Soil biotic legacy effects of extreme weather events influence plant invasiveness

Annelein Meisner[a,1,2], Gerlinde B. De Deyn[a,b], Wietse de Boer[b,c], and Wim H. van der Putten[a,d]

[a]Department of Terrestrial Ecology, Netherlands Institute of Ecology, 6700 AB, Wageningen, The Netherlands; [b]Department of Soil Quality, Wageningen University, 6700 AA, Wageningen, The Netherlands; [c]Department of Microbial Ecology, Netherlands Institute of Ecology, 6700 AB, Wageningen, The Netherlands; and [d]Laboratory of Nematology, Wageningen University, 6700 ES, Wageningen, The Netherlands

Climate change is expected to increase future abiotic stresses on ecosystems through extreme weather events leading to more extreme drought and rainfall incidences [Jentsch A, et al. (2007) Front Ecol Environ 5(7):365–374]. These fluctuations in precipitation may affect soil biota, soil processes [Evans ST, Wallenstein MD (2012) Biogeochemistry 109:101–116], and the proportion of exotics in invaded plant communities [Jiménez MA, et al. (2011) Ecol Lett 14:1277–1235]. However, little is known about legacy effects in soil on the performance of exotics and natives in invaded plant communities. Here we report that drought and rainfall effects on soil processes and biota affect the performance of exotics and natives in plant communities. We performed two mesocosm experiments. In the first experiment, soil without plants was exposed to drought and/or rainfall, which affected soil N availability. Then the initial soil moisture conditions were restored, and a mixed community of co-occurring natives and exotics was planted and exposed to drought during growth. A single stress before or during growth decreased the biomass of natives, but did not affect exotics. A second drought stress during plant growth resetted the exotic advantage, whereas native biomass was not further reduced. In the second experiment, soil inoculation revealed that drought and/or rainfall influenced soil biotic legacies, which promoted exotics but suppressed natives. Our results demonstrate that extreme weather events can cause legacy effects in soil biota, promoting exotics and suppressing natives in invaded plant communities, depending on the type, frequency, and timing of extreme events.

invaded ecosystems | nitrogen cycle | plant invasion | plant–soil interaction | soil microbes

Extreme weather events are expected to increase future abiotic stresses on ecosystems, but the outcomes of these events on the performance of exotic and native plant species in plant communities and the involved mechanisms are poorly understood (1–3). Patterns of drought and rainfall have been predicted to become more extreme under climate change (4, 5). Intensive drought and rainfall can directly affect the productivity and composition of plant communities through altered water supply (6, 7). This may lead to altered dominance of exotic plant species in invaded ecosystems (3, 8–10) when exotics and natives respond differently to extreme weather events (11). Whether extreme weather events also might change plant community composition through changes in soil conditions is less clear. Variations in climate are known to influence the composition of soil microbial communities (12), but the legacy effects in soil of such changes on exotics and natives have not been investigated. In the present study, we examined how extreme weather event-induced changes in soil processes and biota may influence the biomass response of exotics and natives in mixed plant communities. In two mesocosm experiments, we tested how soil biota and the processes that they drive may explain the responses of exotic and native plant species to single and repeated extreme weather events. This knowledge is important for evaluating and improving predictions of current and future climate change on the composition of plant communities.

Extreme drought and rainfall are known to influence soil biota directly (13–16). Drought generally reduces microbial activities in soil, and on rewetting a short-term increase in microbial activity occurs (17–19). Apart from this activity, the microbial community composition also can be altered by exposing soil to drought and rewetting (14, 18, 20). Moreover, previous experiments on drought and rainfall events have shown that such treatments remain as a legacy in soil microbial communities, which become apparent when testing their responses to an additional drying-rewetting event (21). However, whether and how such legacy effects of extreme weather events on soil biota may affect plant species composition is unknown (22).

