1 **TITLE: The Mycorrhizal Tragedy of the Commons**

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30 the model based on experimental data. L.T., J.M., T.N., J.F., and L.E. contributed to

31 experimental design and interpretation of data. All authors contributed to the manuscript

32 text.

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ABSTRACT

Trees receive growth-limiting nitrogen in exchange for allocating carbon to mycorrhizal symbionts, but supplying the fungi with carbon can also cause nitrogen immobilization, which hampers tree growth. We present results from field and greenhouse experiments combined with mathematical modelling, showing that these are not conflicting outcomes. Mycorrhizal networks connect multiple trees, and we modulated C provision by strangling subsets of trees, assuming that carbon supply to fungi was reduced proportionally to the strangled fraction. We conclude that trees gain additional nitrogen at the expense of their neighbors by supplying more carbon to the fungi. But this additional carbon supply aggravates nitrogen limitation via immobilization in the shared fungal biomass. We illustrate the evolutionary underpinnings of this situation by drawing on the analogous *tragedy of the commons*, where the shared mycorrhizal network is the commons, and explain how rising atmospheric CO_2 may lead to greater nitrogen immobilization in the future.

INTRODUCTION

In boreal forests, ectomycorrhizal fungi (EMF) contribute significantly to tree nitrogen (N) acquisition, which is frequently the growth limiting factor in this biome (Högberg *et al.* 2017). But mycorrhizal N is acquired at the cost of photosynthetic carbon (C) (Colpaert *et al.* 1996; Corrêa *et al.* 2008). This is the basis for mycorrhizal trade, but despite the fact that it is one of the most widespread and influential symbioses in boreal forest ecosystems, the ecological nature of this exchange has not been settled (Johnson *et al.* 1997; Alberton *et al.* 2005; Franklin *et al.* 2014; Terrer *et al.* 2019). This represents a critical weak point in any predictions of ecosystem responses to future perturbations of C or N dynamics (Alberton *et al.* 2007; Högberg *et al.* 2017).

Ectomycorrhizal symbioses can vary from mutualism to competition to parasitism, depending on prevailing growth conditions (Johnson *et al.* 1997; Alberton *et al.* 2007; Ågren *et al.* 2019). Under N limitation, host plants have been observed to continue supplying their ectomycorrhizal partner with C, and even increasing the C investment, despite diminishing N returns (Corrêa *et al.* 2008, 2010). If N availability is amended via fertilization, however, EMF transfer a greater proportion of their absorbed N (Näsholm *et al.* 2013). N is thus withheld under conditions of limiting availability, and the host tree cannot unlock it by supplying the EMF with more C, because such an investment results in further diminishing N returns. The eco-evolutionary explanation is that each fungal individual competes with other EMF symbionts of the same plant and can gain a larger share of the plant's C supply by increasing its N export, until its own remaining N matches its C supply (Näsholm *et al.* 2013). Conversely, a larger C flux from the plant allows the fungus to use a greater proportion of the N it absorbs from the soil, as dictated by the stoichiometric requirements of fungal biomass and growth (Alberton *et al.* 2007; Näsholm *et al.* 2013; Franklin *et al.* 2014). Enhanced EMF growth may initially increase N uptake and, by extension, export to host plants but N availability eventually becomes limiting, whereas N immobilization in fungal biomass continues, leading to a negative feedback on the plant's N uptake (Corrêa *et al.* 2010; Näsholm *et al.* 2013). This sequence has been suggested as a mechanism for observed progressive N limitation in forests under increased atmospheric CO_2 concentrations (Alberton *et al.* 2007; Högberg *et al.* 2017). The presence of such an N-immobilizing feedback

82 loop raises the question of how the symbiosis can remain stable over evolutionary time
83 scales and how it has survived natural selection.

