1 **Complementarity and selection effects in early and mid-successional plant communities**

2 **are differentially affected by plant-soil feedback**

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4 Jingying Jing[1][*][+], T. Martijn Bezemer[1], and Wim H. van der Putten[1,2]

5 [1] Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), PO

6 Box 50, 6700 AB Wageningen, The Netherlands

7 [2] Laboratory of Nematology, Wageningen University and Research Centre, PO Box 8123,

8 6700 ES Wageningen, The Netherlands

9 ***** Correspondence author. E-mail: J.Jing@nioo.knaw.nl or Jingyingjing@gmail.com

10 [+] Current address:

11 Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), PO

12 Box 50, 6700 AB Wageningen, The Netherlands

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14 **Running title**: Plant-soil feedback and biodiversity effects

15

16 **Summary**

17 1. Many studies that provided evidence for a positive relationship between plant diversity and

18 productivity have proposed that this effect may be explained by complementarity among

19 species in resources utilization, or selection of particularly productive species in high-

20 diversity plant communities. Recent studies have related the higher productivity in diverse

21 plant communities to suppression of pathogenic soil biota. If soil biota play a role in diversity-

22 productivity relationships, the question remains about how they may influence

23 complementarity and selection effects.

24 2. Here we examine how complementarity and selection effects may depend on soil biota

25 using a plant-soil feedback approach. We used monocultures and mixtures of early

26 successional plant species, which are known to have mostly negative plant-soil feedback

27 effects, and mid-successional plant species, which generally have neutral plant-soil feedback.

28 3. We found that plant-soil feedback effects differed between monocultures and mixed plant

29 communities, as well as between early and mid-succession plants. This resulted in a

30 significant interaction effect between diversity and successional stage. In monocultures, plant-

31 soil feedback tended to be negative for early- and positive for mid-succession plant species.

32 Interestingly, the community feedback responses of the mixed communities were opposite,

33 being positive for early- and negative for mid-succession community.

34 4. Plant-soil feedback differentially affected complementarity and selection effects of early

35 and mid-succession plant communities: it enhanced complementarity effects of early- and

36 decreased selection effects of mid-succession species.

37 5. *Synthesis*. Soil biota that drive plant-soil feedback effects can influence the diversity-

38 productivity relationship not only through decreased biomass production in monocultures

39 compared to mixtures, but also through influencing complementarity and selection effects

40   among species in mixed plant communities. Our results reveal that biodiversity-productivity

41   relationships depend on plant-soil feedback interactions, which depend on the successional

42   position of the plant. We propose that including successional position and trait-based analyses

43   of plant-soil feedback in diversity-functioning studies will enhance understanding

44   consequences of biodiversity loss for productivity and other ecosystem processes.

45   **Key-words**: Biodiversity effect, Biodiversity-productivity relationship, Complementarity

46   effect, Plant-soil feedback, Plant–soil (below-ground) interactions, Selection effect, Soil biota,

47   Succession

48

Introduction

49

50 Numerous studies have reported that primary productivity increases with greater plant species

51 diversity (Tilman, Wedin & Knops 1996; Loreau & Hector 2001; Tilman *et al.* 2001; Hooper

52 *et al.* 2005; Van Ruijven, Berendse & Tilman 2005; Tilman, Reich & Knops 2006). This

53 positive effect of diversity on productivity has been explained by complementarity and

54 selection effects (Loreau & Hector 2001). The complementarity effect refers to niche

55 differentiation or facilitative interactions between species, whereas the selection effect is

56 caused by species with particular traits that disproportionally contributes to the measured

57 parameter (Loreau & Hector 2001; Tilman 2001; Tilman *et al.* 2001; HilleRisLambers *et al.*

58 2004; Hooper & Dukes 2004). These two mechanisms driving the positive diversity-

59 productivity relationship are both based on resource availability and utilization, and a number

60 of studies have shown that complementarity and selection effects can operate simultaneously

61 in affecting productivity (Hooper & Dukes 2004; Roscher *et al.* 2005; Van Ruijven, Berendse

62 & Tilman 2005; Fargione *et al.* 2007).

