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ORIGINAL PAPER

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

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**Abstract** Invasive exotic plant species effects on soil biota and processes in their new range can promote or counteract invasions via changed plant–soil feedback interactions to themselves or to native plant species. Recent meta-analyses reveale that soil influenced by native and exotic plant species is affecting growth and performance of natives more strongly than exotics. However, the question is how uniform these responses are across contrasting life forms. Here, we test the hypothesis that life form matters for effects on soil and plant–soil feedback. In a meta-analysis we show that exotics enhanced C cycling, numbers of meso-invertebrates and nematodes, while having variable effects on other soil biota and processes. Plant effects on soil biota and processes were not dependent on life form, but patterns in feedback effects of natives and exotics were dependent on life form. Native grasses and forbs caused changes in soil that subsequently negatively affected their biomass, whereas native trees caused changes in soil that subsequently positively affected their biomass. Most exotics had neutral feedback effects, although exotic forbs had positive feedback effects. Effects of exotics on natives differed among plant life forms. Native trees were inhibited in soils conditioned by exotics, whereas native grasses were positively

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influenced in soil conditioned by exotics. We conclude that plant life form matters when comparing plant–soil feedback effects both within and between natives and exotics. We propose that impact analyses of exotic plant species on the performance of native plant species can be improved by comparing responses within plant life form.

**Keywords** Alien plant species · Exotic plant species · Life form · Meta-analysis · Plant invasions · Plant–soil feedback · Plant–soil interactions · Soil legacies

## Introduction

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

Overall, native plant species experience variable, but predominantly negative plant–soil feedbacks (Reinhart 2012; Mangan et al. 2010; Fitzsimons and Miller 2010; McCarthy-Neumann and Kobe 2010; Kulmatiski et al. 2008), whereas introduced exotics generally experience neutral or even positive plant–soil feedbacks (Callaway et al. 2004; Reinhart and Callaway 2006; Suding et al. 2013; Engelkes et al. 2008). The magnitude of plant–soil feedback effects for plant species in greenhouse studies has been observed to correlate with the abundance of plant species in the field (Klironomos 2002; Mangan et al. 2010; McCarthy-Neumann and Ibáñez 2013). These findings lead to the conclusion that invasiveness of introduced exotic plant species is because they are subjected to less negative feedback with soil than are native plant species. However, the correlation between the magnitude of plant–soil feedback and plant species abundance in the field is not observed in all studies (Reinhart 2012) and there have been few empirical tests under field conditions (Casper and Castelli 2007). In addition, only a small portion of introduced exotic plant species become invasive (Williamson and Fitter 1996). Moreover, exotics may also indirectly benefit from altered plant–soil feedback when disturbing the positive feedback effect of some native plant species (Suding et al. 2013). For example, because some exotics reduce symbiotic mutualists (Stinson et al. 2006), increase local pathogens (Eppinga et al. 2006) or possibly accumulate allelochemicals (Callaway and Ridenour 2004).

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

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

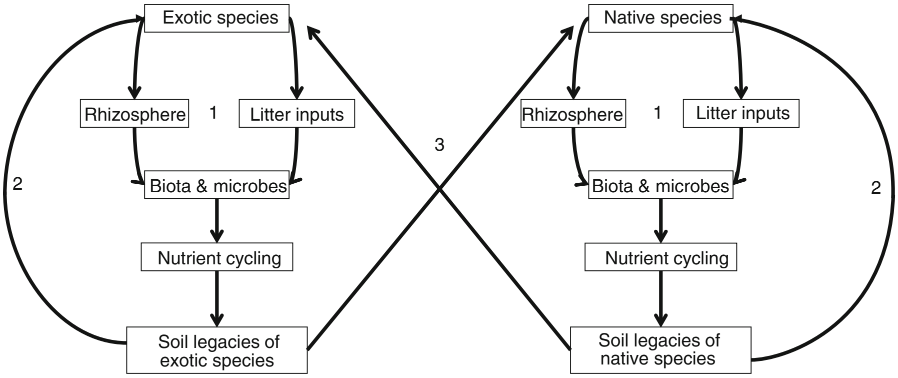

**Fig. 1** Schematic overview of plant–soil feedback. Exotic and native plant species can influence soil legacies via rhizosphere and/or litter inputs (1). These soil legacies can feedback to influence the performance of the plant species that caused the change in the soil properties (2) and the performance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

