

# Responses of common and rare aliens and natives to nutrient availability and fluctuations

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## Summary

**1.** Global environmental change not only includes changes in mean environmental conditions but also in temporal environmental fluctuations. Because it is frequently suggested that common species, and particularly invasive alien species, are phenotypically highly plastic, they might benefit more from these fluctuations than rare native and rare alien species. Experimental tests, however, are still lacking.

**2.** Here, we tested whether alien plant species take more advantage of increases in resource levels and fluctuations therein than native species, and whether common species do so more than rare species. Therefore, we grew seven common alien, seven rare alien, nine common native and six rare native herbaceous plants, in one treatment with constantly low nutrient availability and five treatments with high nutrient availability that differed in temporal availability of nutrients (constant, increasing, decreasing, single large pulse, multiple smaller pulses).

**3.** We found that all species produced more biomass and longer roots, and had a lower root mass fraction under high nutrient conditions than under low nutrient conditions, irrespective of their origin and commonness. Among the high nutrient treatments, the temporal pattern of nutrient supply also influenced biomass production, root allocation and root thickness, but the magnitude and/or directions of these responses varied among the groups of species. Particularly, we found that alien plant species, irrespective of whether they are common or rare, produced more biomass, and had a higher root mass fraction when nutrients were supplied as a single pulse in the middle of the growth period instead of supplied at a constant rate, whereas the reverse was true for the native species.

**4. *Synthesis.*** Our study suggests that species origin does not drive differences in plant biomass production, root morphology and allocation in response to changes in mean environmental nutrient availability. However in our study, alien plant species, in contrast to native plant species, benefited from a large nutrient pulse. This suggests that increased fluctuations in nutrient availability might promote alien plant invasions.

**Key-words:** biological invasion, commonness, exotic plant, invasiveness, non-indigenous, nutrient pulses, plant origin, plant–environment interactions, resource fluctuations

## Introduction

With increasing globalization, more and more plant species have established wild populations in biogeographic regions where they are not native (van Kleunen *et al.* 2015; Seebens *et al.* 2015). Some of these naturalized species successfully spread and now occupy large areas in the introduced range (i.e. have become common), and some of these invasive species threaten native diversity, disrupt ecosystem services, and cause large economic damage (Vitousek *et al.* 1996; Pimentel, Zuniga & Morrison 2005; Vila *et al.* 2011). Consequently, explaining what makes some alien plant species

successful and allows them to displace native plants in the introduced region is an important research topic in ecology (Funk & Vitousek 2007; van Kleunen, Weber & Fischer 2010; Leishman, Thomson & Cooke 2010; Heberling & Fridley 2013; Funk *et al.* 2016; Jia *et al.* 2016).

High phenotypic plasticity is thought to help plants tolerate environmental change and to take advantage of increases in resources (Nicotra *et al.* 2010; Gratani 2014). Consequently, high plasticity could increase the chances of an alien plant species to establish in a new environment, and even to out-compete resident native plant species (Baker & Stebbins 1965; Richards *et al.* 2006). Indeed meta-analyses have shown that invasive species are more plastic (Davidson, Jennions & Nicotra 2011; but see Palacio López & Gianoli 2011) and take more advantage of increased CO<sub>2</sub> levels and

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temperatures (Liu *et al.* 2016b) than native species. So far, empirical studies tested this hypothesis mainly by assessing plastic responses to changes in the means of environmental factors (Leishman & Thomson 2005; Funk 2008; Godoy, Valadares & Castro Díez 2011; van Kleunen *et al.* 2011; Porté *et al.* 2011; Dawson, Fischer & van Kleunen 2012). Environmental change, however, also affects environmental variability (Stenseth *et al.* 2002; Smith 2011; Parepa, Fischer & Bossdorf 2013). As phenotypic plasticity could help species to cope with increasing environmental variability, it is important to test plastic responses of alien and native plant species to such variability, in addition to their responses to changes in mean environmental conditions.

A major global environmental change factor is atmospheric nitrogen deposition (Galloway *et al.* 2008), which has increased nutrient availability in many parts of the world and may have affected the commonness of alien and native plant species. Moreover, in addition to overall increases in nutrient availability, fertilizer spill over from arable fields and grasslands into natural areas, increasing fluctuations in extreme events (e.g. droughts, floodings, heat waves, fires) affecting nutrient cycling and changes in land use types and their associated management practices (e.g. grazing, tilling) could lead to increasing temporal variability in nutrient availability (Davis & Pelsor 2001; Pivello *et al.* 2010; Chen *et al.* 2011; Matias, Castro & Zamora 2011; Verma & Jayakumar 2012). Consequently, the likelihood that nutrients might become available in one or multiple pulses of different magnitudes, and might slowly accumulate or decrease, might increase.

As one of the primary functions of roots is the uptake of nutrients from the soil to enhance plant growth, plastic changes in root allocation and morphology in response to nutrient availability could optimize nutrient acquisition, and thereby plant performance (Hutchings & de Kroon 1994; Grossman & Rice 2012; de Kroon *et al.* 2012). For example, under spatially heterogeneous nutrient supply, plants produce more, longer and thinner roots in the high nutrient patches than in the low nutrient patches, and this increases overall biomass production (Keser *et al.* 2014, 2015). However, little is known about how different patterns of temporal resource availability affect growth and root morphology, and whether this may differ between alien and native plants.