63   It is becoming increasingly clear that soil biota, such as mycorrhizal fungi and soil

64 pathogens, can also play an important role in biodiversity-productivity relationships. For

65 example, several studies have argued that enhanced diversity of arbuscular mycorrhizal fungi

66 may increase plant production (van der Heijden *et al.* 1998), that fungal phylogeny may play a

67 role in maintaining ecosystem functions and services (Maherali & Klironomos 2007), and that

68 the fungi themselves can also have complementarity and selection effects (Wagg *et al.*

69 2011b). Some recent studies have proposed that soil-borne plant pathogens decrease plant

70 biomass production more in low-diversity than in high-diversity plant communities (Maron *et*

71 *al.* 2011; Schnitzer *et al.* 2011; Kulmatiski *et al.* 2012; Hendriks *et al.* 2013). Therefore, both

72 positive (e.g. symbiotic) and negative (e.g. pathogenic) interactions between plants and soil

73 biota can affect diversity-productivity relationships (van der Heijden *et al.* 1998; Maron *et al.*

74   2011; Schnitzer *et al.* 2011; Wagg *et al.* 2011a; Bever, Broadhurst & Thrall 2013). The

75   question is how these plant-soil biota interactions may influence complementarity and

76   selection effects.

77   In the field, plants are exposed to both symbionts and pathogens, as well as other soil biota

78   that altogether impact plant growth and plant community processes. The influence of plants

79   on these soil biota and feedback effects to plant performance is called plant-soil feedback

80   (Bever, Westover & Antonovics 1997). The plant-soil feedback approach provides an

81   effective way to study the net effect of symbiotic, pathogenic, and other soil organisms on

82   plant growth by measuring plant performance in soil that previously has been influenced by

83   the same or by other plant species (Bever *et al.* 2010; Van der Putten *et al.* 2013). A biomass-

84   specific, multi-species model examining the role of plant-soil feedbacks in the diversity-

85   productivity relationship, predicted a negative relationship between plant-soil feedback and

86   species-level overyielding (Kulmatiski *et al.* 2012). According to this model, plant species

87   with negative soil feedbacks produce more biomass in mixed communities than in

88   monocultures, whereas plant species with positive soil feedbacks are expected to perform less

89   well in mixed communities than in monocultures.

90   Traditional plant diversity-functioning studies have been carried out with plant

91   communities of which the species composition has been kept constant (Van Ruijven,

92   Berendse & Tilman 2005; Tilman, Reich & Knops 2006; Roscher *et al.* 2008; Hector *et al.*

93   2010). However, in many field conditions, the composition and structure of natural

94   vegetation changes over time resulting in succession (Walker, Walker & Hobbs 2007).

95   Interestingly, plant-soil feedback interactions also change during succession (Reynolds *et al.*

96   2003; Kardol, Bezemer & Van der Putten 2006). Early successional plant species are

97   generally fast growing and poorly defended against natural enemies, while having low

98   dependence on mutualistic symbionts, such as arbuscular mycorrhizal fungi. Consequently,

99   early successional plant species tend to generate negative plant-soil feedback by building up

100   specific pathogens, which enables pathogen-tolerant later-successional species to enter the

101   community (Van der Putten *et al.* 1993; Kardol, Bezemer & Van der Putten 2006). In

102   contrast, later successional plant species tend to associate with root fungi that positively affect

103   plant growth (Grime 2001), resulting in neutral to positive plant-soil feedback (Kardol,

104   Bezemer & Van der Putten 2006). The contrasting interactions with the soil biota of early and

105   later-successional plant species enabled us to test how plant biomass production in

106   monocultures versus mixed plant communities may depend on the type of plant-soil feedback.

107   We established monocultures and mixed communities consisting of either early- or mid-

108   succession plant species and examined how plant-soil feedback influenced biomass

109   production. We expected that plant-soil feedback would be negative for early- and more

110   neutral for mid-successional plant species. We tested the hypothesis that plant-soil feedback

111   will enhance the positive biodiversity effect on biomass production for early successional

112   communities, but that these effects will be less strong in mid successional communities that

113   have a more neutral soil feedback. We determined the diversity effect of early- and mid-

114   successional communities and established how different plant-soil feedback patterns may

115   affect the net diversity, complementarity, and selection effects.

Material and methods

For each of the two succession stages we selected five grass and five forb species that are typical of recently abandoned ex-arable fields (early succession), or fields that have been abandoned several decades ago (mid succession) according to Kardol *et al.* (2005) and Kardol, Bezemer & Van der Putten (2006): *Echinochloa crus-galli*, *Holcus lanatus*, *Holcus mollis*, *Lolium perenne*, *Poa annua* (early-successional grasses), and *Capsella bursa-pastoris*, *Crepis capillaris*, *Leucanthemum vulgare*, *Rumex acetosa*, *Rumex obtusifolius* (early-successional forbs); *Agrostis capillaris*, *Anthoxanthum odoratum*, *Briza media*, *Festuca filiformis*, *Nardus stricta* (mid-successional grasses), and *Arnica montana*, *Campanula rotundifolia*, *Centaurea jacea*, *Hypericum perforatum*, *Hypochaeris radicata* (mid-successional forbs). Seeds were obtained from specialized suppliers that collect seeds from wild plants (Cruydt-Hoeck, Assen, The Netherlands; B&T World seeds, Paguignan, France).

