Reciprocal Effects of Litter from Exotic and Congeneric Native Plant Species via Soil Nutrients

Annelein Meisner[1]*, Wietse de Boer[2], Johannes H. C. Cornelissen[3], Wim H. van der Putten[1,4]

1 Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands, 2 Department of Microbial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands, 3 Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, Vrije Universiteit (VU) Amsterdam, Amsterdam, The Netherlands, 4 Laboratory of Nematology, Wageningen University, Wageningen, The Netherlands

Abstract

Invasive exotic plant species are often expected to benefit exclusively from legacy effects of their litter inputs on soil processes and nutrient availability. However, there are relatively few experimental tests determining how litter of exotic plants affects their own growth conditions compared to congeneric native plant species. Here, we test how the legacy of litter from three exotic plant species affects their own performance in comparison to their congeneric natives that co-occur in the invaded habitat. We also analyzed litter effects on soil processes. In all three comparisons, soil with litter from exotic plant species had the highest respiration rates. In two out of the three exotic-native species comparisons, soil with litter from exotic plant species had higher inorganic nitrogen concentrations than their native congener, which was likely due to higher initial litter quality of the exotics. When litter from an exotic plant species had a positive effect on itself, it also had a positive effect on its native congener. We conclude that exotic plant species develop a legacy effect in soil from the invaded range through their litter inputs. This litter legacy effect results in altered soil processes that can promote both the exotic plant species and their native congener.

Citation: Meisner A, de Boer W, Cornelissen JHC, van der Putten WH (2012) Reciprocal Effects of Litter from Exotic and Congeneric Native Plant Species via Soil Nutrients. PLoS ONE 7(2): e31596. doi:10.1371/journal.pone.0031596

Editor: Justin Wright, Duke University, United States of America

Received August 24, 2011; **Accepted** January 10, 2012; **Published** February 16, 2012

Funding: This study was funded by the Dutch Research Council ALW-Vici project (number 865.05.002) to WHV. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: A.Meisner@nioo.knaw.nl; AnneleinMeisner@gmail.com

Introduction

Plant species can be introduced into new ecosystems by humans via transport, tourism, trade [1,2] or changes in climate [3,4,5]. Some of these introductions result in biological invasions, which can have profound effects on the invaded habitats and the biodiversity therein [6,7]. One of the strongest impacts of exotic plant species on ecosystem processes operates via altered quality of litter inputs, which can alter the cycling of nutrients [8,9,10]. These altered soil processes have been hypothesized to provide a positive feedback to the exotic plant species through changes in litter inputs [9,11,12,13], but there are very few experimental tests showing that exotic plants indeed influence the legacy of the soil to their own benefit [10]. Here, we present results of an experimental study on litter effects of exotic and congeneric plant species, which are native in the invaded habitat, on soil processes and individual performance of exotic and native congener.

Differences in initial litter chemistry between exotic and native plant species are important for soil processes involved in litter decomposition [14,15] and are mediated indirectly by the soil decomposer subsystem [16,17,18]. For example, a higher lignin content can slow down the phased processes of litter breakdown [19], because this recalcitrant component needs specialist lignolytic fungi for degradation and can shield the more easily available components (*e.g.* cellulose) from decomposers during the earliest phases of litter breakdown [20,21]. Therefore, litter inputs of exotic plant species that differ in litter quality from native species have been shown to increase or decrease soil processes [22,23,24], which may remain in the soil as a legacy.

These litter legacies can affect the performance of exotic or native plant species [25,26]. When litter deposition increases the soil nutrient status, this may create a positive legacy effect to the subsequent plant species, either native or exotic (Fig. 3.11c in [27]). For example, litter addition from an exotic grass has been observed to increase biomass of the exotic grass itself and of a native shrub [28]. In contrast, litter can create a negative legacy effect when litter releases compounds into the soil during litter decomposition that inhibit plant growth [29,30]. A variety of long-term soil legacy effects of exotic plant species has been reported, including positive as well as negative legacy effects to native plant species [31,32].

Altered cycling of nutrients by exotic plant species is often hypothesized to promote exotic plant species exclusively (e.g. [33,34,35]). A relatively large number of studies have analyzed exotic litter effects in a context of plant community interactions. However, less is known about individual effects of exotic plant litter on exotic and native plant species [10]. Here, we study if the legacy of litter from exotics and congeneric natives reciprocally affect their performance when grown in monocultures via changes in soil processes. When litter of exotic plant species is of higher quality than of native plant species, this may increase soil nutrient mineralization [33,36] and nutrient availability [37,38]. Recently established exotic plant species in the Netherlands may have higher litter quality than congeneric native species [39].

Therefore, we test the hypothesis that litter from these exotic plant species provides a positive feedback to itself and inhibits natives through soil legacy effects. In order to avoid confounding effects due to major differences in plant chemistry and other traits that might differ between species [40], we compared exotic plant species with congeneric natives that co-occur in the invaded habitat.

Our hypothesis was tested by three experiments. In the first two experiments, we tested how soil mixed with litter from exotic plant species influenced soil respiration, soil mineralization and soil availability of nitrogen compared to soil mixed with litter from native plants species. In the third experiment, we tested how decomposing litter from exotic and native plant species affected germination rates and plant biomass of both exotic and native plant species. We performed the experiments with three genera of exotic and congeneric native plants that all co-occur in the same invaded habitat (Table 1).

Results

Experiment 1: Soil respiration

Exotic litter-inoculated soils showed (or in the case of *Rorippa* tended to show) a larger increase in cumulative respiration over time (Figure 1) as indicated by the Time by Origin interactions (Table 2).

