1 **Title:** Phylogenetic dependence of plant-soil feedback promotes rare species in a subtropical forest

2 **Running title:** Plant-soil feedback and species coexistence

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Abstract

The widespread observation that rare species have stronger conspecific plant-soil feedback (PSF) than common species raises more questions than answers on how rare species can possibly win the dance with abundant species. Here, we test soil feedback effect of phylogenetically related species on seedlings of contrasting local abundance in a subtropical forest. The results showed that although rare species suffered strong negative PSF in soils of conspecifics or phylogenetically close relatives, no such feedback was found in the soils of distant relatives. In contrast, although common species had weak conspecific PSF, they suffered consistently strong heterospecific soil feedback. These mechanisms ensure that rare species would fare well in the neighborhood of phylogenetically distant heterospecifics but do poorly under their close relatives, while common species perform relatively well in their own neighborhood but poorly in others'. This phylogenetic conservatism in PSF facilitates the persistence of rare species in a community.

Introduction

Negative plant-soil feedback (PSF) has been considered to play a major role in regulating plant diversity worldwide, from tropical to temperate forests and grasslands (Packer & Clay 2000; Klironomos 2002; Petermann *et al.* 2008; Mangan *et al.* 2010b; Bagchi *et al.* 2014; Liu *et al.* 2015; Levi *et al.* 2019). The process accumulates host-specific soil enemies around plant adults that in turn reduce the seedling performance of conspecifics relative to heterospecifics (Bever *et al.* 1997; Bever 2003) so that to prevent dominant species from competitively excluding others (Connell *et al.* 1984; Bever 2003; Chesson & Kuang 2008). However, over the past two decades, much empirical evidence has shown that rare species in plant communities suffer stronger conspecific soil feedback than common species (Klironomos 2002; Mangan *et al.* 2010b; MacDougall *et al.* 2011; Rutten *et al.* 2016), and other studies that model long-term tree mortality data have also shown that their statistical results are consistent with the prediction of stronger rare species PSF although those studies themselves are not a test of PSF (Comita *et al.* 2010; Johnson *et al.* 2012). However, these results are not universally unequivocal (Reinhart 2012; Liu *et al.* 2015; Maron *et al.* 2016; Kempel *et al.* 2018) and they have been questioned to be biased due to study design and analytical approaches (Detto *et al.* 2019). It remains an open question how plant-soil feedback checks the dominance of common species and prevents rare species from competitive exclusion if the negative PSF is stronger for rare species than common species.

Critical to testing biodiversity maintenance is the quantification of the relative strength of intra- vs interspecific density (or frequency) dependence (Chesson 2000; Adler *et al.* 2018). However, similar to competition studies where most experiments were not designed to compare the per-capita strength of intra- and interspecific competition needed to test species coexistence (Inouye 2001), few studies on the PSF effect quantify the per capita effects of host-specific soil microbiota on conspecific and heterospecific performance. For example, as a primary mechanism of PSF, the Janzen-Connell

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70   hypothesis stipulates that host-specific natural enemies in the neighborhood of adult trees limit

71   conspecific regeneration (Janzen 1970; Connell 1971), thus releasing the vicinity of the adult trees for

72   other species to colonize. While the reduced conspecific spatial aggregation is necessary to maintaining

73   biodiversity, little is known how well other species would actually fare in the released space – is the

74   conspecific suppression by the natural enemies strong enough to allow heterospecifics to overwhelm the

75   focal species, or hopelessly weak so that the focal species continues to hold the space in quantity?

76   Plants interact with not only conspecifics but also heterospecifics as seed dispersal frequently leads

77   to seedlings growing near heterospecific adults (Levine & Murrell 2003). It is thus important to

78   understand the effect of soil feedback on the performance of heterospecific seedlings. Fig. 1

79   hypothesizes the possibilities of the relative performance of seedlings of rare and common species under

80   conspecific and heterospecific adults when rare species have stronger conspecific negative PSF. A

81   species could suffer strong conspecific negative PSF but escapes the effect under heterospecific adults

82   (e.g., the common species in Fig. 1a or the rare species in Fig. 1b) or be insensitive to neighbor identity

83   (e.g., the rare species in Fig. 1a or the common species in Fig. 1b). Species coexistence is not possible if

84   rare species suffer stronger suppression than common species, regardless under which adults (Fig. 1a

85   and b). Only in the case of Fig. 1c where common species experience stronger heterospecific negative

86   PSF than rare species can the two species coexist.

87   Much empirical evidence has shown that PSF is phylogenetically dependent, i.e., phylogenetically

88   related host species share common pathogens and the sharing decays phylogenetically (Gilbert & Webb

89   2007; Liu *et al.* 2012). This phylogenetic conservatism in plant-soil microbiota interactions favors plant

90   recruitment under heterospecific trees, which is especially important for species with high dispersal

91   ability, low density, or those having fewer close relatives (Levine & Murrell 2003; Parker *et al.* 2015).

