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14

15 **Title:** Plant-soil feedbacks of exotic plant species across life forms: a meta-analysis

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35 **Abstract (150-250 words)**

36 Invasive exotic plant species effects on soil biota and processes in their new range can promote
37 or counteract invasions via changed plant-soil feedback interactions to themselves or to native
38 plant species. Recent meta-analyses revealed that soil influenced by native and exotic plant
39 species is affecting growth and performance of natives more strongly than exotics. However,
40 the question is how uniform these responses are across contrasting life forms. Here, we test the
41 hypothesis that life form matters for effects on soil and plant-soil feedback.

42 In a meta-analysis we show that exotics enhanced C cycling, numbers of meso-
43 invertebrates and nematodes, while having variable effects on other soil biota and processes.
44 Plant effects on soil biota and processes were not dependent on life form, but patterns in
45 feedback effects of natives and exotics were dependent on life form. Native grasses and forbs
46 caused changes in soil that subsequently negatively affected their biomass, whereas native trees
47 caused changes in soil that subsequently positively affected their biomass. Most exotics had
48 neutral feedback effects, although exotic forbs had positive feedback effects. Effects of exotics
49 on natives differed among plant life forms. Native trees were inhibited in soils conditioned by
50 exotics, whereas native grasses were positively influenced in soil conditioned by exotics. We
51 conclude that plant life form matters when comparing plant-soil feedback effects both within
52 and between natives and exotics. We propose that impact analyses of exotic plant species on
53 the performance of native plant species can be improved by comparing responses within plant
54 life form.

55
56 **Keywords:** alien plant species, exotic plant species, life form, meta-analysis, plant invasions,
57 plant-soil feedback, plant-soil interactions, soil legacies

58 Introduction

59 Plants can affect abiotic and biotic soil properties causing feedback interactions to themselves,
60 their offspring, or to (the offspring of) other plant species (Wardle et al. 2004; Ehrenfeld et al.
61 2005; Bever et al. 2010) (Fig. 1). An increasing number of studies suggest that the abundance
62 of exotic plant species may be influenced by them altering soil conditions in a manner that
63 benefits their own performance through positive feedbacks (Callaway et al. 2004; Reinhart and
64 Callaway 2004; Agrawal et al. 2005; Engelkes et al. 2008; Maron et al. 2014), which may
65 provide them with a competitive advantage in their new range. These suggestions are generally
66 confirmed by recent meta-analyses (Kulmatiski et al. 2008; Suding et al. 2013). However, little
67 is known about how uniform these plant-soil feedback interactions are across life forms both
68 within and between native and exotic plant species.

69 Overall, native plant species experience variable, but predominantly negative plant-soil
70 feedbacks (Reinhart 2012; Mangan et al. 2010; Fitzsimons and Miller 2010; McCarthy-
71 Neumann and Kobe 2010; Kulmatiski et al. 2008), whereas introduced exotics generally
72 experience neutral or even positive plant-soil feedbacks (Callaway et al. 2004; Reinhart and
73 Callaway 2006; Suding et al. 2013; Engelkes et al. 2008). The magnitude of plant-soil
74 feedback effects for plant species in greenhouse studies has been observed to correlate with the
75 abundance of plant species in the field (Klironomos 2002; Mangan et al. 2010; McCarthy-
76 Neumann and Ibáñez 2013). These findings lead to the conclusion that invasiveness of
77 introduced exotic plant species is because they are subjected to less negative feedback with soil
78 than are native plant species. However, the correlation between the magnitude of plant-soil
79 feedback and plant species abundance in the field is not observed in all studies (Reinhart 2012)
80 and there have been few empirical tests under field conditions (Casper and Castelli 2007). In
81 addition, only a small portion of introduced exotic plant species become invasive (Williamson
82 and Fitter 1996). Moreover, exotics may also indirectly benefit from altered plant-soil feedback
83 when disturbing the positive feedback effect of some native plant species (Suding et al. 2013).

84 For example, because some exotics reduce symbiotic mutualists (Stinson et al. 2006), increase
85 local pathogens (Eppinga et al. 2006) or possibly accumulate allelochemicals (Callaway and
86 Ridenour 2004).