Experiment 2: litter effects on soil N, enzyme activities and fungal biomass

Soil with litter from exotic *Artemisia* and *Senecio* accumulated more inorganic N than soil with litter from their congeneric native species (Figure 2A and 2C), as indicated by the origin by time interaction (Table 3). There was also an origin by time interaction for *Rorippa* (Table 2), because soil with litter from exotic *R. austriaca* had lower N concentration than soil with litter from native *R. sylvestris* only after 2 weeks of incubation (Figure 2B). These differences in inorganic N accumulation between soils with litter from exotic and native plant species corresponds with the initial litter N concentrations (Table 1). Soil with litter from exotic plant species had less fungal biomass than soil with litter from native plant species in the case of *Rorippa* and *Senecio*, but not in the case of *Artemisia* (Table 3, Figure 2D, E, F). The highest activity of cellulase was observed after 9 weeks of incubation (Figure 2G, H, I, Table 3). Significant differences at peak activity were observed in the case of *Artemisia* (Table 3), where litter from exotic *A. biennis* induced the highest cellulase activity (Figure 2G). Mn-peroxidase activity in soil with litter was relatively low and did not show significant differences between soil with litter from exotics and natives (Table 3, see Figure S1A, B, C). Soil pH showed some significant, but minor differences (Table 3, see Figure S1D, E, F).

Experiment 3: Litter effects on seedling germination and plant biomass

Seed germination and root sprouting of natives were not inhibited by litter from their congeneric exotic. In contrary, we observed a positive trend that litter from the exotic *R. austriaca* increased the rate of sprouting of both *R. sylvestris* and *R. austriaca* (Table 4, Figure 3). The rates of germination (and sprouting) of exotic plant species were lower than of natives for *Artemisia* and *Rorippa*, whereas the reverse was observed for *Senecio* (Figure 3A, B, C, Table 4).

Litter from exotics did not reduce biomass production of congeneric natives (Figure 3). Instead, *A. biennis and A. vulgaris* produced more biomass in soil with litter from the exotic *A. biennis* than from the native *A. vulgaris* (Table 4, Figure 3D). There was a similar trend for *Senecio* (Table 4, Figure 3F). *Rorippa austriaca* produced more biomass than *R. sylvestris*,whereas biomass was not different between exotic and native species in the case of *Artemisia* and *Senecio* (Table 4, Figure 3).

Discussion

Our results reject the hypothesis that litter from exotic plant species inhibits native plant species while promoting themselves. Instead, we observed that if litter from an exotic plant species increased its own biomass production or germination rate, this litter also promoted biomass and germination of its native congener. Moreover, negative litter effects by litter from exotic plant species were not observed in our study. Our comparison was made within plant genera, but our results are in agreement with two other studies on litter effects of exotic species on natives. *Senecio jacobaea*, an exotic species introduced in New Zealand, increased biomass production of native plant species from New Zealand [41]. In addition, litter of an exotic grass in the USA favored not only its own biomass production, but also biomass production of a native shrub [28]. These studies and our results suggest that not only exotic plant species exclusively, but also native plant species may benefit from the litter of exotic plant species.

The positive effect of litter from exotic plant species may have been due to differences in initial litter quality, because litter from exotics contained less lignin and lower lignin: N ratios than litter of

Table 1. Plant species used in experiments.

Plant name[1]	Plant origin[2]	Time of introduction[2]	Litter chemistry		
			% C	% N	Lignin (mg C/g litter)
Artemisia biennis	North-Asia	1950–1975	44	2.5	121
Artemisia vulgaris	Native[3]		46	1.7	205
Rorippa austriaca	East Europe	1900–1925	35	1.3	43
Rorippa sylvestris	Native[3]		39	2.2	84
Senecio inaequidens	South-Africa	1925–1950	46	2.3	113
Senecio jacobaea[4]	Native[3]		44	1.8	130

[1] Nomenclature according to Van der Meijden [80].
[2] [69].
[3] Native to the Netherlands.
[4] recently *Senecio jacobaea* has been renamed as *Jacobaea vulgaris* [81].

doi:10.1371/journal.pone.0031596.t001

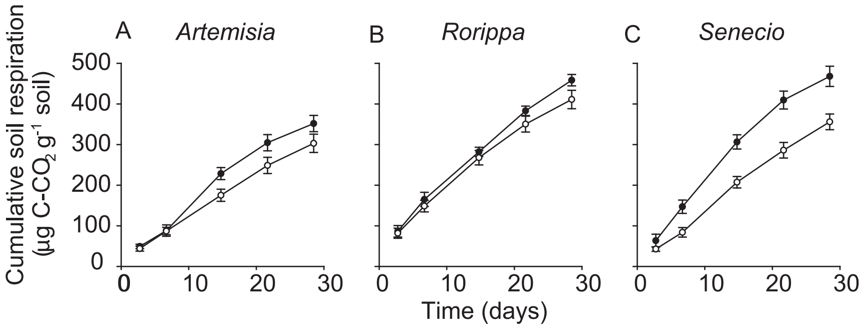

Figure 1. Mean cumulative soil respiration. (± SE). Measured in flasks with litter from exotic (filled circles) and native plant species (open circles) for *Artemisia* (a), *Rorippa* (b), and *Senecio* (c).
doi:10.1371/journal.pone.0031596.g001

the congeneric natives (Table 1). The higher litter quality of exotic species may have increased microbial activity as shown by higher cumulative respiration rates, because the degradable carbon pool in litter from exotics was likely better accessible to decomposers than in litter from natives [42]. Based on cellulase-activities it seems that cellulose was only more available in litter from the exotic *A. biennis*. Soil available N concentrations reflected initial litter N concentrations, which were highest in litter from exotic *Artemisia* and *Senecio* species. In the case of *Rorippa*, there was no such an effect. The increased cumulative respiration rates and mineral N concentration in soil incubated with litter from exotic plant species could be the result of degradation of litter itself as well as from stimulation of degradation of soil organic matter (priming) [43]. This priming-induced increase of soil organic matter mineralization has also been proposed to be an important consequence of exotic grass invasion into hardwood forest [44]. Fungal biomass was more often lower in soil with litter from exotics than litter from natives, which is likely due to the lower initial lignin concentration of exotics [21,45]. Therefore, litter from exotic species may change the soil food-web to a more bacterial dominated one if this litter is of higher quality than litter from native plant species [46,47].

