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Testing the importance of a common ectomycorrhizal network for dipterocarp seedling growth and survival in tropical forests of Borneo

Brearley, Francis Q; Saner, Philippe; Uchida, Ayuho; Burslem, David F R P; Hector, Andy; Nilus, Reuben; Scholes, Julie D; Egli, Simon

Abstract: Background: Connections between mature trees and seedlings via ectomycorrhizal (EcM) hyphal networks existing in dipterocarp-dominated tropical rain forests of South-east Asia could have strong implications for seedling growth and survival and the maintenance of high diversity in such forests. Aim: To test whether EcM hyphal network connections are important for the growth and survival of dipterocarp seedlings. Methods: We conducted four independent experiments that prevented contact of experimental seedlings with an EcM network by using a series of fine meshes and/or plastic barriers. We measured the growth and survival (and foliar $\delta^{13}C$ in one experiment) of seedlings of six dipterocarp species over intervals ranging from 11 to 29 months. Results: Seedling growth (diameter, height or leaf number) was unaffected by exclusion from the EcM network in three experiments and there were no differences in foliar $\delta^{13}C$ values in the fourth. Seedling survival was reduced following exclusion from the EcM network in one experiment. Our results give little support to the hypothesis that dipterocarp seedlings growing in the shaded forest understorey benefit from being connected, through a common EcM network, to surrounding trees. Conclusions: We suggest that our negative results, in contrast to studies conducted in low diversity boreo-temperate or tropical forests, are due to these high diversity forests lacking host species-specific EcM fungi, and therefore providing little opportunity for adaptive support of seedlings via hyphal networks

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1 **Testing the importance of a common ectomycorrhizal network for**
2 **dipterocarp seedling growth and survival in tropical forests of Borneo**

3

4 Francis Q. Brearley^{1,2,+*}, Philippe Saner^{3,+}, Ayuho Uchida⁴, David F. R. P. Burslem⁴,
5 Andy Hector^{3,5}, Reuben Nilus⁶, Julie D. Scholes¹ and Simon Egli⁷

6

7 ¹ Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK; ²
8 School of Science and the Environment, Manchester Metropolitan University, Chester
9 Street, UK; ³ Department of Evolutionary Biology and Environmental Studies,
10 University of Zürich, Zürich, Switzerland; ⁴ School of Biological Sciences, University
11 of Aberdeen, Aberdeen, Scotland, UK; ⁵ Department of Plant Sciences, University of
12 Oxford, Oxford, UK; ⁶ Forest Research Centre, Sabah Forestry Department, Sandakan,
13 Sabah, Malaysia; ⁷ Swiss Federal Research Institute for Forest, Snow and Landscape,
14 Birmensdorf, Switzerland

15 + = Joint first authors

16 *Corresponding author. Email: f.q.brearley@mmu.ac.uk

17

18 **Abstract**

19 **Background:** Connections between mature trees and seedlings *via* ectomycorrhizal
20 (EcM) hyphal networks existing in dipterocarp-dominated tropical rain forests of South-
21 east Asia could have strong implications for seedling growth and survival and the
22 maintenance of high diversity in such forests.

23 **Aim:** To test whether EcM hyphal network connections are important for the growth
24 and survival of dipterocarp seedlings.

25 **Methods:** We conducted four independent experiments that prevented contact of
26 experimental seedlings with an EcM network by using a series of fine meshes and/or
27 plastic barriers. We measured the growth and survival (and foliar $\delta^{13}\text{C}$ in one

28 experiment) of seedlings of six dipterocarp species over intervals ranging from 11 to 29
29 months.

30 **Results:** Seedling growth (diameter, height or leaf number) was unaffected by exclusion
31 from the EcM network in three experiments and there were no differences in foliar $\delta^{13}\text{C}$
32 values in the fourth. Seedling survival was reduced following exclusion from the EcM
33 network in one experiment. Our results give little support to the hypothesis that
34 dipterocarp seedlings growing in the shaded forest understorey benefit from being
35 connected, through a common EcM network, to surrounding trees.

36 **Conclusions:** We suggest that our negative results, in contrast to studies conducted in
37 low diversity boreo-temperate or tropical forests, are due to these high diversity forests
38 lacking host species-specific EcM fungi, and therefore providing little opportunity for
39 adaptive support of seedlings *via* hyphal networks.

40 **Keywords:** Borneo, dipterocarps, ectomycorrhizas, mycorrhizal networks, source-sink
41 relationships

42 **Introduction**

43 Mycorrhizas are a symbiotic association between specialised root-inhabiting fungi and
44 the roots of living plants. The plant provides the fungus with carbon derived from
45 photosynthesis, and, in return, the fungus may improve the nutrient uptake, growth,
46 water relations, pathogen and heavy metal resistance of the plant (van der Heijden and
47 Sanders 2002; Smith and Read 2008 and references therein). Although the majority of
48 tropical trees form arbuscular mycorrhizal (AM) associations, an important minority
49 form ectomycorrhizal (EcM) associations including members of the Dipterocarpaceae
50 (Brearley 2012). Dipterocarp trees dominate the forests of South-east Asia (Slik et al.
51 2003, 2009), and there are more than 250 species on the island of Borneo alone (Ashton
52 2004). Their seeds are produced every 3-8 years in mast-fruiting events (Curran et al.
53 1999; Sakai et al. 2006; Brearley et al. 2007a) after which they germinate and become
54 colonised rapidly by EcM fungi (Lee and Alexander 1996). The main method of
55 colonisation is from the hyphae of fungi already present and forming network in the soil
56 radiating out from roots of adjacent adult trees (Alexander et al. 1992) – during the
57 process of EcM colonisation seedlings become ‘connected’ to this network. After a
58 mast-fruiting event, dipterocarp seedlings are found at high densities close to parent
59 trees forming seedling banks where they are limited in their growth and survival in the
60 shaded forest understorey.

61 Numerous studies have shown the existence of EcM networks in various forest
62 ecosystems with shared fungal species linkages between adults and seedlings (Beiler et
63 al. 2010; Diédhiou et al. 2011; Michaëlla Ebenye et al. in press) and Connell and
64 Lowman (1989) hypothesised that the dominance of dipterocarps in South-east Asian
65 lowland evergreen rain forests was linked to the ability of newly germinated seedlings
66 to link into this EcM-mediated resource acquisition network. Studies conducted in

67 lowland tropical forests of Cameroon found that isolation of seedlings of *Paraberlinia*
68 *bifoliolata* (Leguminosae) from roots and EcM fungi reduced seedling biomass and
69 survival (Onguene and Kuyper 2002), and a similar study in Guyana showed that
70 *Dicycme corymbosa* (Leguminosae) had reduced growth and survival when isolated
71 from an EcM hyphal network using fine meshes (McGuire 2007). Contrasting with
72 these findings, seedlings of only one of three Caesalpinioideae legume species in
73 Cameroon had a higher growth rate in the presence of adult trees and their associated
74 roots and EcM fungi (Newbery et al. 2000). The cause of this difference in outcome
75 between studies in different locations is unknown, and further research is required to
76 extend the range of environments where this is examined including both high and low
77 diversity sites. Whether the connection into an EcM hyphal network has implications
78 for the high species richness observed in dipterocarp-dominated tropical rain forests
79 remains unsolved, and clearly, then, it is important to improve our knowledge of the
80 role of EcM networks in facilitating the regeneration of tropical forest trees.