87 In many studies effects of introduced exotic plant species on soil have been measured in
88 relation to changes in specific soil biota (Stinson et al. 2006; Vogelsang and Bever 2009) and
89 soil processes (Vilà et al. 2011; Kourtev et al. 2003; Meisner et al. 2012). Some of these
90 studies use experimental data, whereas other studies are based on observational differences
91 between uninvaded versus invaded areas. The use of experimental data has an advantage as it
92 enables separation of causes and consequences, but the short duration of most experiments has
93 a disadvantage in that not all soil factors may have had sufficient time to respond to the
94 presence of the exotics. The main disadvantage of observational data is that the observed
95 effects may have been the cause of invasiveness, rather than the consequence. Ideally both
96 observational and empirical studies should run in parallel or need to complement each other.

97 Feedback effects may be dependent on plant species, taxonomic group or life form. For
98 example, grasses and forbs have in general a more negative feedback than trees (Kulmatiski et
99 al. 2008). Thus far, it is unknown if exotic and native species differ in plant-soil feedbacks
100 across plant life form (Liao et al. 2008; Suding et al. 2013). Therefore, in our meta-analysis, we
101 studied effects of both exotic and native species on soil properties and plant-soil feedback
102 effects within plant life form: trees, forbs, grasses, and nitrogen (N)-fixing plant species.

103 We first explored the effects of exotics on specific groups of soil biota and soil
104 processes, in order to advance beyond the black-box approach of plant-soil feedback (Cortois
105 and De Deyn 2012; Van der Heijden et al. 2008; Bever et al. 2010). Then, we explored plant-
106 soil feedback differences in the response of exotic and native plant species to soil conditioned
107 by either the exotic or native species. In this way our meta-analysis, complements the analysis
108 of Vilà et al. (2011) and addresses different questions than the analyses performed by
109 Kulmatiski et al. (2008) and Suding et al. (2013). We determined if the soil-mediated

110 feedbacks of exotics and natives to themselves and other groups of plants (exotics to natives
111 and natives to exotics) differed across plant life forms. We tested the hypotheses that: (1)
112 exotic plant species will enhance process rates and promote soil biota; (2) exotics experience
113 less negative plant-soil feedback from their own soil than do co-occurring native species; (3)
114 native species experience a more negative feedback from soil influenced by exotic species than
115 vice versa. For each hypothesis, we tested to what extent the outcome depended on plant life
116 form.

117

118 **Material and methods**

119 *Literature search*

120 Literature was searched using Web of Science and Scopus with combinations of the following
121 keywords: exotic plant, introduced plant, rhizosphere, invasi* plant, biota, soil, litter, feedback,
122 priority effect, soil legacies. Papers were also selected based on references in other papers and
123 cited papers. A total of 203 papers were selected to screen if the data fitted the inclusion
124 criteria.

125

126 *Inclusion criteria for effects of exotics on soil biota and soil processes*

127 We studied effects of exotics on soil biota and soil processes using soils conditioned by exotic
128 species as treatments and soil conditioned by native species as controls. We used only studies
129 in which the compared exotic and native species were co-occurring in the new range of the
130 exotic plant species. We evaluated effects of both rhizosphere and litter inputs on soil (Fig. 1).
131 If the experiment was performed in both invaded and non-invaded soils, we only used data
132 from the non-invaded soils to determine the effect size of exotic species before entering the
133 new range. We included studies that collected rhizosphere or litter from the field. The type of
134 comparison was noted: with native species (same life form, other life form or congener), plant
135 input (rhizosphere or litter), and type of study (field or greenhouse). Effects of exotics were

136 specified to: AMF, fungal biomass, bacterial biomass, microbial biomass, invertebrate count,
137 nematode count, C cycle, N cycle or P cycle. Supplemental Table S1 presents measurements
138 included within the different categories.

139

140 *Inclusion criteria for feedbacks from their own soil*

141 Here we compared feedbacks of native and exotic species in soil conditioned by conspecifics
142 (own soil). We calculated effect sizes by considering own soil as the treatment and away soil
143 (unconditioned soil, soil conditioned by congeners, soil conditioned by other species or
144 sterilized soil) as the control. Only those studies were included where exotic and native species
145 in the experiment co-occurred in the new range of the exotic plant species. The method used to
146 determine plant biomass was recorded: aboveground biomass, total biomass, or other biomass
147 measure. Native and exotic species were classified according to life forms (grass, forb, tree, N-
148 fixing). One specific nutrient acquisition trait (N-fixing) was added, because this trait may
149 relate to invasiveness (Liao et al. 2008). The studies that met the inclusion criteria are
150 presented in Table S2.