Other studies showed that differences in litter decomposition rates between exotic and native plant species strongly depend on initial litter quality (e.g. [23,33], but see [48]). Our results indicate that these differences in litter decomposition rates between exotic and native plant species can result in altered soil processes and nutrient availability. Moreover, differences in initial litter quality between native and exotic plant species may explain the site-dependent differences in nutrient concentrations, litter decomposition and carbon mineralization between invaded and uninvaded sites in Europe [49,50,51].

Table 2. Repeated-measure ANOVA for soil respiration.

Factors	Plant genera								
	Artemisia			*Rorippa*			*Senecio*		
	d.f.	**F**	**P**	**d.f.**	**F**	**P**	**d.f.**	**F**	**P**
Between subject									
Origin (O)	1	2.77	0.13	1	0.96	0.36	1	13.9	0.004
Error	10			8			10		
Within subject									
Time (T)	1.4	361	<0.001	1.2	1141	<0.001	1.6	635	<0.001
T×O	1.4	5.47	0.027	1.2	4.50	0.054	1.6	13.9	<0.001
Error	14			9.9			16		

Litter from exotic versus native plant species (named Origin) of three genera (*Artemisia, Rorippa* and *Senecio*) were compared.
doi:10.1371/journal.pone.0031596.t002

The native plant species used in our study are also invasive in other parts of the world. It has been proposed that comparisons between exotic plant species and native plant species that are invasive elsewhere, may be complicated, as the natives have traits that can promote their invasiveness [52]. In that case, a congeneric comparison of exotics and natives should not result in differences, whereas our study showed that litter from exotics clearly promoted soil respiration and nitrogen availability compared with litter from natives. Species that are introduced into other regions often pass through environmental filters, which can result in rapid evolution of these plant species [53,54]. As a result, invasive and native populations of the same species do not necessarily have the same traits [55,56]. Our congeneric comparisons made it less likely that differences in litter effect may be due to secondary defense compounds exclusively produced by exotic plants [57]. Nevertheless, in cases of differences in secondary defense compounds, or when slow growing native plant species with poor litter quality are being replaced by fast growing exotics with high litter quality [58], it is possible that exotic species benefit disproportionally from their own litter.

Litter legacy effects are important for the dominance of individual plant species in plant communities in the next growing season [25,26]. Litter legacies that increase soil nutrient concentrations may increase the dominance of exotic plant species when they take more advantage of these nutrients than the competing natives. Therefore, interactions with other mechanisms that increase the performance of exotics more than natives should be considered when explaining exotic plant dominance in ecosystems [59,60]. For example, a modeling study showed that an exotic invasive wetland plant has likely evolved a mechanism to produce litter of lower quality that decomposes slower, which reduces the dominance of the native plant species due to competition for light [61]. Another mechanism that could interact with a positive litter legacy effect on soil processes is the release from belowground enemies when an exotic plant species invades a new range (e.g. [62,63,64]). Indeed, two exotics in our study have been shown to experience a less negative effect from their rhizosphere biota [65]. In that case, litter of exotic plants may cause a legacy effect favoring the exotic over natives when they are released from soil-borne enemies. Therefore, future experiments may be needed to untangle these interacting mechanisms, for example by growing exotic and native species in competition.

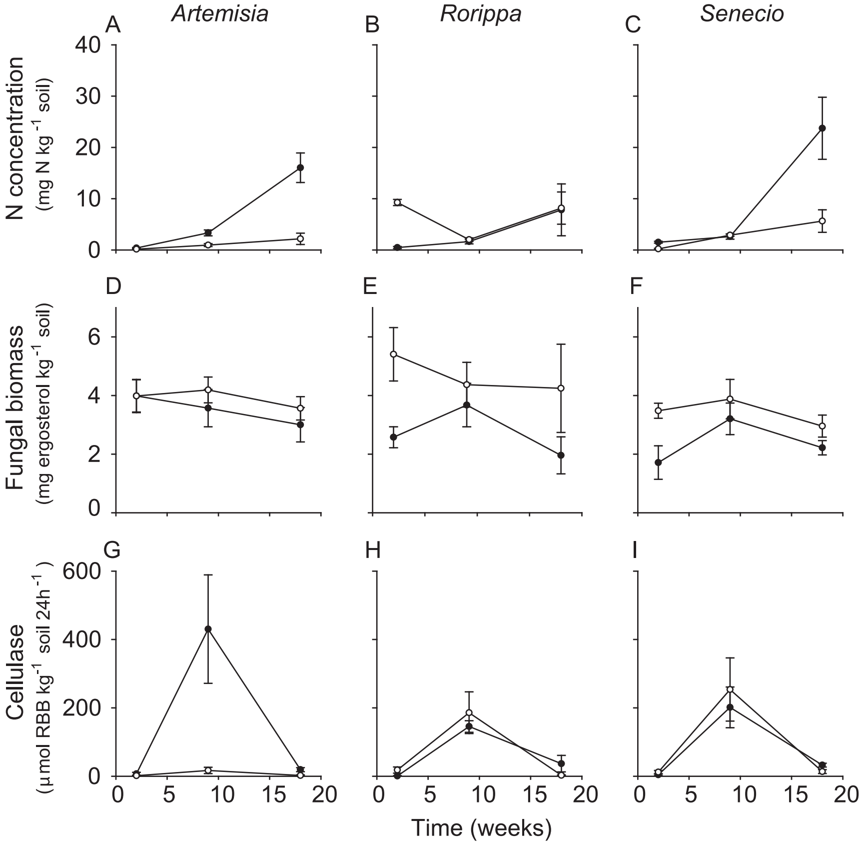

Figure 2. Effects of litter on nitrogen, fungal biomass and cellulase activity. Soil available inorganic nitrogen (N) (A, B, C), fungal biomass (D, E, F) and cellulase activity (G, H, I) in soil mixed with litter from exotic plant species (filled circles) and litter from native plant species (open circles). Means (± SE) are presented for *Artemisia* (A, D, G), *Rorippa* (B, E, H) and *Senecio* (C, F, I).
doi:10.1371/journal.pone.0031596.g002