81 The benefits of being connected into this hyphal ‘wood-wide web’ have been
82 reported from boreo-temperate forests (Simard et al. 2012). For example, carbon has
83 been shown to move between plants or seedlings that form a hyphal network in a
84 'source-sink' fashion whereby plants that are photosynthesising at a rapid rate, such as
85 those under higher irradiance, pass carbon to those that have lower rates of
86 photosynthesis, such as those which are strongly shaded (Francis and Read 1984;
87 Simard et al. 1997; Klein et al. 2016). Support *via* an EcM hyphal network may
88 therefore be beneficial for the survival of seedlings that are growing below the light
89 compensation point in shaded understorey environments. Francis and Read (1984) were
90 the first to show that carbon could move between plants via an AM hyphal network, but
91 not until the milestone study of Simard et al. (1997) was net movement of carbon in

92 EcM systems shown: they found that 6.6% of carbon fixed in *Betula papyrifera*
93 (Betulaceae) was transferred to *Pseudotsuga menziesii* (Pinaceae) and that 45% of this
94 transferred carbon was found in the plant shoots (*i.e.* not fungal structures). Most
95 recently, Klein et al. (2016) showed transfer of carbon from *Picea abies* (Pinaceae)
96 adult trees to roots of adjacent EcM species. However, the ecological importance of
97 this network has been under considerable debate as inter-plant carbon transfer is a
98 complex and variable process. From a phytocentric view, there is a challenge in
99 explaining how this process could be adaptive as it is only likely to be selected for if
100 adults are transferring beneficial compounds, such as carbon, to kin. If considered
101 mycocentrically, however, then the fungus will simply be moving compounds to where
102 they are most required at a given point in time.

103 EcM colonisation in shade tolerant dipterocarps has been shown to improve the
104 growth of seedlings under nursery conditions although far fewer studies have shown a
105 similar benefit under natural field conditions (Brearley 2011, 2012). We report four
106 independent studies on the island of Borneo, using seedlings of six dipterocarp species
107 with contrasting ecological characteristics. We hypothesised that seedlings that were
108 experimentally excluded from an EcM network would display slower growth rates and
109 reduced survival than seedlings that were connected to the network.

110

111 **Materials and methods**

112 *Rationale*

113 In the first three experiments reported, we planted seedlings surrounded by meshes of
114 various pore size with the intention of creating a series of barriers to in-growth by plant
115 roots and fungal hyphae. Therefore, the control treatments allowed free access to fine
116 roots and fungal hyphae, a large mesh treatment had a fine pore-size mesh (35-50 μm)

117 to prevent the access of fine roots but allow access by fungal hyphae and a small mesh
118 treatment had a very fine pore-size mesh (0.5-1.0 μm) and/or a severing treatment to
119 prevent access to both roots and fungal hyphae. It was assumed that seedlings in which
120 fungal hyphae were allowed access through the meshes had the potential to become
121 colonised by hyphae present in the soil outside the meshes, and therefore connect into
122 the EcM hyphal network, whereas those seedlings in the treatments where hyphal access
123 was restricted would only be able to form EcMs *via* spores or hyphal fragments present
124 within their enclosed rooting volume, and would therefore not connect into the EcM
125 network outwith the meshes. This approach has been used successfully to control
126 mycorrhizal colonisation and partition of soil respiration fluxes in previous experiments
127 (Johnson et al. 2001; Heinemeyer et al. 2007; Vallack et al. 2012). A number of the
128 seedlings were raised in a nursery before being transplanted into the forest and, based
129 on prior observations (Brearley 2003), we are confident they were all colonised by EcM
130 fungi, albeit those more common of nursery conditions (*e.g.* Brearley 2006; Brearley et
131 al. 2003, 2007b; Saner et al. 2011). Whilst ‘priority effects’ of EcM colonisation have
132 often been found to affect subsequent competitive replacement by other EcM species
133 (Kennedy et al. 2009), replacement of nursery EcMs with those present in forest soil has
134 been seen within six months for studies in Peninsular Malaysia (Chang et al. 1994,
135 1995) and, given that the length of all our studies was over at least 11 months, we do
136 not consider this to have affected our results.

137 In one experiment we tested whether carbon was measurably transferred from
138 adult trees to seedlings through an EcM hyphal network by trenching the seedlings in
139 order to isolate them from the EcM network and then determining the $\delta^{13}\text{C}$ values of
140 newly produced leaves. This approach is based on the fact that canopy leaves have a
141 less negative $\delta^{13}\text{C}$ signature than seedlings due to differences in the atmospheric-to-

142 intercellular carbon dioxide ratio (O'Leary 1988; Farquhar et al. 1989) and the isotopic
143 signature of the source carbon dioxide in the ambient air taken up for photosynthesis
144 (Medina and Minchin 1980; Medina et al. 1986, 1991; Buchman et al. 1997). For
145 example, if the isotopic difference between adult trees and seedlings were 5‰, using a
146 two-source mixing model, receipt of 10% of carbon by seedlings from adult trees would
147 result in those connected to the EcM network having a foliar $\delta^{13}\text{C}$ value 0.5 ‰ closer to
148 adults than trenched seedlings.

149

150 *Study species*

151 Six dipterocarp species (Table 1) were selected, based on their differences in shade
152 tolerance and maximum growth rates (Experiments 1-3), edaphic preferences
153 (Experiment 3), and on their availability at the start of the experiments (Experiments (1-
154 4).

155

156 *Experiment 1. EcM-network exclusion and fungicide addition effects on two dipterocarp* 157 *species*

158 This experiment was carried out in the northern part of the Kabili-Sepilok Forest
159 Reserve, on alluvial soils (5° 52' N, 117° 56' E; Fox 1973; Nilus 2004). Four plots of ca.
160 7 m x 7 m were cleared of the understorey vegetation and some smaller trees to reduce
161 heterogeneity in the light environment within and between plots. Six-month-old
162 seedlings of *Hopea nervosa* and *Parashorea tomentella* obtained from the INFAPRO
163 nursery, Danum Valley, Sabah that had been potted in forest-derived soil (see Saner et
164 al. 2011 and Paine et al. 2012a for nursery conditions), were planted into the four plots
165 in March 2000. In each plot, 30 seedlings of each of the two species were randomly
166 allocated to planting locations ca. 50 cm apart. Three treatments and two controls were

167 applied to the seedlings: (1) Control: no meshes were used, fungal hyphae and other
168 roots could fully interact with the planted seedling; (2) Sub-Control: a 1 mm pore-size
169 polyester mesh cylinder was installed around the seedling; the aim of this mesh was to
170 attempt to provide some rigidity and to protect the smaller pore-sized meshes in the
171 other treatments from larger soil invertebrates; (3) Root exclusion (-R): one layer of 35
172 μm pore-size nylon mesh (within the 1 mm pore-size polyester mesh cylinder) was
173 installed around the seedlings to allow connection to a mycorrhizal hyphal network; (4)
174 Root and mycorrhizal exclusion (-RM): two layers of 0.5 μm pore-size nylon mesh
175 (within the 1 mm pore-size polyester mesh cylinder) were installed around the
176 seedlings; the cylinders were twisted slightly every four weeks to break any hyphal
177 connections that might have occurred through the meshes; (5) Fungicide (-RM+F): as
178 the -RM treatment but with the addition of Mancozeb fungicide (Bio-Dithane 945, PBI
179 Home & Garden Ltd., Enfield, Middlesex, UK) bi-weekly at a rate of 0.08 g per
180 seedling in 50 ml of water to control the growth of EcMs on the seedling roots (Brearley
181 2003). All the mesh barriers were sewn into cylinders of 7 cm diameter with a lip of 2
182 cm above ground to prevent hyphal entry and dug into the soil to a depth of 25 cm using
183 an auger to create a hole; they remained open at the bottom. All meshes were obtained
184 from, and sewn by, Plastok Associates Ltd. (Birkenhead, Wirral, UK). Apart from the
185 -RM+F treatment all other treatments were given 50 ml of water bi-weekly to control
186 for the addition of water with the fungicide. Other than this bi-weekly fungicide
187 solution or water addition, the seedlings were given supplemental water twice weekly
188 for the first month following planting. Leaf litter and twigs lying across the meshes
189 were removed at monthly intervals to prevent fungal hyphae entering the cylinders *via*
190 this potential pathway. Other vegetation was hand-weeded from the plots throughout the
191 experimental period.