151

152 *Inclusion criteria for feedbacks of exotics to natives and natives to exotics*

153 We compared feedback of exotics to natives and of natives to exotics by considering
154 performance in away soil as treatment and in own soil as control. Away soil of natives was
155 conditioned by the exotics and away soil of exotics was conditioned by natives. As above we
156 noted the method to determine biomass in each study, and the life form of each native and
157 exotic species. The studies that met the inclusion criteria are presented in Table S3.

158

159 *Data extraction and calculating effect sizes*

160 When data met the inclusion criteria, means, variance estimates (SE or SD) and number of
161 replicates (n) were extracted. Out of the 203 papers, we selected 30 papers on feedback effects

162 of home soil, 32 papers on feedback effect of native to exotics and exotic to natives, and 39
163 papers on effects of exotics on soil biota and soil processes (see supplemental information). For
164 papers with multiple plant pairs, we considered plant species as unit of replication (Gurevitch
165 et al. 2001). We extracted data (means and variance estimates) from graphs with DataThief (B.
166 Tummers, DataThief III. 2006 <http://datathief.org/>). When data (mean, variance and/or n) was
167 missing from the study, data were obtained via contacting the corresponding authors of papers.
168 Studies with authors that could not be traced were omitted. To avoid non-independence, we
169 calculated a pooled mean and a pooled standard deviation for the treatment or control when
170 there was more than one treatment and only one control. We also did this for the treatments
171 when there was more than one control and only one treatment (Borenstein et al. 2009; Van
172 Kleunen et al. 2010).

173

174 *Calculating effect sizes*

175 For each parameter of interest, a standardized mean effect size per species was determined by
176 calculating Hedges'd using Metawin 2.0 (Rosenberg et al. 1999). This is the standardized mean
177 difference between the treatment and the control that is weighted by the pooled variance
178 (Borenstein et al. 2009; Gurevitch and Hedges 2001) and multiplied by factor J to correct for
179 bias of small sample size (Gurevitch and Hedges 2001; Rosenberg et al. 1999). These
180 individual effect sizes were combined by calculating a pooled summary effect size over all
181 species for each of the parameters of interest using a random model. A random model is
182 appropriate for ecological data as this takes heterogeneity between species into account
183 (Borenstein et al. 2009; Gurevitch et al. 2001). We calculated bias-corrected 95 % bootstrap
184 confidence intervals using 4999 iterations (Adams et al. 1997). Effect sizes were significantly
185 positive or negative when these confidence intervals did not overlap with 0 at $P < 0.05$ and the
186 sign of the effect size relates to positive and negative feedback, respectively. For effects of

187 exotics on soil biota and processes, a positive effect size indicated that exotics increased the
188 soil parameter of interest, while a decrease was indicated by a negative effect size.

189 We tested the variation between the effect sizes using a homogeneity test (Q), which
190 was evaluated using a chi-square test of significance. This test evaluates the null hypothesis
191 that all studies share the summary effect size (Borenstein et al. 2009). When Q_{total} is
192 significant, it indicates that effect sizes are not equally distributed across the studies in the
193 meta-analysis, or that the direction of effect sizes varies between studies. Provided that
194 sufficient data were available, we calculated the effect sizes per category of origin (native
195 versus exotics), biomass measurement type or life form. We tested if the direction of effect
196 sizes differed between categories (Q_{between}) and the extent to which effect sizes contained
197 variation that was unexplained by categories (Q_{within}).

198

199 *Corrections for non-independence of effect sizes*

200 Some plant species within studies contained more than one effect size, such as when pots were
201 sampled at multiple time points or when studies were performed in soil from multiple
202 locations. Effect sizes within a study were combined by calculating the fixed summary effect
203 size and variation for each plant species to avoid non-independence of the effect sizes, when
204 measurements were from multiple experiments within a study, such as multiple environments
205 or multiple independent time points, (Borenstein et al. 2009; Van Kleunen et al. 2010). When
206 measurements were performed over a time course, we used effect sizes from the final sampling
207 date. When there were more than one measurement on one individual plant species (e.g. two
208 kinds of C cycling measurements), we combined the data as described in chapter 24 of
209 Borenstein et al. (2009) and calculated a pooled mean effect size for the effect sizes from the
210 different measurements. The pooled variation of the mean effect size was calculated with the
211 following formula:

$$var(\bar{Y}_i) = \left(\frac{1}{m}\right)^2 var\left(\sum_{i=1}^m Y_i\right) = \left(\frac{1}{m}\right)^2 var\left(\sum_{i=1}^m V_i + \sum_{i \neq j} (r_{ij} \sqrt{V_i} \sqrt{V_j})\right)$$

212 where $var(\bar{Y}_i)$ is the pooled mean variance of effect size \bar{Y}_i for m variables. The correlation
 213 coefficient r_{ij} describes to which extent \bar{Y}_i and \bar{Y}_j co-vary, but r is often unknown. When $r = 1$,
 214 the variances are completely dependent on the different measurements and when $r = 0$, the
 215 variances are completely independent. The variances will affect the relative weight of the effect
 216 size when calculating the summary effect size with more weight going to the study with lower
 217 variance. We used $r = 1$ as this is the most conservative approach (Davidson et al. 2011) and
 218 we obtained similar results when $r = 0$.