We first explored the effects of exotics on specific groups of soil biota and soil processes, in order to advance beyond the black-box approach of plant–soil feedback (Cortois and De Deyn 2012; Van der Heijden et al. 2008; Bever et al. 2010). Then, we explored plant–soil feedback differences in the response of exotic and native plant species to soil conditioned by either the exotic or native species. In this way our meta-analysis, complements the analysis of Vilà et al. (2011) and addresses different questions than the analyses performed by Kulmatiski et al. (2008) and Suding et al. (2013). We determined if the soil-mediated feedbacks of exotics and natives to themselves and other groups of plants (exotics to natives and natives to exotics) differed across plant life forms. We tested the hypotheses that: (1) exotic plant species will enhance process rates and promote soil biota; (2) exotics experience less negative plant–soil feedback from their own soil than do co-occurring native species; (3) native species experience a more negative feedback from soil influenced by exotic species than vice versa. For each hypothesis, we tested to what extent the outcome depended on plant life form.

## Materials and methods

### Literature search

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

### Inclusion criteria for effects of exotics on soil biota and soil processes

We studied effects of exotics on soil biota and soil processes using soils conditioned by exotic species as treatments and soil conditioned by native species as controls. We used only studies in which the compared exotic and native species were co-occurring in the new range of the exotic plant species. We evaluated effects of both rhizosphere and litter inputs on soil (Fig. 1). If the experiment was performed in both invaded and non-invaded soils, we only used data from the non-invaded soils to determine the effect size of exotic species before entering the new range. We included studies that collected rhizosphere or litter from the field. The type of comparison was noted: with native species (same life form, other life form or congener), plant input (rhizosphere or litter), and type of study (field or greenhouse). Effects of exotics were specified to: AMF, fungal biomass, bacterial biomass, microbial biomass, invertebrate count, nematode count, C cycle, N cycle or P cycle. Supplemental Table S1 presents measurements included within the different categories.

### Inclusion criteria for feedbacks from their own soil

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

### Inclusion criteria for feedbacks of exotics to natives and natives to exotics

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

### Data extraction and calculating effect sizes

When data met the inclusion criteria, means, variance estimates (SE or SD) and number of replicates (n) were extracted. Out of the 203 papers, we selected 30 papers on feedback effects of home soil, 32 papers on feedback effect of native to exotics and exotic to natives, and 39 papers on effects of exotics on soil biota and soil processes (see supplemental information). For papers with multiple plant pairs, we considered plant species as unit of replication (Gurevitch et al. 2001). We extracted data (means and variance estimates) from graphs with DataThief (B. Tummers, DataThief III. 2006 http://datathief.org/). When data (mean, variance and/or n) was missing from the study, data were obtained via contacting the corresponding authors of papers. Studies with authors that could not be traced were omitted. To avoid non-independence, we calculated a pooled mean and a pooled standard deviation for the treatment or control when there was more than one treatment and only one control. We also did this for the treatments when there was more than one control and only one treatment (Borenstein et al. 2009; Van Kleunen et al. 2010).

### Calculating effect sizes

For each parameter of interest, a standardized mean effect size per species was determined by calculating Hedges'd using Metawin 2.0 (Rosenberg et al. 1999). This is the standardized mean difference between the treatment and the control that is weighted by the pooled variance (Borenstein et al. 2009; Gurevitch and Hedges 2001) and multiplied by factor J to correct for bias of small sample size (Gurevitch and Hedges 2001; Rosenberg et al. 1999). These individual effect sizes were combined by calculating a pooled summary effect size over all species for each of the parameters of interest using a random model. A random model is appropriate for ecological data as this takes heterogeneity between species into account (Borenstein et al. 2009; Gurevitch et al. 2001). We calculated bias-corrected 95 % bootstrap confidence intervals using 4,999 iterations (Adams et al. 1997). Effect sizes were significantly positive or negative when these confidence intervals did not overlap with 0 at $P < 0.05$ and the sign of the effect size relates to positive and negative feedback, respectively. For effects of exotics on soil biota and processes, a positive effect size indicated that exotics increased the soil parameter of interest, while a decrease was indicated by a negative effect size.