192

193 *Experiment 2. EcM-network exclusion and distance to adult tree effects on two*
194 *dipterocarp species*

195 This experiment was conducted in the Malua Forest Reserve (5° 05' N, 117° 38' E) that
196 was selectively logged for timber in the 1980s (Marsh and Greer 1992). Twenty large
197 trees (mean dbh = 69.7 ± SD 15.1 cm) of either *Dryobalanops lanceolata* or *Shorea*
198 *parvifolia* were chosen within the Sabah Biodiversity Experiment (Hector et al. 2011;
199 Saner et al. 2012). Trees were only selected if they were among the largest trees and no
200 other large dipterocarp or Fagaceae trees were within 15 m of the plots to ensure that
201 the EcM network of the focal tree was closest to the planted seedlings. At every focal
202 tree, one plot (ca. 1.5 m x 2 m) was cleared of understorey vegetation to reduce within
203 and between plot heterogeneity in the light environment under the tree canopy (2-4 m
204 away from the trunk) and one plot was established and cleared of understorey
205 vegetation outside the tree canopy (15-17 m away from the trunk), based on the
206 assumption that the tree canopy approximately reflected the extension of the rooting
207 system (Baillie and Mamit 1983; Katayama et al. 2009). One control and two treatments
208 were applied to the seedlings: (1) Control: no mesh or tube was used, fungal hyphae and
209 other roots could fully interact with the planted seedling; (2) Root exclusion (-R):
210 seedlings were planted into a PVC tube (15 cm diameter x 70 cm depth) covered at the
211 bottom with 50-µm pore-size mesh allowing fungal hyphae to grow into the tube; (3)
212 Root and mycorrhiza exclusion (-RM): seedlings were planted into a PVC tube as above
213 but with a 1-µm pore-size mesh to prevent the entry of fungal hyphae. The meshes were
214 made of monofilament PET (Sefar PETEX, Heiden, Switzerland) and were glued
215 between the bottom of the PVC tube and an additional PVC ring (15 cm diameter x 5
216 cm depth) with silica and aluminium tape. In every plot, 12 seedlings were planted at a

217 spacing of ca. 50 cm and dug into the soil to a depth of 70 cm. Six seedlings were the
218 same species as the focal tree and six seedlings were of the other tree species. All
219 seedlings were raised in a local nursery at the Malua Field Station, Malua Forest
220 Reserve, Sabah, with conditions similar to those at the INFAPRO nursery noted earlier,
221 and ca. 6 months old and 0.5 m tall when planted into the field. Seedlings were
222 randomly allocated and planted in September 2006. Seedlings were watered once at the
223 beginning of the experiment. Leaf litter and twigs lying across the meshes were
224 removed at monthly intervals to prevent fungal hyphae entering the cylinders. Other
225 vegetation was hand-weeded from the plots throughout the experimental period. An
226 index of light interception (% of canopy openness at the plot level) was measured at the
227 beginning, middle (6 months) and end (11 months) of the experiment, using a Spherical
228 Densiometer Model A.

229

230 *Experiment 3. EcM-network exclusion and soil type effects on four dipterocarp species*

231 This experiment was carried out in the northern and central parts of Kabili-Sepilok
232 Forest Reserve on two contrasting soil types (Nilus 2004; Dent et al. 2006). Ten
233 understorey plots of ca. 5 m x 5 m were chosen within both the sandstone and the
234 alluvial soil types respectively, and understorey vegetation cleared to reduce
235 heterogeneity in the light environment within and between plots. Within each plot,
236 seedlings of *Shorea beccariana*, *S. multiflora* (both sandstone soil specialists),
237 *Dryobalanops lanceolata* and *Parashorea tomentella* (both alluvial soil specialists)
238 were planted in April 2003 at an equal spacing of ca. 1 m (seedlings were grown from
239 seeds collected within the Kabili-Sepilok Forest Reserve during the 2002 mast-fruiting
240 event and were ca. 6 months old when transplanted). They were subjected to three
241 treatments and one control: (1) Control: no tube or mesh was used, fungal hyphae and

242 other roots could fully interact with the planted seedling; (2) Sub-Control: seedlings
243 were planted in PVC tubes of 15 cm in diameter and 35 cm in depth that were open at
244 the bottom (with 5 cm above the soil surface). Three rectangular windows of 7 cm
245 width x 20 cm depth were made in the tube, allowing both mycorrhizal hyphae and
246 plant roots to penetrate. Six small holes (of 5 mm diameter) were cut in the tubes at the
247 level of the soil surface to aid in drainage. (3) Root exclusion (-R): seedlings were
248 planted in PVC tubes as above and the windows were covered in 35 μ m pore-size mesh
249 (Plastok Associates Ltd., Birkenhead, Wirral, UK), allowing only mycorrhizal hyphae
250 to penetrate. (4) Root and mycorrhizal exclusion (-RM): Seedlings were planted in PVC
251 tubes but there were no rectangular windows in the tubes and a knife was used to cut
252 around the edges of the tubes once per week to sever any fungal hyphae that might have
253 entered through the small drainage holes. Once planted, seedlings were not given
254 additional water and there were no on-going manipulations (such as removal of leaf
255 litter and twigs lying across the piping or weeding of vegetation). The two sandstone
256 species (*Shorea beccariana* and *S. multiflora*) grown in the alluvial plots were harvested
257 in July 2004 (after 15 months) due to high mortality rates; all other seedling/soil type
258 combinations were followed for 29 months. An index of light interception (% of canopy
259 openness) was measured at the beginning of the experiment with hemispherical
260 photography using a Minolta X-700 camera with a Rokkor 7.5 mm fisheye lens; images
261 were subsequently analysed using Gap Light Analyser (Frazer et al. 1999).

262

263 *Experiment 4. EcM-network effects on carbon isotope ratios on one dipterocarp species*

264 Twenty areas with seedling banks of *Shorea multiflora* were selected in March 2000 in
265 two separate areas of Kabili-Sepilok Forest Reserve. Ten areas were in the vicinity of
266 research plots in the northern part of the Reserve and another ten were along a trail

267 running north-south through the Reserve. In each area, a circular plot of 68.5 cm
268 diameter was trenched to a depth of 5-10 cm (varying with the local microtopography)
269 and a plastic barrier was placed in the trench. An equally-sized and shaped plot
270 (situated between 0.45-3.2 m from the trenched plot; mean: 1.25 m) was marked out
271 using a circle of plastic, lain on the forest floor but remained otherwise unaltered in
272 order to act as a control. Each plot contained a mean of 13.5 (\pm 4.9 SD) seedlings of
273 which 11.8 (\pm 4.7 SD) were *Shorea multiflora*. The number of leaves and height of each
274 seedling was recorded so that after 13 months, one leaf that had been produced during
275 that interval was randomly selected from one seedling within each plot. The leaves
276 were dried at 50° C for at least one week, ground in liquid nitrogen and a sample of 1
277 mg was analysed for $\delta^{13}\text{C}$ (PDZ Europa ANCA-GSL preparation module connected to a
278 20-20 isotope ratio mass spectrometer, Northwich, Cheshire, UK). Isotope ratios were
279 calculated as: $\delta^{13}\text{C}$ (‰) = $(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ where R is the isotope ratio of
280 $^{13}\text{C}/^{12}\text{C}$ of either the sample or the standard (Pee Dee Belemnite). In addition, one leaf
281 was collected from the canopy of eight large individuals of *Shorea multiflora* (40-45 m
282 tall; C. R. Maycock pers. comm.; R. N. Thewlis pers. comm.) and analysed for $\delta^{13}\text{C}$ as
283 above.

284

285 *Seedling measurements*

286 Non-destructive measurements of seedling height (to the apical meristem), basal
287 diameter and leaf number as well as survival rate were taken periodically. In
288 Experiment 1, six measurements were taken over 24 months (March 2000-February
289 2002), in Experiment 2, three measurements were taken over 11 months (September
290 2006-August 2007), in Experiment 3, 10 measurements were taken over 29 months
291 (April 2003-September 2005). Seedlings that died or were severely damaged by

292 mammals or tree/branch falls, where the meshes were damaged or where there was poor
293 drainage and the tubes became waterlogged (Experiment 2 only) were removed from
294 the growth analyses. For the individual growth analyses a total of n=233 (Experiment 1),
295 n=267 (Experiment 2), and n=317 (Experiment 3) observations were included. Only
296 seedlings grown under dark conditions (<5% canopy openness) were included in the
297 analysis for Experiment 2.