84

85 Here we present an ecological framework to reconcile the observed plant and fungal
86 behaviors summarized above, by recognizing the dual scale of the ectomycorrhizal
87 symbiosis. The critical point is that multiple fungi can colonize the roots of a given tree and
88 that several trees can be connected to the same fungal individual, creating common
89 mycorrhizal networks (Southworth *et al.* 2005). Trees have evolved to maximize their own
90 competitive benefit from the symbiosis at the individual tree scale, but this maximization
91 also has consequences for other trees with whom they share EMF partners at the *network*
92 *scale*.

93

94 The classic paper titled *The Tragedy of the Commons* (Hardin 1968) presents a theory of
95 over-exploitation of shared resources which effectively illustrates the evolutionary
96 underpinnings which have led to the widespread success of a symbiosis in which one partner
97 is in fact maintaining its own resource limitation: Trees do not coordinate their carbon
98 investments within the shared fungal network, but act to increase individual advantages
99 over their neighbors. In Hardin's example, a common pasture was depleted by several
100 herdsmen who all increased the number of cattle they kept there. From each herdsman's
101 perspective, this is the rational course of action, because the cost of the degraded pasture is
102 divided among all users, whereas the individual herdsman receives the entire reward of an
103 extra head of cattle. Analogously, all host trees are competing for enhanced shares of
104 mycorrhizal nutrients, but their combined efforts serve to aggravate the overall nutrient
105 immobilization in fungal biomass.

106

107

108 **HYPOTHESIS**
109 We hypothesize that common EMF symbionts reward the host plants that supply the most C
110 by allocating a greater proportion of their total exported N to them. Conversely, the hosts,
111 which share multiple EMF symbionts, reward the partners that supply the most N by
112 releasing a greater proportion of their total C export to those networks. The "tragedy" from
113 the plant viewpoint arises when the total C export to all fungi is so high that it leads to N

4

immobilization, in which case the proportions cease to matter and all plants suffer. The "tragedy" from the fungal viewpoint arises when exporting more N would reduce their own growth, but exporting less N would reduce their competitiveness for plant C (Näsholm 2013, Franklin 2014).

This hypothesis has specific and predictable implications for plant N uptake in response to C export (mathematically formulated in the Materials & Methods section of this article): A positive linear relationship at the individual plant level and a saturating or hump-shaped relationship at the community level (fig. 1, alternative 3). As stated, the hypothesis should be rejected if a similar relationship between N uptake and C export were observed at both individual and community levels (fig. 1, alternatives 1, 2). Such a result would imply a lack of inter-plant competition for N through a common network.

We conducted two experiments, (in the greenhouse and field conditions), where belowground C flux was reduced by shading and/or stem strangling. Strangling is a treatment whereby belowground C flux is physically restricted by blocking phloem transport. It has been proven to consistently control plant C export to roots and EMF (Björkman 1944; Henriksson *et al.* 2015). Strangling a subset of seedlings growing in the same pot accomplishes two things: 1) the total belowground C flux is decreased, and 2) each seedling's relative contribution to that flux is altered. Shade treatments were also applied to uniformly reduce total C availability to belowground structures in a subset of pots.

MATERIALS AND METHODS

SEEDLING EXPERIMENT

Preparation of mycorrhizal inoculum

A culture of *Suillus variegatus* was prepared based on the protocol described in (Vuorinen *et al.* 2015) with a few modifications. Briefly, ½ MMN medium, was prepared. The media contained 1.25 g/L glucose, 5 g/L malt, 0.5 g/L $(NH4)_2HPO_4$, 0.5 g/L KH_2PO_4, 0.15 g/L $MgSO_4°7H_2O$, 0.05 g/L $CaCl_2*2H_2O$, 0.025 g/L NaCl, 0.02 g/L Fe-EDTA, 0.02 g/l Thiamine-HCl

145 and the pH value adjusted to 5.8 with NaOH-HCl. As inoculum, plugs (5x5 mm) from the

146 actively growing peripheral zone of *S. variegatus* mycelia, growing on solid ½ MMN agar

147 plates, was used. The mycelia were first cultured in 250 ml ½ MMN medium in 1 L

148 Erlenmeyer flasks, sealed with cotton and aluminum foil for 16 days in a dark incubator sat

149 at 23℃ and rotation speed at 100 r/m. Following this, the liquid culture was homogenized

150 and mixed with silica powder (Sipernat 22S, Algol Chemicals AB) moistened with ½ MMN

151 medium to a moisture content of 70%, by weight (250 g silica in each container). The

152 containers were placed in a dark and ventilated space and the mycelium was allowed to

153 grow for another 28 days.