219

220 *Checking for bias in data*

221 We calculated Rosenthal's fail safe numbers to address the "file drawer problem", which is the
 222 problem that studies with strong treatment effects are more likely to be published than studies
 223 with no or weaker treatment effects (Borenstein et al. 2009). Thereto, we calculated the number
 224 of studies needed to change the outcome of a significant summary effect size to non-
 225 significant. Fail safe numbers should be approximately larger than $5n + 10$ where n = number
 226 of studies. We also performed a rank correlation test, Spearman Rho, between effect size and
 227 variance. A significant correlation indicates that larger effect sizes in one direction are more
 228 likely published than smaller effect sizes (Rosenberg et al. 1999). We inspected data visually
 229 for abnormalities in data structure that would indicate publication bias by drawing a funnel plot
 230 and a Normal Quantile Plot.

231

232 **Results**

233 *Effects of exotics on soil biota and processes*

234 Exotics had positive effects on invertebrate abundance, nematode abundance and the processes
 235 involved in the carbon cycling (Fig. 2, see Table S1 for processes measured in experiments).

236 Effect sizes for effects of exotics on AMF, P cycling and N cycling differed between studies
237 (Q_{total} in Table S4), meaning that effect sizes were positive, negative and neutral depending on
238 the study. The comparison with natives (same life form, other life form, or congener), plant
239 input (rhizosphere or litter inputs) or type of study (field, greenhouse) could not explain the
240 differences in effect sizes, as indicated by non-significant values of Q_{between} ($P > 0.1$). There
241 may be a bias in the effects of exotics on soil biota and processes as the fail safe number was
242 548, which should be larger than 700 (see methods for explanation). Moreover, funnel plots
243 showed skewed data (supplement Fig. S1), which suggest that positive effect sizes are more
244 likely to have been published than negative or neutral effect sizes.

245

246 *Feedbacks of exotics and natives from their own soil*

247 Overall, plant species experienced neutral plant-soil feedbacks from their own soil (summary
248 effect size: -0.008; 95 % bootstrap CI -0.16 to 0.14). However, the direction of effect sizes was
249 variable between studies ($Q_{\text{total}} = 274$, $P = 0.001$, d.f. = 208), meaning that plant species
250 experienced negative, positive and neutral effects from their own soil. Part of this variation was
251 explained by the difference in feedback response between exotic and native species (see plant
252 origin effect in Table S5). Exotics had positive feedback when grown in soil conditioned by
253 themselves, whereas natives had negative feedback in their own soil (Fig. 3). However, plant
254 origin (native versus exotic species) did not explain all the variation in the effect sizes (Q_{within}
255 in Table S5). Interestingly, life forms tended to explain a portion of the variation in the effect
256 sizes ($Q_{\text{between}} = 7.62$, $P = 0.054$, d.f. = 3), but not all variation in effect sizes ($Q_{\text{within}} = 261$, $P =$
257 0.001, d.f. = 261).

258 Origin effects (native versus exotic) differed by plant life form (Table S5). Native
259 grasses had negative feedback effects in their own soil, whereas exotic grasses had neutral
260 feedback effects in soil conditioned by themselves (Fig. 3). Native forbs had negative feedback
261 effects from soil conditioned by themselves, whereas exotics had positive feedback effects in

262 their own soil (Fig. 3). In contrast, native trees had positive feedbacks, whereas feedback
263 effects of exotic trees were neutral (Fig. 3). The types of biomass measurement (aboveground
264 biomass, total biomass, or other biomass measure) did not explain differences in effect sizes
265 ($Q_{\text{between}} = 1.06$, $P = 0.59$, d.f. = 1). The type of away soils (sterilized, or conditioned by other
266 species or congener) did explain the differences between effect sizes (see Fig. S2; $Q_{\text{between}} =$
267 11.57 , $P = 0.02$, d.f. = 4). There is no evidence for publication bias as the overall mean effect
268 size was close to zero.