92   Because of this phylogenetic conservatism, plants would suffer from stronger negative effects when

exposed to soil microbiota inoculated by phylogenetically closer heterospecifics (Brandt *et al.* 2009;

Anacker *et al.* 2014; Crawford *et al.* 2019). Phylogenetic conservatism in soil feedback effect also varies

across focal plant species (Brandt *et al.* 2009; Anacker *et al.* 2014; Sweet & Burns 2017; Wilschut *et al.*

2019), arising from the difference in the degree of specificity of soil microbiota in association with host

plants. For example, plants associated with more host-specialized enemies tend to exhibit stronger

phylogenetic conservatism in the strength of negative PSF, while those with more generalized enemies

do not (Liu *et al.* 2012; Crawford *et al.* 2019). This phylogenetic variation in PSF inevitably leads to

different relative performance of species under their own adults versus heterospecific adults, of different

phylogenetic relatedness, as illustrated in Fig. 1, and it is critical for explaining rare species maintenance

in facing stronger negative PSF than abundant species.

To address the question of how phylogenetic dependence in soil feedback effect may promote rare

species in natural communities, we conducted a shade-house sterilization experiment and a reciprocal

field experiment on seedling growth of seven species in a subtropical forest in southern China. The

selected species comprised paired sister species with contrasting local abundances. Conspecific and

heterospecific soil feedback effects on seedling growth were quantified and the phylogenetic signal in

plant-soil feedback was tested. Our results showed that rare species experienced stronger conspecific

negative soil feedback than common species. They also suffered stronger heterospecific negative soil

feedback under closely than distantly related trees and the feedback disappeared with further increase in

phylogenetic distance. In contrast, common species experienced consistently negative soil feedback

from heterospecifics, independent of phylogenetic distance. These results provide empirical evidence

showing that rare species are promoted by soil feedback effects that favor their recruitment under

phylogenetically distant heterospecific trees where the recruitment of common species is restricted, as

predicted by Fig. 1c.

Materials and Methods

Study site, species selection and seed germination

The study site is located in the Heishiding Nature Reserve (N 23°27', E 111°53'; altitude: 150-927

m asl), an evergreen broadleaf subtropical forest in southern China. Tree species, *Ormosia fordiana*, *O.*

glaberrima, *Quercus auricoma* and *Q. macrocalyx* were selected in both shade-house and field

experiments, constituting two pairs of sister species with distinctly low and high abundances in a 50-ha

stem-mapped plot (established in 2012) where our experiments were conducted (see Table S1 and Fig.

S1 in Supporting Information). We additionally used *Canarium album* and *Helicia reticulata* in the

shade-house (*ex situ*) experiment and *Q. pachyloma* in the field (*in situ*) experiment (Table S1). Species

sets were not identical in the two experiments because seeds for some species were not available and we

preferred species from the same genus in the field experiment to generate a phylogenetic distance

gradient of conspecific, congeneric and heterofamilial species. Seeds were collected from the study site

during the autumn and winter (September to December) of 2016, immediately surface-sterilized (1

minute in 70% ethanol, 3 minute 50% commercial bleach and 1 minute 70% ethanol, and 1 minute

distilled water), and then stored in a refrigerator at 4°C. In January 2017, seeds were sowed in sterilized

sandy soil and germinated about 8 weeks later. At the beginning of our experiments in May 2017, we

randomly selected 22 seedlings for each of the seven species. The stem height of each seedling was

measured, and the total leaf area was also measured using an LI-COR LI-3000C portable leaf area meter

to the nearest 0.01 cm^2. The aboveground biomass of each individual was then weighed after oven-dried

at 70°C for 48 h in laboratory. These data were used to estimate initial aboveground biomass for

seedlings that were used in shade-house and field experiments as described below.

Shade-house sterilization experiment

139   A shade-house experiment was designed to test whether the variation in soil feedback from

140   different phylogenetically related species between rare and common species is mediated by soil microbe.

