

1 **Phylogenetic signals and predictability in plant-soil feedbacks**

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25 **Supporting information:** R code to perform the analyses and draw the figures.

26

27 **Summary**

- 28 1. There is strong evidence for a phylogenetic signal in the degree to which species share
29 co-evolved biotic partners and in the outcomes of biotic interactions. This implies there
30 should be a phylogenetic signal in the outcome of feedbacks between plants and soil
31 microbiota they cultivate. However, attempts to identify a phylogenetic signal in plant-
32 soil feedbacks have produced mixed results.
- 33 2. We clarify how phylogenetic signals could arise in plant-soil feedbacks and use a recent
34 compilation of data from feedback experiments to identify: 1) whether there is a
35 phylogenetic signal in the outcome of plant-soil feedbacks; and 2) whether any signal
36 arises through directional or divergent changes in feedback outcomes with evolutionary
37 time.
- 38 3. We find strong evidence for a divergent phylogenetic signal in feedback outcomes.
39 Distantly related plant species show more divergent responses to each other's soil
40 microbiota than closely related plant species. The pattern of divergence implies
41 occasional co-evolutionary shifts in how plants interact with soil microbiota, with
42 strongly contrasting feedback responses among some plant lineages.
- 43 4. Our results highlight that it is difficult to predict feedback outcomes from phylogeny
44 alone, other than to say that more closely related species tend to have more similar
45 responses.

46 **Keywords:** Biotic interactions; Brownian evolution; pair-wise feedbacks; mutualisms;
47 pathogens; plant-soil interactions; symbioses.

48 **Introduction**

49 Phylogenetic signal is the tendency for closely related species to share greater resemblance
50 than species drawn randomly from a phylogenetic tree (Blomberg & Garland, 2002;
51 Münkemüller *et al.*, 2012). Phylogenetic signals arise when similarity between species is
52 related to the time since their evolutionary divergence, or phylogenetic distance. Due to a
53 longer shared evolutionary history, recently diverged species are more likely to share features
54 in common than species that diverged in the more distant past (Harvey & Pagel, 1991).
55 Phylogenetic signals can also arise in the relationships between species and the taxa with which
56 they have strong co-evolutionary interactions (Koyama *et al.*, 2019). For example, as plant
57 species diverge from each other in evolutionary time, their biotic partners (pests, pathogens
58 and symbiotic mutualists) tend also to diverge such that closely related plant species share more

59 co-evolved biotic partners than distantly related plant species (Gilbert & Webb, 2007). A
60 phylogenetic signal in the degree to which species share co-evolved biotic partners should lead
61 to a phylogenetic signal in the outcome of biotic interactions (Gilbert & Parker, 2016). This
62 prediction is supported by empirical studies: closely related plant species tend to respond in
63 similar ways when exposed to the same pathogens (Gilbert *et al.*, 2015), fungal endophytes
64 (Giauque *et al.*, 2019), and symbiotic mutualistic soil microbes (Barrett *et al.*, 2016; Hoeksema
65 *et al.*, 2018), relative to the responses of more distantly related species.

66 Much recent interest has focused on the co-evolutionary relationships that plants form with soil
67 microbiota (van der Putten, 2010; Crawford *et al.*, 2019; Kandlikar *et al.*, 2019), referred to as
68 plant-soil feedbacks. Feedbacks arise because plant species cultivate specific soil microbiota,
69 and soil microbiota in turn affect plant performance. These feedbacks can be positive (the soil
70 microbiota cultivated by a plant species has a net positive effect on its growth relative to either
71 sterilized soil or the soil microbiota cultivated by other plant species) or negative. Because
72 feedbacks between plants and soil biota can differentially alter species performance and
73 competitive ability (Bever, 2003), plant-soil feedbacks are thought to play an important role in
74 community-level processes such as plant species coexistence and invasion (Bonanomi *et al.*,
75 2005; Bell *et al.*, 2006; van der Putten *et al.*, 2007). Consequently, interest has centred on
76 predicting how plant species respond to both their own soil microbiota and the microbiota
77 cultivated by other plant species. As with other biotic interactions, it is widely held that
78 feedback outcomes should be predictable from plant species relatedness, implying a
79 phylogenetic signal (Mehrabi & Tuck, 2015; Fitzpatrick *et al.*, 2016).

80 If there is a phylogenetic signal in plant-soil feedbacks, we expect closely related plant species
81 to cultivate similar soil microbiota, and to respond in a similar way to each other's microbiota,
82 relative to more distantly related species. However, a phylogenetic signal in plant-soil
83 feedbacks could arise in at least two ways, with different implications for how relatedness
84 might predict feedback outcomes. First, a phylogenetic signal could result from a directional
85 trend whereby plant species perform consistently better (positive feedback) or worse (negative
86 feedback) in their own soil relative to other species soil with increasing phylogenetic distance
87 (Fig. 1b). A directional trend implies that feedback strength and direction is predictable from
88 plant species relatedness, which could have consequences for plant community structure. For
89 example, because negative feedbacks can enhance plant species coexistence (Bonanomi *et al.*,
90 2005), stronger negative feedbacks with increasing phylogenetic distance should favour plant
91 communities with greater phylogenetic diversity (Crawford *et al.*, 2019).

92 Evidence for a directional trend is mixed. Studies have variously found that species perform
93 better, worse or much the same when exposed to soil microbiota cultivated by close compared
94 to distant relatives (Dostal & Paleckova, 2011; Liu *et al.*, 2012; Miller & Menalled, 2015;
95 Mehrabi *et al.*, 2015; Sweet & Burns, 2017; Kempel *et al.*, 2018; Kuřáková *et al.*, 2018;
96 Wilschut *et al.*, 2019), with meta-analyses showing either no (Mehrabi & Tuck, 2015) or a
97 slight negative directional trend (Crawford *et al.*, 2019). However, soil feedback experiments
98 usually involve whole soil communities, including both pathogens and symbiotic mutualists.
99 While a higher specificity of pathogens compared with mutualists could result in a negative
100 relationship between feedbacks and phylogenetic distance (see for example Crawford *et al.*
101 2019), there seems no compelling reason why the net effect of pathogens and mutualists on
102 plant performance should generate a consistent directional trend in feedback responses with
103 increasing phylogenetic distance (Jiang *et al.*, 2019). Instead, the observed variation in
104 directional trends could reflect aspects of the experimental design favouring pathogens or
105 mutualists, or affecting plant species response to those pathogens and mutualists.