269

270 *Feedbacks of exotics to natives and natives to exotics*

271 Overall, native and exotic plant species experienced neutral feedback effects in soil
272 conditioned by plants of the other origin (0.08; 95% CI -0.29 to 0.42). However, the direction
273 of the effect sizes varied between species ($Q_{\text{total}} = 200$, $P < 0.001$, d.f. = 88), with positive,
274 negative or neutral effect sizes all occurring. Origin (exotic versus native) did not explain the
275 heterogeneity among effect sizes (Fig. 4). Interestingly, life form explained part of the variation
276 among the effect sizes ($Q_{\text{between}} = 16.5$, $P = 0.003$; d.f. = 4), but not all ($Q_{\text{within}} = 181$, $P < 0.001$,
277 d.f. 82). Moreover, exotic and native species responded differently to each others' soil within
278 plant life form (Table S6, Fig. 4). Changes in soil induced by exotic plant species did not
279 inhibit native species, except for native trees (Fig. 4). Interestingly, native grasses received a
280 positive feedback from soil conditioned by exotics (Fig. 4, Table S6). Native and exotic forbs
281 experienced a neutral plant-soil feedback from each others' soil. Native trees and other life
282 forms experienced negative plant-soil feedback from exotics, whereas exotics had positive
283 feedbacks from natives (Fig. 4, Table S6). The biomass measurement method or type of soil
284 input (rhizosphere or litter) did not explain the variation between effect sizes (Q_{between} for
285 biomass measurement method = 4.07, $P = 0.131$, d.f. = 2; Q_{between} for soil input = 1.22, $P = 0.545$,
286 d.f. = 2). There is no evidence for publication bias as the overall mean effect size was close to
287 zero.

288

289 **Discussion**290 *Effects of exotics on soil biota and processes*

291 Our analysis revealed that effects of exotic species on soil biota and processes were neutral for
292 most measurements, whereas exotics enhanced numbers of nematodes, invertebrates and C
293 cycling. These results confirm the results of a recent meta-analysis based on studies that had
294 taken an observational approach (Vilà et al. 2011). A potential problem of observational data is
295 that causes and consequences may not be separated. The advantage of our use of experimental
296 studies is that treatment effects point at causality, but a potential problem is that short duration
297 experiments may not fully reveal long-term processes, such as influences of exotic plant
298 species on decomposers and decomposition. Therefore, we suggest that both approaches may
299 complement each other in providing a more complete insight in impacts of invasive exotic
300 plant species on community dynamics and ecosystem properties.

301 Our finding that exotic species increased C cycling is consistent with what has been
302 observed for invasive exotic and abundant native species (Liao et al. 2008), suggesting that
303 those effects might be related to abundance rather than origin. However, increased C cycling
304 may be a consequence of trait differences between invasive exotic and native species, because
305 invasive exotic species often have traits associated with greater performance such as higher
306 growth rates (Van Kleunen et al. 2010). In addition, invasive exotic plant species often have
307 higher nutrient concentrations in shoots and higher litter quality than native species (Agrawal
308 et al. 2005; Kurokawa et al. 2010; but see Godoy et al. 2010). These traits could contribute to
309 faster C cycling via for example enhanced decomposition rates (Cornwell et al. 2008).

310 In spite of effects of exotic plant species on some soil properties, it still remains an open
311 question as to what extent changes in soil biota may be responsible for invasiveness of the
312 exotic species. For example, the direction of effects and the effect sizes of the exotic plant
313 species on soil characteristics did not match well with the observed plant-soil feedback

314 responses. This suggests that the drivers of invasiveness of exotic plant species are not
315 necessarily found among the changed soil parameters, but rather in subtle shifts in soil
316 microbes and processes (Inderjit and van der Putten 2010). Alternatively, it may be possible
317 that conditions present in the environment prior to the establishment of an exotic species may
318 be important in contributing to the subsequent success of exotic plant species. As such the
319 ‘vacant niche hypothesis’ suggests that certain exotic species may become successful because
320 they have access to resources in their new community that the native species do not use (Hierro
321 et al. 2005). For example, disturbances such as N deposition in N poor ecosystems may
322 promote invasion of exotic species if the natives are not adapted to high N availabilities (Weiss
323 1999; Huenneke et al. 1990).