298

299 *Statistical analyses*

300 Based on an initial screen, we assumed linear growth, as individual seedlings showed
301 relatively constant increases in diameter, height and leaf number over time. The linear
302 model was fitted for every seedling and the individual regression slope (r) extracted.
303 The slopes were then standardised by dividing by the mean height, diameter or leaf
304 number of the last measurement, termed in this paper as relative growth rate (Paine et al.
305 2012b). A linear mixed-effects model for each study was carried out in R 3.2.0 (R
306 Development Core Team 2015), using the *nlme* library (Pinheiro and Bates 2000).
307 Treatment and species (all experiments), plus planting distance (Experiment 2), or
308 habitat (soil) type (Experiment 3) were treated as fixed effects; as we were specifically
309 interested in selected species effects they were included as fixed, rather than random,
310 effects, plot was included as a random effect. Unequal variance was observed and
311 accounted for by defining a linear increase in variance with time (Experiment 1) or light
312 level by species (Experiments 2 and 3). In the case of Experiment 2, adding
313 conspecificity/heterospecificity did not significantly improve the fit of the model (in all
314 cases: $\chi^2 < 16.5$, $P > 0.15$) so this variable was removed for ease of comparison with the
315 other studies. Analysis of survival rates was made on binomial count data of seedlings
316 that survived compared to those that died, including the same structure of fixed and

317 random effects as outlined above, with the function *glmer()* and a binomial distribution
318 in the *lme4* library (Bates et al. 2015). The statistical tests are reported based on the
319 analysis of relative growth rates for all three non-destructive measurements (height,
320 diameter and leaf number) and for survival, but for simplicity only the increase in
321 diameter is shown graphically (for additional graphical representation of all non-
322 destructive measurements see supplementary material). We present the *F*-test or Chi-
323 square (survival analysis) statistic with associated *P*-values obtained through the
324 *anova()* command and *t*-test statistic with associated *P*-values obtained through the
325 *summary()* command for main effects and their interactions as outlined in Tables 2, 4
326 and 5. Note that with non-orthogonal designs in complex models the outcome from the
327 *anova()* command and the *summary()* command may differ slightly (Hector et al. 2010;
328 Hector 2015). Experiment 4 was analysed using a straightforward one-way ANOVA to
329 compare foliar $\delta^{13}\text{C}$ values between large trees and trenched and untrenched seedlings.

330

331 **Results**

332 *Experiment 1*

333 *Diameter growth.* For relative diameter growth rate, significant main effects of
334 treatment and species were observed (treatment: $F_{4,220}=12.8$, $P<0.0001$; species:
335 $F_{1,220}=19.2$, $P<0.001$) and there was also a significant interaction between treatment and
336 species ($F_{4,220}=2.7$, $P<0.05$). For *Hopea nervosa*, fungicide addition (-RM+F)
337 significantly reduced growth by 40% (mean \pm 95% CI: 5-75%) compared to the
338 seedlings of the root exclusion treatment (-R) ($t_{4,220}=2.2$, $P<0.05$), however for
339 *Parashorea tomentella*, fungicide addition (-RM+F) did not affect diameter growth rate.
340 In contrast to our hypothesis, seedlings of *Parashorea tomentella* in the root and
341 mycorrhizal exclusion treatment (-RM) grew significantly ($t_{4,220}=3.1$, $P<0.01$) faster

342 than seedlings of the root exclusion treatment (-R) (mean \pm 95% CI: 38% \pm 19-50%)
343 (Figure 1 and Table 2, supplementary material Figure S1).

344

345 *Height growth.* There was no effect of the treatments on height growth rates but
346 *Parashorea tomentella* showed a significantly faster relative height growth rate than
347 *Hopea nervosa* ($F_{1,220}=4.1$, $P<0.05$) (Table 2, Figure S2 a and b).

348

349 *Leaf growth.* Relative growth rate in leaf number showed significant main effects of the
350 treatment ($F_{4,220}=5.0$, $P<0.001$) and species ($F_{1,220}=116.3$, $P<0.0001$). *Hopea nervosa*
351 seedlings grew significantly faster those of *Parashorea tomentella* ($t_{1,220}=6.0$,
352 $P<0.0001$). No significant treatment effects were observed for *Parashorea tomentella*,
353 however for *Hopea nervosa*, control seedlings grew significantly faster than both
354 seedlings of the root (-R) and mycorrhizal exclusion (-RM) treatment ($t_{4,220}=2.2$,
355 $P<0.05$ and $t_{4,220}=2.9$, $P<0.01$ respectively). Fungicide addition significantly reduced
356 growth compared to control seedlings ($t_{4,220}=4.2$, $P<0.0001$) (Table 2, Figure S3 a and
357 b).

358

359 *Survival.* No effects of the treatments were observed for seedling survival but seedlings
360 of *Hopea nervosa* showed a significantly greater survival rate compared to *Parashorea*
361 *tomentella* ($\chi^2=6.4$, $P=0.01$) (Tables 2 and 3).

362

363 *Experiment 2*

364 *Diameter growth.* There was no effect with respect to either the treatment or the
365 planting distance from the large trees but *Dryobalanops lanceolata* seedlings showed

366 significantly greater relative diameter growth rates than *Shorea parvifolia* seedlings
367 ($F_{1,238}=10.2$, $P<0.01$; Figure 2 and Table 4, Figure S4).

368

369 *Height growth.* There was no effect of connection to an EcM network or species on
370 height growth. However, the root exclusion (-R) treatment of *Dryobalanops lanceolata*
371 showed a 73% increase in height growth rate when planted close to a large tree
372 compared to those that were planted away from the tree ($t_{1,238}=2.5$, $P<0.05$) (Table 4,
373 Figure S5 a and b).

374

375 *Leaf growth.* Leaf growth in *Shorea parvifolia* was significantly reduced in the root and
376 mycorrhizal exclusion treatment (-RM) compared to the root exclusion (-R) treatment
377 ($t_{2,238}=2.4$, $P<0.05$) (Table 4, Figure S6 a and b).

378

379 *Survival.* A significant treatment effect ($\chi^2=13.3$, $P=0.001$) was found, as seedlings with
380 the root and mycorrhizal exclusion treatment (-RM) showed a lower survival rate than
381 the root exclusion (-R) treatment and the control seedlings. Seedlings of *Dryobalanops*
382 *lanceolata* showed a significantly higher survival rate compared to *Shorea parvifolia*
383 ($\chi^2=4.4$, $P<0.05$) (Tables 3 and 4).

384

385 *Experiment 3*

386 *Diameter growth.* A significant interaction between treatment and soil type ($F_{3,276}=2.7$,
387 $P<0.05$) and between species and soil type ($F_{3,276}=5.4$, $P<0.01$) was found. Seedlings
388 with the root and mycorrhizal exclusion treatment (-RM) of three species (*Parashorea*
389 *tomentella*, *Shorea beccariana* and *S. multiflora*) grew faster in the sandstone soil type
390 compared to seedlings with only the root exclusion treatment (-R). Seedlings of

391 *Dryobalanops lanceolata* with the root exclusion treatment (-R) grew marginally faster
392 on the alluvial soil type ($t_{1,285}=1.7$, $P<0.10$) and also showed more rapid growth
393 compared to seedlings with the root and mycorrhizal exclusion treatment (-RM)
394 ($t_{1,285}=2.2$, $P<0.05$) (Figure 3 and Table 5, Figure S7).

395

396 *Height growth.* Seedlings of all four dipterocarp species showed significantly different
397 height growth rates ($F_{3,276} = 3.6$, $P<0.05$). *Parashorea tomentella* seedlings with the
398 root exclusion treatment (-R) grew faster on the sandstone soil type ($t_{1,276}=2.1$, $P<0.05$)
399 (Table 5, Figure S8 a and b).

400

401 *Leaf growth.* A significant interaction between species and soil type was observed for
402 relative leaf growth rates ($F_{3,276} = 4.7$, $P<0.01$). *Dryobalanops lanceolata* seedlings
403 grew significantly faster on the alluvial compared to the sandstone soil type ($t_{1,276}=2.0$,
404 $P<0.05$); for all other species there were no differences between the soil types (Table 5,
405 Figure S9 a and b).

