Brede, J. P. Gastellu-Etchegorry, N. Lauret, F. Baret, J. G. P. W. Clevers, J. Verbesselt,
342 M. Herold, Monitoring Forest Phenology and Leaf Area Index with the Autonomous,
343 Low-Cost Transmittance Sensor PASTiS-57. *Remote Sens.* **10**, 1032 (2018).

344 46. G. Tyc, J. Tulip, D. Schulten, M. Krischke, M. Oxford, The RapidEye mission design.
345 *Acta Astronaut.* **56**, 213–219 (2005).

346 47. F. Jung-Rothenhäusler, H. Weichelt, M. Pach, RapidEye – A Novel Approach to Space
347 Borne Geo-Information Solutions. *ISPRS Hann. Work.* **2007**, 4–7 (2007).

348 48. G. Chander, M. O. Haque, A. Sampath, A. Brunn, G. Trossset, D. Hoffmann, S. Roloff, M.
349 Thiele, C. Anderson, Radiometric and geometric assessment of data from the RapidEye
350 constellation of satellites. *Int. J. Remote Sens.* **34**, 5905–5925 (2013).

351 49. M. Pfeifer, L. Kor, R. Nilus, E. Turner, J. Cusack, I. Lysenko, M. Khoo, V. K. Chey, A.
352 C. Chung, R. M. Ewers, Mapping the structure of Borneo’s tropical forests across a
353 degradation gradient. *Remote Sens. Environ.* **176**, 84–97 (2016).

354 50. J. Qi, A. Chehbouni, A. R. Huete, Y. H. Kerr, S. Sorooshian, A modified soil adjusted
355 vegetation index. *Remote Sens. Environ.* **48**, 119–126 (1994).

356 51. J. A. Gallardo-Cruz, J. A. Meave, E. J. González, E. E. Lebrija-Trejos, M. A. Romero-
357 Romero, E. A. Pérez-García, R. Gallardo-Cruz, J. L. Hernández-Stefanoni, C. Martorell,
358 Predicting Tropical Dry Forest Successional Attributes from Space: Is the Key Hidden in
359 Image Texture? *PLoS One.* **7**, e30506 (2012).

360 52. M. Vellend, W. K. Cornwell, K. Magnuson-Ford, A. Ø. Mooers, in *Biological Diversity:*

361 *Frontiers in Measurement and Assessment*, A. Magurran, B. McGill, Eds. (Oxford Univ.
362 Press, 2010), pp. 194–207.

363 53. O. L. Petchey, K. J. Gaston, Functional diversity (FD), species richness and community
364 composition. *Ecol. Lett.* **5**, 402–411 (2002).

365 54. F. Barragán, C. E. Moreno, F. Escobar, G. Halffter, D. Navarrete, Negative Impacts of
366 Human Land Use on Dung Beetle Functional Diversity. *PLoS One.* **6**, e17976 (2011).

367 55. E. Laliberté, P. Legendre, A distance-based framework for measuring functional diversity
368 from multiple traits. *Ecology*. **91**, 299–305 (2010).

369 56. C. C. P. Cosset, D. P. Edwards, The effects of restoring logged tropical forests on avian
370 phylogenetic and functional diversity. *Ecol. Appl.* **27**, 1932–1945 (2017).

371 57. B. F. Chabot, D. J. Hicks, The ecology of leaf life spans. *Annu. Rev. Ecol. Syst.* **13**, 229–
372 259 (1982).

373 58. S. J. Wright, K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R.
374 Condit, J. W. Dalling, S. J. Davies, S. Díaz, B. M. J. Engelbrecht, K. E. Harms, S. P.
375 Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, A. E. Zanne, Functional traits
376 and the growth — mortality trade-off in tropical trees. *Ecology*. **91**, 3664–3674 (2010).

377

378 **Acknowledgments**

379 We thank all past and present research assistants for maintaining Sabah Biodiversity
380 Experiment over the last 20 years. We acknowledge assistance and support from the South

381 East Asia Rainforest Research partnership (SEARRP) and Sabah Forestry Department. This
382 publication is Sabah Biodiversity Experiment article 25.