141   The experiment considered three factors: focal species with contrast abundance, phylogenetic distance

142   of soil source species to focal species, and sterilization treatment (soil with gamma radiation versus

143   without), as described below. In March 2017, for each of the six species, *C. album*, *H. reticulata*, *O.*

144   *fordiana*, *O. glaberrima*, *Q. auricoma*, and *Q. macrocalyx*, we collected soils beneath three adults of

145   each conspecific, congeneric, heterogeneric (confamilial), and heterofamilial species (Table S2). For

146   each of the three replicate adults, topsoil (*ca.* 10 cm in depth) at three randomly set directions were

147   sampled and mixed to give a representative sample of soil of the adult. Soil samples were then sieved

148   using meshes (0.2 cm in diameter) to remove any stones, roots and seeds, and divided into two parts.

149   One was sterilized using gamma radiation with a dose of 25 Gy and the other was used as a microbe

150   inoculum source. The species from which soils were sampled and used for cross seedling planting is

151   called soil-source species (also see Fig. 2).

152   To eliminate the interference of nutrition differences, we randomly collected background soils from

153   the study area (not specifically associating with the study species) and sterilized with gamma radiation.

154   These background soils were then mixed with the sterilized or live soil sampled from the soil-source

155   species at a proportion of 93:7 volume/volume following Teste *et al.* (2017). The mixed soils were filled

156   into plastic pots (15 cm in diameter, 17 cm in height) and one seedling was then transplanted into each

157   pot. In total, 48 combinations of experimental treatments (6 seedling species × 4 soil sources × 2

158   sterilization treatments) were replicated eight times, resulting in 384 pots. The position of the pots was

159   randomly shifted every two months and seedlings were watered weekly. After transplanted in May 2017,

160   the stem height and the total leaf area of each seedling were measured. After one year growth, seedlings

161   were harvested, and the aboveground dry weight was determined in June 2018.

Reciprocal field experiment

A reciprocal seedling planting experiment was conducted to test how the strength of soil feedback from different phylogenetically related species is related to the abundance of host species. In March 2017, for each of the five species, *O. fordiana*, *O. glaberrima*, *Q. auricoma*, *Q. macrocalyx*, *Q. pachyloma,* three adults with diameter at breast height larger than 20 cm were selected in the field, and these adults were required to have no neighboring adults belonging to any of the five species within 20 meters. 50 seedlings (10 for each species) were transplanted to a 1.5×2.5 m seedling quadrat beneath a selected adult, with a random mixture of the seedlings in five rows (10 seedlings per row) and 20 cm apart from each other. To minimize the effect of possible transplanting injuries, we replaced the dead or dying seedlings within the first two weeks. In total, 750 seedlings (5 host species × 5 seedling species × 3 host adult replicates × 10 seedling replicates) were planted in the field. Their initial stem height and total leaf area were measured in May 2017. Seedlings were harvested and the aboveground dry weight was determined in November 2018.

Statistical analyses

To estimate the initial aboveground biomass of each transplanted seedling, we used data from the 22 seedlings of each species harvested at the beginning of the experiment to model the aboveground dry weight (B) as a function of the total leaf area (TLA) and stem height (H), with the linear form: $\log(B) = \beta_0 + \beta_1 \cdot \log(TLA) + \beta_2 \cdot \log(H)$. The R^2 of these models was at least 0.78 for all the seven species (Table S3), allowing reliable estimation of initial aboveground biomass using the stem height and total leaf area of those transplanted seedlings. The relative growth rate (RGR) of seedlings was then calculated using the equation: RGR = (log(harvest biomass) - log(initial biomass))/time interval.

For the shade-house experiment, plant-soil feedback was measured as a log-response ratio of RGR

between live and sterilized soils (Kempel *et al.* 2018), where the RGR in sterilized soils was averaged

on the eight replicates in each soil source treatment, and the RGR of each individual in live soils was

used, allowing evaluating the feedback strength for each seedling. By comparing the performance of

seedling growth between sterilized and live soils, we assessed the net effect of soil microbiota on

seedling performance, which was the overall effect of different soil microbiota including pathogenic and

mutualistic fungi. A negative value of plant-soil feedback indicates a lower growth rate in live than

sterile soils and reflects soil pathogenic effects dominate, while a positive value indicates a better growth

in live soil, reflecting mutualistic effects overwhelm.