406

407 *Survival.* A marginal species effect ($\chi^2=7.2$, $P<0.10$) and a significant soil type effect
408 ($\chi^2=6.0$, $P=0.01$) were found, however no effect of the treatments was observed after 15
409 months (Tables 3 and 5). Notably, the sandstone specialists *Shorea beccariana* and *S.*
410 *multiflora* showed lower survival rates on alluvial soil but the species by soil type
411 interaction was not significant.

412

413 *Experiment 4*

414 There was no difference between the foliar $\delta^{13}\text{C}$ values of seedlings grown in trenched
415 ($-35.05\text{‰} \pm 0.22$ SE) or untrenched ($-35.00\text{‰} \pm 0.22$ SE) plots but both were

416 significantly more negative than the value of $-30.31\% \pm 0.34$ SE obtained from the
417 canopy leaves of large trees ($F_{2,45}=79.06$, $P<0.001$). No effect of the treatment (trenched
418 vs. untrenched) on seedling survival rate was observed (Table 3).

419

420 **Discussion**

421 Several studies have addressed the benefits to seedlings of tropical forest trees of being
422 in contact with EcM hyphae radiating out from tree roots (Alexander et al. 1992;
423 Yasman 1995; Newbery et al. 2000), but few have tested the importance of
424 incorporation into a common EcM network under field conditions. Two independent
425 prior studies by Onguene and Kuyper (2002) and McGuire (2007) reported significant
426 increases in seedling mass (35%) and height growth (73%) respectively, that they
427 related to incorporation into the EcM networks of Caesalpinioideae trees in studies in
428 Cameroon and Guyana, respectively. In contrast, the key result from our analysis
429 across four complementary experiments with dipterocarps in South-east Asia is that
430 there are minimal effects of experimentally imposed treatments that alter seedling
431 incorporation into an EcM hyphal network on measures of dipterocarp seedling growth
432 in understory conditions. Only two growth measures (the number of leaves of *Shorea*
433 *parvifolia* in Experiment 2 and the diameter of *Dryobalanops lanceolata* in Experiment
434 3) suggested any importance of an EcM hyphal network. There was some evidence that
435 exclusion from the EcM network reduced seedling survival, as, in Experiment 2,
436 seedling survival was lower in the -RM treatment compared to the -R treatment and the
437 control, although there is the possibility that this was due to waterlogging. In our
438 combined studies we thus did not detect any benefit to seedlings from being connected,
439 through a common EcM network, to surrounding mature trees.

440

441 We suggest that the lack of any effect on seedling growth of being connected to
442 an EcM network, in contrast to boreo-temperate forests (Simard et al. 2012) and low
443 diversity tropical forest (McGuire 2007) is because our lowland dipterocarp forest study
444 sites have high tree diversity and low species preference of EcM fungi. Peay et al.
445 (2015) showed ‘extreme host generalism’ of EcM fungi in similar tropical forests in
446 northern Borneo and it has been found that there is little evidence for host preference by
447 EcM fungal species in other tropical forests with high diversity of trees and a substantial
448 proportion of EcM trees (Tedersoo et al. 2010; Diédhiou et al. 2010; Smith et al. 2011).
449 If considered from a phytocentric perspective, an absence of host-specific EcM
450 associations removes the selective advantage of supporting seedlings *via* an EcM hyphal
451 network because there can be no guarantee that the supported seedling would be
452 conspecific kin.

453

454 Overall, the majority of measurements showed no effect (positive or negative) of
455 inclusion into an EcM network on seedling growth. However, in some cases,
456 experiment-specific findings argue for species-specific growth patterns, sometimes even
457 across the experiments. *Parashorea tomentella* seedlings in Experiments 1 and 3
458 showed increased growth rates when isolated from a common EcM network, suggesting
459 that EcM networks could even have detrimental effects on seedling growth and survival.
460 Two additional species (*Shorea beccariana* and *S. multiflora*) showed this effect in
461 Experiment 3 but only on the sandstone soil type. This result may not be entirely related
462 to an EcM network but in this case we hypothesise that providing exclusive access to
463 EcM hyphae associated with the seedlings to the rooting space inside the mesh tubes
464 prevented competition with hyphae from outside. It could also indicate that the
465 artificially induced limitation of root competition over scarce resources could be

466 directly beneficial for seedling growth (Coomes and Grubb 2000). Furthermore, there
467 was some evidence in Experiment 1 that fungicide addition limited diameter and leaf
468 growth in *Hopea nervosa*, but not in *Parashorea tomentella*. Fungicide addition
469 reduced the growth rate of this one species even though there was no significant
470 reduction in EcM colonisation (Brearley 2003). Clearly, the application of fungicide
471 will have additional effects other than simply reducing EcM colonisation such as effects
472 on soil nutrient status and impacts on pathogenic fungal populations (Newsham et al.
473 1994; Brearley 2003; Teste et al. 2006). In a similar experiment under high light
474 conditions (gaps), Brearley (2003) found that fungicide addition did reduce EcM
475 colonisation but this had a greater impact on seedling nutrient status than on seedling
476 growth. Other aspects of our experimental manipulations that may not have created
477 seedlings that were entirely disconnected from an EcM network include the depth of
478 barriers that were variable among experiment designs (*i.e.* possibly too shallow in
479 Experiment 4) and their open-bottomed nature in some experiments that might have
480 allowed colonisation by EcM hyphae from deeper soil layers (Pickles and Pither 2014).
481 In addition, there is the possibility of confounding the experimental treatments with
482 colonisation by different EcM fungal species; seedling roots isolated from the EcM
483 network would be more likely to be colonised by spore-forming fungi (and perhaps
484 retain initial greenhouse colonising fungi for longer) whereas those connected to the
485 EcM network would be more likely to become colonised via hyphal connections.
486 However, despite the potential for priority effects (Kennedy et al. 2009), there is a rapid
487 turnover of the EcM community on dipterocarp seedlings (Chang et al. 1994,1995; Lee
488 and Alexander 1996). Indeed, it would have been highly beneficial to have determined
489 the EcM fungi present on the seedlings' roots in each of the treatments (both at the
490 beginning and end of the experiments), in addition to those on adult trees, to provide

491 additional support for the efficacy of our experimental manipulations, as well as
492 comparing our different experimental designs. Importantly, it would also provide
493 support for our hypothesis of low EcM host specificity and this should be the key target
494 of future research.

495

496 Whilst we do not question the benefit to seedlings coming into contact with
497 EcM hyphae already present in the soil allowing them to rapidly form EcM associations
498 (Alexander et al. 1992), we did not find any importance of the EcM network for growth
499 of seedlings although survival was affected in one experiment. Whilst the main
500 mechanism through which connections to an EcM network have been hypothesised to
501 benefit seedlings is the provisioning of carbon for seedling growth in low light
502 environments, it could be questioned whether incorporation into an EcM network
503 provides other benefits that we have not measured. These could include improved
504 resistance to herbivores (Booth 2004), drought tolerance through hydraulic uplift
505 (Egerton-Warburton et al. 2007; Bingham and Simard 2011), or access to nutrients
506 being taken up from a larger volume of soil - possibly being more important where light
507 is less limiting. Bingham and Simard (2011) found a greater importance of an EcM
508 network under drought conditions; our sites rarely experience drought but it could be
509 informative to test the effect of EcM networks under an experimentally induced drought
510 or along a climatic gradient. Under very low light conditions, such that light was highly
511 limiting to growth (i.e. below the light compensation point), seedling survival is
512 arguably more important than seedling growth in determining future community
513 composition. In our experiment, light levels were above the light compensation point
514 for seedling growth (Eschenbach et al. 1998) such that growth was a more relevant
515 measure than survival although we did see some suggestions that the EcM network was

516 important for seedling survival. We altered light conditions by removal of some
517 vegetation - this might have influenced our results but as the majority of these would
518 have been AM species the impact of this is considered minor. An isotope labelling
519 study (^{13}C) would be the next step to truly confirm if this lack of importance of an EcM
520 hyphal network is indeed the case although, clearly, this is logistically challenging
521 (Philip and Simard 2008, but see Klein et al. 2016).