Soil was collected from an old field that has been abandoned in 1995. Fertile top soil was collected from a depth of 5-20 cm. The remaining top soil was removed until a depth of 40 cm, and mineral soil was collected from 40-60 cm below the soil surface. All soil was sieved (<0.5 cm) to remove coarse fragments, and homogenized. The top soil and mineral soil were mixed by 1:1 ratio (w:w). Half of the soil was kept at 4 °C to be used as soil for the control treatment in the feedback phase. Each pot was filled with 2 kg (based on dry weight) of the soil mixture.

Conditioning phase

During the conditioning phase two diversity treatments were established with either early- or mid-successional plant species. Monocultures were established consisting of 16 individual plants of the same species. The mixtures were planted with two individuals each of eight

140   species (4 grasses and 4 forbs), so that both monocultures and mixtures contained the same

141   number of plant individuals. In order to vary plant species combinations in the mixture

142   treatment, we established five different mixtures each having four grass and four forb species

143   that had been selected from the pool of five grass and forb species (See Table S1). All

144   monocultures and each mixture were replicated five times. In total there were 100 pots with

145   monocultures: 2 succession stages * 10 species (5 grasses + 5 forbs) * 5 replicates of each

146   species, and 50 pots with mixed plant communities: 2 succession stages * 5 combinations * 5

147   replicates of each combination.

148   Seeds were surface sterilized with 2 % sodium hypochlorite solution for 1 min, rinsed with

149   demineralized water, and germinated on glass beads moistened with demineralized water in a

150   germination cabinet (16/8 hrs light/dark photo regime, 22/18°C). One-week-old seedlings

151   were transplanted to the pots. For the mixtures, seedlings were planted at random positions

152   and the five replicates had different plant configurations to minimize position effects. During

153   the first week after planting, dead seedlings were replaced. Plants were watered three times a

154   week and water content was adjusted (17% w:w) once a week by weighing.

155   To condition the soil, the plants were grown for 12 weeks. From weeks 6-10, the plants

156   received 20 ml half-strength Hoagland nutrient solution twice a week (Hoagland and Arnon,

157   1950). After 12 weeks, shoots were clipped at the soil surface and shoot dry weight was

158   determined after oven-drying (70 °C until constant weight). The main roots were removed

159   from each pot, and the soil was homogenized and placed back in the same pot.

160

161   *Feedback phase*

162   In the feedback phase, the same monocultures and mixtures were replanted and grown for 10

163   weeks in the conditioned soil (150 pots) and in unconditioned soil (150 pots). The growth

164 procedure was as described for the conditioning phase and shoot dry weight was determined

165 after harvesting the plants.

166

167 *Calculations*

168 We calculated the plant-soil feedback effect of one plant species or a mixture of plant species

169 (Brinkman *et al.* 2010):

170 Feedback = Ln(average biomass on conditioned soil/ average biomass on control soil).

171   The additive partitioning method (Loreau & Hector 2001) was used to determine the net

172 diversity effect, the complementarity effect and the selection effect.

173 The net diversity effect was calculated as:

174 Net effect $=\sum Y - \overline{M}$

175 where Y is the observed biomass for each species in mixture, and M represents yield of a

176 species in monoculture.

177   The complementarity effect was calculated as:

178 Complementarity effect $= N \times \overline{M} \times \overline{\Delta RY}$

179 where N is the number of species, and $\Delta RY = (Y/M)-(1/N)$ (the deviation from the expected

180 relative yield of a species in the mixture) .

181   The selection effect was calculated as:

182 Selection effect $= N \times \text{cov}(M, \Delta RY)$.

183

184 *Data analysis*

185 All analyses were performed using the R statistical language, version 3.0.2 (R Development

186 Core Team 2013). In order to investigate whether early- and mid-successional plant species

187 respond differently to soil conditioning, the plant soil feedback effect of each species in

188   monoculture was analyzed using a linear mixed effect model with successional stage (early vs

189   mid), plant functional group (grass vs forb), and their interaction as fixed factors. In this

190   model, plant species was used as random factor. Whether plant-soil feedback effects differed

191   among species in monoculture and in mixed community was analyzed using analysis of

192   variance (ANOVA) with species as factors. T-tests were used to examine whether plant-soil

193   feedback in monocultures differed from zero.