106 Second, a phylogenetic signal can arise if feedback responses diverge over time but in no
107 consistent direction (Fig. 1c, e). As with directional trends, there is evidence from empirical
108 studies for divergent phylogenetic signals in feedback outcomes (Diez *et al.*, 2010; Anacker *et al.*
109 *et al.*, 2014; Fitzpatrick *et al.*, 2016; Senior *et al.*, 2018). A divergent phylogenetic signal is
110 consistent with our understanding of plant-soil feedbacks, since it implies that both pathogens
111 and mutualists can drive plant responses to soil biota. However, it changes our expectations
112 about how predictable feedback outcomes are from knowledge of species relatedness. On the
113 one hand, non-directional divergence over time implies some degree of predictability, in that
114 closely related species should respond in a similar way to each other's microbiota. On the other
115 hand, this pattern of divergence implies the strength and direction of feedbacks becomes more
116 variable, and hence less predictable, among more distantly related species.

117 Nevertheless, if phylogenetic signals do arise though divergence over time, the pattern of
118 divergence could provide insight into the underlying co-evolutionary processes (Fig. 1c-f) and
119 provide some predictability to feedback outcomes. For example, plant species could diverge
120 gradually in their feedback responses over time due to the accumulation of many small changes
121 in the way plants and soil microbiota interact. A process of cumulative gradual change is
122 equivalent to a Brownian motion model of evolutionary change, which should generate
123 approximately normally distributed feedback responses (Fig. 1c, d) with the variance in
124 feedback response increasing in direct proportion to the phylogenetic distance between plant

125 species (Harvey & Pagel, 1991; Elliot & Mooers, 2014). The non-directional accumulation of
126 gradual changes through evolutionary time implies that species will tend to drift apart, such
127 that feedback responses become less predictable among more distantly related species.
128 Alternatively, divergence could include occasional major shifts in the way plants and soil
129 microbiota interact. These shifts could occur if certain plant lineages formed unique co-
130 adaptations with key pathogens or mutualists, such as nitrogen-fixing bacteria or specialized
131 mycorrhizae. Such lineage-based shifts should result in a distribution of feedback responses
132 different to that expected under continuous gradual change, potentially adding some
133 predictability to feedback outcomes. For example, we might expect plant species in the same
134 lineage to respond similarly to each other's soil microbiota if they share a key co-adapted
135 mutualist, but to respond differently to the soil microbiota cultivated by plants in lineages
136 lacking that mutualist. Occasional major co-evolutionary shifts in some lineages should lead to
137 feedback responses having a more peaked distribution with heavier tails relative to a model of
138 continuous gradual change (Fig. 1e,f).

139 The varying ways in which a phylogenetic signal could arise might explain why it has proven
140 difficult to identify a clear signal of relatedness in plant-soil feedbacks. Here, we aim to resolve
141 this issue and gain insight into the nature of co-evolutionary relationships between plants and
142 soil microbiota. We take advantage of a major compilation of data from plant-soil feedback
143 studies (Crawford *et al.*, 2019) to assess the degree to which a phylogenetic signal arises
144 through a directional and/or divergent trend in feedback responses and characterise the pattern
145 of response divergence (e.g., Fig. 1).

146 **Materials and Methods**

147 *The data*

148 We used the data in Crawford *et al.* (2019), which is a compilation of plant-soil feedback data
149 from multiple studies involving pairwise feedbacks where two plant species were grown in soil
150 cultivated by both species. The data [included estimates of the phylogenetic distance between](#)
151 [each plant species pair, as well as details of experimental treatments, whether data were derived](#)
152 [from glasshouse or field experiments, whether the plant species were from grassland or forest](#)
153 [ecosystems and were native or not to those systems, and each species functional group, which](#)
154 [included grasses, forbs and trees](#). The full dataset included studies that used whole soil
155 communities and studies that used some fraction of the soil community, such as mycorrhizal
156 fungi, in measuring feedback responses. We included only studies using whole soil

157 communities because feedbacks involving a subset of the soil biota are likely to differ from
158 those generated by whole soil communities, potentially obscuring the pattern we were
159 interested in. Where whole soil communities were used, an inoculum of the whole soil was
160 typically added to pots of sterile soil, with the proportion of whole soil inoculum relative to
161 sterile soil ranging from less than 0.01 to 1. Adding a small amount of inoculum to sterilized
162 soil is a technique used to introduce soil microbiota while minimising changes to species'
163 performance due to differences in abiotic soil properties. While abiotic feedbacks are expected
164 to be small relative to biotic feedbacks (Crawford *et al.* 2019), feedback responses will reflect
165 changes to both biotic and abiotic soil properties caused by the cultivating species, and
166 phylogenetic signals could arise due to the differing response of species to both components.

167 The data we analysed comprised 968 feedbacks from 470 unique species pairs involving 165
168 species from 39 plant families. Consequently, over half of the 968 feedbacks involved
169 replicates of a species pair, most associated with different experimental treatments that were
170 reported separately in [the dataset compiled by](#) Crawford *et al.* (2019), such as feedbacks
171 involving the same species pair measured in soil with different resource levels. To identify a
172 phylogenetic signal in feedbacks, we considered each species pair in our analysis (see
173 *Phylogenetic signal in plant-soil feedbacks*) to be an independent data point with multiple
174 feedbacks per pair treated as pseudoreplicates (Hurlbert, 1984). [We used the estimates of](#)
175 [phylogenetic distance provided in the dataset.](#)

176 *Estimating the similarity of species responses to soil microbiota*

177 Crawford *et al.* (2019) raised the issue that differences in study design or methodology might
178 confound comparisons [among studies](#). For example, variation in factors such as soil type and
179 nutrient status can alter plant responses to soil microbiota, potentially obscuring efforts to
180 identify a phylogenetic signal. This problem can be overcome using data from pairwise plant-
181 soil feedback experiments, allowing data from different experiments and studies to be
182 compared directly (Crawford *et al.* 2019). [We next describe a method to estimate the](#)
183 [disimilarity in feedback response when two plant species are exposed to two soil communities,](#)
184 [regardless of the origin of those soil communities. We then show how a measure of feedback](#)
185 [dissimilarity can be calculated using data from pairwise feedback experiments, and how this](#)
186 [dissimilarity measure should change as a function of phylogenetic distance given different](#)
187 [models of evolutionary divergence in feedback response.](#)

188 Consider two soil microbial communities, 1 and 2. If we conduct a pairwise experiment where
189 we grow two plant species, *A* and *B*, in association with each soil community, we can measure
190 the relative performance of species in each soil as the log ratio of the biomass of species *A* to
191 species *B* (or vice versa): $\ln\left(\frac{A_1}{B_1}\right)$ and $\ln\left(\frac{A_2}{B_2}\right)$, where A_1 is the biomass of species *A* when grown
192 with soil community 1. The log transformation ensures that a proportional difference in
193 biomass has the same magnitude whether positive or negative.