Extreme weather events may promote exotics over native plant species through several mechanisms. Exotics that become dominant in native vegetation often have specific traits associated with better performance than natives, such as faster growth rates, which may enable them to recover faster after a pulse of abiotic stress (23). Another possibility is that extreme weather events indirectly influence exotics and natives in plant communities via soil biota (24), which can influence interactions between plant species (22, 25). Exotics may be less influenced than natives by effects of extreme weather events on soil biota, because exotics experience weaker negative and positive effects from interactions with soil biota (26–28). For example, promotion of soil pathogens by extreme weather events may reduce the proportion of natives, because exotics are less influenced by soil pathogens in the new range (27, 29). On the other hand, when exotic plant species lack a co-evolutionary history with the symbionts, positive effects of plant growth-promoting soil biota might enable native plant species to cope better with drought stresses (30). Thus, if soil biota effects on plants are enforced by extreme weather events either before or during plant growth, then exotic and native plant species might be facilitated or suppressed differently by soil biotic legacy effects.

We tested the hypothesis that a history of a drought and/or rainfall event before plant growth would affect exotic and native plant biomass in mixed plant communities via changed soil conditions. We studied how natives and exotics respond to an additional drought event during plant growth when grown in soils with or without a legacy of drought and/or rainfall. We tested our hypothesis in a mesocosm experiment, exposing the mesocosms to eight different drought and rainfall scenarios (Fig. S1). These are realistic scenarios predicted for northwestern Europe (4). In experiment 1, the mesocosms were filled with field soil and then exposed to an extreme drought and/or rainfall event before planting. Then the original soil moisture conditions were restored, and a mixed plant
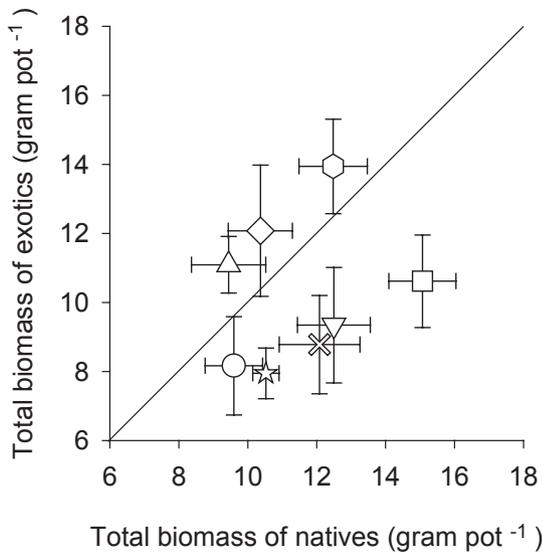
ECOLOGY

Fig. 1. Exotic versus native species responses to water stresses. Biomass (mean ± SE) of exotics and natives as affected by the different water stresses. Plant communities were exposed to control conditions (square; $n = 7$), drought before plant growth (hexagon; $n = 7$), rainfall before plant growth (down-pointing triangle; $n = 7$), drought during plant growth (up-pointing triangle; $n = 7$), drought and rainfall before plant growth (diamond; $n = 7$), drought before and during plant growth (cross; $n = 6$), rainfall before and drought during plant growth (circle; $n = 8$), or rainfall and drought before and drought during plant growth (star; $n = 7$). The 1:1 line indicates when exotics and natives have the same biomass.

community of exotic and related (congeneric) native species was planted (Table S1). All plant species used in our study co-occur in invaded riverine ecosystems of northwestern Europe. Soil processes, microbial biomass, and fungal biomass were measured before planting. During plant growth, one-half of the mesocosms were exposed to an extreme drought event (*Materials and Methods* and Fig. S1).

In a second mesocosm experiment, we examined whether the shifts in the plant community biomass between natives and exotics observed in the first experiment might have been related to legacy effects of extreme weather events on soil biota (including symbionts and pathogens) (31). We tested this by inoculating living or sterilized soil from the first experiment in sterilized field soil (1:8 proportion; the sterilized field soil was of the same origin as that used in experiment 1) and growing the same plant communities again under the same conditions as in experiment 1.