522

523 In conclusion, we found that incorporation into a common EcM network has few
524 measurable beneficial effects on dipterocarp seedling growth. That is not to say that the
525 EcM network is unimportant, but, that within the constraints of short-term experiments
526 ($< 2 \frac{1}{2}$ years), we could not detect a signal of its influence on seedling growth. We did
527 determine suggestions of an effect on seedling survival but this was only in one
528 experiment and may have been an experimental artefact. We recommend that further
529 studies should focus on the role that EcM networks play in resilience to drought periods
530 or nutrient limitation of dipterocarp seedlings. In addition, we propose a working
531 hypothesis, that needs further experimental testing, that the high tree species diversity
532 and lack of benefit to trees of supporting heterospecific seedlings through a generalist
533 EcM network is the reason for the minimal effects seen here. We welcome additional
534 experiments and note that they need to be supported by identification of EcM fungi on
535 seedling roots to aid interpretation. Currently, incorporation into an EcM network
536 cannot categorically be invoked as affecting dipterocarp seedling growth or determining
537 patterns of community diversity in dipterocarp-dominated tropical forests of Borneo.

538

539

540

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550

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554

555 **Disclosure statement**

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559

560 **Notes on Contributors**

561 **Francis Q. Brearley** is an ecologist interested in the functional importance of plant-soil
562 interactions for ecological processes in tropical forests

563 **Philippe Saner** is an environmental scientist with a main interest in tropical plant
564 community ecology and the restoration of tropical forests

565 **Ayuhō Uchida** was a Ph.D. student examining the importance of root competition and
566 ectomycorrhizal fungi for dipterocarp seedling growth
567 **David F.R.P. Burslem** is interested in the community and ecosystem ecology of
568 tropical forests with a particular focus on the maintenance of species diversity and the
569 conservation of tropical forests
570 **Andy Hector** is a community ecologist interested in biodiversity loss and its
571 consequences for the stability and functioning of ecosystems and the provision of
572 ecological services
573 **Reuben Nilus** is an ecologist working on the diversity, distribution and conservation of
574 the forests of Sabah
575 **Julie D. Scholes** is a physiologist/molecular biologist interested in the role of pathogens
576 and mycorrhizas in the maintenance of dipterocarp diversity in tropical forests
577 **Simon Egli** has a main interest in mycorrhizal fungi and how they support the
578 resistance and resilience of forest ecosystems in a changing environment

579

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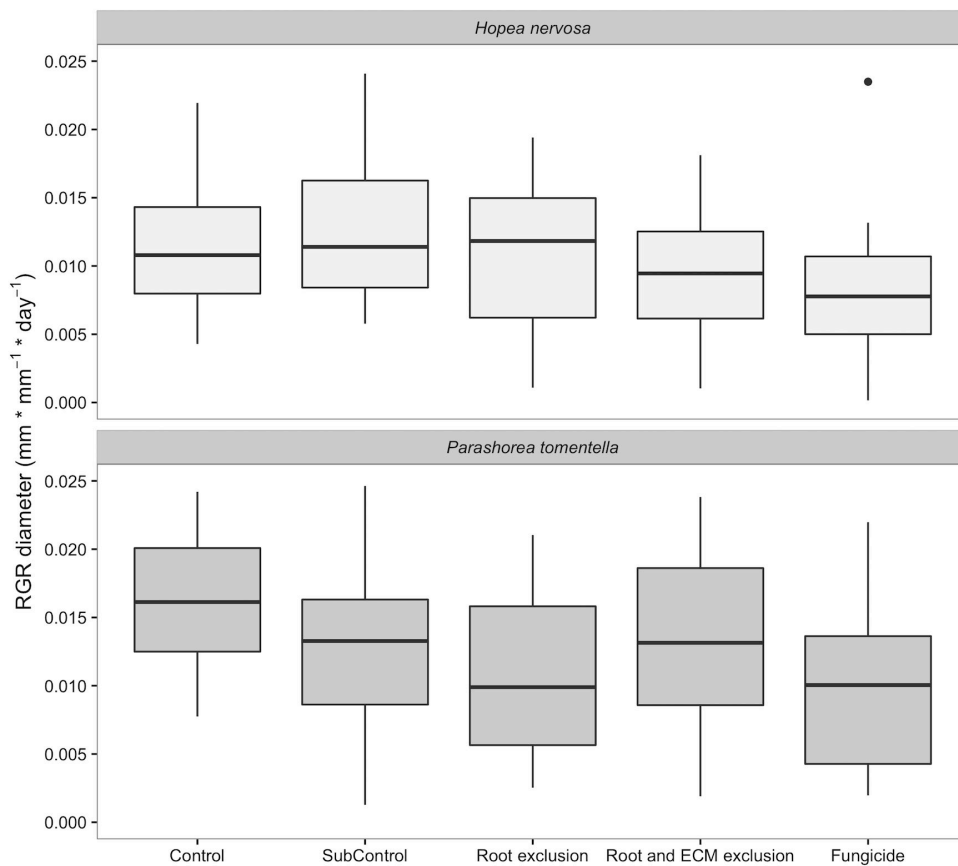
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787 **Figure legends**

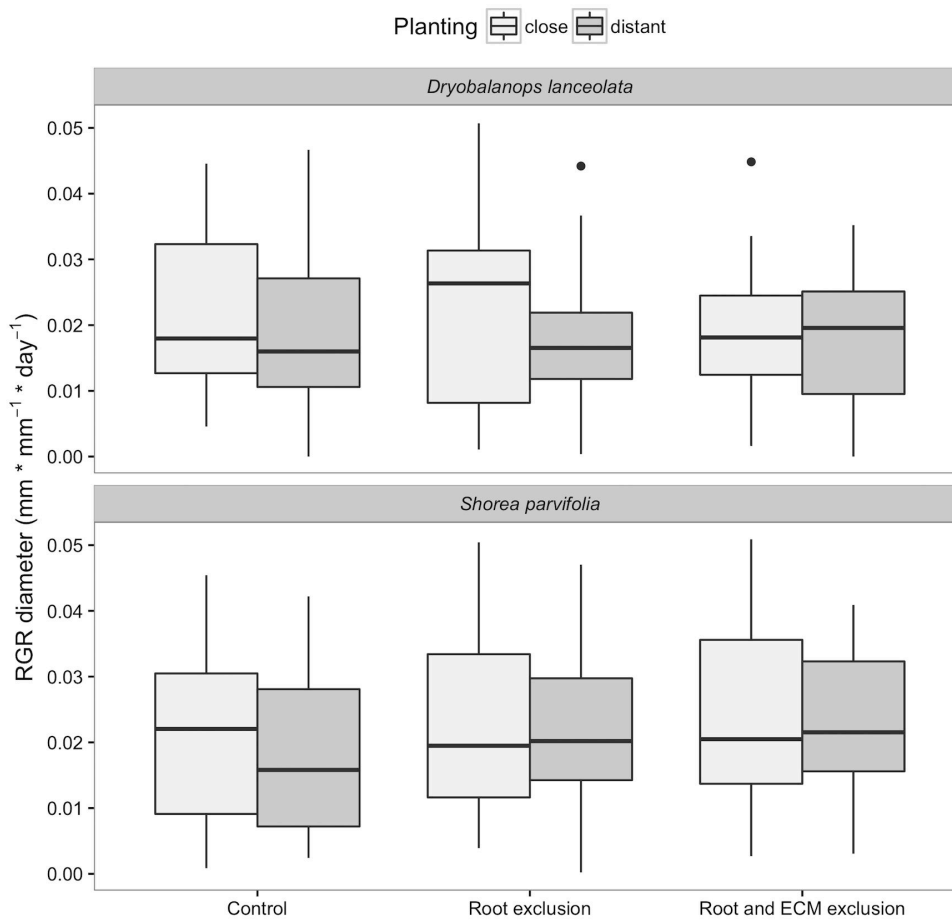
788 **Figure 1:** Effect of fungicide addition, but no effect of exclusion from an ectomycorrhizal hyphal
789 network on the relative diameter growth rate (RGR) of two species of dipterocarp seedlings (top: *Hopea*
790 *nervosa* and bottom: *Parashorea tomentella*) over a 24-month period at Kabili-Sepilok Forest Reserve in
791 Sabah (Malaysian Borneo). The box indicates the data range from the lower quartile (25%) to the upper
792 quartile (75%) and covers 50% of the data with the solid horizontal line within the box indicating the
793 median. Whiskers indicate the data range from the lower 10% to the upper 90% (1.5 times the lower or
794 upper quartile); outliers are indicated separately with a dot. See text for full details of experimental
795 treatments.