Plants can have different strategies to adjust to constant and fluctuating environments. There is evidence that, in contrast to plants from constant environments, plants from fluctuating environments have higher nutrient uptake rates and show a stronger increase in potential uptake rates when nutrient availability increases (Craine 2009). Plant strategy theory suggests that only plants possessing characteristics related to competitive ability (e.g. high growth rates) could achieve success under high resource availability while competing with other plants (Grime 1977; Jabot & Pottier 2012; Grime, Hodgson & Hunt 2014). Consequently, highly competitive invasive alien, and also common native, plant species are predicted to be able to take more advantage of resource peaks under temporal nutrient fluctuations. In line with this idea, the fluctuating resource availability hypothesis poses that habitats

become more susceptible to invasion when resources availability increases (Davis, Grime & Thompson 2000). Indeed, studies have shown that alien plants benefited more than native plants in the community when water availability (Blumenthal *et al.* 2008) or nutrients increased (Brooks 2003; Jiménez *et al.* 2011; Lai *et al.* 2015; Flores Moreno *et al.* 2016). Not only increases in the mean levels of resource availability, but also increases in the variability of resource availability are thus likely to increase plant invasion. Few experiments, however, have tested explicitly whether and to what extent invasive alien plant species benefit from resource fluctuations (but see Davis & Pelsor 2001; Parepa, Fischer & Bossdorf 2013; Koerner *et al.* 2015 for notable exceptions).

Invasive alien species are widespread, but some native species are equally common. Similarly, there are not only rare native species but also rare alien species. It has been suggested that the factors that drive invasion success of alien species are the same as the ones that drive commonness of native species (Thompson & Davis 2011; also see van Kleunen & Richardson 2007). While this may seem plausible, it still needs to be explicitly tested (van Kleunen, Dawson & Dostal 2011; Knapp & Kühn 2012). Dawson, Fischer & van Kleunen (2012) found that common alien plant species did not differ from common native plant species in their responses to nutrient addition, but that both groups of common species exhibited stronger responses to nutrient addition compared to rare alien and native species. Therefore, commonness might affect the outcomes of comparisons between alien and native plant species in response to nutrient changes, and should be tested.

To test whether alien and common plant species take more advantage of increases in resource levels and fluctuations therein than native and rare species, we did a multispecies, common garden experiment. We compared the plastic responses in biomass production and in root allocation and morphology to nutrient addition and fluctuations therein among seven common alien, seven rare alien, nine common native and six rare native plant species. We applied six treatments differing in the mean and temporal availability of nutrients. By comparing biomass production, root morphology and allocation of the four groups of plant species in the different treatments, we addressed the following specific questions: (i) Do alien and common plant species exhibit stronger plastic responses in root morphology and allocation, and take more advantage of increased mean nutrient levels than native and rare plant species? (ii) Do alien and common plant species exhibit stronger plastic responses in root morphology and allocation, and take more advantage of gradual changes in nutrient availability over time than native and rare plant species? and (iii) Do alien and common plant species take more advantage of nutrient pulses than native and rare plant species?

## Materials and methods

### STUDY SPECIES

To test for differences in plant responses to nutrient availability and temporal fluctuations therein among common alien, rare alien,

common native and rare native species, we selected a total of 29 terrestrial herbs belonging to seven families and all occurring in Germany (Methods S1, Supporting Information). We classified the species as alien or native to Germany based on information in the BiolFlor database (<http://www2.ufz.de/biolflor/index.jsp>). All selected alien species are considered to be naturalized (i.e. have established long term populations in the wild). We classified the species as common and rare based on their frequency of occurrence in Germany according to the FLORKART database, which provides distributional data for the vascular flora of Germany (<http://www.flora-web.de/>). In the FLORKART database, Germany is divided into 3000 grid cells of 10 minutes longitude  $\times$  6 minutes latitude (corresponding to c. 12 km  $\times$  11 km). We assigned a species as common if it has been recorded in more than 1000 grid cells (33% of the total number of grid cells in Germany), and as rare (or less common) if it has been recorded in fewer than 500 grid cells (17% of the total number of grid cells in Germany). To avoid confounding of origin and commonness with taxonomy, we aimed to include at least one common alien, one rare alien, one common native and one rare native species per family. However, because of difficulties in obtaining seeds and insufficient germination of some species, our final species set was not fully balanced with regard to taxonomy; we used seven common alien, seven rare alien, nine common native and six rare native species (Methods S1). Four families were represented by at least one species from each group, and three families lacked representatives of one or two groups. Seeds of the study species were collected in natural populations, or acquired from commercial seed companies or botanical gardens (Methods S1).