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

### Corrections for non-independence of effect sizes

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

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

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

### Checking for bias in data

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

## Results

### Effects of exotics on soil biota and processes

Exotics had positive effects on invertebrate abundance, nematode abundance and the processes involved in the carbon cycling (Fig. 2, see Table S1 for processes measured in experiments). Effect sizes for effects of exotics on AMF, P cycling and N cycling differed between studies ($Q_{total}$ in Table S4), meaning that effect sizes were positive, negative and neutral depending on the study. The comparison with natives (same life form, other life form, or congener), plant input (rhizosphere or litter inputs) or type of study (field, greenhouse) could not explain the differences in effect sizes, as indicated by non-significant values of $Q_{between}$ ($P > 0.1$). There may be a bias in the effects of exotics on soil biota and processes as the fail safe number was 548, which should be larger than 700 (see methods for explanation). Moreover, funnel plots showed skewed data (supplement Fig. S1), which suggest that positive effect sizes are more likely to have been published than negative or neutral effect sizes.

### Feedbacks of exotics and natives from their own soil

Overall, plant species experienced neutral plant–soil feedbacks from their own soil (summary effect size:

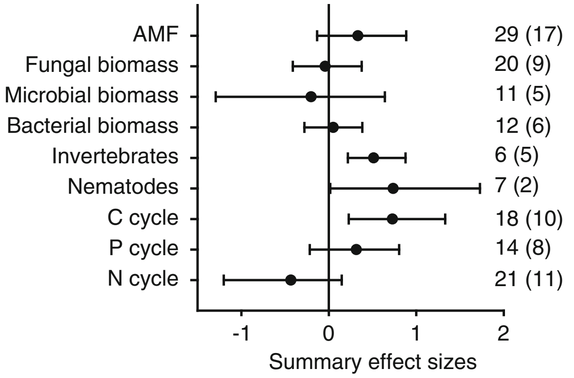

**Fig. 2** Effects of exotics on soil biota and processes. Effect sizes of effects from exotics on soil variables were calculated as the difference between soil conditioned by the exotic species and soil conditioned by the native species. Confidence intervals that do not overlap 0 indicate that exotics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

−0.008; 95 % bootstrap CI −0.16 to 0.14). However, the direction of effect sizes was variable between studies ($Q_{\text{total}} = 274, P = 0.001, df = 208$), meaning that plant species experienced negative, positive and neutral effects from their own soil. Part of this variation was explained by the difference in feedback response between exotic and native species (see plant origin effect in Table S5). Exotics had positive feedback when grown in soil conditioned by themselves, whereas natives had negative feedback in their own soil (Fig. 3). However, plant origin (native vs. exotic species) did not explain all the variation in the effect sizes ($Q_{\text{within}}$ in Table S5). Interestingly, life forms tended to explain a portion of the variation in the effect sizes ($Q_{\text{between}} = 7.62, P = 0.054, df = 3$), but not all variation in effect sizes ($Q_{\text{within}} = 261$, $P = 0.001, df = 261$).

Origin effects (native vs. exotic) differed by plant life form (Table S5). Native grasses had negative feedback effects in their own soil, whereas exotic grasses had neutral feedback effects in soil conditioned by themselves (Fig. 3). Native forbs had negative feedback effects from soil conditioned by themselves, whereas exotics had positive feedback effects in their own soil (Fig. 3). In contrast, native trees had positive feedbacks, whereas feedback effects of exotic trees were neutral (Fig. 3). The types of biomass measurement (aboveground biomass, total biomass, or other biomass measure) did not explain differences in effect sizes ($Q_{\text{between}} = 1.06, P = 0.59, df = 1$). The type of away soils (sterilized, or conditioned by other species or congener) did explain the differences between effect sizes (see Fig. S2; $Q_{\text{between}} = 11.57$, $P = 0.02$, $df = 4$). There is no evidence for publication bias as the overall mean effect size was close to zero.

