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Relationships between plant-soil feedbacks and functional traits

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1 **Relationships between plant-soil feedbacks and functional traits**

2

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19

20 Abstract

21 1. Plant-soil feedbacks (PSF) and functional traits are two active but not well
22 theoretically integrated areas of research. However, PSF and traits are both affected
23 by life history evolution, so the two should theoretically be related.

24 2. We provide a conceptual framework to link plant functional traits to two types of
25 PSF metrics, and hypothesize that individual PSF (**plant performance in conspecific**
26 **versus heterospecific soil**) should be related to the fast-slow trait spectrum, while
27 pairwise PSF (**the sum of the individual feedbacks for two species growing in each**
28 **other's soils**) should be related to trait dissimilarity. We performed meta-analyses to
29 test these hypotheses by compiling two datasets, one dataset consisting of individual
30 PSF values and plant trait values (specific leaf area, SLA; leaf N concentration, LNC;
31 specific root length, **SRL**; fine root diameter, FRD; plant height; seed mass), and the
32 second consisting of pairwise PSF values and trait dissimilarity.

33 3. Our meta-analyses showed that individual PSF values were more negative in faster-
34 growing species with greater SLA, LNC and SRL, supporting the growth-defence
35 trade-off hypothesis. Plant height was positively correlated with individual PSF,
36 perhaps because large, long-lived plants defend against pathogens better than smaller,
37 shorter-lived plants. We also found that larger-seeded species had more positive or
38 less negative PSF, likely reflecting greater tolerance of soil pathogens. **The direction**
39 **of relationships between trait dissimilarity and pairwise PSF varied with trait identity.**

40 Dissimilarities in SRL and FRD were negatively correlated with pairwise PSF, while
41 height dissimilarity was positively correlated with pairwise PSF. The contrasting

42 relationships may reflect distinct links between trait dissimilarity and niche and
43 fitness differences.

44 4. *Synthesis*. Our results demonstrate how an integration of PSF and trait-based
45 approaches can advance plant community ecology.

46

47 **KEYWORDS**

48 growth-defence trade-off, functional traits, niche differentiation, phenotypic
49 dissimilarity, plant–soil (below-ground) interactions, species coexistence, species-
50 specialized pathogens/mutualists

52 1 | INTRODUCTION

53 Plant-soil feedbacks (PSF) express how plants interact with soil microbes and soil
54 biogeochemical and physical properties. Negative PSF, where soil microbes and
55 abiotic properties reduce plant performance, can theoretically contribute to species
56 coexistence via conspecific negative density-dependence (Bever et al., 2015;
57 Kandlikar et al., 2019). This has provided a useful framework for evaluating the
58 influence of soil microbes on community dynamics and biodiversity maintenance
59 (Bever, 2003; Crawford et al., 2019; van der Putten et al., 2013). However, there is
60 considerable variation in the strength of feedbacks observed across a broad range of
61 species. This variation may reflect differences in local abiotic factors such as soil
62 nutrients, moisture and climate factors (Bennett & Klironomos, 2019; De Long et al.,
63 2019; Smith-Ramesh & Reynolds, 2017) or it could also be related to variation in
64 plant functional traits (Bever et al., 2012; Ke et al., 2015). Although recent
65 experimental studies tested the relationship between PSF and plant traits (Baxendale
66 et al., 2014; Cortois et al., 2016; Kuřáková et al., 2018; Münzbergová & Šurinová,
67 2015; Semchenko et al., 2018; Teste et al., 2017; Wilschut et al., 2019), there remain
68 gaps in the conceptual framework theoretically relating these two areas and a global
69 test for this relationship.

70 Life history evolution has produced distinct plant strategies that are positioned
71 along the fast-slow trait spectrum. For example, plants can invest in traits that
72 promote rapid growth (e.g., via nutrient acquisition) or in traits that provide defence
73 against antagonists (Díaz et al., 2016; Weiher et al., 1999; Westoby, 1998) but not

74 both to the same degree, which leads to a growth-defence trade-off. For seed traits,
75 previous studies provide evidence for a trade-off between investment in numerous
76 small seeds versus fewer larger seeds. The seed number-seed size trade-off predicts
77 that small-seeded species have an advantage in fecundity and colonization, which may
78 aid in pathogen escape through increased dispersal ability, while large-seeded species
79 have greater seedling survival, competitive ability and pathogen tolerance (Bagchi et
80 al., 2014; Dalling et al., 2011; Moles, 2018; Moles & Westoby, 2004; Muller-Landau,
81 2010). Plant height may indicate plant lifespan and competitive ability for light
82 (Moles et al., 2009). A long-lived plant species, such as a tree, likely invests more in
83 defence traits (e.g., structural traits, chemical defence) than a short-lived species, such
84 as an herbaceous species, which should allocate more resources to nutrient acquisition
85 or reproduction to maximize fitness (Kulmatiski et al., 2017).

86 Given the important roles of soil microbes in both nutrient acquisition and plant
87 disease, we should expect relationships between PSF and the plant strategies
88 traditionally linked with functional traits. Furthermore, plant traits should feed back to
89 influence the composition and functioning of soil microbial communities by
90 controlling the quality and quantity of resources entering into soil (Bardgett, 2017; de
91 Vries et al., 2012; Delgado-Baquerizo et al., 2018; Legay et al., 2014). In other words,
92 traits influence both the effect of a plant on the soil community and the response of
93 the plant to the soil community. Based on the likely linkages between PSF and
94 functional traits, we hypothesize a strong relationship between traits involved in the
95 growth-defence trade-off and individual PSF (the absolute performance of a plant in

96 conspecific soil versus heterospecific soil) (Figure 1a). Specifically, fast-growing
97 plant species with traits, such as small seed size, short lifespan, high leaf N
98 concentration, specific leaf area and specific root length and low fine root diameter,
99 should experience more negative feedback effects than slow-growing plants with the
100 opposite trait syndrome, because the former have high growth rate/ nutrient
101 acquisition but low defence against natural enemies (Coley, 1988; Coley et al., 1985;
102 Comas & Eissenstat, 2009; Laliberté et al., 2015; Lind et al., 2013; Teste et al., 2017).