154

155 **Seedling growth conditions**

156 On May 10th, 2018 (DOY 130), two-year-old *Pinus sylvestris* seedlings were bare-rooted,

157 weighed and potted in a soil mix containing 10 % *S. variegatus* inoculum and 90 % soil (50-50

158 mixture of peat and commercial non-fertilized potting soil). No measures were taken to

159 exclude fungal species already present on the roots of the seedlings. Each pot (23 cm x 17

160 cm x 6 cm) contained six seedlings, planted as shown in fig. 1b. Seedling fresh weight was

161 measured before planting. Seedlings were randomly selected to pots and there was no

162 significant difference in initial fresh weight among seedlings that would subsequently be

163 allotted to different treatments (P = 0.74).

164

165 To allow the seedlings to establish themselves in their pots, they were kept in controlled

166 greenhouse conditions for 53 days. They were then transferred outdoors, first to partial

167 shade for 10 days, to avoid damage to the needles from sudden exposure to direct sunlight,

168 and then into the open. After 18 days in direct sunlight, the experimental treatments were

169 initiated. Thus, the experimental treatments were begun on July 30th 2018 (DOY 211), 81

170 days after the seedlings were potted. Finally, all the pots were transferred back inside the

171 greenhouse for the final month of the study. This was done to avoid loss of ^{15}N tracer in

172 autumn rains. All pots were watered daily throughout the experiment duration.

173

174 **Shading and strangling treatments**

175 Half of the pots were covered by individual shade tents constructed of DeWitt UV PE knitted

176 shade cloth (Agriculture Solutions, LLC, Strong, Maine), reducing incoming photosynthetic

177 radiation (PAR) by 78.8 ± 4.8 % (mean ± SD).

178 Within each pot, the six seedlings could be either strangled or left unstrangled, and the

179 treatments were designed so that 0, 1, 5, or 6 seedlings were strangled. Thus, there were

180 four levels of the strangling treatment, and two levels of the light treatment (Fig. 1). This

181 resulted in a total of eight factorial combinations of treatments that were replicated 5 times

182 in a blocked design.

183 Seedlings were strangled by tightly wrapping iron wire (0.7 mm diameter) around the stems

184 below the lowest branch (Björkman 1944). This method, and modified versions for large

185 trees, have been shown to effectively reduce belowground C flux in *P. sylvestris* and *Pinus*

186 *ponderosa* (Björkman 1944; Henriksson *et al.* 2015). In Björkman (1944) strangling of 3-year-

187 old pine seedlings for one entire season was shown to strongly reduce root soluble

188 carbohydrate levels as well as ectomycorrhizal colonization rate (< 5 % of root tips,

189 compared to c. 65 % in control seedlings). In that publication, the strangling wire was

190 removed from a subset of the seedlings after three months, resulting in intermediary levels

191 of both measurements.

192

193 **^{15}N application**

194 Thirty-two days after the initiation of shade and strangling treatments, ^{15}N was applied to

195 the soil surface of each pot (DAY 243), in the form of KNO_3 (Larodan AB, Karolinska Institutet

196 Science Park, Stockholm, Sweden). The total added quantity corresponded to 0.3 g ^{15}N / m^2,

197 which was applied in three doses over the course of six days to avoid flushing the system

198 with nitrogen. Each pot thus received a total of 0.012 g ^{15}N.

199 To avoid loss of ^{15}N from the bottom of the pots, as well as isotopic contamination between

200 pots, the pots were placed in individual trays before isotopic label was applied, and

201 remained in these for the duration of the study. Any water that drained out the bottom was

202 used to re-water the same pot using a syringe.