We conclude that monocultures of the exotic plant species and their congeneric native can benefit from increased soil nutrient availability through the legacy of exotic litter. Litter legacy effects on soil processes alone may, therefore, disproportionally benefit exotic over native plant species only in interaction with other mechanisms [66].

Materials and Methods

Ethics Statement

All necessary permits to collect soil and plant material from the Gelderse Poort region were obtained from Staatsbosbeheer regio Oost, the Netherlands.

Plant selection

We made a phylogenetically controlled comparison of exotics and congeneric natives (e.g. [23,37,67]), to ensure that differences in litter effects would not be influenced by differences in major classes of plant chemistry within a plant pair. The three plant pairs all co-occurred in the same riverine habitat and the exotic and native congeners occurred in mixed stands [68]. Therefore, species interactions through litter are realistically occurring in the field. Three exotic and their congeneric native plant species were selected using the national standard list of the Dutch flora [39,65,69]. We chose exotic plant species that are recent invaders and have increased in frequency in the second half of the 20th century in order to include exotic species with invasive potential [5]. Finally, a practical point was that sufficient amounts of litter, and seeds or root fragments had to be available to conduct the experiment. All plants co-occurred in the Gelderse Poort region, which is where the River Rhine enters the Netherlands. Three species pairs that could be selected according to the above-mentioned criteria were: *Artemisia biennis* and *A. vulgaris*; *Rorippa austriaca* and *R. sylvestris*; *Senecio inaequidens* and *S. jacobaea* (Table 1). The three native species are all invasive in other parts of the world [70,71,72].

Collection of plant and soil material

Soil, litter, seeds and root fragments were all collected from the Gelderse Poort region. Root fragments were collected for *Rorippa*, because this genus and especially the exotics has very difficult seeds to collect [73]. Soil was collected from 5 locations in Millingerwaard, a nature reserve within this region (51°52′N; 5°59′E). After sampling, soil was homogenized and sieved through a 10 mm mesh to remove coarse fragments and plant material. The homogenized soil had a pH of 7.8 and a moisture content of 14.7% (w/w) [39].

In autumn 2008, litter was collected from the Gelderse Poort region by selecting senesced leaves from standing plants [74]. Litter was collected from at least 10 individuals per plant species at multiple locations within the Gelderse Poort region. Litter was air-dried, stored in paper bags until use, chopped into 0.5×0.5 cm pieces and mixed for subsequent use in the experiment. Initial chemical composition of litter was determined on dried (at 70°C) and then ground litter (see Table 1). Total carbon (C) and nitrogen (N) were determined using a NC analyzer (Thermo flash EA

Table 3. ANOVA for effects of litter on soil properties.

Factors	Plant genera					
	Artemisia[1]		*Rorippa*[1]		*Senecio*[1]	
	F	**P**	**F**	**P**	**F**	**P**
Soil Inorganic N						
Origin (O)	51.7	<0.001	12.0	0.005	18.6	<0.001
Time (T)	55.0	<0.001	6.82	0.01	34.7	<0.001
OxT	13.1	<0.001	10.6	0.002	5.91	0.008
Fungal biomass						
Origin (O)	0.80	0.38	5.10	0.043	7.57	0.01
Time (T)	1.00	0.38	0.49	0.63	2.70	0.087
OxT	0.20	0.82	0.54	0.59	0.85	0.44
Cellulase activity						
Origin (O)	28.1	<0.001	0.02	0.89	0.05	0.83
Time (T)	16.7	<0.001	16.5	<0.001	30.7	<0.001
OxT	2.97	0.07	5.77	0.018	3.03	0.07
Mn-peroxidase activity						
Origin (O)	0.89	0.35	0.44	0.42	0.18	0.67
Time (T)	14.2	<0.001	0.36	0.67	6.29	0.006
OxT	0.57	0.57	0.44	0.34	0.29	0.75
pH						
Origin (O)	4.40	0.046	11.9	0.005	4.00	0.057
Time (T)	43.9	<0.001	23.7	<0.001	36.8	<0.001
OxT	1.90	0.17	0.78	0.78	4.30	0.026

Litter from exotic or native species (Origin) were compared for three plant genera (*Artemisia*, *Rorippa* and *Senecio*) at three destructive sampling points (Time).

[1] Numerator d.f. is 2 for time, 1 for origin and 2 for Time×Origin. Denominator d.f. is 24 for *Artemisia* and *Senecio* and 12 for *Rorippa* pair.

doi:10.1371/journal.pone.0031596.t003

Table 4. ANOVA for effects of litter effects on plant performance.

Factors	Plant genera					
	Artemisia[1]		*Rorippa*[1]		*Senecio*[1]	
	F	**P**	**F**	**P**	**F**	**P**
Germination/sprouting						
Litter (L)	1.78	0.20	4.13	0.06	1.86	0.19
Plant (P)	23.7	<0.001	17.7	<0.001	13.9	0.002
LxP	0.02	0.88	0.06	0.81	0.79	0.39
Plant biomass						
Litter (L)	9.54	0.007	1.23	0.29	3.56	0.078
Plant (P)	1.04	0.32	7.47	0.016	0.03	0.87
LxP	0.02	0.89	1.52	0.24	0.86	0.37

Litter effects from exotic versus native plant species (Litter) on germination or (in the case of *Rorippa*) sprouting rates and plant biomass production as well as the differences between exotic and native plant species (Plant) within three genera (*Artemisia*, *Rorippa*, and *Senecio*).