103 In contrast to the individual PSF, pairwise PSF, which essentially represent the
104 sum of the individual feedbacks for two species growing in each other's soils, should
105 be related to ecological dissimilarity rather than absolute trait values. Negative values
106 of pairwise PSF indicate that plants influence soils in a way that favours
107 heterospecific over conspecific individuals, stabilizing coexistence through
108 conspecific negative density dependence, whereas positive values indicate the
109 opposite patterns (Bever et al., 1997). Crawford et al. (2019) recently showed that
110 plant phylogenetic distance has a linearly negative correlation with pairwise PSF.
111 However, Wandrag et al. (2020) showed that there was a divergent trend in feedback
112 responses to soil biota with increasing phylogenetic distance, and thus it is difficult to
113 predict feedback outcomes using phylogeny alone. This trend may reflect high trait
114 similarity among closely related plants, while trait similarity decreases – or at least
115 becomes less predictable – with increasing phylogenetic distance. However, little is
116 known about correlations between pairwise PSF and trait dissimilarity. Directly
117 linking pairwise PSF to trait dissimilarity may be more powerful for understanding

118 the role of PSF in species coexistence and biodiversity maintenance, but it remains a
119 key knowledge gap.

120 Modern coexistence theory asserts that species coexistence depends on two non-
121 exclusive processes, stabilizing differences, which promote coexistence, and average
122 fitness differences, which promote competitive exclusion (Chesson, 2000, 2018). In
123 theory, trait dissimilarity can reflect niche differences or average fitness differences,
124 depending on the traits considered and the biotic and abiotic context (Kraft et al.,
125 2015; Mayfield & Levine, 2010). If PSF and traits represent two aspects of a
126 coordinated life history strategy, then their effects on coexistence should be
127 reinforcing (Figure 1b): Negative pairwise PSF (i.e. species perform better in
128 heterospecific than conspecific soil) should correlate with trait dissimilarities that
129 contribute to niche differences by promoting use of different soil nutrients [such as
130 specific leaf area, specific root length (Cadotte, 2017)] or the accumulation of
131 specialized soil pathogens (Smith-Ramesh & Reynolds, 2017). In contrast, positive
132 pairwise PSF should correlate with trait dissimilarities that drive fitness differences
133 favouring one competitor over the other regardless of their relative abundance,
134 thereby reflecting competitive hierarchy (Chesson, 2000). For example, positive
135 pairwise PSF have been observed in natural ecosystems such as ecto-mycorrhizal tree
136 dominated temperate forests (Nuñez & Dickie, 2014; Reynolds et al., 2003; Smith-
137 Ramesh & Reynolds, 2017), because plant species associated with ecto-mycorrhizal
138 fungi can gain competitive advantages over plants associated with arbuscular
139 mycorrhizal fungi by efficiently capturing soil nutrients and lowering nutrient

140 availability that is diminishing growth of arbuscular mycorrhizal species.
141 Theoretically, trait dissimilarity reflecting average fitness difference/competitive
142 hierarchy [e.g. height, a key trait for size-asymmetric competition for light (Cadotte,
143 2017)] should correlate with positive pairwise PSF (Figure 1b)

144 Empirical support for these two hypotheses (Figure 1) would help explain the
145 large variation of PSF for co-occurring plants, facilitate prediction of PSF for plant
146 species for which no experiments have been conducted, and advance our
147 understanding of the factors driving plant community dynamics. To meet this need,
148 we conducted a comprehensive literature review and meta-analysis to test our
149 hypotheses about plant traits and both individual and pairwise PSF. Specifically, we
150 tested the hypotheses that 1) individual PSF will be negatively correlated with fast life
151 history traits; and 2) pairwise PSF will be correlated with trait dissimilarity.

152

153 2 | METHODS

154 2.1 | Data compilation

155 In this meta-analysis, we calculated individual and pairwise PSF using two
156 different datasets. For individual PSF, we searched ISI Web of Science on 3 August
157 2018 without restriction on publication year using the key search term “plant soil
158 feedback”. We added extra studies from recent meta-analyses of Crawford et al.
159 (2019) and Lekberg et al. (2018), resulting in a total of 2585 papers. We screened
160 paper titles and abstracts to ensure that they were in the correct subject area, and thus
161 2208 papers were removed. After this screening, 377 papers were assessed for

162 eligibility using the following criteria: (1) plants were grown in conspecific and
163 heterospecific soil; (2) conspecific soil had to be clearly influenced by one single
164 plant species in the conditioning phase, and heterospecific soil was not affected by the
165 focal species (we included studies where the authors stated that field soil was
166 collected from certain species and used as soil inoculum); (3) PSF were tested for
167 natural plants and studies for cultivated or crop plants were avoided; (4) studies
168 reported means, standard errors or standard deviations or 95% confidential intervals
169 and sample sizes for plant performance in the feedback phase. In total, 63 papers met
170 these criteria (Figure S1, Appendix 1).

171 Data were extracted from text, tables, figures or supplementary materials. We
172 used ImageJ to extract means, standard errors or standard deviations of plant biomass
173 from figures in the chosen papers (Schneider et al., 2012). Multiple experimental
174 treatments from the same study were included in our analysis to take complete
175 advantage of published results. Species names of focal plants and paper identity
176 (authors, publication years) were recorded. In total, we constructed a dataset
177 consisting of 2110 observations and 216 plant species representing a variety of
178 functional groups (e.g., herbs, trees and shrubs).

179 For pairwise plant-soil feedbacks, we used the dataset compiled by Crawford et
180 al. (2019). This dataset consisted of 1038 observations for 508 species pairs that were
181 extracted from 69 peer-reviewed papers. The dataset included studies that conducted
182 in forest and grassland ecosystems, and used lab or field experimental approaches.
183 The plant species included trees and herbs. Effect sizes of pairwise PSF were

184 calculated using species average performance in **conspecific** versus **heterospecific**
 185 soils, standard errors and replicates (see the following details) for each species pair
 186 and each observation. We obtained effect sizes, variances and species pairs for our
 187 meta-analysis.

188

189 **2.2 | Effect size of individual PSF**

190 Effect size of individual **PSF** was calculated using the natural log of response
 191 ratio (Hedges et al., 1999; **Brinkman et al., 2010**)

$$192 \quad rr = \text{Ln}\left(\frac{X_e}{X_c}\right)$$

193 where X_e and X_c are plant biomass in conspecific and heterospecific soil respectively.

194 Variance of each effect size was estimated

$$195 \quad v_{rr} = \frac{(SD_e)^2}{n_e(X_e)^2} + \frac{(SD_c)^2}{n_c(X_c)^2}$$

196 where SD_e and SD_c are standard deviations of plant biomass in conspecific and
 197 heterospecific soil respectively, and n_e and n_c are sample sizes for conspecific and
 198 heterospecific soil treatments respectively.

