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Plant–soil feedbacks of exotic plant species across life forms: a meta-analysis

Meisner, Annelein; Hol, WH Gera; de Boer, Wietse; Adams Krumins, Jennifer; Wardle, David A; van der Putten, Wim H

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14

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

16 Authors: Annelein Meisner<sup>1,2\*</sup>, W.H. Gera Hol<sup>1</sup>, Wietse de Boer<sup>3,4</sup>, Jennifer Adams Krumins<sup>5</sup>,  
17 David A. Wardle<sup>6</sup>, Wim H. van der Putten<sup>1,7</sup>

18  
19 <sup>1</sup>Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW),  
20 P.O.Box 50, 6700 AB, Wageningen, The Netherlands; <sup>2</sup>Microbial Ecology, Department of  
21 Biology, Lund University, Ecology Building, SE 22362 Lund, Sweden; <sup>3</sup>Department of Soil  
22 Quality, Wageningen University, P.O. Box 47, 6700 AA, Wageningen, The Netherlands;  
23 <sup>4</sup>Department of Microbial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O.  
24 Box 50, 6700 AB, Wageningen, The Netherlands; <sup>5</sup>Department of Biology and Molecular  
25 Biology, Montclair State University, Montclair, NJ 07043, USA; <sup>6</sup>Department of Forest  
26 Ecology and Management, Swedish University of Agricultural Sciences, SE 90183, Umeå,  
27 Sweden; <sup>7</sup>Laboratory of Nematology, Wageningen University, P.O. Box 8123, 6700  
28 ES, Wageningen, The Netherlands

29  
30 \*corresponding author: Annelein Meisner, Email: AnneleinMeisner@gmail.com, Telephone:  
31 +46 46 2223763

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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  $Q_{\text{total}}$  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 ( $Q_{\text{between}}$ ) and the extent to which effect sizes contained  
197 variation that was unexplained by categories ( $Q_{\text{within}}$ ).

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 ( $Q_{\text{total}}$  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  $Q_{\text{between}}$  ( $P > 0.1$ ). 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 ( $Q_{\text{within}}$   
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 ( $Q_{\text{between}}$  for  
285 biomass measurement method = 4.07,  $P = 0.131$ , d.f. = 2;  $Q_{\text{between}}$  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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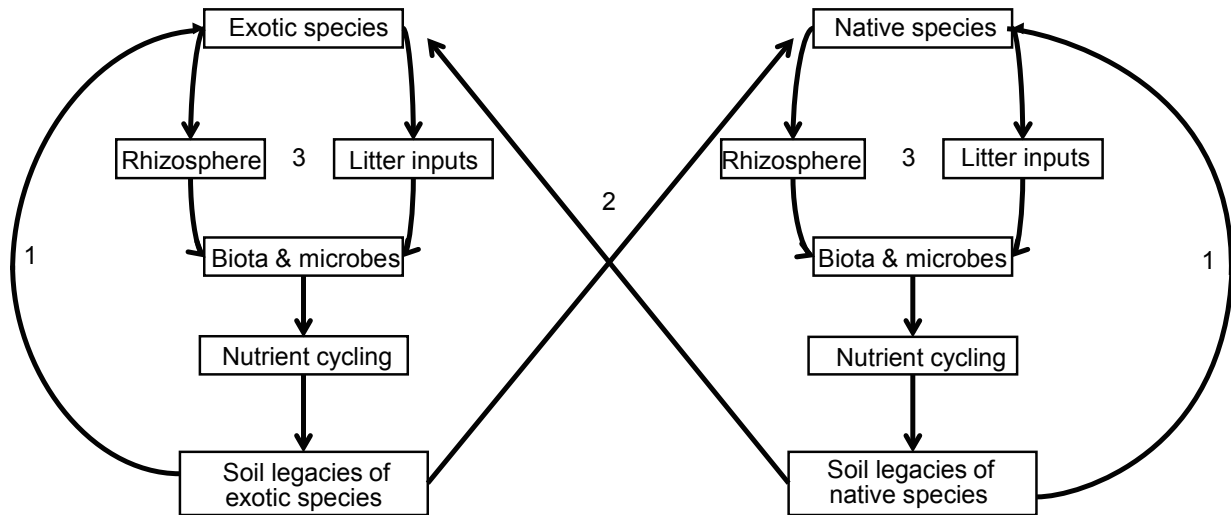
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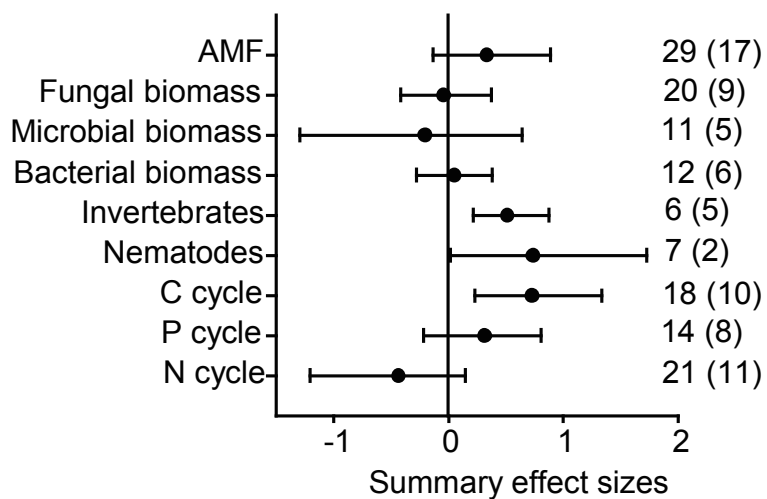