194 If the two species respond in the same way to the different soil communities, we expect the two
195 log ratios to be equal. That is, if the net effect of soil community 2 is to reduce (or increase)
196 the biomass of species *A* by 20% relative to soil community 1, we expect the same proportional
197 reduction (or increase) in biomass for species *B* if it responds the same way as species *A*.
198 Because we measure relative differences, this holds regardless of any absolute difference in
199 biomass between species *A* and *B*, and independent of the origin of the two soil communities.
200 A difference in the log ratios indicates that plant species differ in their response to the two soil
201 communities, with the magnitude of difference a measure of the dissimilarity in response: a
202 large difference indicates a more divergent response. For example, relative to soil community
203 1, if the net effect of soil community 2 is to reduce the biomass of species *A* by 20% but reduce
204 the biomass of species *B* by 10%, the difference in log ratio is 0.12. If the difference in response
205 is more pronounced, such that the net effect of soil community 2 is to reduce the biomass of
206 species *A* by 20% but increase the biomass of species *B* by 30% relative to soil community 1,
207 the difference in log ratio increases to 0.49.

208 *Using data from pairwise plant-soil feedback experiments to calculate dissimilarity in response*

209 Pairwise feedback experiments measure the performance of two species in association with
210 their own soil microbiota and with the microbiota of the other species. We can calculate the
211 dissimilarity in response, r , to soil microbiota [cultivated by one species relative to that](#)
212 [cultivated by the other as the difference in the log ratios of the biomass of species *A* and *B* in](#)
213 [association with each soil microbiota:](#)

$$214 \quad r = \ln\left(\frac{A_a}{B_a}\right) - \ln\left(\frac{A_b}{B_b}\right) \quad \text{Equation 1}$$

215 Where A_a is the biomass of species *A* grown with its associated soil community a . [The log](#)
216 [transformation ensures that the magnitude of \$r\$ is the same regardless of which species is chosen](#)
217 [as the numerator and which as the denominator. However, for whichever species is chosen as](#)
218 [the numerator, how we interpret the direction of \$r\$ \(positive or negative\) depends on whether](#)

219 the numerator in the left-hand log ratio denotes performance in conspecific (e.g., A_a , as in
220 equation 1) or heterospecific soil (e.g., A_b). Specifying the numerator in the left-hand log ratio
221 as performance in conspecific soil means that a positive value of r is associated with species
222 performing better overall in conspecific relative to heterospecific soil, which is the usual
223 definition of a positive soil feedback. Equation 1 is the dissimilarity measure that Crawford *et*
224 *al.* (2019) analysed for a directional trend in feedback outcomes with phylogenetic distance.
225 Here, we use this measure to test for both a directional trend in feedback outcomes (values of
226 r increasingly diverge from zero with greater phylogenetic distance in a consistent positive or
227 negative direction) and a divergent trend in feedback outcomes (values of r increasingly
228 diverge from zero but in no consistent direction), and quantify the pattern of divergence.

229 *Phylogenetic signal in plant-soil feedbacks*

230 We used the dissimilarity response measure, r , to test for a phylogenetic signal in plant-soil
231 feedbacks by comparing the fit of six models to the data, with the different models specifying
232 different types of phylogenetic signal (Fig. 1). For each pairwise feedback, we used the
233 estimates of A_a , A_b , B_a and B_b in Crawford *et al.* (2019) to calculate r_{ij} , the dissimilarity response
234 of the i th replicate for the j th species pair (with one to 11 replicates per species pair), using
235 equation 1. We used the corresponding standard errors of the estimates to calculate the
236 variance, $\sigma_{r_{ij}}^2$, of each r_{ij} using the formula in Crawford *et al.* (2019).

237 For each pairwise feedback, we assumed there was a true value for r_{ij} but this had not been
238 observed directly. Instead, each r_{ij} was an estimate of the true value with uncertainty $\sigma_{r_{ij}}^2$. To
239 allow this uncertainty to propagate through the analysis, we modelled each r_{ij} as sampled from
240 a normal distribution with mean given by the true response value r_{ij}^* :

$$241 \quad r_{ij} \sim \text{Normal}(r_{ij}^*, \sigma_{r_{ij}}^2)$$

242 To deal with non-independence due to replicated species pairs, we modelled each r_{ij}^* as
243 sampled from a distribution with a different mean dissimilarity response for each species pair,
244 r_j^* , and variance estimated from the data, with the variance, σ_w^2 , quantifying the variation in r_{ij}^*
245 among replicates *within* species pairs:

$$246 \quad r_{ij}^* \sim \text{Normal}(r_j^*, \sigma_w^2)$$

247 We then used estimates of r_j^* as the response variable in six models that specified different
248 ways in which a phylogenetic signal could arise (Fig. 1). Our aim was to identify the model

249 that best fitted the data as a basis for inferring the nature of the phylogenetic signal in plant-
250 soil feedbacks.

251 *The models*

252 Model 1 (equivalent to Fig. 1a) assumed no phylogenetic signal in the data by modelling the
253 r_j^* as drawn from a normal distribution with mean zero, implying no directional trend in
254 dissimilarity with increasing phylogenetic distance, and constant variance, σ^2 , which quantifies
255 the variation in dissimilarity response *among* species pairs:

$$256 \quad r_j^* \sim \text{Normal}(0, \sigma^2) \qquad \text{Model 1}$$

257 Model 2 (e.g. Fig. 1b) assumed a directional trend in mean response but constant variance:

$$258 \quad r_j^* \sim \text{Normal}(\beta t_j, \sigma^2) \qquad \text{Model 2}$$

259 where t_j is the phylogenetic distance between the j th plant species pair, and β measures the
260 tendency for the mean value of r_j^* to become either increasingly positive or negative with
261 increasing phylogenetic distance ([Fig. 1b shows \$r\$ becoming increasingly negative, but the](#)
262 [model tests for shifts in either direction](#)).