199

200 **2.3 | Effect size of pairwise PSF**

201 To compare pairwise PSF across species that differ in their growth rates and sizes
 202 across experiments that differ widely in their methodologies, plant **biomass** was log-
 203 transformed (Crawford et al., 2019). The pairwise PSF for two plant species, A and B,
 204 and their respective soils, α and β , is

$$205 \quad rr(I_s) = Ln(\alpha_A) - Ln(\alpha_B) - Ln(\beta_A) + Ln(\beta_B)$$

206 where α_A is plant A performance in conspecific soil, α_B is plant B performance in
 207 heterospecific soil, β_A is plant A performance in heterospecific soil, and β_B is plant B
 208 performance in conspecific soil. Variance of $rr(I_s)$ was estimated using the equation

$$209 \quad v_{rr(I_s)} = \frac{v_{\alpha_A}}{n_{\alpha_A}(\alpha_A)^2} + \frac{v_{\alpha_B}}{n_{\alpha_B}(\alpha_B)^2} + \frac{v_{\beta_A}}{n_{\beta_A}(\beta_A)^2} + \frac{v_{\beta_B}}{n_{\beta_B}(\beta_B)^2}$$

210 where v and n are variance and sample size of plant performances respectively.

211

212 **2.4 | Calculating species-level average individual and pairwise PSF**

213 In our dataset, there were multiple observations (i.e., effect size values) for one
 214 plant species or one species pair. We did not consider variations within plant species
 215 or within species pair, and thus species-level average PSF values were calculated by
 216 one mixed effect model using the ‘metafor’ package (Viechtbauer, 2010) in R. In this
 217 model, species identity or species pair were used as the fixed effect and study as the
 218 random effect to overcome possible data dependence (i.e., from multiple effect sizes
 219 in single studies) (Nakagawa et al., 2017). Average effect size and its variance for
 220 each species were calculated using the formulas in this model (Borenstein, 2009)

$$221 \quad \bar{rr} = \frac{\left(\sum_{i=1}^k \frac{rr_i}{v_i + \tau^2} \right)}{\left(\sum_{i=1}^k \frac{1}{v_i + \tau^2} \right)}$$

$$222 \quad \bar{v} = \frac{1}{\sum_{i=1}^k \frac{1}{v_i + \tau^2}}$$

223 where rr_i , v_i and τ^2 are effect size, within-experiment variance and between-

224 experiment for experiment i within each subgroup (i.e. each species) respectively. τ^2
225 was estimated using the restricted maximum likelihood approach. We also computed
226 average pairwise PSF value and its variance for each species pair by performing one
227 mixed effects models with species pair as one fixed effect and study as one random
228 effect and using the formulas mentioned above.

229

230 **2.5 | Plant functional traits**

231 To test linkages between PSF values and plant traits or trait dissimilarity, we
232 chose six plant functional traits that are closely associated with plant life history
233 strategies: specific leaf area (SLA, the one-sided area of a fresh leaf divided by its dry
234 mass, $\text{mm}^2 \text{mg}^{-1}$), leaf nitrogen (N) concentration (LNC, the total amounts of N per
235 unit of dry leaf mass, mg g^{-1}), specific root length (SRL, the ratio of root length to dry
236 mass of fine roots, cm g^{-1}), fine root diameter (FRD, mm), plant height (the shortest
237 distance between the upper boundary of the main photosynthetic tissues on a plant
238 and the ground level, m) and seed dry mass (SM, the dry mass of an average seed of a
239 species, mg). SLA, LNC, SRL and FRD are important plant economic traits that are
240 related to carbon and soil nutrient acquisition and reflect trade-offs between growth
241 and defence (Kong et al., 2019; Reich, 2014; Westoby, 1998; Wright et al., 2004).
242 Plant height reflects plant size and lifespan. Seed mass reflects a trade-off between
243 investment in numerous small seeds and fewer larger seeds.

244 We obtained all trait data from the TRY Database (Kattge et al., 2020). Trait
245 values from different locations or populations were averaged to obtain mean values

246 for each species; we did not consider intraspecific trait variability. Average trait
247 values were natural log-transformed for each species and each trait prior to analyses
248 because of large difference in orders of magnitude across plant species. Trait
249 dissimilarity was calculated using the Euclidian distance for each species pair, and
250 they were log-transformed prior to meta-analyses if needed to reduce the influences of
251 differences in value sizes.

252 Previous work, including one of the meta-analyses we pulled data from for our
253 study (Crawford et al., 2019), has found that plant relatedness significantly predicts
254 PSF (see also Anacker et al., 2014). Testing for relationships between plant
255 phylogeny and plant traits (e.g., testing for phylogenetic signal in plant traits or testing
256 for correlations between phylogenetic distance and trait dissimilarity) would help
257 inform the extent to which the relationship between plant relatedness and PSF is
258 driven by closely related individuals sharing similar traits. However, we cannot make
259 robust predictions with our data because of the inequality of sample sizes of plant
260 traits and low phylogenetic resolution. We recommend that future studies, using
261 rigorous experimental design (consistent trait sample sizes, robust phylogenetic
262 relatedness, and a large range of plant species), are required to address the connection
263 between trait dissimilarity, phylogenetic distance, and PSF (e.g., similar to Fitzpatrick
264 et al., 2017).

265

266 **2.6 | Data analyses**

267 A random effects model was used to estimate the overall weighted effect sizes

268 using the *ram* function in the ‘metafor’ package in R (Viechtbauer, 2010). A *Z* test
269 was used to determine if the weighted effect size was equal to zero. The total
270 heterogeneity of effect size was tested using the *Q* statistic, which follows a chi-
271 squared distribution under the null hypothesis that the effect size is the same for all
272 experiments (Borenstein, 2009). Based on the results from this model, publication
273 bias of non-significant results was tested by constructing a funnel plot and calculating
274 Rosenthal’s fail-safe numbers to check for asymmetry or gaps in the data (Sterne &
275 Egger, 2001).

276 We performed a series of univariate meta-regressions rather than single
277 multivariate meta-regressions to test our hypotheses for fully exploiting our datasets.
278 We are aware that it is of interest to assess the relative importance of different traits in
279 driving the variation of PSF, but it is not the goal of this present study, and this study
280 aims to generalize the relationships between PSF and key traits that reflect plant life
281 history strategy. Meta-regressions were then performed to evaluate the relationships
282 between each individual plant trait, or each measure of trait dissimilarity, and species-
283 average PSF effect sizes using random effects models. **The random-effects models in**
284 **meta-analysis incorporate an assumption that the different studies are estimating**
285 **different treatment effects, and these models allow us to test if variables cause the**
286 **heterogeneity of effect sizes (Borenstein, 2009).** For each trait model, the total
287 heterogeneity of effect sizes (Q_T) was partitioned into residual heterogeneity (Q_E) and
288 variate-explained heterogeneity (Q_M) (Borenstein, 2009). The Q_M statistic follows a
289 chi-squared distribution under the null hypothesis that the effect size is the same for

290 all subgroups. For data of traits or trait similarities, values were log-transformed, if
291 necessary, to meet the requirements of regression analyses. All analyses were
292 performed in R (R Core Team, 2020).