For the field experiment, conspecific plant-soil feedback was defined as the difference of seedling

performance in 'home vs. alien' soils, which was calculated as a pairwise linear contrast of $RGR(A)_\alpha -$

$RGR(A)_\beta + RGR(B)_\beta - RGR(B)_\alpha$, where A refers to focal seedlings and B as the seedlings of another

species; α and β are the soils from adults A (home soil) and B (alien soil), respectively; and $RGR(A)_\alpha$,

for example, indicates the relative growth rate of A seedlings in conspecific (home) soils α (Bever 1994,

2003; Bever *et al.* 1997). The averaged *RGR* of the seedlings per species per seedling quadrat was

calculated to represent the growth of seedlings in that soil. There were three *RGR* values in home soil

and 12 in alien soil for each of the five species, resulting in a total of 180 pairwise feedbacks.

Similarly, the congeneric plant-soil feedback was defined as the relative seedling performance of

two species, e.g., focal species A and another species B, in soils from the congeneric species of A and

from B, respectively. The strength of congeneric PSF was calculated in the same way as that for

conspecific PSF shown in the above, where the home soil α was defined as soil from congenerics. The

same procedure was also applied to calculate the strength of heterofamilial plant-soil feedback. In total,

288 congeneric and 432 heterofamilial soil feedbacks were calculated as each focal species in *Quercus*

had two congeneric and heterofamilial species, and each focal species in *Ormosia* had one congeneric

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208 and three heterofamilial species in our study.

209   In both the shade-house and field experiments, linear mixed-effects models were used to test the

210 significance of phylogenetic relatedness between focal species and the soil-source species, the

211 abundance of focal species and their interaction term in determining the strength of PSF. The

212 phylogenetic relationships between focal species and the soil-source species (Fig. S2) were obtained by

213 pruning the GBOTB.extended mega-tree for our species set using the "phylo.maker" function of the

214 "V.PhyloMaker" package (Jin & Qian 2019). The mixed-effects models included phylogenetic distance,

215 abundance and their interaction as fixed effects while seedling species identity as a random effect using

216 "lme" function in "nlme" package of R software (Pinheiro & Bates 2000). To detect phylogenetic signal

217 in PSF, we used nonparametric Kruskal-Wallis rank-sum test and Dunnett modified Tukey-Kramer

218 multiple comparison test to test the variation in the effect of PSF from different phylogenetically related

219 host tree species on seedlings of focal species. We further used one-sided Wilcoxon signed-rank test to

220 test whether the strength of the soil feedback is significantly negative. All analyses were conducted in R

221 v.3.6.2 (https://www.r-project.org/).

222

223 **Results**

224 **Plant-soil feedback in the shade-house sterilization experiment**

225   The results from shade-house experiment showed that plant seedlings grew worse in live than in

226 sterilized soil (Fig. S3; two-sample Wilcoxon test, $W = 15206$, one-sided $P = 0.003$), suggesting an

227 overall negative effect of soil microbiota on seedling performance. The strength of this negative effect

228 decreased with the phylogenetic distance between the focal species and soil-source species for rare

229 species (Fig. 2; Kruskal-Wallis test, $\chi^2 = 30.53$, $df = 3$, $P < 0.001$), while this relationship disappeared

230 for common species (Fig. 2; Kruskal-Wallis test, $\chi^2 = 1.02$, $df = 3$, $P = 0.797$). Conspecific negative soil

231   feedback was found in both rare and common species (Fig. 2) and the strength of this effect was weaker

232   for common than rare species (two-sample Wilcoxon test, $W = 394$, two-sided $P = 0.011$). However,

233   common species were strongly affected by negative effects of heterofamilial soil feedback while rare

234   species were not (Fig. 2), and the strength of soil feedback from distantly related adults, e.g.

235   heterofamilials, was stronger for common than rare species (two-sample Wilcoxon test, $W = 146$, two-

236   sided $P = 0.003$).

237   The difference in PSF strength between common and rare species can be further compared by the

238   performance of the six species in conspecific versus heterospecific soils (Fig. 3). The rare species

239   experienced significant conspecific negative soil feedback, while the common species showed no or

240   weak negative conspecific PSF (Fig. 3a). In contrast, plant-soil feedback from heterofamilials showed

241   no effects of soil microbiota on rare species but strong negative feedback on common species (Fig. 3b).

242   These results were confirmed by a linear mixed-effects model where the strength of PSF was modeled

243   by abundance of focal species and the phylogenetic distance between the focal species and soil-source

244   species (Table 1). The model showed that the strength of PSF was positively associated with the

245   phylogenetic distance but negatively associated with the interaction term between the phylogenetic

246   distance and local abundance (Table 1; $P < 0.001$), suggesting that rare species had a stronger

247   relationship between the phylogenetic distance and the strength of soil feedback (Fig. 2). Overall, this

248   experiment showed significant phylogenetic conservatism in the effects of soil microbiota for rare

249   species but not for common species; and common species but not rare species suffered strong negative

250   soil feedbacks from phylogenetic-distant relatives, e.g., heterofamilials.