263 Model 3 (equivalent to Fig. 1c) assumed non-directional divergence over time. Under a model
264 in which feedback responses diverge gradually through incremental changes drawn from a
265 random distribution, the sum of increments over time will follow a normal distribution with
266 variance increasing in direct proportion to time since divergence: a Brownian motion model of
267 evolutionary change used widely to model continuous trait variation (Harvey & Pagel, 1991;
268 Elliot & Mooers, 2014). We specified this model as:

$$269 \quad r_j^* \sim \text{Normal}(0, \sigma^2 + kt_j) \qquad \text{Model 3}$$

270 which has mean zero, indicating no directional trend, and variance $\sigma^2 + kt_j$, where k measures
271 the rate of change in the variance of r_j^* with increasing phylogenetic distance.

272 Model 4 (Fig. 1d) specified a phylogenetic signal resulting from both a directional trend (as in
273 model 2) and gradual divergence in feedback response over time (as in model 3):

$$274 \quad r_j^* \sim \text{Normal}(\beta t_j, \sigma^2 + kt_j) \qquad \text{Model 4}$$

275 In contrast to models of continuous gradual divergence (models 3 and 4), gradual change
276 coupled with occasional major co-evolutionary shifts in some lineages could constrain

277 feedback responses leading to a more peaked distribution with more extreme outcomes, and
278 thus heavier tails, than captured by a normal distribution (Elliot & Mooers, 2014). We modelled
279 this outcome (model 5) using a three parameter Student's t distribution, which is widely used
280 to model heavy-tailed continuous distributions (Anderson *et al.*, 2017).

281 Model 5 (Fig. 1e) specified that response outcomes followed a Student's t distribution with
282 mean zero (no directional trend), scale parameter s^2 , and parameter v controlling the degree of
283 kurtosis, with smaller values of v implying a more heavy-tailed distribution (more extreme
284 values) with higher variance. We allowed the kurtosis, and hence the variance, to change with
285 phylogenetic distance, specified by rate parameter k , with smaller values of k indicating a more
286 heavy-tailed distribution with higher variance:

$$287 \quad r_j^* \sim \text{Student's } t(0, s^2, v + kt_j) \quad \text{Model 5}$$

288 Model 6 (Fig. 1f) was the same as model 5 but allowed for a directional trend in mean response
289 along with non-gradual divergence through evolutionary time:

$$290 \quad r_j^* \sim \text{Student's } t(\beta t_j, s^2, v + kt_j) \quad \text{Model 6}$$

291 *Are feedback responses more similar within families?*

292 A heavy-tailed distribution could arise if feedback responses in some plant lineages were
293 constrained by unique co-adaptations with soil microbiota. The variance of r appears to
294 increase among species pairs separated by more than 300 million years (myr; Fig. 2), which
295 equates to an increase in variation among plant families relative to within plant families.
296 Constraints at the family level might be expected, since we know that plant species in some
297 families share unique co-adaptations with soil biota (e.g., Fabaceae, Orchidaceae, Ericaceae),
298 and recent evidence suggests that plant species are more responsive to mycorrhizal fungi
299 cultivated by plants in the same family (Hoeksema *et al.* 2018). Such constraints could result
300 in more similar feedback responses among plant species in the same family but greater
301 differences in feedback response among species in different families. To examine this, we
302 expanded model 6 to include terms estimating the mean feedback response between each pair
303 of plant families for which responses had been measured, with the pairwise family means
304 modelled hierarchically:

$$305 \quad r_j^* \sim \text{Student's } t(\beta t_j + \alpha_f, s^2, v + kt_j) \quad \text{Model 7}$$

306 $\alpha_f \sim \text{Student's } t(0, s_\alpha^2, \nu_\alpha)$

307 Where α_f is a parameter estimating the deviation in response from the overall mean for the f th
308 plant family pair, with the parameters modelled hierarchically as drawn from a Student's t
309 distribution with scale parameter s_α^2 and kurtosis parameter ν_α , allowing the values to have a
310 heavy-tailed distribution. If unique co-adaptations between plants and soil microbiota at the
311 family level account for the heavy-tailed distribution of feedback responses, then adjusting for
312 pairwise family-level differences should account for much of the phylogenetic signal in the
313 data, leading to little or no increase in residual variance over time (i.e., after adjusting for
314 pairwise family-level differences, the pattern of residual variation should shift from Fig. 1c or
315 1e to Fig. 1a).

316 *Fitting the models*

317 To allow the uncertainty at all levels to propagate through the analysis, we fitted the models in
318 a Bayesian framework using JAGS (Just Another Gibbs Sampler; Plummer, 2003), specifying
319 relatively uninformative priors to allow the data to drive parameter estimation. For continuous
320 variables, we used normally distributed priors with mean zero and variance 10, and for variance
321 terms used uniformly distributed priors on the standard deviation in the range 0-10, [which](#)
322 [correspond to relatively uninformative priors](#). We ran the models with three chains for 10,000
323 iterations following a burn-in of 1000 iterations and checked parameters for convergence using
324 the Gelman-Rubin statistic (Gelman & Rubin, 1992), which was less than 1.1 for all parameters
325 indicating adequate convergence. We identified the best performing model using the
326 approximate leave-one-out cross-validation (LOO) criteria (Vehtari *et al.*, 2017), which
327 estimates the predictive accuracy of each model. LOO is considered an improvement on other
328 information-criterion based model selection measures such as Akaike Information Criterion,
329 Watanabe-Akaike Information Criterion and Deviance Information Criterion that are widely
330 used to compare model performance (see Vehtari *et al.*, 2017 for details). We compared models
331 by calculating the difference in expected predictive accuracy (ΔLOO) between each model and
332 the best-fitting model on the deviance scale using the *loo* package in R (Vehtari *et al.*, 2019),
333 with smaller values implying a model with better predictive accuracy. The R code used to fit
334 the models is provided in Supporting Information S1, along with code to draw all figures.

335 **Results**

336 Figure 2 plots the measure of response dissimilarity, r , against phylogenetic distance for the
337 whole soil community feedback data in Crawford *et al.* (2019), revealing that more distantly
338 related species (greater phylogenetic distance) appear to show greater variation in r values.