293

294 3 | RESULTS

295 3.1 | Linkages between plant traits and individual PSF

296 Across all studies, average individual PSF was negative (95% confidence interval
297 = -0.0924 ± 0.0741 , $Z = -2.4437$, $P = 0.014$). However, there was a significant
298 variation in effect size ($Q = 13599.67$, $df = 2109$; $P < 0.001$). Without considering the
299 influence of moderators (i.e., plant species identity and plant traits), 90.79% of total
300 variance in the true effects was due to heterogeneity rather than sampling variance
301 (i.e., $I^2 = 90.79\%$), **reflecting the inconsistency across the effect sizes that needs to be**
302 **explained using moderators**. Individual PSF values were inconsistent across plant
303 species ($Q_M = 4310.44$, $df = 215$, $P < 0.001$). We did not detect publication bias for
304 this model, because the funnel plot did not show asymmetry in effect size distribution
305 (effect size vs. standard error, Figure S2), and the Rosenthal's fail-safe number
306 showed that 485803 null records would have to be added to change the results of this
307 model.

308 Trait-based relationships with individual PSF were consistent with Hypothesis 1
309 (Figure 1a). PSF values decreased (i.e., they became more negative) with increased
310 specific leaf area (slope = -0.2272 , $Q_M = 7.49$, $P = 0.006$, $n = 134$, Figure 2a), leaf N
311 concentration (slope = -0.0095 , $Q_M = 3.99$, $P = 0.045$, $n = 153$, Figure 2b) and

312 specific root length (slope = -0.0994, $Q_M = 5.26$, $P = 0.022$, $n = 78$, **Figure 2c**). Plant
313 species with greater FRD (slope = 0.3018, $Q_M = 5.28$, $P = 0.022$, $n = 64$, **Figure 2d**),
314 plant height (slope = 0.082, $Q_M = 21.71$, $P < 0.001$, $n = 171$, **Figure 2e**) and seed mass
315 (slope = 0.0261, $Q_M = 4.49$, $P = 0.034$, $n = 181$, **Figure 2f**) showed less negative or
316 even more positive individual PSF values.

317

318 **3.2 | Linkages between trait dissimilarity and pairwise PSF**

319 Pairwise PSF values were associated with dissimilarity in SRL, FRD and height,
320 but the direction of the relationship varied between these traits; these findings
321 partially supported hypothesis 2 (**Figure 1b**). There was no relationship between PSF
322 values and SLA dissimilarity ($Q_M = 0.42$, $P = 0.516$, $n = 183$, **Figure 3a**) or between
323 PSF values and LNC dissimilarity ($Q_M = 0.48$, $P = 0.488$, $n = 197$, **Figure 3b**).
324 However, pairwise PSF values were negatively related to SRL dissimilarity (slope = -
325 0.1091, $Q_M = 6.39$, $P = 0.012$, $n = 103$, **Figure 3c**) and FRD dissimilarity (slope = -
326 0.5989, $Q_M = 5.56$, $P = 0.018$, $n = 91$, **Figure 3d**), and they were positively related to
327 height dissimilarity (slope = 0.2012, $Q_M = 4.41$, $P = 0.036$, $n = 224$, **Figure 3e**). No
328 relationship was detected between PSF values and SM dissimilarity ($Q_M = 0.1862$, P
329 = 0.666, $n = 230$, **Figure 3f**).

330

331 **4 | DISCUSSION**

332 Plant-soil feedbacks (PSF) and functional traits are two active research areas of
333 ecology, but global evidence linking traits with **PSF** remains scarce. Integrating traits

334 and PSF could explain variation in PSF among species in natural communities and
335 advance our understanding of the role of PSF in generating niche and fitness
336 differences and thus species coexistence. Our results help fill this knowledge gap by
337 demonstrating that (1) individual PSF were related to plant traits in directions
338 consistent with known trade-offs between growth and defence or between seed
339 number and seed size, and (2) the direction of relationships between trait dissimilarity
340 and pairwise PSF varied with trait identity, from negative, neutral to positive.

341

342 4.1 | Variation of individual PSF along the fast-slow trait spectrum

343 We tested the growth-defence hypothesis in the context of plant-soil feedbacks
344 (Hypothesis 1, Figure 1a) and found evidence of the negative relationships between
345 PSF and traits associated with fast life histories, i.e. specific leaf area, leaf N
346 concentration and specific root length, and positive relationship between PSF and
347 traits for slow life history, i.e. fine root diameter, seed mass and plant height (Figure
348 2), presumably because the fast-growing plants have lower defence against soil
349 pathogens (Semchenko et al., 2018). This finding is consistent with evidence that
350 slow-growing species with greater seed mass are more tolerant of conspecific
351 neighbours (Lebrija-Trejos et al., 2016), and that plant–soil feedbacks are a key
352 mechanism driving conspecific negative density dependence (Mangan et al., 2010;
353 Maron et al., 2016). The plant height-PSF relationship may reflect the fact that taller
354 plants have closer associations with mycorrhizal fungi than shorter plants, because
355 they are not limited by light and can exchange carbon for nutrients with mycorrhizal

356 fungi (Cheeke et al., 2019).