[1] Numerator d.f. is 1 for all factors. Denominator d.f. is 16, except for Rorippa-pair where denominator d.f. is 14.

doi:10.1371/journal.pone.0031596.t004

1112). Lignin content was determined according to Poorter and Villar [75]. Briefly, the litter material was subjected to polar, non-polar and acid extraction steps. The mass of the remaining residue was corrected for ash and the ash-adjusted C and N content of the residue was used to calculate lignin concentrations. This lignin fraction has been used successfully as litter quality index, but may contain small amounts of other recalcitrant C compounds besides lignin [29].

Seeds were collected in autumn 2008. Root fragments were collected for *Rorippa*-pair in spring 2009. Root fragments and seeds were surface-sterilised in a 0.5% sodium hypochlorite solution to kill potential root and seed pathogens. Root fragments of *R. sylvestris* were also rinsed with 70% ethanol, because a pilot showed higher root sprouting.

Experiment 1: litter effects on soil respiration

In order to determine the effects of litter on soil respiration, each litter was mixed with field soil and placed in flasks. Per plant species, six flasks of 315 ml were used (four flasks for *R. austriaca* due to limited amount of available litter). Each flask received an amount of field-moist soil equivalent to 40 gram dry weight and on top of this soil a 29.6 gram mixture of soil and litter (71.6:1) was placed, representing an average yearly amount of litter per unit of soil in temperate systems [76]. Six flasks without litter in the top layer were included as control. Soil was kept at 50% water holding capacity (WHC), which equals 17.7% w/w. Flasks were closed with a rubber septum, placed in randomized order in an incubation chamber and incubated at 10°C, which is the yearly average temperature of the Netherlands (www.knmi.nl). At days 3, 7, 15, 22 and 29, gas samples were collected from the headspace using a gastight syringe and stored in an Exetainer® vial until analysis. After each sampling, flasks were opened to allow ventilation for an hour to prevent high CO_2 levels in the flasks and to adjust the moisture if needed by adding demineralized water. CO_2-concentrations were measured against a reference line on a Thermo FOCUS GC equipped with a RT-QPLOT column from Restek (30 m long and 0.53 mm diameter). The average CO_2 concentration in control pots was subtracted from the CO_2 concentration in the pots that contained litter. Cumulative CO_2 production was calculated for each litter type.

Experiment 2: litter effects on soil N, enzyme activities and fungal biomass

In order to determine how litter influenced soil N availability, enzyme activities and fungal biomass, litter of each plant species was mixed with field soil and placed in cubic microcosms of 0.5 L with a surface area of 81 cm^2. There were 15 replicates for each litter (8 replicates for *R. austriaca* and 10 for *R. sylvestris* due to limited availability of litter). Each microcosm received an amount of field-moist soil equivalent to 450 gram dry soil and on top of this soil 83 gram of the same litter-soil mixture as used in experiment 1 was added. The microcosms were incubated in a climate room at 10°C, 83% humidity and soil was kept at 50% WHC (= 17.7% w/w). Five random microcosms were harvested after 2, 9 and 18 weeks of incubation, after which the top layer of soil was analyzed.

Available mineral N was extracted by shaking moist soil (equivalent to 10 g dry weight) in 50 ml 1 M KCl for 2 h. N-NH_4^+ and N-NO_3^- concentrations were measured on a Technicon TrAAcs 800 auto-analyzer. pH_{water} was measured in a 1: 2.5 soil to water ratio. Ergosterol, a specific fungal biomarker in the cell wall, was used to measure fungal biomass. This biomarker is not present in arbuscular mycorrhizal fungi (AMF) [77]. Ergosterol was extracted from soil using an alkaline-extraction method and measured on a Dionex HPLC equipped