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574 **Figures**

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).

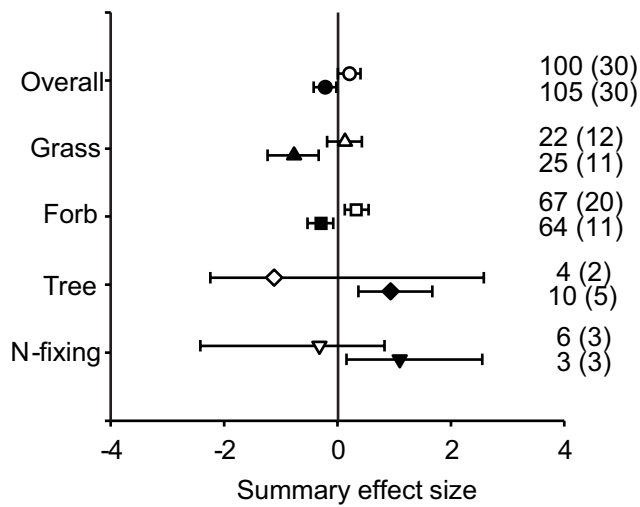
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584  
 585 **Fig. 2** Effects of exotics on soil biota and processes. Effect sizes of effects from exotics on soil  
 586 variables were calculated as the difference between soil conditioned by the exotic species and  
 587 soil conditioned by the 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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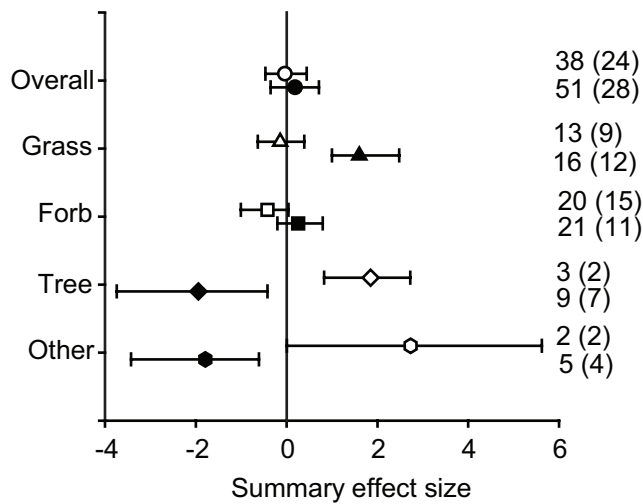
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592

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) ( $Q_{\text{between}}$   
 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,  $Q_{\text{between}}$ ). 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