357 Based on the trait-PSF relationships we observed, we can now make predictions
358 about how PSF may vary across environmental gradients. Fertile habitats are usually
359 dominated by plant species with fast traits, while slow-growing species dominate
360 infertile habitats (Diaz et al., 2004; Reich, 2014; Wright et al., 2004). Under nutrient-
361 rich conditions, negative PSF should be pervasive and play more important roles in
362 community dynamics than that under nutrient-poor conditions; under nutrient-poor
363 conditions, soil mutualisms (e.g. mycorrhizas, N₂ fixers) that drive positive plant-soil
364 feedbacks would be expected to be more important in community dynamics (Laliberté
365 et al., 2015; Png et al., 2019). The same reasoning suggests that PSF should play a
366 role in succession: early-successional plants that are characterized by fast growth,
367 high nutrient acquisition, small seed size and short lifespan should be more negatively
368 influenced by soil biota than late-successional plants with the opposite traits (Bauer et
369 al., 2015; Kardol et al., 2006). Moreover, unpacking the relationship between fast-
370 slow traits and individual PSF may enable us to better understand plant population
371 ecology, including transient and stochastic dynamics (Stott et al., 2010; Thuiller et al.,
372 2007), and can be used to inform vegetation management, such as restoration and
373 species invasions (Suding et al., 2013; Wubs et al., 2016). Observed time lags
374 between alien species arrival and dominance (Coutts et al., 2018) and alien population
375 booms-and-busts (Simberloff & Gibbons, 2004) may be at least partly attributed to
376 the time required for plant-soil feedbacks to accumulate and take effect, with slow-
377 growing and fast-growing plant invaders experiencing different effects.

378

379 **4.2 | Correlations between trait dissimilarity and pairwise PSF are complex**

380 PSF theory has clearly shown that predicting species coexistence requires
381 measurement of pairwise PSF, i.e. the relative performance of species on conspecific
382 and heterospecific soil (Bever et al., 1997). Our results indicated that trait
383 dissimilarity showed positive or negative or no correlations with pairwise PSF;
384 greater SRL dissimilarity caused more negative PSF, while the opposite pattern was
385 observed for height dissimilarity (Figure 3). These findings partially supported our
386 prediction that pairwise PSF is related to trait dissimilarity (Hypothesis 2, Figure 1b),
387 but they indicated that the links between trait dissimilarity and pairwise PSF may be
388 more complicated than previously expected. Our findings are consistent with the idea
389 that many relationships between trait differences and coexistence are possible, with
390 differing implications for competitive outcomes (Gross et al., 2015; Kraft et al.,
391 2015).

392 The negative relationship we observed between SRL dissimilarity and pairwise
393 PSF may reflect differences in plant strategies related to resource acquisition and
394 defence. Plants with different SRL dominate habitats with different resource
395 availability, and SRL dissimilarity is a predictor of niche difference across herb and
396 tree species (Fort et al., 2015; Valverde-Barrantes et al., 2013). Fast-growing species
397 with high SRL tend to condition soil with high abundance of pathogens and nutrient
398 availability, and slow-growing species with low SRL produce soil with the opposite
399 characters (Bagchi et al., 2014; Bever et al., 2015; Wardle et al., 2004). Consequently,

400 fast-growing species are promoted in soil conditioned by slow-growing species
401 because of low infection from pathogens, whilst slow-growing species are promoted
402 in soil conditioned by fast-growing species due to high nutrient availability. Of
403 course, we cannot rule out the possibility that fast-growing might not establish in soil
404 conditioned by slow-growing species due to low nutrient availability or allelopathic
405 chemicals.

406 In contrast, between-species difference in height were associated with
407 increasingly positive PSF, which should promote competitive exclusion. Differences
408 in this trait likely reflects the differential ability of species to pre-empt the same
409 resources (e.g. light) or to form associations with ecto-mycorrhizal fungi, creating a
410 competitive hierarchy and leading to average fitness differences (Cadotte, 2017;
411 Gross et al., 2015; Herben & Goldberg, 2014; Kraft et al., 2015). The trait-PSF
412 relationships we observed would further reinforce such competitive hierarchies. In
413 principle, these patterns should help explain competitive exclusion and abundance
414 patterns in natural ecosystems. For example, trees can outcompete herbaceous species
415 because of size-asymmetric advantages concerning light competition in the early
416 successional stage of forest ecosystems, and thus dominate the forests in the late
417 successional stage. However, incorporating plant traits and plant-soil feedbacks into
418 modern species coexistence theory remains a considerable challenge due to limited
419 experimental evidence and even theory [but see Ke & Wan (2020)]. Our work
420 suggests that finding plant trait dissimilarity – pairwise PSF correlations can reduce
421 the number of potential niche dimensions, if they reflect one coordinated life history

422 strategy. Empirical research is needed to test if PSF and trait dissimilarity mirror two
423 aspects of a coordinated life history strategy.

424

425 **5 | CONCLUSIONS**

426 Our analyses provided evidence for relationships between plant-soil feedbacks
427 and functional traits. The trade-off between growth and defence can drive variation of
428 individual plant-soil feedbacks. Individual PSF was more negative in faster-growing
429 species, but taller and larger-seeded species have more positive or less negative
430 individual PSF likely because of greater tolerance to soil pathogens. Pairwise PSF,
431 normally used to deduce species coexistence, was related to trait dissimilarity in terms
432 of some functional traits. However, our results showed SRL differences had negative
433 relationships with pairwise PSF, and height differences had positive relationships with
434 PSF, mediating distinct links between trait dissimilarity and species coexistence
435 (niche difference versus fitness difference). Together, these results suggest that PSF
436 may reinforce the effect of trait dissimilarities on coexistence. However, knowledge
437 of how trait dissimilarity affects species coexistence must improve before this
438 conjecture can be rigorously tested. Extrapolating from our results, we suggest that
439 considering plant-soil feedbacks in modern species coexistence theory can help build
440 a more comprehensive understanding of when plant-soil feedbacks contribute to
441 species coexistence (Ke & Wan, 2020).

442

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454

455 **AUTHORS' CONTRIBUTIONS**

456 NX conceived the idea and designed the research. NX and CC constructed the
457 conceptual frameworks, with contributions from PBA, KC and MB. DC, HW and KC
458 conducted literature search and collected data. DC and NX performed data analyses.
459 NX, PBA, CC, KC, JC, PMVB and MB discussed and interpreted the results. NX and
460 PBA wrote the manuscript, with inputs from CC, KC, JC, PMVB and MB.

461

462 **DATA AVAILABILITY**

463 The data supporting the results will be archived in a Dryad and the data DOI will be
464 included at the end of the article upon acceptance.