194   Plant-soil feedback effects were calculated for each species both in the monocultures and in

195   the mixed communities. We compared the feedback response in early and mid-successional

196   monocultures using a mixed model with species as random factor, and stage (early vs mid),

197   functional group, and their interactions as factors. We also calculated the community plant-

198   soil feedback based on the total biomass of each mixed-community pot. We then analyzed

199   whether monospecific and community plant soil feedback responses differed between early

200   and mid-successional stages using a mixed model with stage and diversity (monoculture vs

201   mixture) as fixed factors. For this analysis we used assemblage as random factor (i.e. true

202   replicates). Each assemblage consists of eight plant species and each species was present in

203   four assemblages. For each species there were five replicate monocultures. We randomly

204   allocated the five replicates of each monoculture to the four appropriate assemblages to avoid

205   using the same data multiple times. If there were two replicates of the same monoculture

206   allocated to a single assemblage, this data was averaged so that within each assemblage there

207   were eight data points for the monocultures and five for the mixtures. We repeated the

208   analysis with average values for each monoculture; the outcome of these two analyses was

209   very similar and the interaction term was highly significant in both analyses. T-tests were

210   used to examine whether plant-soil feedback in monocultures and community feedback

211   effects differed from zero using averages of each assemblage as replicate.

212   The biodiversity effects (net, complementarity, and selection effect) were assessed using a

213   linear mixed model with successional stage (early vs mid), soil conditioning (conditioned vs

214   unconditioned) and their interaction as fixed factors. In this model, plant assemblage was used

215   as random factor. T-tests were used to examine whether biodiversity effects differed from

216   zero using averages of each assemblage as replicate.

217

218

219   **Results**

220   In monocultures, early-successional plant species tended to have negative plant-soil

221   feedbacks, while mid-successional species had positive plant-soil feedbacks (Figs. 1 & 2).

222   However, due to the large variation between species this was not significant (stage: $F_{1,16}$ =

223   1.86, P = 0.19). Independent of successional stage, grasses had positive and forbs negative

224   plant-soil feedbacks (Functional group: $F_{1,16}$ = 7.78., P =0.013). The plant-soil feedback

225   effects differed significantly among species in both early and mid-successional plants (Fig. 1

226   & S1; early successional species: $F_{9,40}$= 9.87, P < 0.001; mid successional species: $F_{9,40}$=

227   5.75, P < 0.001). For early-successional plant species, plant-soil feedback was positive for *P.*

228   *annua* and negative for *C. capillaris* and *L. vulgare*. For mid-successional plant species, plant-

229   soil feedback was positive for *A. capillaris* and *N. stricta* and negative for *H. radicata*. In the

230   mixture, species-specific plant-soil feedback also differed significantly among species in both

231   early- and mid-successional plant communities (Fig. S2 & S3; early successional species: F

232    $_{9,30}$= 5.41, P < 0.001; mid successional species: $F_{9,30}$= 15.76, P < 0.001).

233   The community feedback in mixtures was positive for early- and negative for mid-

234   successional species, and these effects were opposite to what was observed for feedbacks in

235   the monospecific plant cultures. This resulted in a highly significant interaction between stage

236   (early vs mid) and plant diversity (monoculture vs mixture; stage* diversity: $F_{1,118}$ = 11.87, P

237   = 0.0008; Fig. 2; Fig. S4).

238   Interestingly, the different responses of early- and mid-successional plant species to soil

239   conditioning between monocultures and mixtures affected the net, complementarity and

240   selection effects in a stage-dependent way (Table S2). The net effect of plant diversity

241   differed significantly between early- and mid-successional plant communities (Fig. 3a; $F_{1,8}$

242   =39.63, P < 0.001) and the magnitude and direction differed between conditioned and

243 unconditioned soil (successional stage * soil conditioning: $F_{1,88} = 16.19$, $P < 0.001$). Soil

244 conditioning evened-out the net diversity effects to some extent: it increased the net diversity

245 effect in the early-successional communities to become more neutral, whereas it decreased the

246 net diversity effect in the mid-successional communities to become less positive.