324

325 *Feedbacks of exotics and natives from their own soil*

326 The results supported part of our hypothesis in that overall exotics have positive plant soil-
327 feedbacks in their own soil, whereas natives have negative feedback effects in their own soil.
328 This result is in contrast with a previous meta-analysis where both exotics and natives had
329 overall negative feedback effects in their own soil (Kulmatiski et al. 2008). This difference
330 may be due to the recent increase in studies with plant-soil feedback for exotic species
331 resulting in a larger sample size of 19 papers. However, opposite to our prediction, exotics did
332 not have less negative plant-soil feedbacks than natives when analyzing the data across all life
333 forms. This turned out to be due to a difference between grasses and forbs on the one hand and
334 trees on the other. Native grasses and forbs experienced negative plant-soil feedbacks, whereas
335 soil feedback effects of native trees were positive. That finding is in line with a previous meta-
336 analysis where trees had more positive feedbacks with their soil than forbs and grasses
337 (Kulmatiski et al. 2008). Our data suggest that this does not apply to exotic grasses, forbs and
338 trees as grasses and trees had neutral feedbacks with their soil while forbs had positive
339 feedbacks. Therefore, when comparing feedback effects of exotics with natives, care should be

340 taken to ensure proper comparisons, such as within life forms. Moreover, future experiments
341 may enhance understanding of invasiveness when they include factors, such as successional
342 position (Kardol et al. 2006), or time since introduction (Diez et al. 2010), which allows to
343 study why invasiveness of exotic species declines over time (Simberloff and Gibbons 2004).

344 In their own soil, all life forms of exotic species had neutral feedback effects, whereas
345 native grasses had negative feedback (Fig. 3). This could be due to a lack of specialist
346 pathogens and less dependence on specialist mutualists for exotic plant species (Van der Putten
347 et al. 2007). For example, part of the success of *Prunus serotina* as an invader in Europe is
348 because virulent soil pathogens that keep this plant in check in its native range in the USA
349 appear to be absent in the invaded range (Reinhart et al. 2010). In most studies, data on
350 pathogen species and their virulence, however, are not available. Another explanation for the
351 neutral plant-soil feedback effect of exotics may be that their dependence on belowground
352 symbiotic mutualists is lower than for native plant species (Seifert et al. 2009; Vogelsang and
353 Bever 2009). Also in the case of symbiotic mutualists, data on community composition and
354 effects on plant performance are too rare for inclusion in a meta-analysis.

355

356 *Effects from exotics to natives and natives to exotics*

357 The soil feedback effects of exotics on natives depended on plant life form. Native trees
358 experienced overall negative feedbacks from soil conditioned by exotic species, whereas native
359 grasses experienced positive feedbacks from exotics (Fig. 4). These conclusions appear to be in
360 contrast with a recent meta-analysis showing that soil from exotic species had a negative effect
361 on native species in comparison to performance in their own soil (Suding et al. 2013). Different
362 inclusion criteria may have been a reason for the discrepancies between these two studies.
363 While we included studies with feedback effects of exotics to natives or natives to exotics,
364 Suding et al. (2013) had a smaller subset to work with because of including only those studies
365 that reported both feedback effects from exotics to natives and vice versa. Moreover, in our

366 study some older papers have been included further enlarging our dataset. Our result confirms
367 the suggestion (Suding et al. 2013) that plant life form may matter for plant-soil feedbacks of
368 exotic species to natives.

369 Soil conditioned by exotics had a positive effect on native grasses, which may result
370 from effects of the exotic species on microbial community composition (e.g. Hawkes et al.
371 2006; Kourtev et al. 2003; Morriën and van der Putten 2013) and by increased faunal
372 abundance and C cycling (Fig. 2). The literature contains some examples of individual exotic
373 species that inhibit native species via the accumulation of local pathogens (Eppinga et al. 2006;
374 Mangla et al. 2008) or through inputs of novel allelochemicals into the soil that inhibit native
375 trees by a reduction in their symbiont (Stinson et al. 2006). However, our results do not suggest
376 that exotic plant species in general inhibit native plant species via altered plant-soil feedbacks.

377 Overall exotic species had neutral feedback effects in soil conditioned by natives. This
378 applied to most plant life forms, except that exotic trees had positive feedback effects in soil
379 conditioned by native trees. These results would suggest that exotic trees might benefit from (at
380 least some) of the symbiotic mutualists of the native tree species as suggested previously
381 (Richardson et al. 2000; Gundale et al. 2014).