465

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772 **Figure legends**

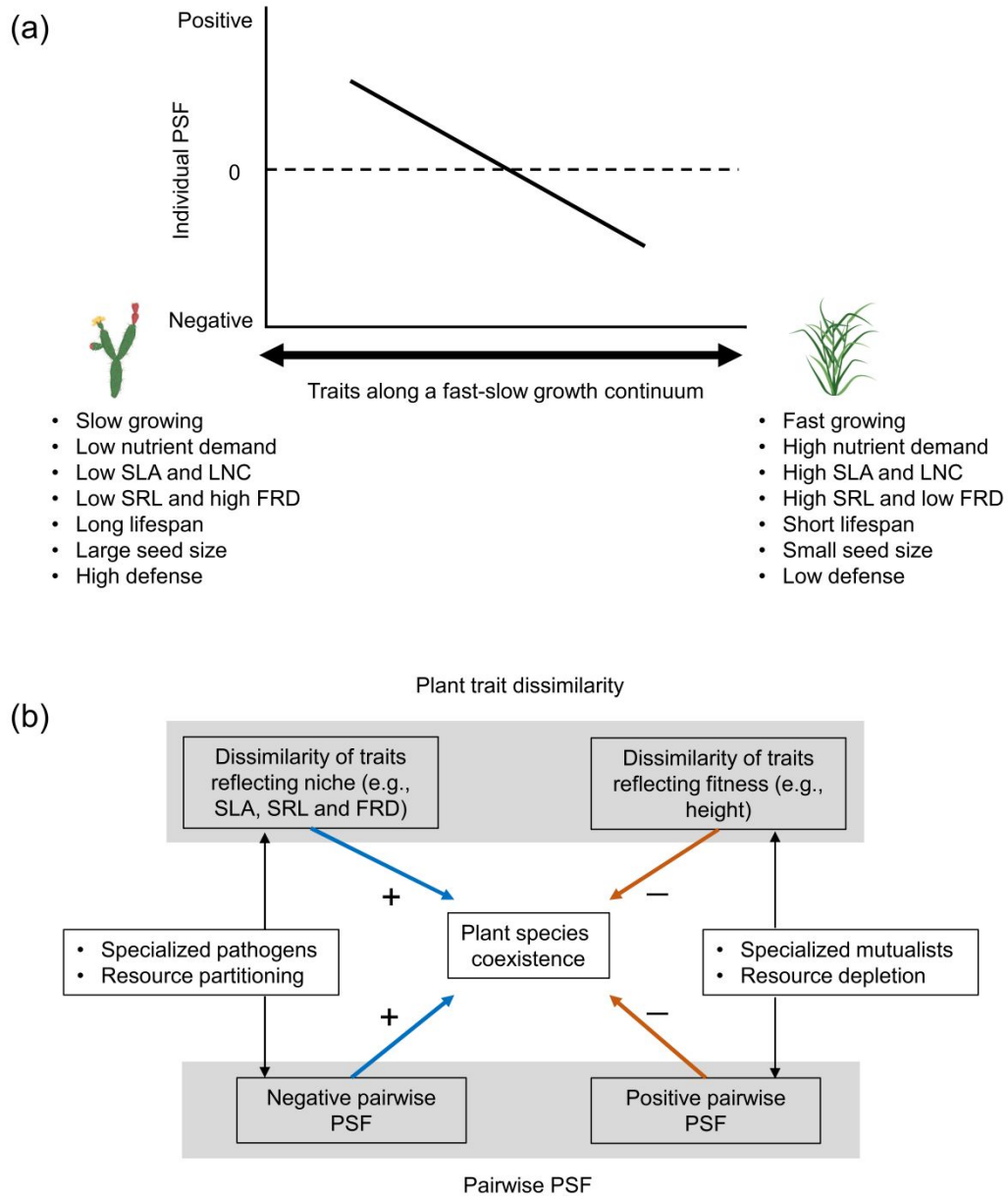
773 **Figure 1** A conceptual framework connecting plant traits and PSF showing the key
774 hypotheses tested in this study. (a) Individual PSF hypothetically varies with plant
775 fast-slow growth continuum in accordance with the growth-defence hypothesis
776 (Hypothesis 1). (b) Trait dissimilarity can lead to negative pairwise PSF when traits
777 reflect resource niche partitioning or accumulation of specialized soil pathogens,
778 while they can correlate to positive pairwise PSF in cases where traits reflect average
779 fitness differences driven by species-specialized mutualists or resource depletion. We
780 predicted that trait dissimilarity is related to pairwise PSF (Hypothesis 2). The blue
781 and red arrows indicate “strengthening” (+) and “weakening” (–) effects. SLA =
782 specific leaf area; LNC = leaf N concentration; SRL = specific root length; FRD =
783 fine root diameter.

784 **Figure 2** Relationships between individual plant-soil feedbacks and (a) specific leaf
785 area, (b) leaf N concentration, (c) specific root length, (d) fine root diameter, (e) plant
786 height and (f) seed mass, which test Hypothesis 1 (Figure 1a). The solid lines indicate
787 the fitted relationships, and the dashed red lines indicate the 95% confidence intervals
788 based on univariate regression analyses. SLA = specific leaf area; LNC = leaf N
789 concentration; SRL = specific root length; FRD = fine root diameter; SM = seed mass.