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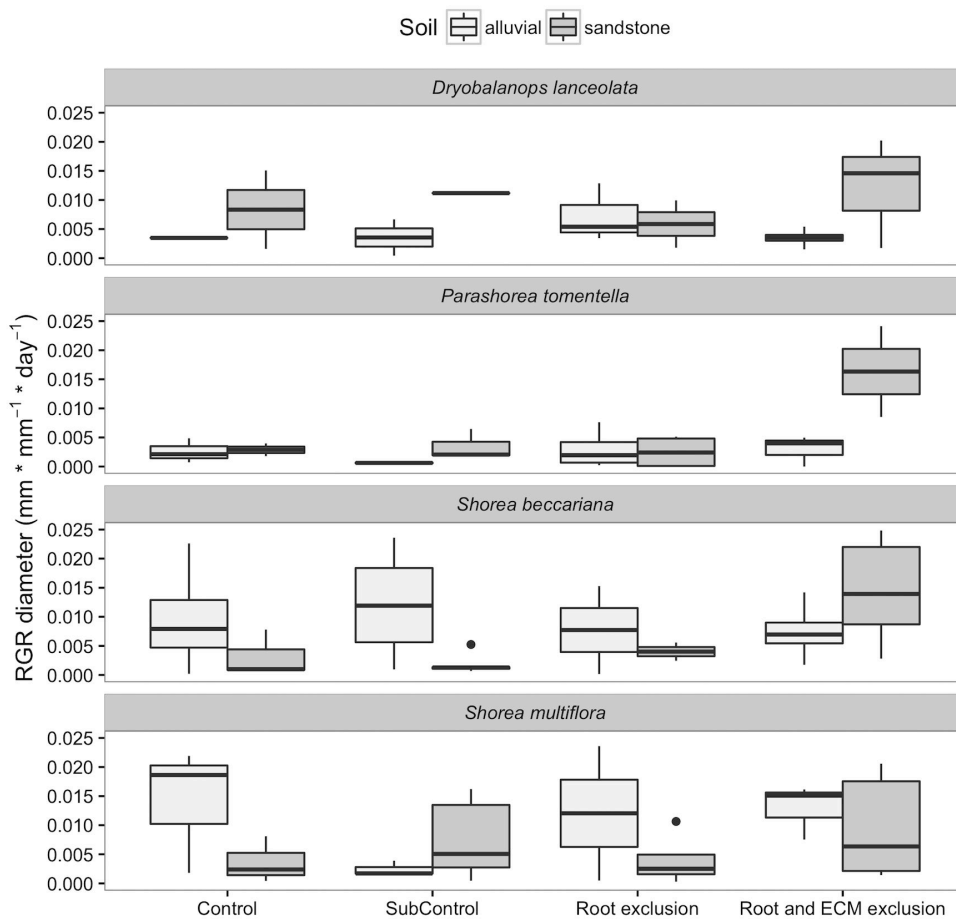
798 **Figure 2:** No effect of exclusion from an ectomycorrhizal hyphal network on the relative diameter
 799 growth rate (RGR) of two species of dipterocarp seedlings by distance from adult tree (top: *Dryobalanops*
 800 *lanceolata* and bottom: *Shorea parvifolia*) over an 11-month period at Malua Forest Reserve in Sabah
 801 (Malaysian Borneo). The box indicates the data range from the lower quartile (25%) to the upper quartile
 802 (75%) and covers 50% of the data with the solid horizontal line within the box indicating the median.
 803 Whiskers indicate the data range from the lower 10% to the upper 90% (1.5 times the lower or upper
 804 quartile); outliers are indicated separately with a dot. See text for full details of experimental treatments.



805

806

807 **Figure 3:** No effect of exclusion from an ectomycorrhizal hyphal network on the relative diameter
 808 growth rate (RGR) of four species of dipterocarp seedlings (top: *Dryobalanops lanceolata*, middle top:
 809 *Parashorea tomentella*, middle bottom: *Shorea beccariana* and bottom: *Shorea multiflora*) across soil
 810 types over a 29-month period at Kabili-Sepilok Forest Reserve in Sabah (Malaysian Borneo). Note that *S.*
 811 *beccariana* and *S. multiflora* growing in the alluvial soil type were harvested after 15 months due to high
 812 mortality rates. The box indicates the data range from the lower quartile (25%) to the upper quartile
 813 (75%) and covers 50% of the data with the solid horizontal line within the box indicating the median.
 814 Whiskers indicate the data range from the lower 10% to the upper 90% (1.5 times the lower or upper
 815 quartile); outliers are indicated separately with a dot. See text for full details of experimental treatments.



816

817 **Table 1:** Ecological information on seedlings of six dipterocarp species used to
 818 experimentally assess the important of incorporation into a common EcM network on
 819 seedling growth in tropical forests of Malaysian Borneo.

Name	Size	Wood density	Distribution	Experiment(s)
<i>Dryobalanops lanceolata</i>	Very large emergent	Medium / heavy	Common on fertile clay-rich soils in lowland northern Borneo	2,3
<i>Hopea nervosa</i>	Medium-sized	Heavy	Locally common in eastern Sabah	1
<i>Parashorea tomentella</i>	Large emergent	Light	Locally common on fertile lowland soils with occasional flooding (only on the east coast of northern Borneo)	1,3
<i>Shorea beccariana</i>	Medium-sized to large	Light	Common in northern Borneo on sandy soils and particularly ridge-tops associated with sandstone rocks.	3
<i>Shorea multiflora</i>	Small to medium-sized	Light	Common throughout Borneo on nutrient-poor or sandy soils and coastal hill slopes.	3,4
<i>Shorea parvifolia</i>	Large emergent	Light	Common throughout Borneo on better-drained clay soils.	2

820 Information collated from Ashton (2004), Meijer and Wood (1964), Newman *et al.* (1996, 1998) and
 821 personal observations.
 822

823 **Table 2:** Experiment 1: Statistical summary table and biological interpretation of
824 exclusion from an ectomycorrhizal hyphal network on relative growth rates (diameter,
825 height and number of leaves) and survival for two species of dipterocarp seedlings
826 (*Hopea nervosa* and *Parashorea tomentella*) over a 24-month period at Kabili-Sepilok
827 Forest Reserve in Sabah (Malaysian Borneo). -R = Root exclusion, -RM = Root and
828 ectomycorrhiza exclusion, -RM+F = Root and ectomycorrhiza exclusion plus fungicide
829 addition.

Effect	F_{df}	<i>P</i>	Interpretation
Diameter			
Treatment	$F_{4,220}=12.8$	<0.0001	-RM+F reduced growth of <i>Hopea nervosa</i> -RM treatment showed faster growth rate compared to -R in <i>Parashorea tomentella</i>
Species	$F_{1,220}=19.2$	<0.0001	Seedlings of <i>Parashorea tomentella</i> grew faster than <i>Hopea nervosa</i>
Treatment x Species	$F_{4,220}=2.7$	<0.05	Slower growth with =RM+F for <i>Hopea nervosa</i> but not <i>Parashorea tomentella</i>
Height			
Treatment	$F_{4,220}=1.4$	ns	No ectomycorrhizal network effect
Species	$F_{1,220}=4.1$	<0.05	<i>Parashorea tomentella</i> grew faster than <i>Hopea nervosa</i>
Treatment x Species	$F_{4,220}=0.8$	ns	No significant interaction term
Leaves			
Treatment	$F_{4,220}=5.0$	<0.001	<i>Hopea nervosa</i> control seedlings grew faster than -R and -RM -RM+F significantly reduced growth in <i>Hopea nervosa</i>
Species	$F_{1,220}=116.3$	<0.0001	<i>Hopea nervosa</i> seedlings grew faster than <i>Parashorea tomentella</i> seedlings
Treatment x Species	$F_{4,220}=1.8$	ns	No significant interaction term
Survival			
Treatment	$\chi^2_{3,7}=4.0$	ns	No effect of treatment on survival
Species	$\chi^2_{6,7}=6.4$	<0.01	Seedlings of <i>Hopea nervosa</i> showed higher survival compared to <i>Parashorea tomentella</i>
Treatment x Species	$\chi^2_{7,11}=4.2$	ns	No significant interaction term

830

831

832 **Table 3:** Survival rates (%) of dipterocarp seedlings following exclusion from an
833 ectomycorrhizal hyphal network in four independent experiments conducted in Borneo.
834 See text for full details of experimental set-up in each experiment. Dash (-) indicates
835 that the treatment noted was not present in the given experiment. Asterisk (*) indicates
836 15 months to harvest whilst all other values are for the entire experimental period. -R =
837 Root exclusion, -RM = Root and ectomycorrhiza exclusion, -RM+F = Root and
838 ectomycorrhiza exclusion plus fungicide addition.