382

383 **Conclusion**

384 Our results show that plant life form matter when studying potential effects of exotic invaders
385 on native plant community composition. Exotic species may promote native grasses, whereas
386 they may inhibit native trees. Therefore, we suggest that when assessing effects of exotic plant
387 species on subsequent potential establishment of native plant species (Grman and Suding
388 2010), effects of plant life form need to be explicitly taken into account. Our results suggest
389 that plant life forms are not only important to consider when comparing plant traits (Tecco et
390 al. 2010), but also when comparing plant-soil feedback effects between native and exotic plant

391 species. Further studies might as well reveal other traits that relate to patterns in plant-soil
392 feedback effects of native and exotic plant species.

393 The observed feedback responses of exotics and natives could not be related directly to
394 their influences on general soil biotic and abiotic characteristics. Therefore, more subtle effects
395 on soil conditions, such as the population abundance of specialist pathogens and symbionts,
396 may need to be addressed. In addition, the effects of changed composition of these soil
397 specialists on the performance of native and exotic plant species need to be quantified in order
398 to further understand the observed patterns in plant-soil feedback effects.

399

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407

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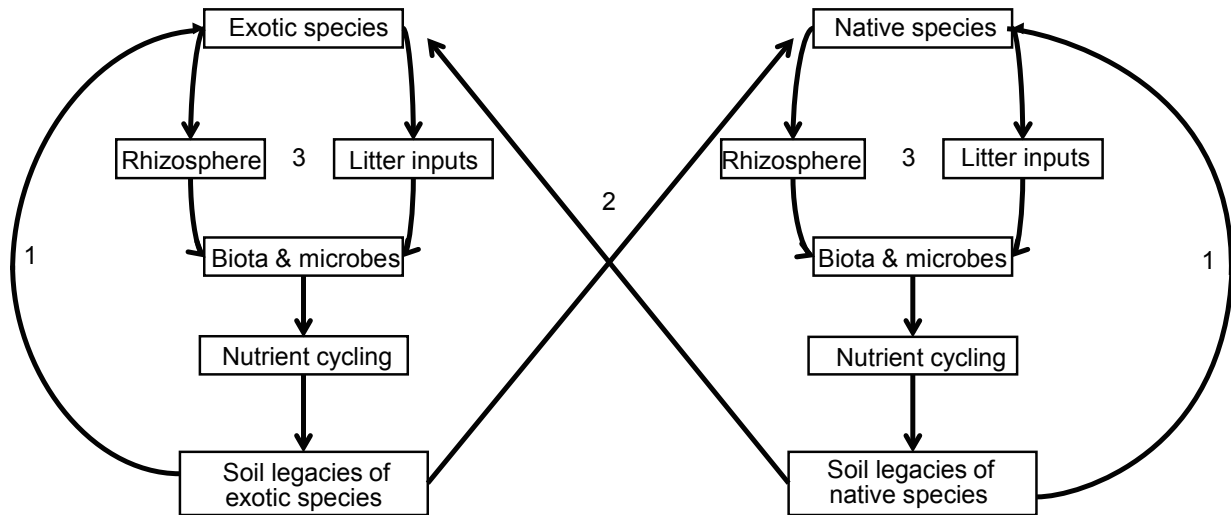
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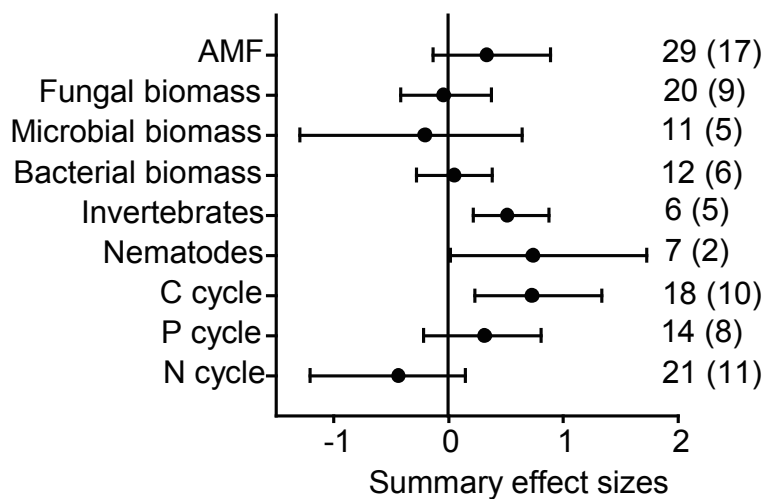
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574 **Figures**

575
 576 **Fig. 1** Schematic overview of plant-soil feedback. Exotic and native plant species can influence
 577 soil legacies via rhizosphere and/ or litter inputs. These soil legacies can feedback to influence
 578 the performance of the plant species that caused the change in the soil properties (1) and the
 579 performance of a neighbouring plant (2). In the present study, we have compared plant-soil
 580 feedbacks within and between native and exotic plant species. We further have studied effects
 581 of exotic species on soil biota, microbes and soil processes (3). Scheme is adapted from Bever
 582 (Bever 2003; Bever et al. 1997).