339 The six models shown in Fig. 1 (see section below for model 7) produced widely differing fits
340 to the data as revealed by substantial differences in LOO values (Table 1). If we interpret
341 differences in LOO values similarly to other information-criterion measures, a difference in
342 LOO >10 indicates very strong support for one model relative to another (Lunn *et al.*, 2012).
343 Models 3-6 fit the data better than models 1 and 2, which specified constant variance among
344 species pairs. This implies a phylogenetic signal arising, at least in part, through divergence in
345 feedback responses over evolutionary time.

346 Among the models specifying that feedback responses diverged over time (models 3-6), models
347 5 and 6 were the best performing, with both having similar predictive accuracy. Models 5 and
348 6 specified heavy-tailed distributions and, for model 6, the parameter estimates identified a
349 clear negative directional trend (a negative β parameter; Fig. 3) and increasing kurtosis with
350 greater phylogenetic distance (a negative k parameter; Fig. 3). Comparing the fit of model 4
351 (the best-fitting of the models that specified a normal distribution) with model 6 revealed that
352 the better fit of model 6 to the data was due to the distribution of feedback responses being
353 more peaked and having heavier tails than could be accommodated by the normal distribution
354 specified in model 4, especially at large phylogenetic distances (Fig. 4).

355 While the negative β parameter for model 6 (Fig. 3; see also Crawford *et al.* 2019) implied that
356 feedback responses tended to be more negative among plant species separated by a greater
357 phylogenetic distance, this negative trend was of small magnitude relative to the increase in
358 variance with increasing phylogenetic distance due to non-directional divergence. The β
359 parameter for model 6 implies that a 600 myr increase in phylogenetic distance between plant
360 species results in the mean value of r declining by about 0.13, which is of much smaller
361 magnitude than the shifts that result from increase in variance over an equivalent time span
362 (Fig. 2).

363 *Are feedback responses more similar within families?*

364 The distribution of feedback responses was consistent with divergence that involved occasional
365 major shifts rather than continuous gradual change through evolutionary time (Elliot & Mooers,
366 2014), an outcome that could arise if feedback responses in some plant lineages became
367 constrained by unique co-adaptations with soil microbiota. Model 7 attempted to accommodate

368 this, and had much better predictive accuracy than other models (Table 1). The magnitude of
369 parameter k (measuring the change in kurtosis with phylogenetic distance) in model 7 was
370 substantially less than in model 6, with 95% credible intervals that overlapped zero (Fig. 3).
371 This implies that much of the increase in variance with increasing phylogenetic distance in
372 model 6 could be accounted for by the pair-wise family level estimates in model 7. The family-
373 level mean estimates for r in model 7 identified 7 family pairs that differed significantly from
374 the overall mean in their feedback responses (Fig. 5).

375 **Discussion**

376 Plant-soil feedbacks can influence plant species performance and competitive ability, with
377 implications for community assembly (Bever, 2003; Bonanomi *et al.*, 2005). Consequently,
378 considerable effort has been invested in understanding how plant species respond to their own
379 soil biota and to soil biota cultivated by other species, including whether feedback responses
380 can be predicted from plant species relatedness. Despite evidence that both the identity of biotic
381 partners and the response of plant species to those partners are linked to phylogenetic
382 relatedness (Barrett *et al.*, 2016; Hoeksema *et al.*, 2018; Giauque *et al.*, 2019), attempts to
383 identify a phylogenetic signal in feedback responses have produced mixed results. Using an
384 extensive dataset compiled from plant-soil feedback studies (Crawford *et al.*, 2019), we show
385 that: 1) there is a strong phylogenetic signal in plant-soil feedbacks; 2) the phylogenetic signal
386 arises primarily through non-directional divergence of feedback responses over time with a
387 slight tendency for responses to become more negative with greater phylogenetic distance (see
388 also Crawford *et al.* 2019); and 3) the pattern of divergence is consistent with occasional major
389 co-evolutionary shifts between plants and soil microbes rather than continuous gradual
390 divergence.

391 Much research has examined whether there is a directional trend in feedback responses linked
392 to phylogenetic relatedness. This is due largely to the putative importance of negative
393 feedbacks in promoting coexistence and invasion, and positive feedbacks in promoting
394 dominance by single species (Mehrabi & Tuck, 2015; Fitzpatrick *et al.*, 2016; Kempel *et al.*,
395 2018; Kuřáková *et al.*, 2018). Our findings reiterate those of Crawford *et al.* (2019) in showing
396 some evidence for a slight negative trend in feedback response with increasing phylogenetic
397 distance. Such an outcome should favour coexistence among more distantly related species and
398 thus promote communities with greater phylogenetic diversity (Bonanomi *et al.*, 2005).

399 Nevertheless, our analysis highlights that any negative trend in feedback outcomes is slight
400 compared with the overall increase in variance due to divergence in both directions over time.
401 An increase in the variance of feedback responses over evolutionary time based on data from
402 multiple studies is consistent with our understanding of plant-soil feedbacks, where the net
403 effect of pathogens, mutualists and other components of the soil biota, does not consistently
404 alter plant performance in a particular direction (Jiang *et al.*, 2019). Strong directional trends
405 should only arise in specific situations where there are compelling reasons to expect a
406 disproportionate influence of either pathogens or mutualists on focal species (e.g., Liu *et al.*,
407 2012). The slight negative trend we observe could reflect a higher specificity of soil pathogens
408 relative to soil mutualists, which could result in plants benefiting more through the loss of
409 pathogens in soils of more distantly related species, relative to the cost of losing mutualists.
410 The difference between what theory might predict about phylogenetic signals in specific
411 situations or case studies and what theory predicts when integrating across data from multiple
412 studies may be one reason it has proven difficult to identify a clear phylogenetic signal in the
413 outcome of plant-soil feedbacks.

414 The increase in the variance of feedback responses due to divergence in both directions over
415 evolutionary time implies that close relatives tend to respond to each other's soil microbiota in
416 similar ways, but that the magnitude and direction of feedback responses become more variable
417 with greater phylogenetic distance. Consequently, it may only be possible to predict feedback
418 outcomes with any accuracy among closely related species: phylogenetic distance is of less
419 help in predicting the response among distantly related species.