251

252   **Plant-soil feedback in the reciprocal field experiment**

253   In addition to the shade-house *ex situ* experiment, we also conducted an *in situ* seedling growth

254   experiment involving transplanting 750 seedlings into the forest (see Methods). 643 (86%) of the

255   seedlings still survived after 18 months when the experiment was ended (Table S4). We found that for

256   the rare species, the strength of plant-soil feedback from conspecifics was stronger than that from

257   heterofamilials but showed no difference between the conspecifics and congenerics (Fig. 4 and Fig. S4a,

258   b; Kruskal-Wallis test, $\chi^2 = 25.55$, $df = 2$, $P < 0.001$). In contrast, seedlings of common species suffered

259   similar PSF strengths beneath the adults of conspecifics and heterospecifics (Fig. 4 and Fig. S4d, e;

260   Kruskal-Wallis test, $\chi^2 = 2.65$, $df = 2$, $P = 0.265$). Furthermore, for sister species pairs, the soils beneath

261   conspecific adults had a stronger negative effect on seedling growth of rare species but did not affect

262   that of common species (Fig. 5a), while the heterofamilial negative soil feedback was stronger for the

263   common than the rare species (Fig. 5b). The linear mixed-effects model for the strength of plant-soil

264   feedback showed consistent results with that of the shade-house experiment (Table 1).

265

266   **Discussion**

267   The observation of stronger conspecific PSF for locally rare than common species has been widely

268   reported (Klironomos 2002; Comita *et al.* 2010; Mangan *et al.* 2010b; MacDougall *et al.* 2011; Johnson

269   *et al.* 2012; McCarthy-Neumann & Ibáñez 2012; Rutten *et al.* 2016). This however raises more

270   questions than answers in explaining how rare species can possibly persist if they experience stronger

271   self-limitation (Metz *et al.* 2010; Zhu *et al.* 2015; Detto *et al.* 2019). Answers to this question are

272   ultimately important for understanding the maintenance of plant diversity. Our results from both shade-

273   house and field experiments consistently support the observation that rare species experience stronger

274   conspecific negative PSF than common species. In the meantime, we also found rare species had

275   stronger phylogenetic conservatism in plant-soil feedback than common species (Figs. 2 and 4; Table 1).

276   This conservatism in PSF shelters rare species from the effect of negative soil-feedback under distantly

277 related adults as hypothesized by Fig. 1c and provides them recruitment advantage under heterospecific

278 herd protection by lowering chance to encounter host-specific natural enemies (Peters 2003; Bachelot *et*

279 *al.* 2016). In contrast, although common species had weak negative conspecific PSF, they suffered

280 consistently strong heterospecific soil feedback, independent of phylogenetic distance (Figs. 3 and 5). In

281 other words, different from rare species, the recruitment of common species is less restricted under their

282 own adults but more restricted under heterospecifics. This contrast PSF between rare and common

283 species offers a promising answer to the puzzle of rare species-common species coexistence.

284 The variation in the strength of soil feedback from heterospecific adults in maintaining plant

285 diversity has been largely overlooked in the past. Our study highlights the importance of heterospecific

286 PSF in mediating seedling recruitment and species coexistence. Recruitment in the proximity of

287 heterospecifics is crucial for rare species whose seedlings are more likely surrounded by heterospecific

288 individuals than conspecific individuals. For example, the majority of seeds and seedlings of less

289 abundant species were found to be away from the conspecific adults in our study site (Fig. S5), and rare

290 tree species in most forests are more scattered in distribution than common species (He *et al.* 1997). The

291 variation in spatial distribution of recruitments suggested that heterospecific instead of conspecific soil

292 feedback is often the trouble that rare species have to deal with in nature, and thus weaker soil feedback

293 from heterospecific trees would facilitates recruitment of rare species and promote species coexistence.

294 Our finding that rare species had stronger conspecific but weaker heterospecific PSF than common

295 species suggests higher specificity in the effect of soil microbiota on rare species. This mechanism

296 would protect rare species from other adversaries, e.g., stochastic extinction. When facing disturbance,

297 the decrease in population density of rare species would reduce associated soil enemies and weaken the

298 strength of conspecific negative soil feedback. This, coupled with the fact that soil enemies maintained

299 by heterospecifics would have weak or no negative effects on rare species recruitment, could make rare

species rebound quickly to equilibrium abundance (Yenni *et al.* 2012, 2017; Liu *et al.* 2015). In contrast, for common species, the decrease in population density does not necessarily promote recruitment as they often experience strong negative feedback from the soil enemies of heterospecifics (McCarthy-Neumann & Kobe 2010).