Results

The results support our hypothesis that extreme weather events before the growth season leave legacies that affect the performance of exotics and natives during the growth season. The drought and rainfall treatments influenced the biomass of both exotics ($F_{7,49} = 2.33$, $P = 0.04$) and natives ($F_{7,49} = 3.67$, $P = 0.003$). Drought and/or rainfall reduced the biomass of the native plant species in most treatments (Fig. 1 and Fig. S2*B*). In contrast, exotics were resistant to a single drought and/or rainfall before or during plant growth (Fig. 1 and Fig. S2*A*). However, in soil with a legacy of drought, exotics produced less biomass when exposed to drought during plant growth compared with their performance in soil exposed to drought before plant growth (Fig. 1 and Fig. S2*A*). In contrast, natives did not produce less biomass when exposed to drought during plant growth compared with their performance in soil preexposed to drought (Fig. 1 and Fig. S2*B*). Redundancy analysis revealed that four of the five exotics responded positively and all natives responded negatively

to the legacy of drought before plant growth (Fig. S3). In contrast, drought before and during plant growth resulted in the opposite response (Fig. S3). Drought before plant growth tended to increase the average ratio of exotic to total plant pair biomass (Table S2). On average, drought during plant growth reduced the biomass of the total plant community from 24.0 ± 0.6 g to 19.3 ± 0.5 g ($F_{7,49} = 6.31$, $P < 0.001$) (Fig. S2*C*).

The potential N mineralization (arginine-N mineralization) rate was influenced by drought and rainfall before plant growth, but the direction of the effects depended on the type of extreme event (Table S3 and Fig. S4). Drought increased and rainfall decreased N mineralization before soil moisture was reset. By the time soil moisture was restored and before plant growth, the N mineralization rate was still marginally lower in soil preexposed to both drought and rainfall compared with control soils. Soil respiration was not affected by drought and/or rainfall (Table S3). Rainfall before plant growth slightly decreased total microbial biomass (Fig. S5). Inorganic N in control soil remained different from that in soil exposed to drought and/or rainfall before plant growth. The availability of inorganic N immediately before planting was highest in soil exposed to drought and lowest in soil exposed to rainfall (Fig. 2 and Table S3). In mesocosms not exposed to additional drought during plant growth, total plant biomass was higher in soil with higher N availability (Spearman rho = 1, $P < 0.01$; $n = 4$). In these mesocosms, exotic species appeared to be more favored than natives by the higher N concentrations (Fig. S6).

In the inoculation experiment, drought and rainfall before plant growth influenced the effect of soil biota on exotics ($F_{3,24} = 3.75$, $P = 0.024$) and natives ($F_{3,24} = 4.49$, $P = 0.011$). Interestingly, soil biota exposed to drought and/or rainfall before plant growth had a positive effect on exotics and a negative effect on natives, whereas soil biota from control soil had the opposite effect (Fig. 3). In contrast to the responses of the exotics and natives, the soil biotic effect on the total plant community was unaffected by a legacy of drought and/or rainfall ($F_{3,24} = 0.53$, $P = 0.67$), demonstrating that native biomass had been replaced by exotic biomass.