247   These effects of soil conditioning on net diversity effects turned out to be due to different

248 underlying complementarity and selection effects, depending on plant successional stage. Soil

249 conditioning influenced the complementarity effect in the two successional stages differently

250 (Fig. 3b; $F_{1,88} = 4.66$, $P < 0.05$). For early-successional plant species, the complementarity

251 effect was negative in control soil, whereas it was positive in conditioned soil. However, the

252 complementarity effect did not differ significantly between the two soils ($t = 2.18$, $P = 0.061$).

253 For mid-successional plant species, the complementarity effect did not significantly differ

254 between conditioned and control soil (Fig. 3b; Table S2). The selection effect was negative

255 for early-successional and positive for mid-successional plant species (Fig. 3c; $F_{1,8} = 51.20$, P

256 < 0.001). The magnitude and direction of the selection effect differed between conditioned

257 and unconditioned soils (successional stage * soil conditioning: $F_{1,88} = 25.73$, $P < 0.001$). Soil

258 conditioning did not affect the selection effect of early-successional species, but for mid-

259 successional species the selection effect was significantly reduced in conditioned soil (Table

260 S2).

261

262

Discussion

In our study, plant species from early- and mid-successional plant communities had a variety of responses to soil conditioning, but overall soil conditioning affected grass species positively and forb species negatively, independent of succession stage. Soil conditioning also differentially affected the community feedback responses, as well as the net, complementarity and selection effects of the early- and mid-successional plant communities. Clearly, the impact of soil conditioning on biodiversity effects depended on the successional position of the plant communities. Soil conditioning changed the complementarity effect from negative in control soil to positive in conditioned soil for early successional communities, whereas it decreased the selection effect in mid successional plant communities. Such soil-mediated effects reveal a mechanism that may explain differences in the effects of plant diversity on productivity among plant communities, for example when comparing early- and mid-successional plant communities.

Recently, Schnitzer and colleagues (2011) proposed that the positive relationship between diversity and productivity is due to pathogenic soil fungi, because in their study plants suffered more from host-specific soil pathogens in low-diversity than in high-diversity communities. These results were supported by several other studies (Maron *et al.* 2011; Kulmatiski *et al.* 2012; Hendriks *et al.* 2013), showing that positive plant diversity-productivity relationship may be due to less negative plant-soil feedback effects in mixtures than in monocultures. Traditionally, the positive effect of biodiversity on productivity has been explained by niche complementarity among plant species and the presence of few dominant, productive species. A recent study has shown that selection and complementarity effects among fungal species may act as insurance for maintaining plant productivity (Wagg *et al.* 2011). However, in the field soil biota can have positive and negative effects on plant diversity depending on which soil biota prevail: symbionts and decomposers, or pathogens

288   (Hartnett & Wilson 1999; De Deyn *et al.* 2003). Here, we show for the first time that

289   differences in how plant diversity influences the productivity of early- and mid-successional

290   plant communities can also be caused by differential effects of plant-soil feedback on

291   selection and complementarity effects.

292   A previous study with communities in which early-, mid- and late-successional plant

293   species were grown together has shown that soil pathogen effects may be confined to early-

294   successional species, whereas later successional plant species may interact in more neutral or

295   even positive ways with soil biota (Kardol, Bezemer & Van der Putten 2006). This previous

296   observation using the same type of ecosystem is different from our observation in which we

297   grew early and mid-successional communities separately. In our study, plant-soil feedbacks

298   between early- and mid-succession plant species were not statistically different, but tended to

299   be negative in monocultures of early- and positive in monocultures of mid-successional plant

300   species. In mixed plant communities, however, the effects were completely the opposite,

301   suggesting that plant-soil feedback can change diversity effects in a succession stage-

302   dependent way. It is important to note that in the previous study by Kardol, Bezemer & Van

303   der Putten (2006) all early-, mid-, and late-successional plant species were grown in one

304   mixed community, so that the plant-soil feedbacks are calculated as the responses of these

305   species when they were all exposed at the same time to the same soil community. In the

306   present study, however, all plant species were grown in monocultures and early vs mid

307   successional species mixtures were grown separately, which may explain the difference in

308   plant-soil feedback effects of early- and mid-successional plant species with the study by

309   Kardol *et al.* (2006).

310   In our study we also found that grasses and forbs had different plant-soil feedback effects.

311   Plant functional traits control many aspects of ecosystem functions, including soil physical

312   and biochemical characteristics (Eviner & Chapin 2003; De Deyn, Cornelissen & Bardgett

313 2008), and govern the primary productivity (Diaz & Cabido 2001; Roscher *et al.* 2012;

314 Polley, Isbell & Wilsey 2013). In an earlier study (De Deyn, Raaijmakers & Van der Putten

315 2004), soil sterilization greatly affected the relative abundance of plant functional groups in

316 the community. In that study, over time, the proportion of forb biomass decreased in sterilized

317 soil while it increased in non-sterilized soil indicating that soil biotic and abiotic conditions

318 can greatly affect plant community composition. Moreover, grasses and forbs can differ in

319 how they respond to changes in soil abiotic and biotic properties (Bezemer *et al.* 2006, Milcu

320 *et al.* 2006), which in turn may have caused the different plant-soil feedback effects between

321 the two functional groups.