	Control	Sub-Control	-R	-RM	-RM+F
Experiment 1					
<i>Parashorea tomentella</i>	79	83	80	71	80
<i>Hopea nervosa</i>	96	92	100	88	83
Experiment 2					
Near					
<i>Dryobalanops lanceolata</i>	98	-	97	95	-
<i>Shorea parvifolia</i>	98	-	97	89	-
Far					
<i>Dryobalanops lanceolata</i>	99	-	100	97	-
<i>Shorea parvifolia</i>	98	-	98	90	-
Experiment 3					
Alluvial					
<i>Dryobalanops lanceolata</i>	50	70	60	70	-
<i>Shorea beccariana</i>	30*	30*	30*	20*	-
<i>Shorea multiflora</i>	20*	30*	40*	10*	-
<i>Parashorea tomentella</i>	20	20	40	20	-
Sandstone					
<i>Dryobalanops lanceolata</i>	40	40	50	60	-
<i>Shorea beccariana</i>	60	60	40	30	-
<i>Shorea multiflora</i>	50	30	40	30	-
<i>Parashorea tomentella</i>	40	70	60	30	-
Experiment 4					
<i>Shorea multiflora</i>	92	-	-	88	-

839

840 **Table 4:** Experiment 2: Statistical summary table and biological interpretation of
 841 exclusion from an ectomycorrhizal hyphal network and distance from adult tree on
 842 relative growth rates (diameter, height and number of leaves) and survival for two
 843 species of dipterocarp seedlings (*Dryobalanops lanceolata* and *Shorea parvifolia*) over
 844 an 11-month period at the Malua Forest Reserve in Sabah (Malaysian Borneo).
 845 Interaction terms not included were not statistically significant for any of the parameters
 846 measured. -R = Root exclusion, -RM = Root and ectomycorrhiza exclusion.

Effect	F_{df}	P	Interpretation
Diameter			
Treatment	$F_{2,238}=0.6$	ns	No ectomycorrhizal network effect
Distance	$F_{1,238}=1.1$	ns	No effect of distance from adult tree
Species	$F_{1,238}=10.2$	<0.01	<i>Dryobalanops lanceolata</i> grew faster than <i>Shorea parvifolia</i>
Treatment x Species	$F_{2,238}=0.3$	ns	No significant interaction term
Height			
Treatment	$F_{2,238}=1.2$	ns	No ectomycorrhizal network effect
Distance	$F_{1,238}=9.3$	<0.01	<i>Dryobalanops lanceolata</i> grew faster closer to adult trees
Species	$F_{1,238}=0.1$	ns	No species differences
Treatment x Species	$F_{2,238}=2.5$	<0.10	<i>Shorea parvifolia</i> control seedlings grew marginally faster than -R and significantly faster than -RM but no effect on <i>Dryobalanops lanceolata</i>
Leaves			
Treatment	$F_{2,238}=3.1$	<0.05	<i>Shorea parvifolia</i> -RM seedlings grew slower than the -R treatment
Distance	$F_{1,238}=0.9$	ns	No effect of distance from adult tree
Species	$F_{1,238}=0.1$	ns	No species differences
Treatment x Species	$F_{2,238}=3.2$	<0.05	<i>Dryobalanops lanceolata</i> -RM seedlings grew slower, but no effect on <i>Shorea parvifolia</i>
Survival			
Treatment	$\chi^2_{3,5}=13.3$	<0.0001	-RM showed significantly lower survival for both species
Distance	$\chi^2_{5,6}=1.0$	ns	No effect of distance from adult tree
Species	$\chi^2_{4,5}=4.4$	<0.05	Survival rate in <i>Shorea parvifolia</i> lower than in <i>Dryobalanops lanceolata</i>
Treatment x Species	$\chi^2_{5,7}=0.4$	ns	No significant interaction term

847

848 **Table 5:** Experiment 3: Statistical summary table and biological interpretation of
849 exclusion from an ectomycorrhizal hyphal network and soil type on relative growth
850 rates (diameter, height and number of leaves) for four species of dipterocarp seedlings
851 (*Dryobalanops lanceolata*, *Parashorea tomentella*, *Shorea beccariana* and *Shorea*
852 *multiflora*) over a 29-month period at Kabili-Sepilok Forest Reserve in Sabah
853 (Malaysian Borneo). The three-way interaction term is not included as it was not
854 statistically significant for any of the parameters measured. -R = Root exclusion, -RM =
855 Root and ectomycorrhiza exclusion.

Effect	F_{df}	P	Interpretation
Diameter			
Treatment	$F_{3,276}=2.6$	<0.10	See interactions below
Soil type	$F_{1,276}=0.8$	ns	No soil type effect
Species	$F_{3,276}=0.8$	ns	No species effect
Treatment x Species	$F_{9,276}=1.3$	ns	No significant interaction term
Treatment x Soil type	$F_{3,276}=2.7$	<0.05	-RM of <i>Parashorea tomentella</i> , <i>Shorea beccariana</i> and <i>Shorea multiflora</i> grew faster on sandstone soil than -R for all three species
Species x Soil type	$F_{3,276}=5.4$	<0.01	-R of <i>Dryobalanops lanceolata</i> grew faster on alluvial soil and overall faster than -RM
Height			
Treatment	$F_{3,276}=1.0$	ns	No ectomycorrhizal network effect
Soil type	$F_{1,276}=0.9$	ns	No soil type effect
Species	$F_{3,276}=3.6$	<0.05	-R of <i>Parashorea tomentella</i> grew faster on sandstone soil
Treatment x Species	$F_{9,276}=1.0$	ns	No significant interaction term
Treatment x Soil type	$F_{3,276}=1.1$	ns	No significant interaction term
Species x Soil type	$F_{3,276}=0.4$	ns	No significant interaction term
Leaves			
Treatment	$F_{3,276}=1.1$	ns	No ectomycorrhizal network effect
Soil type	$F_{1,276}=0.1$	ns	No soil type effect
Species	$F_{3,276}<0.1$	ns	No species effect
Treatment x Species	$F_{9,276}=1.4$	ns	No significant interaction term
Treatment x Soil type	$F_{3,276}=2.0$	ns	No significant interaction term
Species x Soil type	$F_{3,276}=4.7$	<0.01	<i>Dryobalanops lanceolata</i> seedlings grew faster on alluvial soil than sandstone soil
Survival			
Treatment	$\chi^2_{6,9}=1.2$	ns	No effect of treatment on survival
Soil type	$\chi^2_{8,9}=6.0$	<0.01	Survival on alluvial soil was significantly lower compared to sandstone soil
Species	$\chi^2_{6,9}=7.2$	<0.10	Seedlings of <i>Shorea multiflora</i> and <i>Shorea beccariana</i> showed lowest survival after 15 months
Treatment x Species	$\chi^2_{9,18}=4.3$	Ns	No significant interaction term
Treatment x Soil type	$\chi^2_{9,12}=2.3$	ns	No significant interaction term
Species x Soil type	$\chi^2_{9,12}=4.6$	ns	No significant interaction term

856