Our sterilized treatment that removed all soil microbiota including mutualists and antagonists showed an overall positive effect on seedling performance (Fig. S3), implying the shared antagonists (e.g., pathogens) among phylogenetically related plant species are responsible for the effect of negative plant-soil feedback (Dyer *et al.* 2007; Gilbert & Webb 2007; Barrett & Heil 2012; Gilbert *et al.* 2012; Parker *et al.* 2015; Kempel *et al.* 2018). A possible reason that phylogenetic signal in PSF was detected for rare species but not for common species (Figs. 2 and 4) could be because rare species are associated with more host-specific pathogens than common species. Pathogens of a focal tree, theoretically, can spillover onto phylogenetically related species, and species with greater abundance are likely to produce and receive more pathogen inocula which would dilute specialized pathogens in those abundant species (Power & Mitchell 2004; Parker *et al.* 2015). An alternative possibility is that the specialized effect of soil microbiota on rare species could result from the co-infection of (strong) pathogens and (weak) mycorrhizal fungi (Corradi & Bonfante 2012). Common species are generally considered to have a stronger association with mycorrhizal fungi and rely more on their mutualists compared to rare species (Hart *et al.* 2003). The beneficial effects of mycorrhizal fungi could also be host specialized (Mangan *et al.* 2010a), which counteracts negative pathogenic effects on seedling recruitment, and thus lead to the host-general net effect of soil microbiota on common species (Bennett *et al.* 2017; García-Parisi & Omacini 2017; Wang *et al.* 2019). Although we did not directly identify the specific pathogens and mycorrhizal fungi, the net effects of these two fungal guilds have been suggested to be important in plant-soil feedback (Bever *et al.* 2012). We suggest future studies to isolate these host-specific microbes

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323 and also to analyze both fungal and bacterial community composition for better understanding the

324 effects of plant-soil feedback.

325   Our study quantified phylogenetic variation in plant-soil microbiota interactions between rare and

326 common species in a subtropical forest in China. We detected strong phylogenetic conservatism in the

327 strength of soil feedback for rare species but not for common species. Consequently, rare species

328 suffered stronger negative soil feedback from close relatives (e.g. conspecifics) but weaker or no

329 feedback from distant relatives (e.g. heterofamilials), while common species were less affected by

330 conspecific negative effects but more strongly affected by heterospecific negative effects. Our study

331 highlights the importance of quantifying asymmetric heterospecific plant-soil feedback for

332 understanding the role of plant-soil feedback in maintaining plant diversity, particularly rare species-

333 common species coexistence.

334

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468 **Tables and Figures**

469 **Table 1 Linear mixed-effect models for testing effects of phylogenetic relatedness, species relative**

470 **abundance and their interaction term on the strength of plant-soil feedback.** The estimates of the

471 effects are shown for the shade-house sterilization experiment and the reciprocal field experiment,

472 respectively. Phylogenetic distance was measured as the distance between focal seedling species and

473 soil-source species. Boldfaced values indicate significance at $P < 0.05$.

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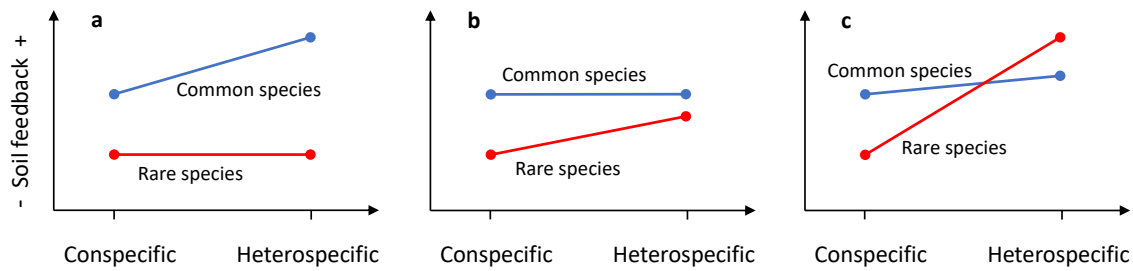|	Effect	Estimate	Std.Error	$P(>|t|)$
	Intercept	-1.331	0.402	**0.002**
	Phylogenetic distance	0.006	0.001	**< 0.001**
Shade-house	Log(Abundance)	0.175	0.065	0.054
experiment	Phylogenetic distance	-0.001	0.0002	**< 0.001**
	Random effect:		Std.Dev	
	Species (intercept)		0.120	
	Intercept	-0.013	0.004	**0.004**
	Phylogenetic distance	0.0001	0.00003	**< 0.001**
Field experiment	Log(Abundance)	0.001	0.0008	0.184
	Phylogenetic distance	-0.00001	0.000005	**0.006**
	Random effect:		Std.Dev	
	Species (intercept)		2.91e-07	