383

384 **Funding**

385 Natural Environment Research Council grant D4T003300 (RV)
386 Natural Environment Research Council grant NE/K016253/1 (AH, SB, DFRPB, GR)
387 Comunidad de Madrid Atracción de Talento Modalidad I Fellowship 2018-T1/AMB-11095
388 (MJOB)
389 University of Zurich Research Priority Program on Global Change and Biodiversity (BS)
390 National Key Research and Development Program of China grant 2016YFA0600101 (JW)

391

392 **Author contributions**

393 Conceptualization: MJOB, HCJG, AH, GR, BS, PS, RV, JW, YSW
394 Data curation: SB, DFRPB, BC, AH, SL, RV, JW, JX
395 Formal analysis: AH, RV, JW
396 Funding acquisition: MJOB, HCJG, AH, GR, BS, RV, JW
397 Investigation: SB, DFRPB, BC, AH, SL, RV, JW, JX,
398 Project administration: RA, MJOB, EG, AH, GR, YSW
399 Supervision: MJOB, EFMC, EG, AH, GR
400 Visualization: AH, RV, JW
401 Writing – original draft: AH, RV

402 Writing – review & editing: RA, SB, DFRPB, MJOB, BC, EFMC, HCJG, EG, AH, SL, GR,
403 PS, BS, RV, JW, YSW, JX

404 **Competing interests**

405 Authors declare that they have no competing interests.

406 **Data and materials availability:**

407 All data and code for analysis can be found at https://github.com/RVeryard/Satellite_SBE.

408 **List of Supplementary materials:**

409 **Supplementary materials**

410 Materials and Methods

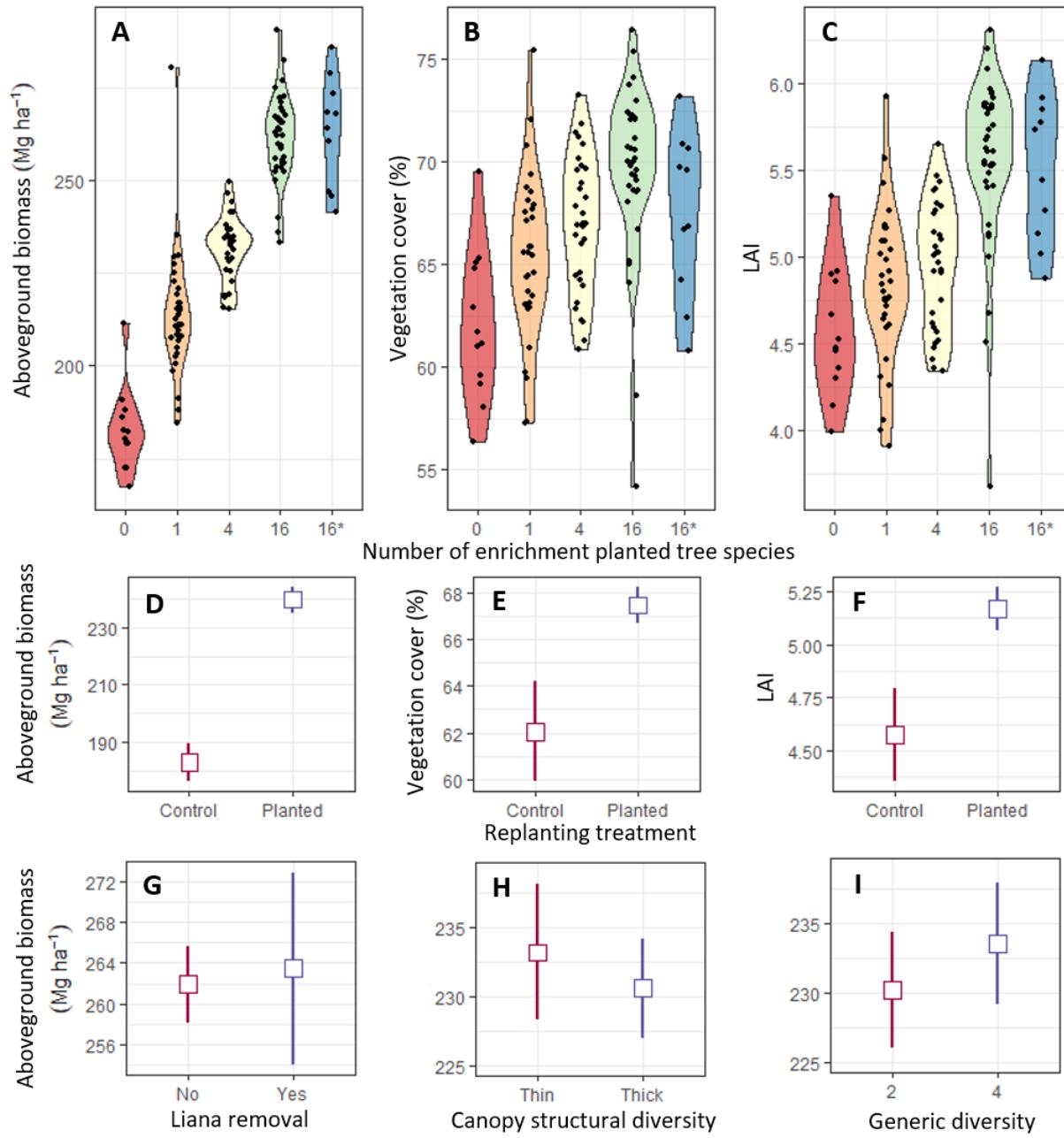
411 Supplementary Text

412 Tables S1 to S8

413 Figs. S1 to S4

414 References (32 – 58)

415



416

417

418

419

420

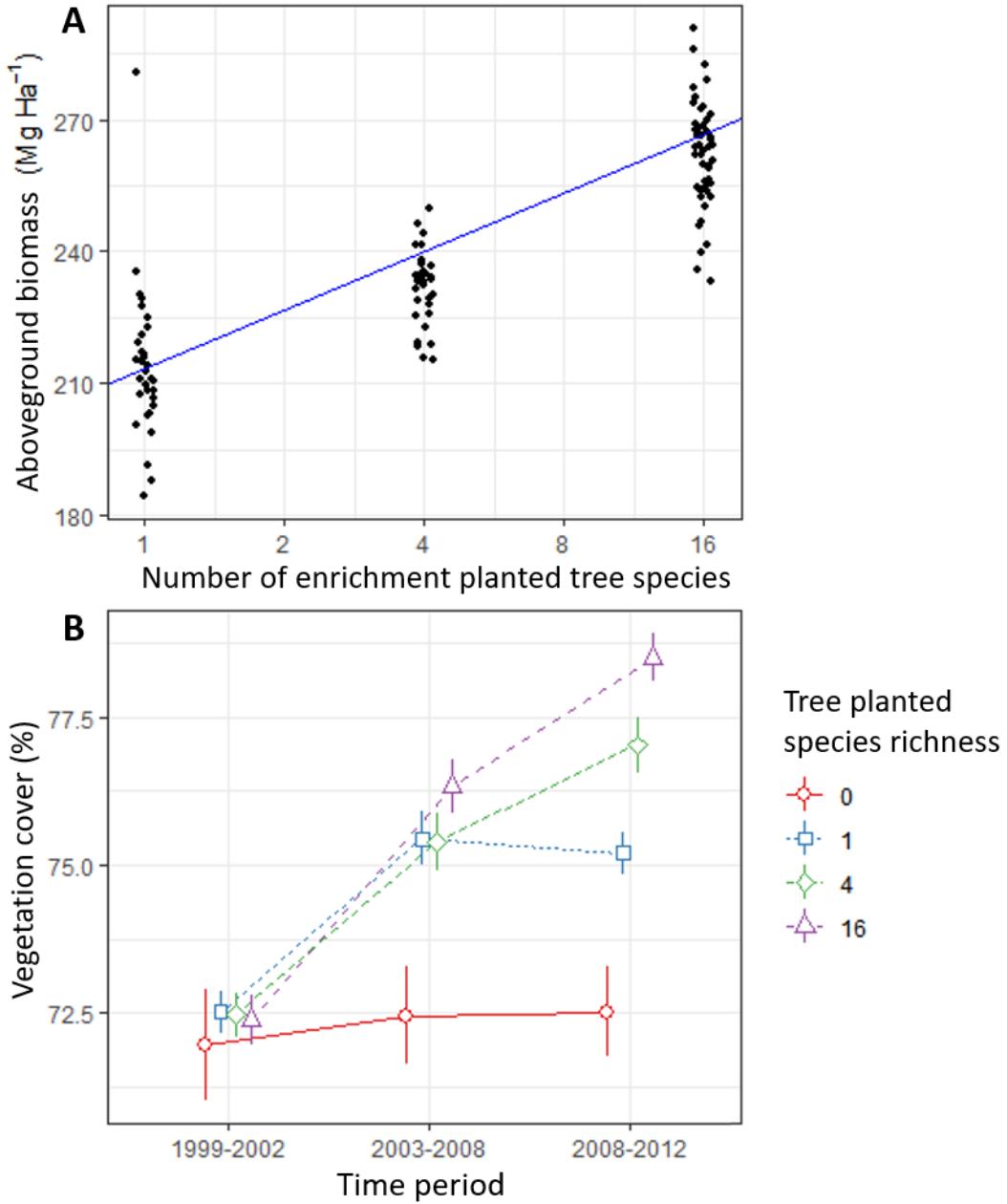
421

Fig. 1. RapidEye satellite remote sensing estimates as a function of restoration treatment

a decade after initial planting. (A to C) Data points for experimental plots overlaid on violin plots showing (left to right) aboveground biomass, percent vegetation cover and Leaf Area Index (LAI) in relation to enrichment planting with seedlings of 0, 1, 4, or 16 species of dipterocarp tree species (16*: enrichment planting with sixteen species plus liana cutting). (D

422 to **F**) Treatment means (with 95% confidence intervals) for unplanted controls versus
423 enrichment planted plots (panels as in top row). (**G** to **I**) Aboveground biomass as a function
424 of (left to right) generic diversity of plots enrichment planted with four-species (2 genera vs
425 4 genera); canopy complexity (low vs high); and liana removal ('climber cutting').