322   Several long-term studies have shown that the positive impact of plant diversity on biomass

323 production increases over time (Van Ruijven, Berendse & Tilman 2005; Fargione *et al.* 2007;

324 Marquard *et al.* 2009), which has been attributed to increasing complementarity in resource

325 use and facilitative interactions (Cardinale *et al.* 2007). Recently, these temporal patterns in

326 diversity-functioning relationships have been suggested to be due primarily to plant-soil

327 feedback (Schnitzer *et al.* 2011, Maron *et al.* 2011, Kulmatiski *et al.* 2012, Hendriks *et al.*

328 2013). Our results show that plant-soil feedback effects can influence community productivity

329 by differentially influencing complementarity effect among plant species in early and mid-

330 successional plant communities. Complementarity effect was not altered by plant-soil

331 feedback in mid-successional plant communities. A possible explanation is that soil

332 conditioning caused a reduction in the biomass of the dominant species *H. radicata*, without

333 facilitating biomass production of other plant species to the same extent as the negative

334 community-level plant-soil feedback effect of mid-successional plant community. The

335 implication of our results is that the role of plant-soil feedback in diversity-functioning

336 relationships depends on the proportion of plant species in the community that respond to soil

337   feedback by negative versus positive responses, as well as to the strength of these negative

338   and positive feedback effects.

339   In several long-term studies, a positive selection effect initially operates via promoting a

340   productive dominant species, but over time these positive selection effects become negative

341   (Fargione *et al.* 2007; Marquard *et al.* 2009). We identified a decreased net biodiversity effect

342   of mid-successional plant species in the conditioned soil, which could be explained by a

343   decrease in the selection effect. This decline in the selection effect of mid-successional plant

344   communities in conditioned soil may be due to the performance of certain species in the

345   community: a more neutral, or positive plant-soil feedback in monoculture may not

346   necessarily be associated with the competitive ability of that plant species in a mixed plant

347   community. Several studies have reported that negative plant-soil feedback can maintain

348   species richness by preventing species from dominating the plant community (Bever 2003;

349   Adler & Muller-Landau 2005; Petermann *et al.* 2008; Mangan *et al.* 2010). In the present

350   study, the most productive mid-successional plant species, *Hypochaeris radicata*, suffered

351   from negative plant-soil feedback in monoculture, as well as in mixtures. This suggests that

352   soil conditioning decreased the selection effect in mid-successional plant communities by

353   suppressing the performance of a dominant species through negative plant-soil feedback.

354   In conclusion, plant-soil feedback has been considered as an important mechanism driving

355   plant population dynamics, community structure and ecosystem functioning in terrestrial

356   ecosystems. Here, we show that plant-soil feedback can influence the diversity-productivity

357   relationship via differentially influencing the complementarity and selection effects of early-

358   and mid-successional plant communities despite that in monoculture plant-soil feedback

359   effects of the early- and mid-successional plant species did not differ significantly. The

360   positive effect of diversity on productivity may be explained by less negative effects of soil

361   pathogens in multi-species plant communities, but also through enhanced soil microbe-

362   mediated complementarity effect among plant species. More studies are needed to investigate

363   how plant-soil feedback may influence biodiversity-productivity relationships in different

364   ecosystems under natural field conditions. Such studies should also attempt to elucidate the

365   underlying mechanisms by quantifying the contributions of the various abiotic and biotic soil

366   components to plant-soil feedback effects.

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374   **Data accessibility**

375   Data available from the Dryad Digital Repository, doi: 10.5061/dryad.sg770 (Jing *et al.*

376   2015).

377

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518   **Figure legends**

519   **Fig 1.** Plant-soil feedback effects of early- (a) and mid- (b) successional plant species. Grass

520   species are depicted left of the dashed line and forbs right. Asterisks indicate significant

521   differences between control and conditioned soil. **, * represent significant differences from

522   zero at $P<0.01$ and $P<0.05$, respectively. Each species is identified by abbreviated Latin

523   names (full names are provided in the Material and Methods section).