203

204 **Final harvest and sampling**

205 Three weeks after the ^{15}N labelling (on DOY 269-276), the seedlings were harvested. All 240

206 seedlings (6 seedlings x 40 pots) were washed and their roots separated. The needles, roots,

7

207   stem, and buds of each seedling were separated, and weighed. For strangled seedlings, the

208   wire was removed before weighing the stem. The material was then dried at 60°C for 48

209   hours before being weighed again.

210

211   The dried needles, roots and stem of each seedling were milled in a chamber mill (IKA-Werke

212   GmbH & Co.KG). Using isotope ratio mass spectrometry, the total C and N contents (% C and

213   % N) and the isotopic enrichment of ^{15}N was analyzed for each plant compartment.

214

215   The current setup allows quantification of the ^{15}N abundance in the entire seedling biomass,

216   rather than relying on foliage concentration, which is commonly used as a measure of N

217   uptake in field conditions   (Hasselquist *et al*. 2016). By measuring each seedling

218   compartment separately (needles, roots, stem), we avoid problems in distinguishing actual N

219   mobilization from a potential shade avoidance response in the trees (Henry & Aarssen 1997),

220   which could shift internal N partitioning toward the foliage.

221

222   **Statistical analyses**

223   Seedling dry weights, elemental and isotopic composition, and photosynthetic rates were

224   compared using a standard least squares means model where light level and the number of

225   strangled seedlings per pot were considered as fixed effects in a factorial design. Where the

226   initial tests yielded F-scores < 0.05, Student's t-test or Tukey's HSD were used post-hoc, to

227   perform pairwise comparisons within groups. The statistical analyses were carried out in JMP

228   (JMP® pro 15.0.0, SAS Institute Inc.).

229

230

231   **FIELD EXPERIMENT**

232   **The study site**

233   The experiment was conducted in a 15-20-year-old, naturally regenerated *Pinus sylvestris*

234   stand located in northern Sweden (64°14'N, 19°46'E, and 175 m above sea level). The soil is

235   weakly podsolized sandy silt sediment, and the field layer consists mainly of lichens, with

236   infrequent occurrences of *Calluna vulgaris* and *Vaccinium vitis-ideae*. The organic mor layer

237   is 1-3 cm thick, and has a C-N ratio of 37 ± 1 and pH of 4.0 ± 0.1 (Hasselquist *et al*. 2016).

238

8

239   The trees were between three and five meters tall with stem diameters at breast height of

240   7.4 ± 2.6 cm (mean ± 1 SD). The site is very N-poor and has an uneven stand density,

241   including bald patches as well as patches where the trees grow closer together.

242

243   **Study design**

244   We selected 23 circular plots with radius of two meters, using a tree as the center. All trees

245   growing within this area were considered as part of the plot. Plots contained 5-11 trees (7.1

246   ±1.7 mean ± SE) and had a total basal area at breast height of 3.2 ± 1.2 dm^2 (mean ± SE). The

247   plots were placed around trees growing in the denser patches of the site, so that they were

248   naturally semi-discrete in the landscape. We had two reasons for doing this: First, the higher

249   tree-density in these patches allowed us to assume that these trees were occupying the

250   same soil volume and were more likely connected to the same mycorrhizal network. Second,

251   the surrounding low-density areas should help reduce the influence from trees whose stems

252   grew outside the plot boundary.

253

254   We designed four plot-level treatments using stem strangling to reduce the trees'

255   belowground C-transport (detailed description in Henriksson et al., 2015). In Henriksson *et*

256   *al*. (2015) canopy ^{13}C labelling and subsequent isotopic analysis of phloem carbohydrates

257   showed that none of the $^{13}CO_2$ absorbed after strangling was transported past the strangling

258   point to the lower part of the stem. The experiment described in that publication was

259   performed on similar trees to the current study, and in the same study area. Plots were

260   considered to have two types of trees – the center tree, and neighbor trees –which could be

261   either strangled or not strangled. In other words, we either strangled the stems of all trees,

262   none of them, only the center tree, or all except the center tree (figure 2). The plots were

263   divided into six blocks and then randomly assigned one of the four treatments. One of the

264   blocks only had space for 3 plots, and thus one of the treatments (all trees strangled except

265   one) was only replicated five times, but all the rest were replicated six times. In each plot,

266   two trees were selected for needle sampling (3 weeks after ^{15}N-application), the central tree

267   and one neighbor tree.