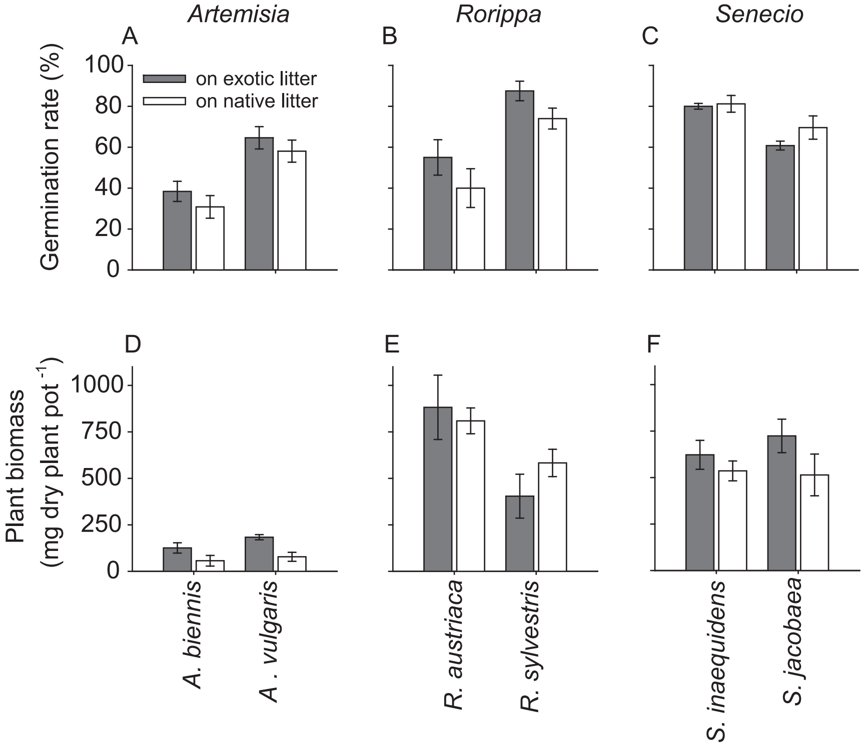

Figure 3. Effects of litter on germination rates and plant biomass production. Mean (± SE) for germination or (in the case of *Rorippa*) sprouting rate (A, B, C) and plant biomass (D, E, F) production of exotic and native plant species in litter from exotic (grey bars) or native plant species (white bars) belonging to three genera. Exotic plant species are: *A. biennis, R. austriaca* and *S. inaequidens*. Native plant species are: *A. vulgaris, R. sylvestris* and *S. jacobaea*. Significances of litter effects and plant effects are given in Table 4.
doi:10.1371/journal.pone.0031596.g003

with a C 18 reverse-phase column and a UV-detector set at 282 nm [78]. Lignin degrading enzyme activity (Mn-peroxidase) and cellulose degrading enzyme activity (endo-1,4-β-glucanase) were measured according to Van der Wal et al. [79], modified by extracting 6 gram of soil with 9 ml of milli-q water. Endo-1,4-β-glucanase is an indicator of cellulase activity and is therefore called cellulase in the main text.

Experiment 3: litter effects on seedling germination and plant biomass production

In order to determine how litter influenced seedling germination and plant biomass production, seeds of exotic and native plant species were placed on soil that had been incubated with their own litter, as well as on soil that had been incubated with the litter of the congener. We created a series of 10 microcosms (8 for *R. austriaca*) per litter origin, which were pre-incubated for 18 weeks as in experiment 2 in order to mimic litter decomposition in winter prior to plant growth in spring. For *Artemisia* and *Senecio*, 50 seeds of exotic or native plant species were placed on half of the microcosm within the genera to create five microcosms per litter origin for each plant origin within genera. For *Rorippa*, 10 root fragments of exotic or native species were placed in the soil of half of the microcosm. Germination or sprouting rates were registered after 17 days for *Senecio*, after 22 days for *Rorippa*, and after 36 days for *Artemisia*, because the time of germination or sprouting differed between genera. After germination, seedlings or cuttings were thinned so that one seedling with median length was left. Microcosms were harvested after 9.5 weeks of incubation. All harvested plants were dried to constant weight at 70°C and weighed. Microcosms were placed in a climate chamber at 19°C/10°C and 83% humidity (average May–September growing conditions for plant species in the Netherlands, www.knmi.nl) with daylight for 16 h per 24 h.

Data analysis

The results were analyzed with Statistica version 9.0 (StatSoft, Inc. (2009), Tulsa, USA) by considering the three genera separately. Repeated measures ANOVAs were performed per genus-pair for soil respiration with origin (litter from exotic or native plant species) as the between-subject factor. As the sphericity assumption was violated for all genus-pairs, Greenhouse-Geisser adjusted P values and degrees of freedom were calculated (Table 2). An ANOVA was performed for the effects of litter on soil per genus-pair with origin (litter from exotic or native plant species) and time (2, 9 and 18 weeks of incubation) as fixed factors. Cellulase was log-transformed to meet assumptions of ANOVA. Inorganic N concentration was log-transformed for the genera *Artemisia* and *Rorippa* and fourth-root transformed for *Senecio* to meet assumptions of ANOVA. Effects of litter origin on germination rates and plant biomass production were analyzed per genus-pair by ANOVA with litter (litter from exotic or native plant species) and plant (exotic or native plant species) as fixed factors. Germination rates were arcsine transformed and biomass was log transformed to meet assumptions of ANOVA.

Supporting Information

Figure S1 Effects of litter on Mn-peroxidase activity and pH. Mn-peroxidase activity (A, B, C) and pH (D, E, F) in soil incubated with litter from exotic plant species (filled circles) or with litter from native plant species (open circles). Means (± SE) are presented for *Artemisia* (A, D), *Rorippa* (B, E) and *Senecio* (C, F). (PDF)

Acknowledgments

We thank Staatsbosbeheer regio Oost for giving us permission to collect plant and soil material in the Gelderse Poort region. We thank Ciska Raaijmakers, Wiecher Smant, Gera Hol, Henk Duyts, Paulien Klein Gunnewiek and Richard van Logtestijn for their help and advice during the experiment; Heike Schmitt for advice on respiration measurements; Daan Blok for help with setting up the experiment and for helpful comments on the manuscript; Fernando Monroy Martinez, Remy Hillekens, Mirka Macel and Tim Engelkes for discussion about the experiment; Koen Verhoeven, Martijn Bezemer and Arjen Biere for discussions about statistics; two anonymous referees for comments on previous versions of this manuscript. This is NIOO publication 5204.

Author Contributions

Conceived and designed the experiments: AM WD WHV JHCC. Performed the experiments: AM. Analyzed the data: AM. Contributed reagents/materials/analysis tools: WHV JHCC. Wrote the paper: AM WD JHCC WHV.