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Figure 1 Variation in soil feedback from conspecifics and heterospecifics between rare and common species. The *x* axis indicates conspecific versus heterospecific soils and *y* axis indicates the strength of soil feedback, ranging from negative to positive. (**a**) Rare species shows no change in conspecific and heterospecific soil feedback strength, while common species has weaker heterospecific effect (positive slope), leading to recruitment advantage in heterospecific soils, thus preventing colonization of rare species. (**b**) Common species shows no change in soil feedback, while rare species has weaker negative feedback in heterospecific soils, leading to recruitment advantage under heterospecifics but the strength is not strong enough to overwhelm the common species. (**c**) Rare species has stronger conspecific soil feedback but weaker heterospecific feedback than common species, leading to species coexistence. Note negative slopes are unlikely to occur as predicted by the natural enemy hypothesis of invasive species and thus are not considered here.

Figure 2 Boxplots showing the change of plant-soil feedback strength in relation to phylogenetic distance between seedlings of focal species and soil-source species for rare and common species, as measured in shade-house experiment. Rare species: *Helicia reticulata*; *Ormosia fordiana*; *Quercus macrocalyx*; Common species: *Canarium album*; *O. glaberrima*; *Q. auricoma*. "conspecific" means conspecific seedlings grew in soils taken under conspecific adults, "congeneric" means seedlings grew in soils taken from adult trees of congeneric sister species, etc. The species that donated soils is called "soil-source species". Letter labels indicate the significant difference in the strength of plant-soil feedback across phylogenetic relatedness at $P < 0.05$ by the Dunnett's