268

269   Mean basal area did not differ between plot treatments (p = 0.14, ANOVA), although the

270   variance was unequal: the basal area of control plots varied more than the other treatments

     9

271 (p = 0.001, Levine's test). The number of trees per plot was not significantly different

272 between treatments (p = 0.23, ANOVA).

273

274 **Sampling and treatments**

275 All strangling treatments began on July 21st, 2015 (DOY 202). On August 10th (DOY 222), we

276 applied 2.62 g of ^{15}N-labeled KNO_3 (0.39 g ^{15}N) dissolved in water, which could be detected in

277 needle samples taken three weeks later. This N form was chosen for the high C requirement

278 associated with its reduction and assimilation, which should lead to lower efficiency of N

279 immobilization by free-living soil microbes than would be the case with N sources like

280 ammonium or organic N. The application was equivalent to 0.02 kg ^{15}N ha^{-1} and the solution

281 corresponded to 2 liters m^{-2}, which was evenly distributed from above and allowed to soak

282 into the soil, over a circular area with a radius of 2.5 meters (plot radius + 0.5m), in order to

283 treat a larger proportion of edge trees' root systems. The isotopic enrichment of N in the

284 foliage of trees that received different treatments could then be compared to detect

285 changes in uptake patterns among the treatments.

286

287 **MODEL DESCRIPTION**

288 Our hypothesis is formulated in terms of a model describes the C-N exchange between

289 plants and mycorrhizal fungi, both at the stand (or network) level and from the perspective

290 of an individual plant. It was tested and evaluated based on the data from the pot

291 experiment, which allowed better control and isolation, and more complete quantification of

292 the ^{15}N uptake by all plants than was possible in the field experiment. Strangling of a seedling

293 predictably reduces its C provision below ground, to roots and the fungal network

294 (Henriksson *et al.* 2015).Thus, we assume that the C supply to fungi is proportional to root

295 biomass but that it is reduced by strangling according to a strangling factor estimated by the

296 model.

297

298 **Stand level C-N exchange**

299 The growth of mycorrhizal fungi is fueled by C supply by the plants ($\dot{C}_s$), which we consider

300 in relative terms (compared to mean of control plants) because its absolute value cannot be

301 estimated and is not important for our conclusions. We assume that C supply to fungi from

302 an individual plant ($\dot{C}_{si}$) is proportional to its root mass (C_{ri})(Rouhier & Read 1998; Neumann

10

303   & Matzner 2013) and further reduced by strangling by a constant factor (see *supplementary*

304   *information* for model parameterization).

305

306   We assume that fungal N uptake ($\dot{N}_u$), is a saturating function of fungal growth (which is

307   proportional to its biomass):

308    $$\dot{N}_u = \frac{N_a \dot{C}_s}{\dot{C}_s + \dot{C}_{sh}}$$ (1)

309

310   In eq. 2 N_a = soil N availability (maximum potential N uptake) and $\dot{C}_{sh}$ = half-saturation $\dot{C}_s$.

311   N immobilization in fungal biomass is:

312    $$\dot{N}_f = \dot{C}_s \cdot I_f$$ (2)

313

314   The N immobilization factor, $I_f = N:C_f \cdot e_f$, where $N:C_f$ = N:C ratio of fungal biomass and e_f

315   = C use efficiency of fungal growth.