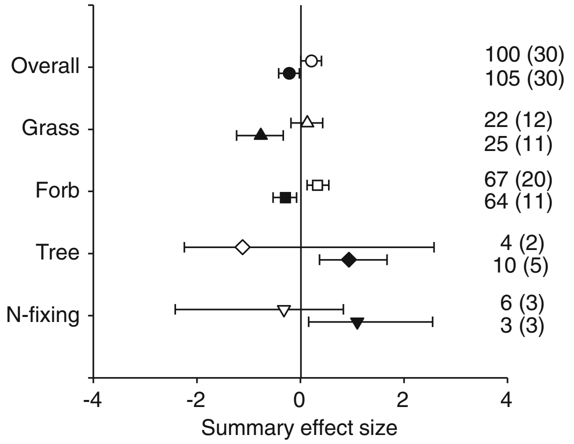

**Fig. 3** Plant–soil feedbacks of home soil for exotics (*open circles*) versus natives (*closed circles*). Effect sizes were calculated by the difference between soil conditioned by own plant species (home soil) and sterilized soil or soil conditioned by other plant species (away soil). Exotics differed from natives for overall feedback (*circles*), grasses (up facing *triangle*), forbs (*squares*) and trees (*diamond*), but not for N-fixing species (down-facing triangle) ($Q_{\text{between}}$ Table S5). Bootstrap bias corrected 95 % confidence intervals that do not overlap 0 indicate positive or negative plant–soil feedbacks at $P < 0.05$. Number of species and numbers of studies (in *brackets*) are presented on the right side of the graph

### Feedbacks of exotics to natives and natives to exotics

Overall, native and exotic plant species experienced neutral feedback effects in soil conditioned by plants of the other origin (0.08; 95 % CI −0.29 to 0.42). However, the direction of the effect sizes varied between species ($Q_{\text{total}} = 200, P < 0.001, df = 88$), with positive, negative or neutral effect sizes all occurring. Origin (exotic vs. native) did not explain the heterogeneity among effect sizes (Fig. 4). Interestingly, life form explained part of the variation among the effect sizes ($Q_{\text{between}} = 16.5, P = 0.003$; $df = 4$), but not all ($Q_{\text{within}} = 181$, $P < 0.001$, $df = 82$). Moreover, exotic and native species responded differently to each others' soil within plant life form (Table S6, Fig. 4). Changes in soil induced by exotic plant species did not inhibit native species,

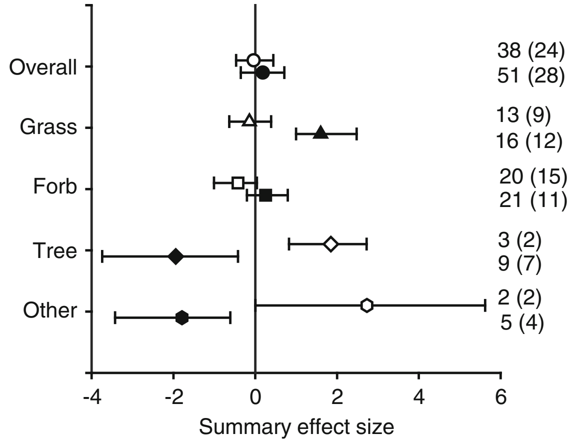

**Fig. 4** Plant–soil feedbacks of natives to exotics (*open circles*) versus exotics to natives (*closed circles*). For natives, effect sizes were calculated by the difference between soil conditioned by the exotic (away soil) and soil conditioned by themselves (home soil). For exotic, effect sizes were calculated by the difference between soil conditioned by the native species (away soil) and soil conditioned by themselves (home soil). Exotics and natives differed in response to each other's plant–soil feedback for grasses (up-facing *triangle*), trees (*diamond*) and other species (*hexagon*), but not for overall (*circles*) and forbs (*square*) (Table S6, $Q_{\text{between}}$). Bootstrap corrected 95 % confidence intervals that do not overlap 0 indicate positive or negative plant–soil feedbacks at $P < 0.05$. Number of species and number of studies (in *brackets*) are presented on the right side of the graph