Discussion

Our mesocosm study reveals a mechanism by which extreme weather events influence the performance of exotics and natives in plant communities, namely through legacy effects of drought and
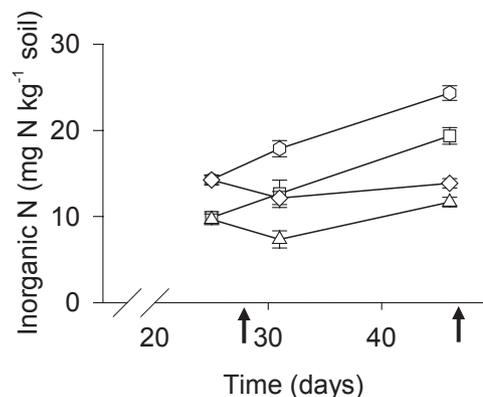
Fig. 2. Extreme event effects on soil N concentration over time. Mean ± SE values are presented for control soil (square; $n = 8$), soil with legacies of drought before plant growth (hexagon; $n = 8$), rainfall before plant growth (triangle; $n = 8$), or soils with both legacies (diamond; $n = 8$). The first arrow at 28 d indicates up to when one-half of the soils were exposed to drought. At day 28, one-half of the mesocosms received rainfall before plant growth. The second arrow at day 48 indicates when plant communities were established. The first sampling point was during the drought stress, the second sampling point was 3 d after rainfall, and the third sampling point was just before plant establishment (Fig. S1).

Fig. 3. Soil biota effects to natives versus exotics. Biomass (mean ± SE) of communities of exotics and natives grown in sterilized soil mixed with a sterilized (s) or living (l) inoculum from control soil (square), or soil with legacies of drought before plant growth (hexagon), rainfall before plant growth (triangle) or both (diamond). B, plant biomass. The effect of legacy on exotics and natives of soil biota that had been exposed to drought and/or rainfall before plant growth were different from that of control soils ($P < 0.05$, t test; n = 7).

rainfall events on soil biota. The influence of soil biota on plant performance depended on the type of extreme weather event (drought or rainfall), the timing (before or during plant growth), and frequency (single or repeated). Effects of a preseason drought on soil were detectable during plant growth even when soil moisture levels had been restored before plant establishment. The native biomass was sensitive to a single drought and/or rainfall stress before or during plant growth, whereas exotics appeared to be resistant. As such, natives seemed to be more responsive than exotics to the extreme weather events before the growing season. However, a subsequent stress—in this case, drought during plant growth—reversed the effect of a single stress before plant growth. Indeed, in soil with a legacy of an extreme weather event, natives were resistant to drought during plant growth, whereas exotic biomass decreased. Our observation that extreme weather events before plant establishment can change the response of native and exotic plant species to drought during plant growth reveals that extreme drought or rainfall can leave a legacy effect that can cause a previously undescribed priority effect (32). Thus, far, such legacy effects have been demonstrated only through plant-induced changes in the soil biota (33, 34), not through extreme weather-induced changes in the soil biota and plant responses.

We found evidence that the soil legacy effect is mediated through changes in the soil biota and the processes in which they are involved. It is well known that rewetting a dried soil can affect soil processes (16), and in our study N mineralization was directly affected by drought and/or rainfall before plant growth, which might have altered inorganic nitrogen concentrations. The increased soil nitrogen availability appeared to favor exotics more than natives. This is in line with the fluctuations in resource hypothesis, which states that an increase in nutrient availability favors exotic plant species (35). However, we cannot exclude the possibility that the advantage for exotics might have been caused by the reduction of biomass of natives.

The net effect of all soil biota (including beneficial plant symbionts and pathogens) was less significant for exotics than for natives. This is in line with observations that exotics may experience weaker impact from soil pathogens and symbionts than

natives (26–28). As such, extreme weather events may have caused a legacy effect in soil biota, which might have changed plant–plant interactions within the plant community owing to stronger responses of natives than exotics to altered soil biotic conditions.