316

317   Combining eqs. 1 and 2, N export to plants ($\dot{N}_p$), can be written as:

318    $$\dot{N}_p = \dot{N}_u - \dot{N}_f = \frac{N_a \cdot \dot{C}_s}{\dot{C}_s + \cdot \dot{C}_{sh}} - \dot{C}_s \cdot I_f$$ (3)

319

320   **Competition for N among individual plants**

321   We assume that the fungi are attached to all plants in a pot and deliver N to each plant

322   depending on its C supply relative to its competitors, which is postulated by eco-evolutionary

323   theory (Wyatt *et al.* 2014) and indicated by experiments (Kiers *et al.* 2011; Fellbaum *et al.*

324   2014). This N competition effect was estimated in terms of N uptake of a plant *i* ($\dot{N}_{pi}¿¿$

325   relative to mean N uptake of all plants in the pot ($\overline{\dot{N}_p}$) as

326    $$\frac{\dot{N}_{pi}}{\overline{\dot{N}_p}} - 1 = d \cdot \left[\left(\frac{\dot{C}_{si}}{\overline{\dot{C}_s}} \right)^z - 1 \right]$$ (4)

327

328   In eq. 4, $\dot{C}_{si}$ = C supply from plant *i*, $\overline{\dot{C}_s}$ = mean C supply from all plants, and *d* = degree of

329   fungal N export discrimination according to plant C supply. *d* is approximately equal to the

330   marginal tree N gain per C supply for a tree, or the marginal C gain from each tree per N

11

331   export for a fungus. Theoretically, $d=1$ maximizes the total C a fungus receives from all its

332   tree partners, because a larger or smaller d would mean that the fungus could increase C

333   supply by redistributing N supply among its tree partners. The parameter z allows for a

334   potential non-linear effect of individual C supply on N uptake (for $z \neq 1$), e.g. due to N

335   limitation of fungal partners.

336

337   The modelled relationships between individual plant scale and network scale C and N

338   exchange is illustrated in fig. 3. Detailed descriptions of parameter estimation and model

339   testing are presented in the supplementary information for this article.

340

341

342   ## RESULTS

343

344   We found that seedlings growing in shaded communities (78.8 ± 4.8 % reduction of PAR,

345   mean ± SD) for two months had 36 % smaller dry mass at the time of harvest than seedlings

346   in sun pots ($p < 0.0001$, fig. 4a). Phloem strangling of individual seedlings did not affect their

347   biomass, but it did cause a decrease in root/shoot ratio ($p < 0.0001$, fig. 4b).

348

349   Three weeks before harvest, 12 mg traceable nitrogen isotope ^{15}N was applied to the soil

350   surface of each pot. Shading led to 50% higher recovery of applied ^{15}N in seedling biomass

351   (1.07 mg ^{15}N per seedling, compared to 0.71 mg ^{15}N per seedling, fig. 4c; $p < 0.0001$). Thus, a

352   total of 54 % of applied ^{15}N was accounted for in plant biomass in shaded pots, and only 36 %

353   in sun pots. Further, strangled seedlings received significantly less ^{15}N than non-strangled

354   ones (fig. 4c). This supports the stoichiometric model of mycorrhizal C-N exchange, which

355   predicts that decreased C export to fungi mobilizes soil N to the plant host and *vice versa*.

356

357   In shaded seedlings, ^{15}N allocation to foliage was higher than for seedlings grown in full sun

358   ($p < 0.0001$, fig. 4d). Strangling individual seedlings had the opposite effect on ^{15}N allocation,

359   compared to shading – more N remained in the mycorrhizal roots of the seedlings, which

360   included both a fungal and a plant component ($p < 0.032$).

361

12

362 In the field, we found that reducing belowground C flux, by strangling one tree per plot,

363 improved total mobilization of applied ^{15}N label to the trees (fig. 5a, b). In such plots, the

364 strangled tree received less N than its neighbors (fig. S3). Strangling a greater subset of trees,

365 thereby further impairing the capacity for plot-scale belowground C export, caused total ^{15}N

366 uptake to fall significantly, as was observed in plots where 82-100 % of tree basal area was

367 strangled (fig. 5a, b).