420 Much of the increase in variability in feedback responses over evolutionary time was due to
421 more extreme values than expected under a model of gradual divergence. This is consistent
422 with major shifts associated with some plant lineages being constrained by co-evolution with
423 specialist microbiota. Such lineages should disproportionately benefit from escaping specialist
424 natural enemies or disproportionately suffer from losing specialist mutualists, an outcome
425 known to occur in some plant families. For example, the Orchidaceae (orchids) and Ericaceae
426 (heaths) form specialized associations with orchid and ericoid mycorrhizal fungi, Fabaceae
427 (legumes) rely on soil bacteria (rhizobia) for nitrogen fixation, and Poaceae (grasses) cultivate
428 distinct microbial communities and are more responsive to those communities than other life-
429 forms (Hoeksema *et al.*, 2010; Davison *et al.*, 2020). In the data we analysed, 7 family pairs
430 had more extreme feedback responses than average, which included the families Fabaceae and
431 Poaceae (Fig. 5; there were no Orchidaceae in the data). While it is important not to over-

432 interpret these results, since most between-family comparisons involved relatively few species
433 and feedback responses, modelling the variation associated with family-level mean responses
434 (Fig. 5) explained much of the increase in variation in feedback responses with increasing
435 phylogenetic distance, leaving a weaker residual phylogenetic signal (parameter k was much
436 closer to zero in model 7; Fig. 3). Hence, increasing divergence in feedback response with
437 greater phylogenetic distance could be largely explained by the differing response of species
438 in certain families to the microbiota associated with species in other families. Understanding
439 variation in feedback responses within and among families may be one way to increase the
440 predictability of feedback outcomes among more distantly related species.

441 **Conclusions**

442 While relatedness can help predict the outcome of some biotic interactions (Parker *et al.*, 2015;
443 Bufford *et al.*, 2016), attempts to predict how plant species will respond to each other's soil
444 microbiota based on relatedness have produced mixed results. We have clarified how
445 phylogenetic signals in plant-soil feedback outcomes could arise and used a recent compilation
446 of data to quantify the nature of the phylogenetic signal. Our results reiterate other studies that
447 provide evidence for, at best, a weak directional trend and highlights that knowledge of plant
448 species relatedness is most likely a weak predictor of community-level outcomes for plant-soil
449 feedbacks. Our results indicate that it is difficult to predict how species will respond to each
450 other's soil microbiota from a knowledge of the phylogenetic distance between plant species
451 alone, other than to say that more closely related species tend to have more similar responses.
452 Nevertheless, this apparent loss in predictability could be offset by a divergence pattern that
453 suggests feedbacks become constrained in some lineages by co-evolution with specialist
454 mutualists or enemies. If so, feedback outcomes among distantly related species might be
455 predictable from knowledge of the lineages involved and how species in those lineages respond
456 to each other's soil biota (e.g., Fig. 5). Identifying families for which feedback responses have
457 been constrained by co-evolution with specialist soil microbiota and examining feedback
458 outcomes for species within and among those families could improve our ability to predict
459 outcomes.

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466 **Author Contributions**

467 E.M.W, R.P.D and S.E.B conceived the idea, with input from all authors. E.M.W and R.P.D
468 designed the methodology. R.P.D designed and performed the analyses. E.M.W and R.P.D led
469 the writing of the manuscript with critical input from all authors. All authors gave final approval
470 for publication.

471 **Data Availability**

472 Data from Crawford et al. (2019) When and where plant-soil feedback may promote plant
473 coexistence: a meta-analysis. *Figshare*. <https://doi.org/10.6084/m9.figshare.7985195.v1>. The
474 code used to perform the analyses and draw Figs 1 – 5 is in Appendix S1.

475 **References**

- 476 **Anacker BL, Klironomos JN, Maherali H, Reinhart KO, Strauss SY. 2014.** Phylogenetic conservatism
477 in plant-soil feedback and its implications for plant abundance. *Ecology Letters* **17**: 1613–1621.
- 478 **Anderson SC, Branch TA, Cooper AB, Dulvy NK. 2017.** Black-swan events in animal populations.
479 *Proceedings of the National Academy of Sciences* **114**: 3252–3257.
- 480 **Barrett LG, Zee PC, Bever JD, Miller JT, Thrall PH. 2016.** Evolutionary history shapes patterns of
481 mutualistic benefit in Acacia-rhizobial interactions. *Evolution* **70**: 1473–1485.
- 482 **Bell T, Freckleton RP, Lewis OT. 2006.** Plant pathogens drive density-dependent seedling mortality in
483 a tropical tree. *Ecology Letters* **9**: 569–574.
- 484 **Bever JD. 2003.** Soil community feedback and the coexistence of competitors: conceptual
485 frameworks and empirical tests. *New Phytologist* **157**: 465–473.
- 486 **Blomberg SP, Garland T. 2002.** Tempo and mode in evolution: Phylogenetic inertia, adaptation and
487 comparative methods. *Journal of Evolutionary Biology* **15**: 899–910.
- 488 **Bonanomi G, Giannino F, Mazzoleni S, Setälä H. 2005.** Negative plant-soil feedback and species
489 coexistence. *Oikos* **111**: 311–321.
- 490 **Bufford JL, Hulme PE, Sikes BA, Cooper JA, Johnston PR, Duncan RP. 2016.** Taxonomic similarity,
491 more than contact opportunity, explains novel plant-pathogen associations between native and
492 alien taxa. *New Phytologist* **212**: 657–667.
- 493 **Crawford KM, Bauer JT, Comita LS, Eppinga MB, Johnson DJ, Mangan SA, Queenborough SA,
494 Strand AE, Suding KN, Umbanhowar J, et al. 2019.** When and where plant-soil feedback may
495 promote plant coexistence: a meta-analysis. *Ecology Letters*.

496 **Davison J, León DG de, Zobel M, Moora M, Bueno CG, Barceló M, Gerz M, León D, Meng Y, Pillar**
497 **VD, et al. 2020.** Plant functional groups associate with distinct arbuscular mycorrhizal fungal
498 communities. *New Phytologist* n/a.

499 **Diez JM, Dickie I, Edwards G, Hulme PE, Sullivan JJ, Duncan RP. 2010.** Negative soil feedbacks
500 accumulate over time for non-native plant species. *Ecology Letters* **13**: 803–809.

501 **Dostal P, Paleckova M. 2011.** Does relatedness of natives used for soil conditioning influence plant-
502 soil feedback of exotics? *Biological Invasions* **13**: 331–340.

503 **Elliot MG, Mooers AØ. 2014.** Inferring ancestral states without assuming neutrality or gradualism
504 using a stable model of continuous character evolution. *BMC Evolutionary Biology* **14**: 226.