Our results demonstrate that the response of plant communities subjected to drought stress may operate via legacy effects of earlier extreme weather events on the soil biota and the processes that they drive. It is well known that extreme weather events can directly influence soil conditions (14–16) and plant species composition (6, 7). Here we show that the responses of native and exotic species in mixed plant communities to drought depend on whether or not the soil also has been subjected to a drought stress before plant growth. Thus, our results indicate that consequences of changed climate conditions for plant community composition cannot rely solely on predicted averages, but need to explicitly incorporate the dynamic nature of the extreme weather events that may go along with such global change (2). Recently, several extreme spring drought events have occurred in northwestern Europe, for example, in 2011 (www.knmi.nl). The frequency of spring droughts is predicted to increase with ongoing climate warming (4, 5). We show that extreme spring droughts may promote the performance of exotics while reducing that of natives in invaded plant communities. Exotics were not promoted by repeated droughts, before and during plant growth. Natives were less resistant than exotics to extreme weather events. Thus, we conclude that extreme weather events can promote invasiveness of exotic plant species, depending on the type, frequency, and timing of the events. These effects are caused not only by changes in nutrient availability, but also by changes in biotic conditions in the soil that are not directly related to plant nutrition.

Materials and Methods

Soil. Soil was collected from the upper 15 cm at five locations within the nature reserve Millingerwaard, located in the Gelderse Poort region along the Rhine River in The Netherlands (51°52′N; 6°00′E). After sampling, soil was homogenized and sieved through a 10-mm mesh to remove coarse fragments and plant material. Part of this soil was sterilized by γ-irradiation to obtain sterile bulk soil for experiment 2 (see below).

Plant Species. We selected exotic and congeneric native plant species that co-occur in the Gelderse Poort region in The Netherlands (26, 36, 37). The selected plant species were from three different families (Table S1). Seeds were collected from the field or bought from small seed suppliers that collect seeds locally. All seeds were surface-sterilized with a 0.5% hypochlorite solution, germinated on glass beads, moistened with demineralized water and placed in a germination cabinet. Seeds of *Vicia* sp. were exposed to sulfuric acid for 45 min to overcome seed dormancy. Because not all seeds germinated at the same moment, seedlings were placed in a 4 °C climate chamber with 11 h daylight until the start of the experiment. The experiment was carried out in a greenhouse at 21 ± 2 °C day temperature and 16 ± 2 °C night temperature and 16 h of daylight obtained by supplementing 225 μmol m^{-2} s^{-1} if light levels dropped below that level.

Experiment 1: Effects of Soil Legacies and Drought on the Plant Community. In the first experiment, we tested the legacy effect in soil exposed to previous drought and/or rainfall events and the direct effect of drought to a plant community. Mesocosms (64 in total) of 7 L were filled with nonsterilized soil (equivalent to 6,000 g of dry soil) on day 0 of the experiment and preexposed to one of the four water treatments (Fig. S1): no water stress, drought stress for 28 d, simulated heavy rainfall at 28 d, or a combined drought and rainfall event.

Soil samples were collected from half the mesocosms per pretreatment (a total of 32 mesocosms) after 25, 31, and 46 d of incubation. Soil mineral N was extracted by shaking wet soil (equivalent to 10 g dry weight) in 50 mL of 1 M KCl for 2 h (38). N mineralization was measured as arginine ammonification (39) with minor modifications (38). Basal respiration was measured according to Orwin and Wardle (40). C-CO$_2$ was measured against a reference line on a Thermo Scientific FOCUS gas chromatograph equipped with an RT-QPLOT column (Restek) (30 m long and 0.53 mm in diameter). Fungal biomass was measured as ergosterol content (41). Total microbial biomass was measured at 46 d with fumigation extraction method (42). After 46 d of incubation, soil samples were also collected for experiment 2 (see below).

At day 48 after initiating the experiment, each mesocosm was planted with 10 seedlings, one of each exotic and native plant species that co-occur in riparian areas in northwestern Europe (Table S1). Seedlings were planted in a random order with 5 cm distance and grown for 69 d. After 21 d of plant growth, half the planted mesocosms received a 14-d drought period until the soil moisture was 3.6% wt/wt, after which soils were rewetted up to 20% wt/wt (Fig. S1). Mesocosms were placed randomly in a greenhouse and received 16 h daylight per 24 h. At day 117, roots and shoots were harvested, sorted to species and dried to constant weight at 70 °C. Seven of the 64 mesocosms, which were distributed across the eight treatments, were excluded from further analyses because they did not contain the intended plant species owing to seed pollution. Fig. 1 shows the number of mesocosms per treatment.