368

369 Both shading and strangling reduce the belowground C flux that fuels the activity of

370 mycorrhizal fungi. Based on the greenhouse experiment, we developed a model to test the

371 connection between belowground C export and plant N acquisition at both the *individual*

372 *tree-scale* (seedling) and at the *network-scale* (whole pot). The model explained 58% of the

373 variation among individuals in the same pot, and 25% of the variation between pots in plant

374 N uptake. In addition to the measured effects on root mass, the model indicated that C flux

375 to mycorrhiza per root mass was significantly reduced by strangling (by 55%) but not by

376 shading (Supplementary).

377

378 The model, supported by our measurements, shows that the greatest N-mobilization for

379 plant use occurred at an intermediate level of belowground C export (fig. 6 a). Initially, N

380 uptake and export to plants increases steeply with C supply to mycorrhizal fungi, but the rate

381 of increase gradually declines as hyphae fill up the soil and N becomes limiting. At the same

382 time N immobilization in fungal biomass increases linearly with C supply, which eventually

383 results in declining net N export to plants. Thus, the model corroborates the hypothesis that

384 maximum *network-scale* N mobilization occurs at an intermediate level of *network-scale* C

385 export. At the individual tree-scale, the marginal increase in the share of N that the plant

386 receives per share C supplied is approximately equal to one (0.95), as theoretically predicted

387 (fig. 6b). This drives a competition for N among trees where each tree at first gains N by

388 fueling fungal growth, but later the whole community suffers from N immobilization in the

389 shared fungal network.

390

391

392 **DISCUSSION**

13

393 We show that belowground C allocation to can fuel N immobilization, reducing the amount
394 of N to be distributed among the trees. But we also found that individual trees received
395 nutritional benefits in proportion to their carbon contribution to the fungal network in
396 accordance with our hypothesis (fig. 1, alternative 3). This apparent incongruity can be
397 explained by invoking the concept of the *tragedy of the commons*, as described by Hardin in
398 1968 (Hardin 1968).

399

400 Our estimates of plant C export to EMF are constrained by root measurements and a
401 strangling effect (previously shown to predictably reduce below ground C export (Henriksson
402 et al 2015)). The only free parameter affecting the modelled C export was the magnitude of
403 the strangling effect per root biomass. As an additional test, we used respiration
404 measurements to make independent estimates of the C export to EMF at the pot
405 (community) level, which were well correlated the model results, and suggesting that the
406 model explains 39% of the variation in EMF respiration (Supplementary information). The
407 underlying details of the strangling effect on C export are not relevant for our conclusions
408 but may include reduced EMF colonization of roots (Björkman 1944), and reduced growth of
409 extraradical mycelia extending from strangled roots. Either way, the strangled plants cannot
410 have been completely ejected from the EMF network, or their N uptake would not fall on the
411 same line as the non-strangled plants in figure 6b.

412

413 The most plausible alternative scenarios and their implications are displayed in fig. 1: (1)
414 direct N uptake without EMF and (2) N uptake via EMF but without a common network. In
415 alternative 1, plant N uptake would increase with below ground C allocation to roots and
416 would tend to saturate, but never decline, at higher C allocation. Competition would lead to
417 slightly less saturation at the individual than at the community level (Franklin et al 2012).
418 Alternative 2 would lead to initially increasing but eventually saturating plant N uptake with
419 C export, due to linearly increasing fungal growth and N immobilization with C export. The
420 response would be similar at both the individual level and the community level as there is no
421 strong inter-plant competition for EMF-derived N. Only if plants take up and compete for N
422 via a common EMF network (Alternative 3 in fig. 1) is it possible to obtain the contrasting
423 results shown in fig. 6, i.e. a linear increase in plant N uptake with C export at the individual
424 level (scaling exponent = 1.038, Supplementary) and a hump shaped relationship at the

14

425 community level. The linearity of the individual response was tested, resulting in a. We

426 conclude that the most reasonable interpretation of this data is the presence of common

427 EMF network (Nara 2006; Beiler *et al.* 2010) in which multiple fungi connect the host plants

428 to each other (Franklin *et al.* 2014).