505 **Fitzpatrick CR, Gehant L, Kotanen PM, Johnson MTJ. 2016.** Phylogenetic relatedness, phenotypic
506 similarity, and plant-soil feedbacks. *Journal of Ecology* **105**: 786–800.

507 **Gelman A, Rubin DB. 1992.** Inference from iterative simulation using multiple sequences. *Statistical*
508 *Science* **7**: 457–472.

509 **Giauque H, Connor EW, Hawkes C V. 2019.** Endophyte traits relevant to stress tolerance, resource
510 use and habitat of origin predict effects on host plants. *New Phytologist* **221**: 2239–2249.

511 **Gilbert GS, Briggs HM, Magarey R. 2015.** The impact of plant enemies shows a phylogenetic signal.
512 *PLoS ONE* **10**: 1–11.

513 **Gilbert GS, Parker IM. 2016.** The evolutionary ecology of plant disease: a phylogenetic perspective.
514 *Annual Review of Phytopathology* **54**: 549–578.

515 **Gilbert GS, Webb CO. 2007.** Phylogenetic signal in plant pathogen–host range. *Proceedings of the*
516 *National Academy of Sciences* **104**: 4979–4983.

517 **Harvey PH, Pagel MD. 1991.** *The Comparative Method in Evolutionary Biology*. Oxford, UK: Oxford
518 University Press.

519 **Hoeksema JD, Bever JD, Chakraborty S, Chaudhary VB, Gardes M, Gehring CA, Hart MM,**
520 **Housworth EA, Kaonongbua W, Klironomos JN, et al. 2018.** Evolutionary history of plant hosts and
521 fungal symbionts predicts the strength of mycorrhizal mutualism. *Communications Biology* **1**: 1–10.

522 **Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C,**
523 **Bever JD, Moore JC, et al. 2010.** A meta-analysis of context-dependency in plant response to
524 inoculation with mycorrhizal fungi. *Ecology Letters* **13**: 394–407.

525 **Hurlbert SH. 1984.** Pseudoreplication and the design of ecological field experiments. *Ecological*
526 *Monographs* **54**: 187–211.

527 **Jiang J, Abbott KC, Baudena M, Eppinga MB, Umbanhowar JA, Bever JD. 2019.** Pathogens and
528 mutualists as joint drivers of host species coexistence and turnover: implications for plant
529 competition and succession. *The American Naturalist*: 000–000.

530 **Kandlikar GS, Johnson CA, Yan X, Kraft NJB, Levine JM. 2019.** Winning and losing with microbes:
531 how microbially mediated fitness differences influence plant diversity. *Ecology Letters* **22**: 1178–
532 1191.

- 533 **Kempel A, Rindisbacher A, Fischer M, Allan E. 2018.** Plant soil feedback strength in relation to large-
534 scale plant rarity and phylogenetic relatedness. *Ecology* **99**: 597–606.
- 535 **Koyama A, Maherali H, Antunes PM. 2019.** Plant geographic origin and phylogeny as potential
536 drivers of community structure in root-inhabiting fungi. *Journal of Ecology* **107**: 1720–1736.
- 537 **Kuťáková E, Herben T, Münzbergová Z. 2018.** Heterospecific plant–soil feedback and its relationship
538 to plant traits, species relatedness, and co-occurrence in natural communities. *Oecologia* **187**: 679–
539 688.
- 540 **Liu X, Liang M, Etienne RS, Wang Y, Staehelin C, Yu S. 2012.** Experimental evidence for a
541 phylogenetic Janzen-Connell effect in a subtropical forest. *Ecology Letters* **15**: 111–118.
- 542 **Lunn D, Jackson C, Best N, Thomas A, Spiegelhalter D. 2012.** *The BUGS book: a practical introduction*
543 *to Bayesian analysis*. Chapman and Hall/CRC.
- 544 **Mehrabi Z, Bell T, Lewis OT. 2015.** Plant-soil feedbacks from 30-year family-specific soil cultures:
545 phylogeny, soil chemistry and plant life stage. *Ecology and Evolution* **5**: 2333–2339.
- 546 **Mehrabi Z, Tuck SL. 2015.** Relatedness is a poor predictor of negative plant–soil feedbacks. *New*
547 *Phytologist* **205**: 1071–1075.
- 548 **Miller ZJ, Menalled FD. 2015.** Impact of species identity and phylogenetic relatedness on
549 biologically-mediated plant-soil feedbacks in a low and a high intensity agroecosystem. *Plant and Soil*
550 **389**: 171–183.
- 551 **Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffers K, Thuiller W. 2012.** How to
552 measure and test phylogenetic signal. *Methods in Ecology and Evolution* **3**: 743–756.
- 553 **Parker IM, Saunders M, Bontrager M, Weitz AP, Hendricks R, Magarey R, Suiter K, Gilbert GS. 2015.**
554 Phylogenetic structure and host abundance drive disease pressure in communities. *Nature* **520**: 542–
555 544.
- 556 **Plummer M. 2003.** JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.
557 *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)* **124**:
558 20–22.
- 559 **van der Putten WH. 2010.** Impacts of soil microbial communities on exotic plant invasions. *Trends in*
560 *Ecology & Evolution* **25**: 512–519.
- 561 **van der Putten WH, Klironomos JN, Wardle DA. 2007.** Microbial ecology of biological invasions. *The*
562 *ISME Journal* **1**: 28–37.
- 563 **Senior JK, Potts BM, O’Reilly-Wapstra JM, Bissett A, Wooliver RC, Bailey JK, Glen M, Schweitzer JA.**
564 **2018.** Phylogenetic trait conservatism predicts patterns of plant-soil feedback. *Ecosphere* **9**.
- 565 **Sweet DD, Burns JH. 2017.** Plant performance was greater in the soils of more distantly related
566 plants for an herbaceous understory species. *AoB Plants* **9**.
- 567 **Vehtari A, Gabry J, Magnusson M, Yao Y, Gelman A. 2019.** *loo: Efficient leave-one-out cross-*
568 *validation and WAIC for Bayesian models*.

569 **Vehtari A, Gelman A, Gabry J. 2017.** Practical Bayesian model evaluation using leave-one-out cross-
570 validation and WAIC. *Statistics and Computing* **27**: 1413–1432.