References

1. Hodkinson DJ, Thompson K (1997) Plant dispersal: the role of man. J Appl Ecol 34: 1484–1496.
2. Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, et al. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. Ecol App 10: 689–710.
3. Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.
4. Walther GR, Roques A, Hulme PE, Sykes MT, Pysek P, et al. (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24: 686–693.
5. Tamis WLM, Van't Zelfde M, Van der Meijden R, De Haes HAU (2005) Changes in vascular plant biodiversity in the Netherlands in the 20th century explained by their climatic and other environmental characteristics. Climatic Change 72: 37–56.
6. Chapin FSI, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, et al. (2000) Consequences of changing biodiversity. Nature 405: 234–242.
7. Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: A significant component of human-caused global change. N Z J Ecol 21: 1–16.
8. Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41: 59–80.
9. Liao C, Peng R, Luo Y, Zhou X, Wu X, et al. (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phyt 177: 706–714.
10. Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, et al. (2003) Mechanisms underlying the impacts of exotic plant invasions. P Roy Soc Lond B Bio 270: 775–781.
11. Farrer EC, Goldberg DE (2009) Litter drives ecosystem and plant community changes in cattail invasion. Ecol App 19: 398–412.
12. Raizada P, Raghubanshi AS, Singh JS (2008) Impact of invasive alien plant species on soil processes: A review. Proc Nat Acad Sci India Sect B 78: 288–298.
13. Ehrenfeld JG (2004) Implications of invasive species for belowground community and nutrient. Weed Technology 18: 1232–1235.
14. Wardle DA, Barker GM, Bonner KI, Nicholson KS (1998) Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? J Ecol 86: 405–420.
15. Meier CL, Bowman WD (2008) Links between plant litter chemistry, species diversity, and below-ground ecosystem function. Proc Natl Acad Sci U S A 105: 19780–19785.
16. Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van der Putten WH, et al. (2004) Ecological linkages between aboveground and belowground biota. Science 304: 1629–1633.
17. Aerts R, Chapin FSI (2000) The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. Adv Ecol Res 30: 1–67.
18. Hobbie SE (1992) Effects of plant-species on nutrient cycling. Trends Ecol Evol 7: 336–339.
19. Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, et al. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol Lett 11: 1065–1071.
20. De Boer W, Folman LB, Summerbell RC, Boddy L (2005) Living in a fungal world: impact of fungi on soil bacterial niche development. FEMS Microbiol Rev 29: 795–811.
21. Osono T (2007) Ecology of ligninolytic fungi associated with leaf litter decomposition. Ecol Res 22: 955–974.
22. Rothstein DE, Vitousek PM, Simmons BL (2004) An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. Ecosystems 7: 805–814.
23. Godoy O, Castro-Diez P, Van Logtestijn RSP, Cornelissen JHC, Valladares F (2010) Leaf litter traits of invasive species slow down decomposition compared to Spanish natives: a broad phylogenetic comparison. Oecologia 162: 781–790.
24. Drenovsky RE, Batten KM (2007) Invasion by *aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpetine grassland. Biol Invasions 9: 107–116.
25. Facelli JM, Facelli E (1993) Interactions after death - plant litter controls priority effects in a successional plant community. Oecologia 95: 277–282.
26. Berendse F (1994) Litter decomposability - a neglected component of plant fitness. J Ecol 82: 187–190.
27. Bardgett RD, Wardle DA (2010) Aboveground- belowground linkages: biotic interactions, ecosystem processes and global change. New York, USA: Oxford University Press.
28. Wolkovich EM, Bolger DT, Cottingham KL (2009) Invasive grass litter facilitates native shrubs through abiotic effects. J Veg Sci 20: 1121–1132.
29. Dorrepaal E, Cornelissen JHC, Aerts R (2007) Changing leaf litter feedbacks on plant production across contrasting sub-arctic peatland species and growth forms. Oecologia 151: 251–261.
30. Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2: 436–443.
31. Scharfy D, Funk A, Olde Venterink H, Güsewell S (2011) Invasive forbs differ functionally from native graminoids, but are similar to native forbs. New Phyt 189: 818–828.
32. Yelenik SG, Levine JM (2011) The role of plant–soil feedbacks in driving native-species recovery. Ecology 92: 66–74.
33. Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141: 612–619.
34. Hawkes CV, Wren IF, Herman DJ, Firestone MK (2005) Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecol Lett 8: 976–985.
35. Sperry LJ, Belnap J, Evans RD (2006) *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. Ecology 87: 603–615.
36. Petsikos C, Dalias P, Troumbis AY (2007) Effects of *Oxalis pes-caprae* L. invasion in olive groves. Agricult Ecosys Environ 120: 325–329.
37. Ashton IW, Hyatt LA, Howe KM, Gurevitch J, Lerdau MT (2005) Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. Ecol App 15: 1263–1272.
38. Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6: 503–523.
39. Meisner A, de Boer W, Verhoeven KJF, Boschker HTS, van der Putten WH (2011) Comparison of nutrient acquisition in exotic plant species and congeneric natives. J Ecol 99: 1308–1315.
40. Pyšek P, Richardson DM (2007) Traits Associated with Invasiveness in Alien Plants: Where Do we Stand? In: Nentwig W, ed. Biological Invasions: Springer Berlin Heidelberg. pp 97–125.
41. Wardle DA, Nicholson KS, Rahman A (1995) Ecological effects of the invasive weed species Senecio jacobaea L. (ragwort) in a New Zealand pasture. Agricult Ecosys Environ 56: 19–28.
42. Berg B, McClaugherty C (2008) Plant litter: decomposition, humus formation, carbon sequestration. Berlin-Heidelberg: Springer.
43. Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. Soil Biol Biochem 32: 1485–1498.
44. Strickland MS, Devore JL, Maerz JC, Bradford MA (2010) Grass invasion of a hardwood forest is associated with declines in belowground carbon pools. Global Change Biol 16: 1338–1350.
45. Cadisch G, Giller KE (1997) Driven by nature: plant litter quality and decomposition. Wallingford, UK: CAB International.
46. Bardgett RD (2005) The biology of soil: A community and ecosystem approach. Oxford: Oxford University Press.
47. Coleman DC, Reid CPP, Cole CV (1983) Biological strategies of nutrient cycling in soil systems. Adv Ecol Res 13: 1–55.
48. Kurokawa H, Peltzer DA, Wardle DA (2010) Plant traits, leaf palatability and litter decomposability for co-occurring woody species differing in invasion status and nitrogen fixation ability. Funct Ecol 24: 513–523.
49. Koutika LS, Vanderhoeven S, Chapuis-Lardy L, Dassonville N, Meerts P (2007) Assessment of changes in soil organic matter after invasion by exotic plant species. Biol Fertil Soils 44: 331–341.
50. Dassonville N, Vanderhoeven S, Vanparys V, Hayez M, Gruber W, et al. (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. Oecologia 157: 131–140.
51. Vila M, Tessier M, Suehs CM, Brundu G, Carta L, et al. (2006) Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. J Biogeography 33: 853–861.