429

430 A stable evolutionary strategy for a multi-partner trade network is achieved when individuals

431 allocate resources among symbionts of the other species in proportion to the relative

432 benefits they receive from each partner. This is called proportional discrimination and has

433 been applied to modelled mycorrhizal networks (Wyatt *et al.* 2014). The fact that our model

434 (where plant N uptake was measured and relative C contribution to fungi was modelled)

435 resulted in a linear proportionality (with slope 0.94, not significantly different from 1)

436 between relative C investment and N uptake strongly indicates the presence of a common

437 mycorrhizal network.

438

439 In our experiment, seedlings were potted in soil containing inoculum of the EMF *Suillus*

440 *variegatus*. This was done to ensure a minimum degree of comparability among the plant-

441 fungal systems established in the pots. As mentioned in the Methods section, seedlings were

442 2 years old at the time of planting, and any EMF species already present on the root systems

443 from their time at the nursery were not excluded. We consider this to be a strength of the

444 current study, as the presence of multiple fungal species improves the comparability of the

445 results to those of the field study. Further, mycorrhizal market theory (Franklin *et al.* 2014;

446 Wyatt *et al.* 2014), upon which our hypotheses were based, does not rely on species

447 differences or a particular species being present, it is the competition between multiple

448 individuals (regardless of species) that drives the dynamics.

449

450 Rising atmospheric CO_2 could significantly increase mycorrhizal fungal biomass (Treseder

451 2004), which could drive progressive N limitation in forests via mycorrhizal immobilization

452 (Alberton *et al.* 2007; Alberton & Kuyper 2009; Steidinger *et al.* 2019). Our results support

453 this notion. In fact, the field-studied Scots pines were observed to export higher-than-

454 optimal quantities of C under untreated conditions (fig. 5). Therefore, any increase in the C

455 supply to EMF should further exacerbate the network-scale N limitation in the studied forest

456 stand (fig. 3, 6a). However, this may not be the case in locations where soil N availability is

457   greater, or in situations where increased C supply allows EMF to have access to more
458   energy-demanding N sources, such as complex organic substrates.

459

460   Although a global model meta-analysis of elevated CO_2 experiments (Terrer *et al*. 2019)
461   concluded that rising atmospheric CO_2 would continue to stimulate plant growth in boreal
462   forests in general, empirical evidence for N-poor boreal forests is scant. Of the two
463   experiments from forests similar to ours included in the meta-analysis, one showed a small
464   negative CO_2 effect (Sigurdsson *et al*. 2013). In support of our prediction, Alberton *et al*.
465   (2005) observed that, in laboratory conditions, the growth-enhancing effect of elevated CO_2
466   was greater in the fungal component of an ectomycorrhizal symbiosis than it was in the
467   plant. They concluded that this should eventually cause increased plant-fungus competition
468   for N, and suggested this as a mechanism for future progressive N limitation, in line with our
469   model predictions. This further suggests that the risk of losing forests dominated by
470   ectomycorrhizal tree species   due to climate change (Steidinger *et al*. 2019) may be
471   unfounded, as that study did not account for increasing N limitation (relative to C) caused by
472   rising CO_2, which should reinforce the stability of the ectomycorrhizal symbiosis (Franklin *et*
473   *al*. 2014).

474

475   That the *tragedy of the commons* mechanism has gone almost unnoticed by scientists until
476   now may be due to many mycorrhizal C-N trade experiments having used setups containing
477   a single plant, paired with a fungal partner (Colpaert *et al*. 1996; Corrêa *et al*. 2010). Such a
478   design cannot capture network-scale drivers of EMF-plant interactions.   Arbuscular
479   mycorrhiza connected to multiple host plants can preferentially supply nutrients to the
480   plants presenting greater C-sources for the fungi (Fellbaum *et al*. 2014; Weremijewicz &
481   Janos 2013; Weremijewicz *et al*. 2016). However, the current study is the first to show the
482   link between plant-plant competition within EMF networks and the resulting N
483   immobilization as measured at the system level.

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