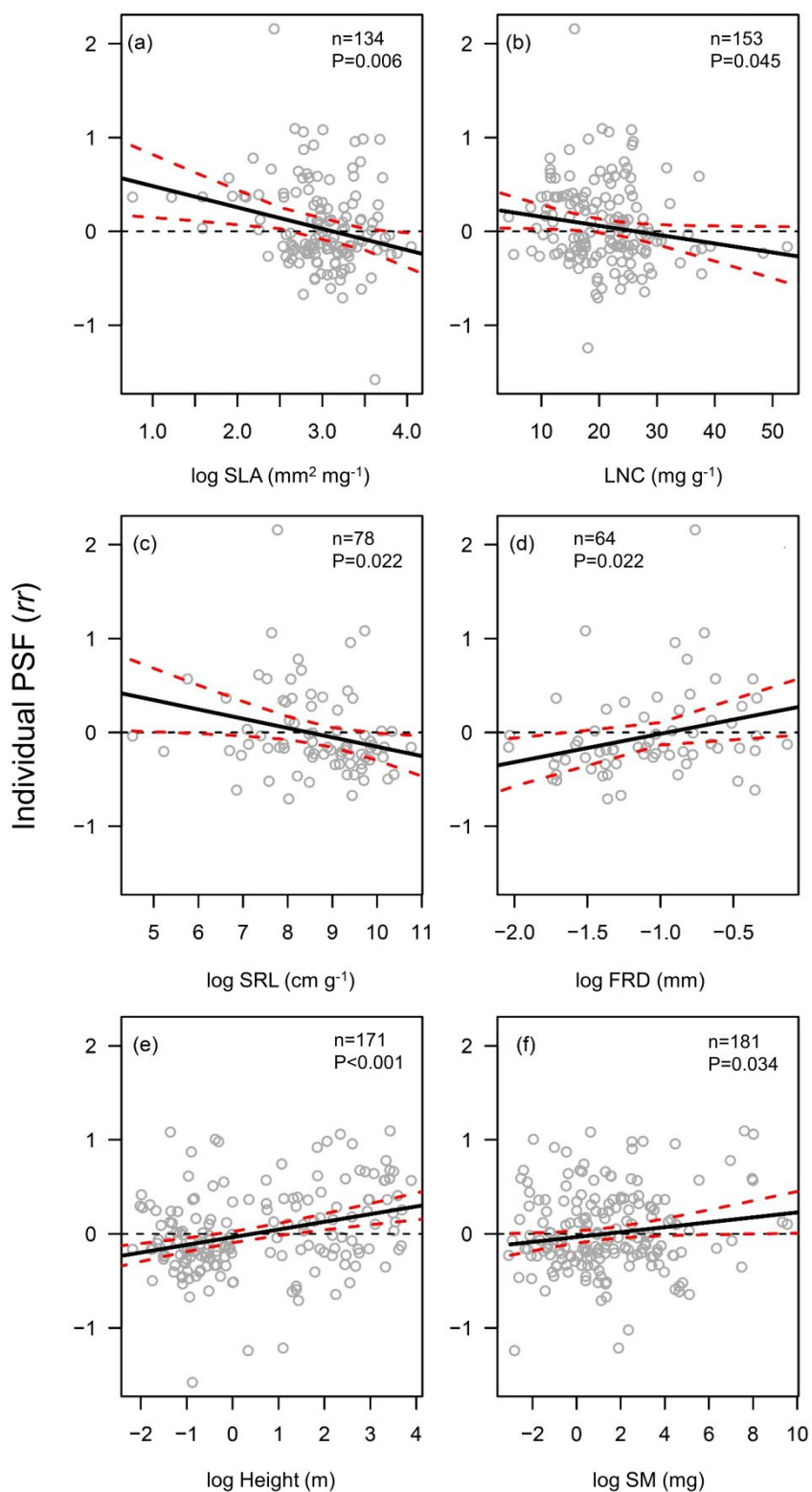
790 **Figure 3** Relationship between pairwise plant-soil feedback and (a) SLA
791 dissimilarity, (b) LNC dissimilarity, (c) SRL dissimilarity, (d) FRD dissimilarity, (e)
792 Height dissimilarity and (f) SM dissimilarity, which test Hypothesis 2 (Figure 1b).
793 The solid lines indicate the fitted relationships, and the dashed red lines indicate the

794 95% confidence intervals based on univariate regression analyses. Panels that do not
795 show the trend lines imply there were not statistically significant relationships ($P >$
796 0.05). SLA = specific leaf area; LNC = leaf N concentration; SRL = specific root
797 length; FRD = fine root diameter; SM = seed mass.