52. Van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM, Fischer M (2010) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecol lett 13: 947–958.
53. Müller-Schärer H, Schaffner U, Steinger T (2004) Evolution in invasive plants: implications for biological control. Trends Ecol Evol 19: 417–422.
54. Lachmuth S, Durka W, Schurr FM (2011) Differentiation of reproductive and competitive ability in the invaded range of Senecio inaequidens: the role of genetic Allee effects, adaptive and nonadaptive evolution. New Phyt 192: 529–541.
55. Güsewell S, Jakobs G, Weber E (2006) Native and introduced populations of Solidago gigantea differ in shoot production but not in leaf traits or litter decomposition. Funct Ecol 20: 575–584.
56. Feng YL, Lei YB, Wang RF, Callaway RM, Valiente-Banuet A, et al. (2009) Evolutionary tradeoffs for nitrogen allocation to photosynthesis versus cell walls in an invasive plant. Proc Natl Acad Sci U S A 106: 1853–1856.
57. Inderjit, Evans H, Crocoll C, Bajpai D, Kaur R, et al. (2011) Volatile chemicals from leaf litter are associated with invasiveness of a Neotropical weed in Asia. Ecology 92: 316–324.
58. Walker LR, Vitousek PM (1991) An invader alters germination and growth of a native dominant tree in Hawaii. Ecology 72: 1449–1455.
59. Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Divers Distrib 15: 22–40.
60. Blumenthal D, Mitchell CE, Pysek P, Jarosik V (2009) Synergy between pathogen release and resource availability in plant invasion. Proc Natl Acad Sci U S A 106: 7899–7904.
61. Eppinga MB, Kaproth MA, Collins AR, Molofsky J (2011) Litter feedbacks, evolutionary change and exotic plant invasion. J Ecol 99: 503–514.
62. Van Grunsven RHA, Van der Putten WH, Bezemer TM, Berendse F, Veenendaal EM (2010) Plant- soil interactions in the expansion and native range of a poleward shifting plant species. Global Change Biol 16: 380–385.
63. Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731–733.
64. Reinhart KO, Packer A, Van der Putten WH, Clay K (2003) Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. Ecol lett 6: 1046–1050.
65. Engelkes T, Morriën E, Verhoeven KJF, Bezemer MT, Biere A, et al. (2008) Successful range expanding plants have less aboveground and belowground enemy impact. Nature 456: 946–948.
66. Inderjit, van der Putten WH (2010) Impacts of soil microbial communities on exotic plant invasions. Trends Ecol Evolut 25: 512–519.
67. Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, et al. (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86: 2979–2989.
68. Dirkse GM, Hochstenbach SMH, Reijerse AI (2007) Flora van Nijmegen en Kleef 1800–2006/Flora von Nimwegen und Kleve 1800–2006. Mook, The Netherlands: KNNV, printed at Zevendal.
69. Tamis WLM, Van der Meijden R, Runhaar J, Bekker RM, Ozinga WA, et al. (2005) Anex: standaardlijst van de Nederlandse flora 2003. Gorteria supplement 6: 135–229.
70. Barney JN (2006) North American history of two invasive plant species: phytogeographic distribution, dispersal vectors, and multiple introductions. Biol Invasions 8: 703–717.
71. Wardle DA (1987) The ecology of ragwort (*Senecio-jacobaea* l) - a review. N Z J Ecol 10: 67–76.
72. Stuckey RL (1966) The distribution of *Rorippa sylvestris* (Cruciferae) in North America. Sida 2: 361–376.
73. Dietz H, Köhler A, Ullmann I (2002) Regeneration Growth of the Invasive Clonal Forb Rorippa austriaca (Brassicaceae) in Relation to Fertilization and Interspecific Competition. Plant Ecol 158: 171–182.
74. Cornelissen JHC (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J Ecol 84: 573–582.
75. Poorter H, Villar R (1997) The Fate of Acquired Carbon in Plants: Chemical Composition and Construction Costs. In: Bazzaz FA, Grace J, eds. Plant Resource Allocation. San Diego: Academic Press. pp 39–72.
76. Penuelas J, Prieto P, Beier C, Cesaraccio C, de Angelis P, et al. (2007) Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. Global CHange Biol 13: 2563–2581.
77. Olsson PA, Larsson L, Bago B, Wallander H, van Aarle IM (2003) Ergosterol and fatty acids for biomass estimation of mycorrhizal fungi. New Phyt 159: 7–10.
78. De Ridder-Duine AS, Smant W, Van der Wal A, Van Veen JA, De Boer W (2006) Evaluation of a simple, non-alkaline extraction protocol to quantify soil ergosterol. Pedobiologia 50: 293–300.
79. Van der Wal A, De Boer W, Smant W, Van Veen JA (2007) Initial decay of woody fragments in soil is influenced by size, vertical position, nitrogen availability and soil origin. Plant Soil 301: 189–201.
80. Van der Meijden R (2005) *Heukels'* flora van Nederland. , The Netherlands: Wolters-Noordhoff bv.
81. Pelser PB, Veldkamp J-F, Van der Meijden R (2006) New combinations in *Jacobaea* Mill. (Asteraceae - Senecioneae). Compositae Newsletter 44: 1–11.