Experiment 2: Effect of Biotic Legacy on Plant Species. For this experiment, we established the same plant communities as in experiment 1 in 56 mesocosms and grew the plants for 70 d. The mesocosms contained the sterilized bulk soil (see above) that was mixed with either living or sterilized soil inocula collected at day 46 of experiment 1. The inocula originated from seven replicates of the four drought/rainfall soil treatments (Fig. S1A). The inoculum from each pot was kept separate and split into two halves (equivalent to 325 g dry soil each). One half was sterilized twice at 120 °C for 1 h in an autoclave with a 48-h time interval to kill all soil biota present in the inocula (41). We used autoclaving instead of γ-irradiation, because of accessibility limitations of the irradiation facilities for small soil samples. The other half of the soil was kept untreated and served as living inoculum. The sterilized and living

soil inocula were mixed with the sterilized bulk soil according to a 1:8 mixture of inoculum and bulk soil. The soil mixture was placed in 3-L mesocosms and planted after 3 d. It is well known that soil sterilization increases soil nutrient availability (43, 44). Considering that we added one part of inoculum to 8 parts (wt/wt) of sterilized background soil, and given that we worked with a nutrient-poor sandy soil, effects of nutrient flush differences between sterilized and living inocula will have been overwhelmed by nutrients in the sterilized background soils. This will have increased the likelihood that differences among treatments will have been caused by changes in soil biota. We established the same plant communities as in experiment 1 in all mesocosms and grew, harvested, and weighed plants as in experiment 1.

Data Analysis. Data were analyzed using SPSS 17 (IBM) and CANOCO 2.55 (Ter Braak and Šmilauer). Details are presented in *SI Materials and Methods*.

1. Peñuelas J, 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. *Glob Change Biol* 13(12):2563–2581.
2. Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: Events, not trends. *Front Ecol Environ* 5(7):365–374.
3. Walther GR, et al. (2009) Alien species in a warmer world: Risks and opportunities. *Trends Ecol Evol* 24(12):686–693.
4. Royal Netherlands Meteorological Institute (KNMI) (2009) *Klimaatverandering in Nederland: Aanvullingen op de KNMI'06 Scenarios*, eds Klein Tank AMG, Lenderink G (KNMI, De Bilt, The Netherlands).
5. Intergovernmental Panel on Climate Change (2007) *Climate Change 2007 – The physical science basis; Contribution of working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*, eds Solomon SD, et al. (Cambridge University Press, Cambridge, UK).
6. Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Glob Change Biol* 17(2):927–942.
7. Kardol P, et al. (2010) Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Glob Change Biol* 16(10):2676–2687.
8. Jiménez MA, et al. (2011) Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities. *Ecol Lett* 14(12):1227–1235.
9. Verlinden M, Nijs I (2010) Alien plant species favoured over congeneric natives under experimental climate warming in temperate Belgian climate. *Biol Invasions* 12(8):2777–2787.
10. Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol Evol Syst* 3(1):52–66.
11. Sorte CJB, et al. (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecol Lett* 16(2):261–270.
12. de Vries FT, et al. (2012) Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecol Lett* 15(11):1230–1239.
13. de Vries FT, et al. (2012) Land use alters the resistance and resilience of soil food webs to drought. *Nature Climate Change* 2(4):276–280.
14. Fierer N, Schimel JP, Holden PA (2003) Influence of drying-rewetting frequency on soil bacterial community structure. *Microb Ecol* 45(1):63–71.
15. Schimel J, Balser TC, Wallenstein M (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88(6):1386–1394.
16. Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Glob Change Biol* 15(4):808–824.
17. Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* 10(1):9–31.
18. Butterly CR, Bunemann EK, McNeill AM, Baldock JA, Marschner P (2009) Carbon pulses but not phosphorus pulses are related to decreases in microbial biomass during repeated drying and rewetting of soils. *Soil Biol Biochem* 41(7):1406–1416.
19. Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biol Biochem* 34(6):777–787.
20. Degens BP, Schipper LA, Sparling GP, Duncan LC (2001) Is the microbial community in a soil with reduced catabolic diversity less resistant to stress or disturbance? *Soil Biol Biochem* 33(9):1143–1153.
21. Evans SE, Wallenstein MD (2012) Soil microbial community response to drying and rewetting stress: Does historical precipitation regime matter? *Biogeochemistry* 109(1-3):101–116.
22. van der Heijden MGA, Bardgett RD, van Straalen NM (2008) The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol Lett* 11(3):296–310.