524   **Fig 2.** Monoculture (Mono) and community-level plant-soil feedback effects (Mean + SE;

525   n=5) of early- and mid-successional plant species. Asterisks between bars indicate if

526   differences between monospecific and community plant-soil feedbacks are significant.

527   Asterisks within bars indicate a significant difference from zero. *, $P<0.05$.

528   **Fig 3.** The net diversity effect (a), complementarity effect (b), and selection effect (c) of

529   early- and mid-successional plant communities in control and conditioned soils. Asterisks

530   between two bars indicate significant differences between control and conditioned soil.

531   Asterisks within bars indicate significant differences from zero. **, $P<0.01$; *, $P<0.05$.

532   Means are shown + SE (n=5).
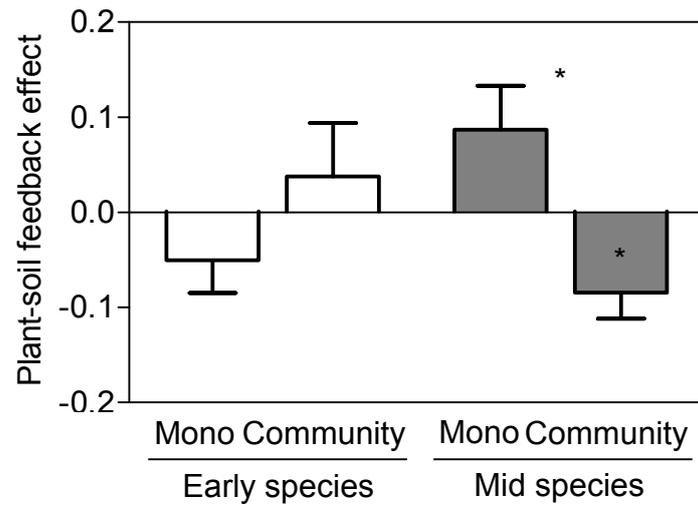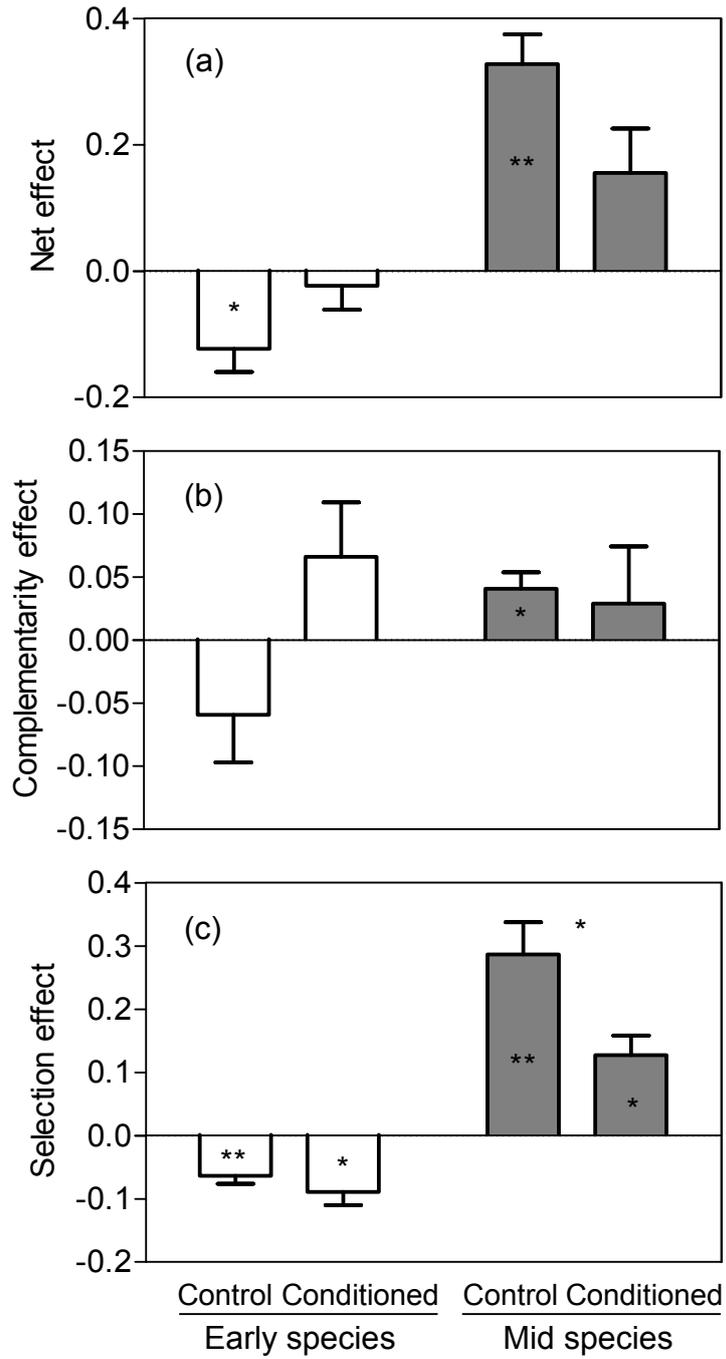
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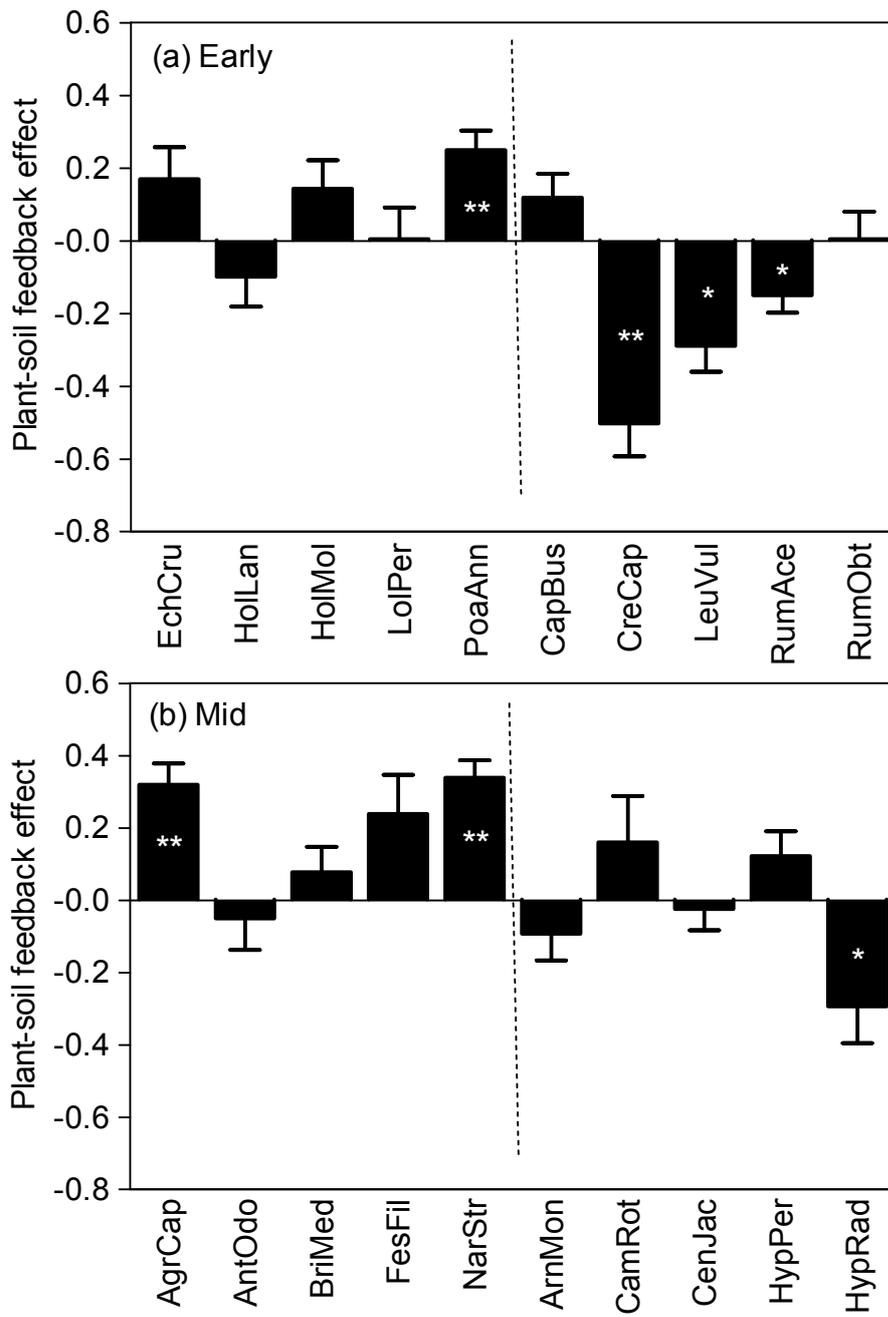
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536   Fig. 1

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