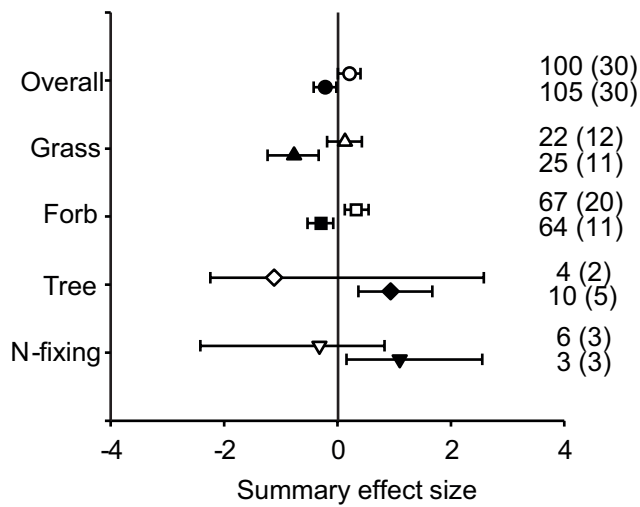
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 585 **Fig. 2** Effects of exotics on soil biota and processes. Effect sizes of effects from exotics on soil
 586 variables were calculated as the difference between soil conditioned by the exotic species and
 587 soil conditioned by the native species. Confidence intervals that do not overlap 0 indicate that
 588 exotics had an effect on the soil parameter at $P < 0.05$. Number of species and in brackets
 589 numbers of studies are presented on the right side of the graph.

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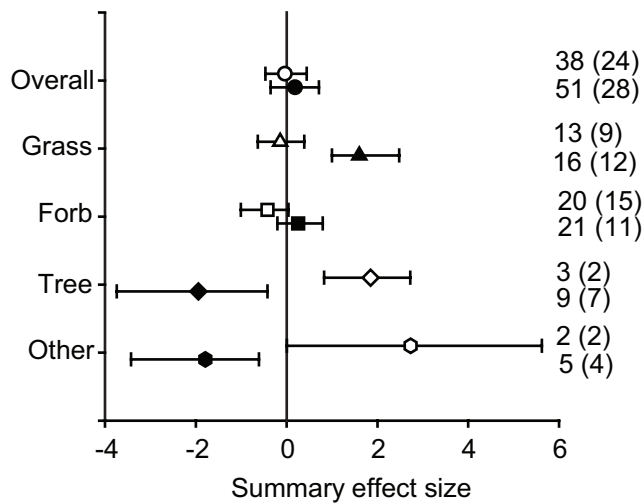
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593 **Fig. 3** Plant-soil feedbacks of home soil for exotics (open circles) versus natives (closed
 594 circles). Effect sizes were calculated by the difference between soil conditioned by own plant
 595 species (home soil) and sterilized soil or soil conditioned by other plant species (away soil).
 596 Exotics differed from natives for overall feedback (circles), grasses (up facing triangle), forbs
 597 (squares) and trees (diamond), but not for N-fixing species (down-facing triangle) (Q_{between}
 598 Table 1). Bootstrap bias corrected 95 % confidence intervals that do not overlap 0 indicate
 599 positive or negative plant-soil feedbacks at $P < 0.05$. Number of species and numbers of studies
 600 (in brackets) are presented on the right side of the graph.

601



602
 603 **Fig. 4** Plant-soil feedbacks of natives to exotics (open circles) versus exotics to natives (closed
 604 circles). For natives, effect sizes were calculated by the difference between soil conditioned by
 605 the exotic (away soil) and soil conditioned by themselves (home soil). For exotic, effect sizes
 606 were calculated by the difference between soil conditioned by the native species (away soil)
 607 and soil conditioned by themselves (home soil). Exotics and natives differed in response to
 608 each other's plant-soil feedback for grasses (up-facing triangle), trees (diamond) and other
 609 species (hexagon), but not for overall (circles) and forbs (square) (Table 2, Q_{between}). Bootstrap
 610 corrected 95 % confidence intervals that do not overlap 0 indicate positive or negative plant-
 611 soil feedbacks at $P < 0.05$. Number of species and number of studies (in brackets) are
 612 presented on the right side of the graph.

613