except for native trees (Fig. 4). Interestingly, native grasses received a positive feedback from soil conditioned by exotics (Fig. 4, Table S6). Native and exotic forbs experienced a neutral plant–soil feedback from each others' soil. Native trees and other life forms experienced negative plant–soil feedback from exotics, whereas exotics had positive feedbacks from natives (Fig. 4, Table S6). The biomass measurement method or type of soil input (rhizosphere or litter) did not explain the variation between effect sizes ($Q_{\text{between}}$ for biomass measurement method = 4.07, $P$ 0.131, $df = 2$; $Q_{\text{between}}$ for soil input = 1.22, $P = 0.545$, $df = 2$). There is no evidence for publication bias as the overall mean effect size was close to zero.

## Discussion

### Effects of exotics on soil biota and processes

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

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

In spite of effects of exotic plant species on some soil properties, it still remains an open question as to what extent changes in soil biota may be responsible for invasiveness of the exotic species. For example, the direction of effects and the effect sizes of the exotic plant species on soil characteristics did not match well with the observed plant–soil feedback responses. This suggests that the drivers of invasiveness of exotic plant species are not necessarily found among the changed soil parameters, but rather in subtle shifts in soil microbes and processes (Inderjit and van der Putten 2010). Alternatively, it may be possible that conditions present in the environment prior to the establishment of an exotic species may be important in contributing to the subsequent success of exotic plant species. As such the 'vacant niche hypothesis' suggests that certain exotic species may become successful because they have access to resources in their new community that the native species do not use (Hierro et al. 2005). For example, disturbances such as N deposition in N poor ecosystems may promote invasion of exotic species if the natives are not adapted to high N availabilities (Weiss 1999; Huenneke et al. 1990).

### Feedbacks of exotics and natives from their own soil

The results supported part of our hypothesis in that overall exotics have positive plant soil-feedbacks in their own soil, whereas natives have negative feedback effects in their own soil. This result is in contrast with a previous meta-analysis where both exotics and natives had overall negative feedback effects in their own soil (Kulmatiski et al. 2008). This difference may be due to the recent increase in studies with plant–soil feedback for exotic species resulting in a larger sample size of 19 papers. However, opposite to our prediction, exotics did not have less negative plant–soil feedbacks than natives when analyzing the data across all life forms. This turned out to be due to a difference between grasses and forbs on the one hand and trees on the other. Native grasses and forbs experienced negative plant–soil feedbacks, whereas soil feedback effects of native trees were positive. That finding is in line with a previous meta-analysis where trees had more positive feedbacks with their soil than forbs and grasses (Kulmatiski et al. 2008). Our data suggest that this does not apply to exotic grasses, forbs and trees as grasses and trees had neutral feedbacks with their soil while forbs had positive feedbacks. Therefore, when comparing feedback effects of exotics with natives, care should be taken to ensure proper comparisons, such as within life forms. Moreover, future experiments may enhance understanding of invasiveness when they include factors, such as successional position (Kardol et al. 2006), or time since introduction (Diez et al. 2010), which allows to study why invasiveness of exotic species declines over time (Simberloff and Gibbons 2004).

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

### Effects from exotics to natives and natives to exotics

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

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

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

## Conclusion

Our results show that plant life form matter when studying potential effects of exotic invaders on native plant community composition. Exotic species may promote native grasses, whereas they may inhibit native trees. Therefore, we suggest that when assessing effects of exotic plant species on subsequent potential establishment of native plant species (Grman and Suding 2010), effects of plant life form need to be explicitly taken into account. Our results suggest that plant life forms are not only important to consider when comparing plant traits (Tecco et al. 2010), but also when comparing plant–soil feedback effects between native and exotic plant species. Further studies might as well reveal other traits that relate to patterns in plant–soil feedback effects of native and exotic plant species.

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

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