799 **Figure 1**

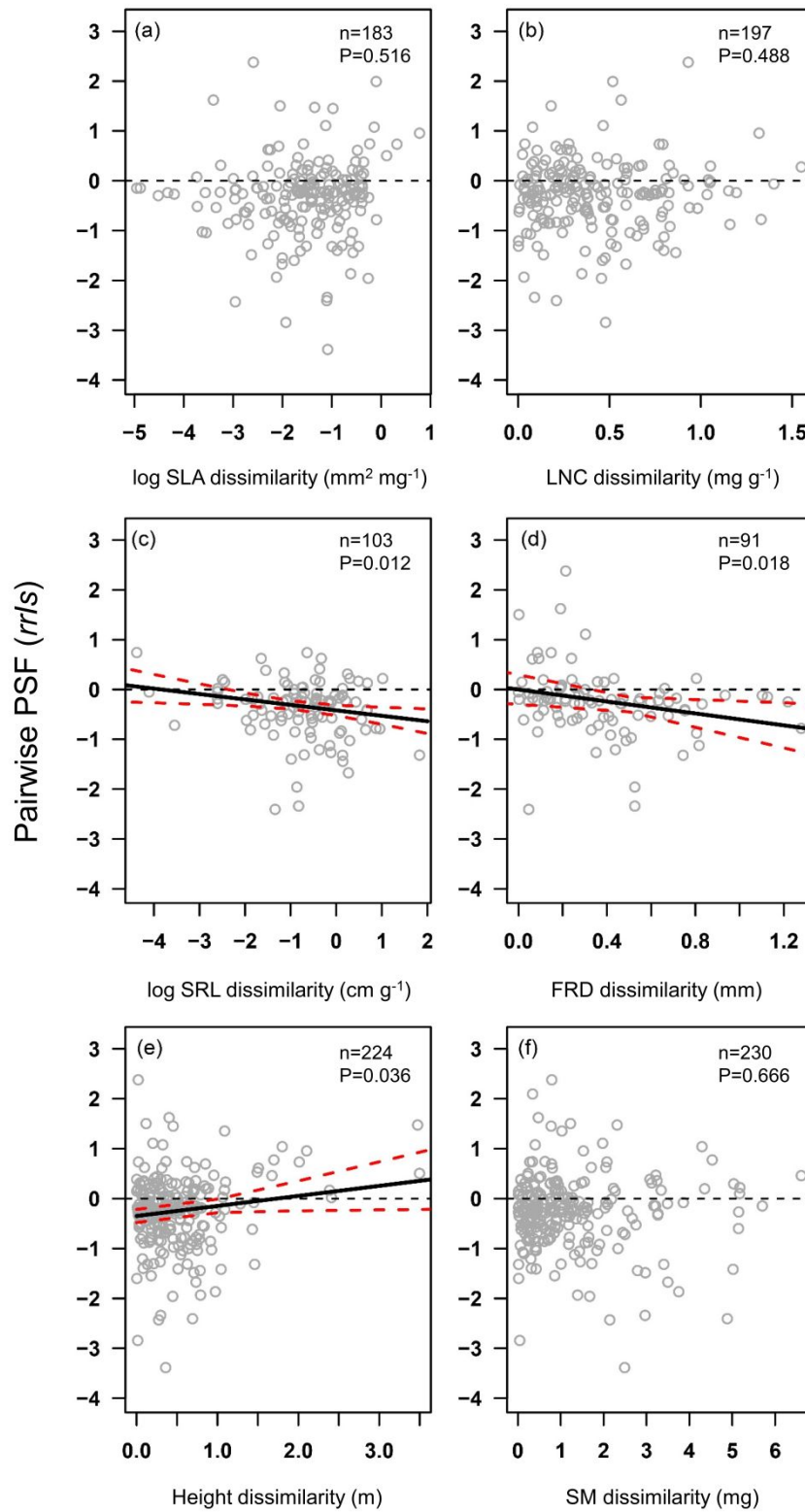


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802 **Figure 2**

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805 **Figure 3**

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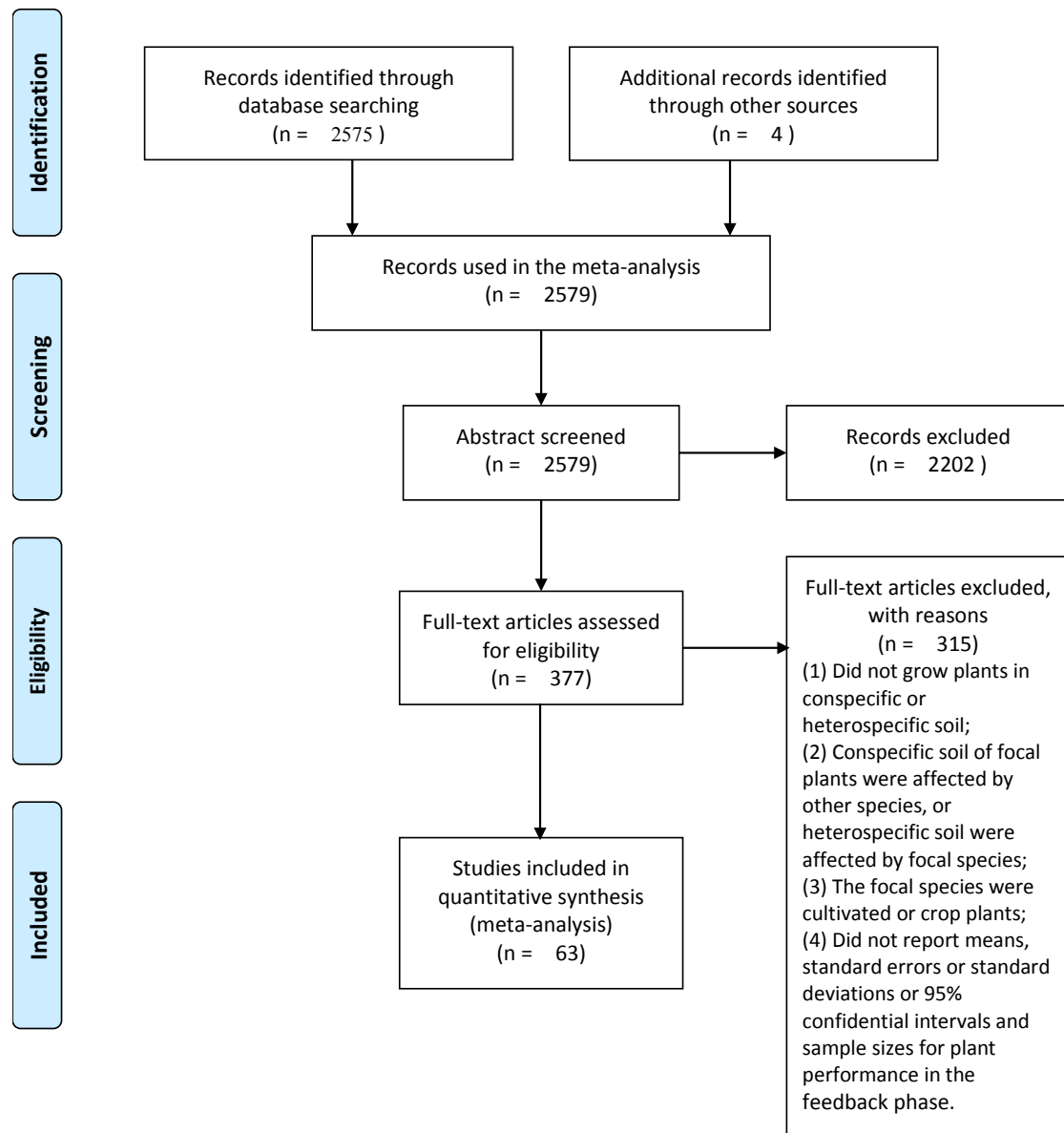


Fig. S1 PRISMA flow diagram of this meta-analysis.

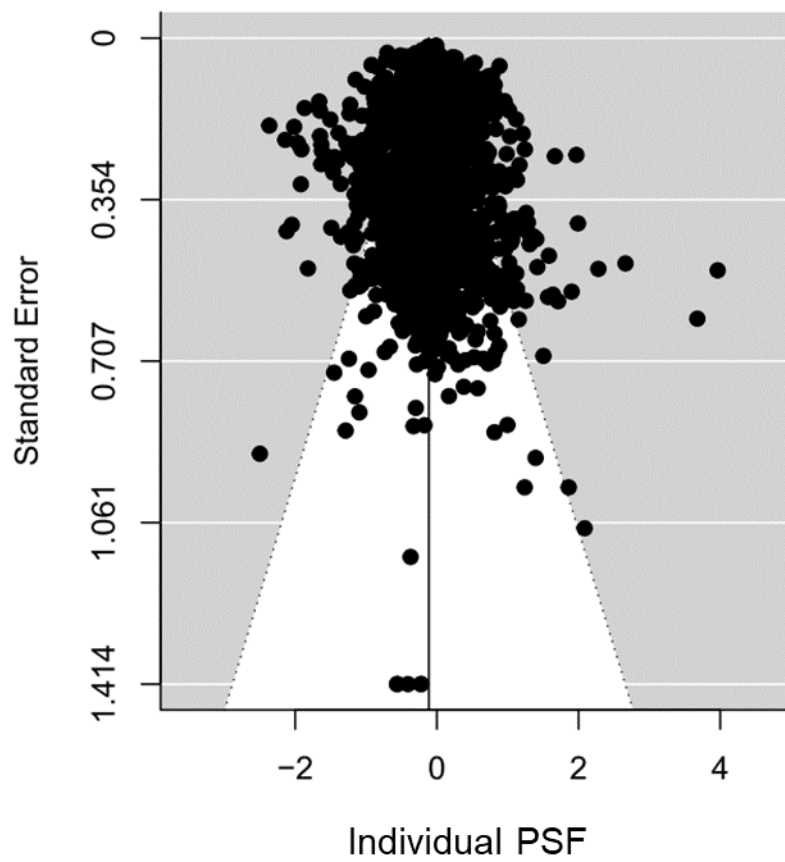


Fig. S2 Funnel plot to detect publication bias for this meta-analysis.

Appendix 1 Selected papers

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