Modified Tukey-Kramer Pairwise Multiple Comparison Test. Asterisks indicate whether the strength of plant-soil feedback is significantly negative using one-sided Wilcoxon signed-rank test (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The sample size for each box is given by *n*.
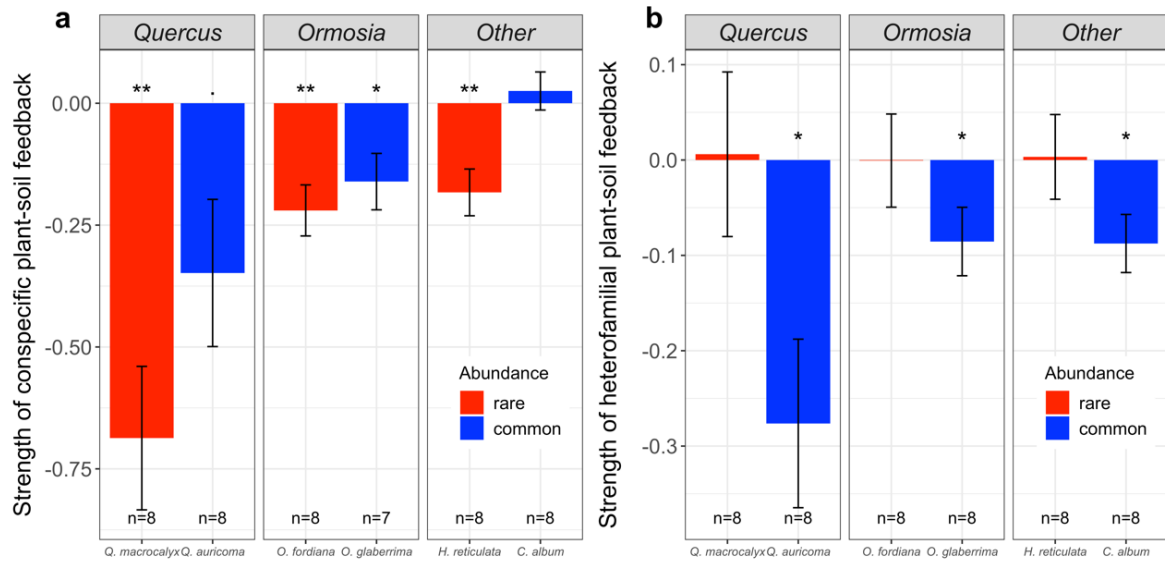
Figure 3 Variation in the strength of plant-soil feedback from (a) conspecifics and (b) heterofamilials between the rare and common sister species pairs in the shade-house experiment. Bars indicate ±one standard error, and asterisks indicate whether the mean in strength is significantly negative (· $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The sample size for each bar is given by n.
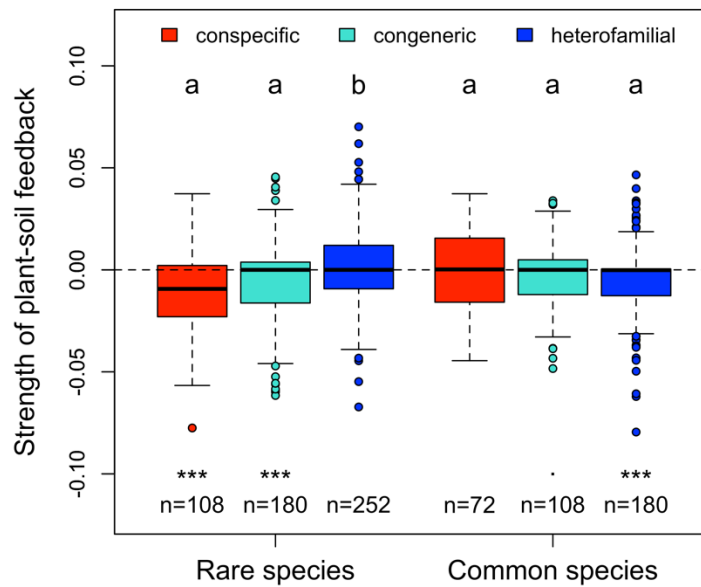
Figure 4 Boxplots showing the strength of plant-soil feedback in relation to phylogenetic distance between focal seedling species and soil-source species for rare and common species, in the *in situ* field experiment. Rare species: *Ormosia fordiana*; *Quercus macrocalyx*; *Q. pachyloma*; Common species: *O. glaberrima*; *Q. auricoma*. Letter labels indicate the significant difference in plant-soil feedback across phylogenetic relatedness at $P < 0.05$ by the Dunnett's Modified Tukey-Kramer Pairwise Multiple Comparison Test. Asterisks indicate whether the strength of plant-soil feedback is significantly negative ($\cdot$ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The sample size for each box is given by *n*.
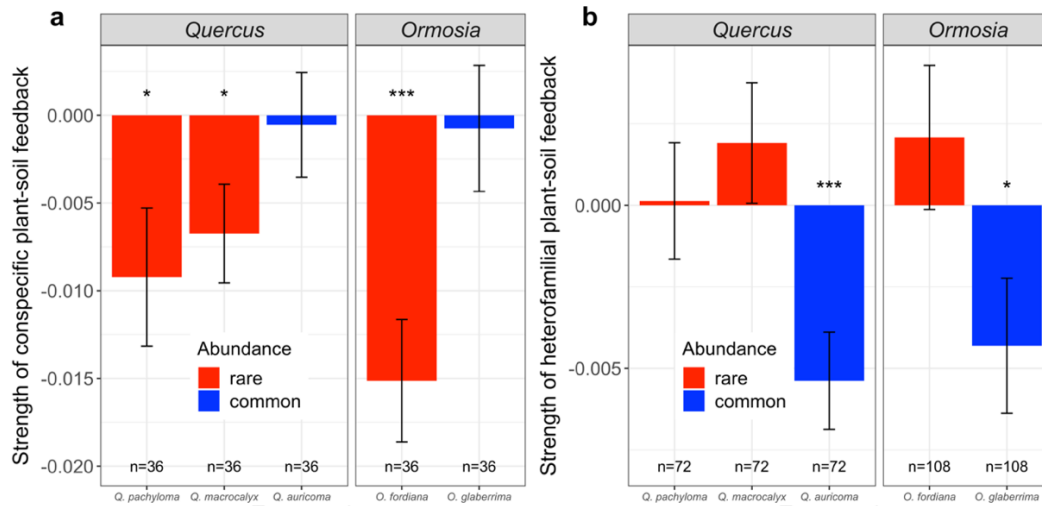
Figure 5 Variation in the strength of conspecific plant-soil feedback (a) and heterofamilial feedback (b) between the rare and common sister species pairs in the field experiment. Bars indicate ±one standard error, and asterisks indicate significantly negative plant-soil feedback (* $P <$ 0.05; ** $P < 0.01$; *** $P < 0.001$). The sample size for each bar is given by *n*.