426

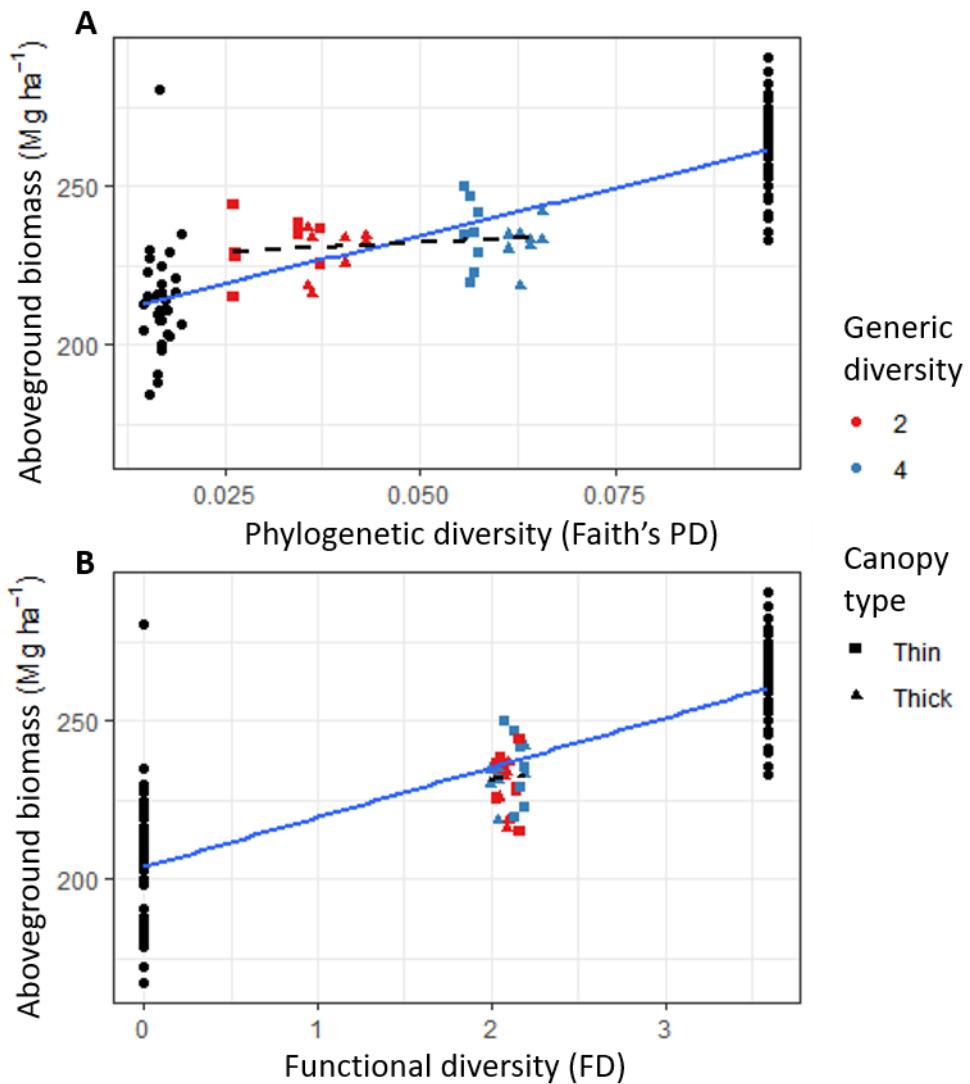


427

428 **Fig. 2. Effects of the diversity of enrichment planted trees on aboveground biomass and**
429 **vegetation cover.** (A) Estimated aboveground biomass (RapidEye) as a function of the
430 number of enrichment-planted tree species a decade after initial planting. The line is the
431 regression slope with the log2 number of tree species from the mixed-effects model analysis
432 (points jittered to reduce overlap). (B) Changes in vegetation cover over time as a function

433 of the number of enrichment-planted tree species. Estimates of mean cover (with 95%
434 confidence intervals) for the LANDSAT monitoring periods 1999-2002 (prior to planting),
435 2003-2008 and 2008-2012 for plots enrichment planted with seedlings of 0, 1, 4, or 16
436 species. Individual species richness treatment levels staggered for clarity.

437



438
439

Fig. 3. Estimated biomass as a function of phylogenetic and functional diversity.

440 Measures of phylogenetic diversity (Faith's PD, (A)) and functional diversity (FD, (B))
441 increase across the full diversity gradient from 1 to 16 species but not in relation to the
442 treatments applied to the subset of four-species plots that manipulate generic diversity (2 vs
443 4 genera) and canopy complexity (lower vs higher). Solid blue lines show the positive
444 relationship between estimated aboveground biomass and PD and FD across the full gradient
445 from 1 to 16 species and dashed lines show the weaker, non-significant relationships for the
446 subset of plots enrichment planted with four-species only.

447 **Table 1. Sabah Biodiversity Experiment treatments.** Treatments include number of
448 species and genera of enrichment planted trees, predicted resulting canopy complexity,
449 whether lianas are removed and the number of replicate plots.

450

Number of species	Number of genera	Canopy complexity	Liana removal?	Number of replicate plots
0	0	N/A	No	12
1	1	Low	No	32
4	2	Low	No	8
4	2	High	No	8
4	4	Low	No	8
4	4	High	No	8
16	5	High	No	32
16	5	High	Yes	16

451

452

453

454