571 **Wilschut RA, van der Putten WH, Garbeva P, Harkes P, Konings W, Kulkarni P, Martens H, Geisen S.**
572 **2019.** Root traits and belowground herbivores relate to plant–soil feedback variation among
573 congeners. *Nature Communications* **10**.

574 **Supporting Information.**

575 **S1:** R code used to perform the analyses and draw the figures.

576

577 **Table 1.** Comparison of model performance with a lower LOO (Leave-one-out cross-validation) indicating a better performing model, and the
578 difference in LOO (Δ LOO) between each model and the best fitting model. r_j^* is the mean dissimilarity response for the j th species pair. β measures
579 the tendency for the mean value of r_j^* to become increasingly positive or negative with increasing phylogenetic distance (t_j). For normal
580 distributions, σ^2 is the variance in response among species pairs, which is either constant or changing with phylogenetic distance at a rate estimated
581 by parameter k . For Student's t distributions, s^2 is a scale parameter and v is a parameter controlling the degree of kurtosis, which changes with
582 phylogenetic distance at a rate estimated by parameter k .

583	Model	Model specification	Model summary	LOO	ΔLOO
584					
585	7	$r_j^* \sim \text{Student's } t(\beta t_j + \alpha_j, s^2, v + kt_j)$	Family-level shifts with directional trend	1550.3	0
586	6	$r_j^* \sim \text{Student's } t(\beta t_j, s^2, v + kt_j)$	Co-evolutionary shifts with directional trend	1592.6	42.3
587	5	$r_j^* \sim \text{Student's } t(0, s^2, v + kt_j)$	Co-evolutionary shifts without directional trend	1593.2	42.8
588	4	$r_j^* \sim \text{Normal}(\beta t_j, \sigma^2 + kt_j)$	Gradual divergence with directional trend	1615.4	65.0
589	3	$r_j^* \sim \text{Normal}(0, \sigma^2 + kt_j)$	Gradual divergence without directional trend	1616.6	66.3
590	2	$r_j^* \sim \text{Normal}(\beta t_j, \sigma^2)$	Constant variance with directional trend	1635.4	85.1
591	1	$r_j^* \sim \text{Normal}(0, \sigma^2)$	Constant variance without directional trend	1637.2	86.8

592

593 **FIGURE LEGENDS**

594 **Figure 1.** Phylogenetic signals arise when closely related species tend to be more similar (less
595 dissimilar) than distantly related species. In panels **a-f** dashed lines show mean trend in
596 dissimilarity with increasing phylogenetic distance (where dissimilarity can be in a positive or
597 negative direction) and blue shading indicates variation in dissimilarity around the mean. In (a)
598 (dis)similarity among species is the same, on average, regardless of phylogenetic distance,
599 meaning there is no phylogenetic signal due to no change in mean dissimilarity and no change
600 in variation with increasing phylogenetic distance. Panel (b) shows a phylogenetic signal
601 arising from a directional trend in mean dissimilarity with increasing phylogenetic distance,
602 resulting in more distantly related species being more dissimilar to each other (here, in a
603 negative direction) relative to closely related species. In both (c) and (e) a phylogenetic signal
604 arises due to an increase in variance but no directional trend, with more distantly related species
605 being more likely to differ from each other in either direction relative to more closely related
606 species. In (c), continuous gradual divergence over time leads to normally distributed responses
607 while in (e), occasional major co-evolutionary shifts lead to a heavy-tailed distribution of
608 responses. Panels (d) and (f) show a phylogenetic signal arising due to both an increase in
609 variance and a directional trend, with a normally distributed (d) or heavy-tailed (f) distribution
610 of responses.

611 **Figure 2.** Values of r , a measure of feedback response dissimilarity (a value of zero means two
612 species responded in the same way to their own and each other's soil), plotted against
613 phylogenetic distance. Blue circles are the data for 968 feedback responses from a compilation
614 of pairwise plant-soil feedback experiments using whole soil communities (Crawford *et al.*,
615 2019). Red circles are the mean feedback responses for each unique species pair ($n = 470$). The
616 x axis values have been jittered so points are visible.

617 **Figure 3.** β (a) and k (b) parameter estimates for models 2 to 7 (model 1 did not include β or
618 k) where β measures the tendency for feedback outcomes to become increasingly positive or
619 negative with increasing phylogenetic distance and k measures the rate of change in the
620 variance of feedback outcomes. Here, the estimates for β and k assume that one unit of
621 phylogenetic distance equates to 100 myr. The value of β was set to zero in models 3 and 5 (no
622 directional trend), and the value of k was set to zero in model 2 (constant variance). For normal
623 distributions (models 3-4), positive k values imply increasing variance in feedback responses
624 with increasing phylogenetic distance. For Student's t distributions (models 5-7), negative k

625 values imply increasing kurtosis and increasing variance in feedback responses with increasing
626 phylogenetic distance.

627 **Figure 4.** Density histograms of feedback response r (grey shaded bars) for phylogenetic
628 distances involving feedbacks among species in the same family (**a**) and feedbacks among
629 species in different families (**b**). The fit of model 4 (assuming a normal distribution of
630 responses) to the density data at the median phylogenetic distance for data in the range is
631 shown as a black line; the fit of model 6 (assuming a Student's t distribution of responses) is
632 shown as a red line, with the red dashed line showing the mean for model 6. Numbers to the
633 right of the histograms are the variances of the data in each group.

634 **Figure 5.** Estimates of the mean value of feedback response r for each family pair (model 7),
635 expressed as a deviation from the overall mean, as a function of the mean phylogenetic
636 distance between the species pairs in each family pair. Estimates of mean feedback response
637 between species in the same family are to the left of the dashed line, estimates of mean
638 feedback response between species in different families are to the right. Red circles identify
639 family pairs where the mean response differed from zero as judged by 95% credible intervals.
640 Labels above the red circles are abbreviated names for the family pairs: Ast-Com =
641 Asteraceae-Commelinaceae ($n = 15$), Ast-Ona = Asteraceae-Onagraceae ($n = 2$), Ast-Ros =
642 Asteraceae-Rosaceae ($n = 2$), Car-Poa = Caryophyllaceae-Poaceae ($n = 2$), Com-Fab =
643 Commelinaceae-Fabaceae ($n = 2$), Com-Poa = Commelinaceae-Poaceae ($n = 19$), Ona-Poa =
644 Onagraceae-Poaceae ($n = 8$), with n = the number of feedback responses in each family pair.

645