23. van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol Lett* 13(2):235–245.
24. Lau JA, Lennon JT (2012) Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proc Natl Acad Sci USA* 109(35):14058–14062.
25. Wardle DA, et al. (2004) Ecological linkages between aboveground and belowground biota. *Science* 304(5677):1629–1633.
26. Engelkes T, et al. (2008) Successful range-expanding plants experience less aboveground and below-ground enemy impact. *Nature* 456(7224):946–948.
27. Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417(6884):67–70.
28. Vogelsang KM, Bever JD (2009) Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. *Ecology* 90(2):399–407.
29. 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(12):1046–1050.
30. Compant S, van der Heijden MGA, Sessitsch A (2010) Climate change effects on beneficial plant–microorganism interactions. *FEMS Microbiol Ecol* 73(2):197–214.
31. Bever JD (2003) Soil community feedback and the coexistence of competitors: Conceptual frameworks and empirical tests. *New Phytol* 157(3):465–473.
32. Young TP, Chase JM, Huddleston RT (2001) Community succession and assembly: Comparing, contrasting and combining paradigms in the context of restoration ecology. *Ecol Res* 19(1):5–18.
33. Kardol P, Cornips NJ, van Kempen MML, Bakx-Schotman JMT, van der Putten WH (2007) Microbe-mediated plant–soil feedback causes historical contingency effects in plant community assembly. *Ecol Monogr* 77:147–162.
34. Grman E, Suding KN (2010) Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restor Ecol* 18(5):664–670.
35. Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: A general theory of invasibility. *J Ecol* 88(3):528–534.
36. Dirkse GM, Hochstenbach SMH, Reijerse AI (2007) *Flora van Nijmegen en Kleef 1800–2006/Flora von Nimwegen und Kleve 1800–2006* (KNNV, Mook, The Netherlands).
37. Tamis WLM, Van't Zelfde M, Van der Meijden R, Udo de Haes HA (2005) Changes in vascular plant biodiversity in the Netherlands in the 20th century explained by their climatic and other environmental characteristics. *Clim Change* 72(1-2):37–56.
38. 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(6):1308–1315.
39. Alef K, Kleiner D (1987) Applicability of arginine ammonification as indicator of microbial activity in different soils. *Biol Fertil Soils* 5(2):148–151.
40. Orwin KH, Wardle DA (2005) Plant species composition effects on belowground properties and the resistance and resilience of the soil microflora to a drying disturbance. *Plant Soil* 278(1-2):205–221.
41. 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 (Jena)* 50(4):293–300.
42. Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass-C. *Soil Biol Biochem* 19(6):703–707.
43. McNamara NP, Black HIJ, Beresford NA, Parekh NR (2003) Effects of acute gamma irradiation on chemical, physical and biological properties of soils. *Appl Soil Ecol* 24(2):117–132.
44. Troelstra SR, Wagenaar R, Smant W, Peters BAM (2001) Interpretation of bioassays in the study of interactions between soil organisms and plants: Involvement of nutrient factors. *New Phytol* 150(3):697–706.