## EXPERIMENTAL DESIGN

To test for differences in growth performance, and root morphology and allocation among the four groups of species, we did a multi-species experiment (van Kleunen *et al.* 2014) in a greenhouse of the botanical garden of the University of Konstanz (Germany). From 4 to 26 August 2014, we sowed the seeds of each species separately into trays (12  $\times$  12  $\times$  4.5 cm) filled with potting soil (Topferde<sup>®</sup>, Einheitserde Co., Sinntal Altengronau, Germany; pH 5.8; 2.0 g L<sup>-1</sup> KCl; 340 mg L<sup>-1</sup> N; 380 mg L<sup>-1</sup> P<sub>2</sub>O<sub>6</sub>; 420 mg L<sup>-1</sup> K<sub>2</sub>O; 200 mg L<sup>-1</sup> S; 700 mg L<sup>-1</sup> Mg). As some species were known, from previous experiments, to germinate earlier than others, we sowed the species on different dates (Methods S1) to ensure that the seedlings were in a similar developmental stage at the start of the experiment. Sowing dates of rare alien, common alien, rare native and common native species differed on average by less than 1 day. The trays with sown seeds were kept in a greenhouse at a temperature between 22 and 28 °C, and a light cycle of 16 h : 8 h (day : night). After 4 weeks, we selected 24 similar sized seedlings per species, and transplanted them into 2.5 L circular plastic pots filled with a 1 : 1 mixture of sand and fine vermiculite. We transplanted one seedling into each pot. The resulting 696 pots were assigned to positions across eight greenhouse benches according to a fully randomized experimental design, and watered to saturation. We randomized the positions of the pots among and within the benches 5 weeks after the start of the experiment. We kept the temperature between 22 and 28 °C, and we used supplemental lighting to supply the plants with 14 hours of light each day.

One week after transplanting the seedlings, we started to apply different nutrient treatments. We used a Hoagland solution as fertilizer (Methods S2), which was applied at weekly intervals for a total of

10 weeks. To test the effects of different overall nutrient supply and different temporal patterns of nutrient supply on common alien, rare alien, common native and rare native plant species, we created six different nutrient supply patterns (Fig. 1): (i) constant low, (ii) constant high, (iii) gradual increase, (iv) gradual decrease, (v) single large pulse and (vi) multiple pulses of different magnitudes. The total (i.e. cumulative) amount of nutrients supplied during the 10 weeks was the same in all treatments except for the constant low treatment. In other words, treatments (ii) to (vi) were all high nutrient treatments, but differed in the temporal pattern of nutrient supply (Fig. 1). To increase the statistical power for detecting differences among the four groups of studied species, we had maximized the number of species per group over the number of replicate pots per species (van Kleunen *et al.* 2014). Therefore, we had only four individuals per species for each of the six nutrient treatments. We added 5 mL of 400% strength Hoagland solution to pots in the constant low nutrient treatment, and 40 mL of the same Hoagland solution to the constant high nutrient treatment each week. To avoid introducing a potential bias because of differences in water supply among the six treatments, we added extra water to the specific amount of 400% strength Hoagland solution of each treatment to ensure that each plant received a total of 100 mL nutrient solution each time.

Among the high nutrient treatments in this study, the temporal pattern of nutrient supply might influence plant growth differently because of shifts in the degree of nutrient limitation over time. If nutrient supply is not limiting in the high nutrient treatments, the effects of fluctuations in nutrient availability over time on plant growth should be similar to when nutrients are supplied at a constant rate. Therefore, to ensure that the high nutrient treatments were still limiting for plant growth, we had previously done a pilot experiment with a wider range of nutrient levels (Methods S3). For the current experiment, we chose the high nutrient level so that plants produced significantly more biomass than at the lowest nutrient level of the pilot experiment, but also still significantly less biomass than at the highest nutrient level of the pilot experiment (Methods S3). For the gradual increase treatment, we increased the weekly amount of Hoagland solution per pot during the 10 weeks of the experiment as follows: 5, 5, 21, 21, 40, 40, 58, 58, 76 and 76 mL (Fig. 1). For the gradual decrease treatment, we applied the opposite sequence of nutrient solution amounts (Fig. 1). The single large pulse treatment started after 3 weeks, and lasted for 4 weeks; the sequence was 5, 5, 5, 92.5, 92.5, 92.5, 92.5, 5, 5 and 5 mL (Fig. 1). For the multiple pulses treatment, we supplied to all replicates the same random order of 5, 76, 40, 40, 21, 58, 76, 58, 21 and 5 mL nutrient solution (Fig. 1). To ensure that water was not limiting for plant growth, we checked all pots every day during the experiment. We watered the plants when the soil looked dry, and supplied the same amounts of water to all plants.

## MEASUREMENTS

To be able to account for variation in initial sizes of plants in the analyses, we counted at the start of the experiment the number of true leaves (i.e. excluding the cotyledons), and measured the length and width of the largest leaf on each plant, and the height of each plant. On 24 November 2014, we began to harvest the plants. On the first day, we harvested the above ground biomass of all plants, and then started to harvest the below ground biomass. As eight plants died during the experiment (Table S1), the total number of harvested plants was 688 instead of 696. As the entire below ground biomass harvest took 8 days, we stored all pots outside at low temperatures after the

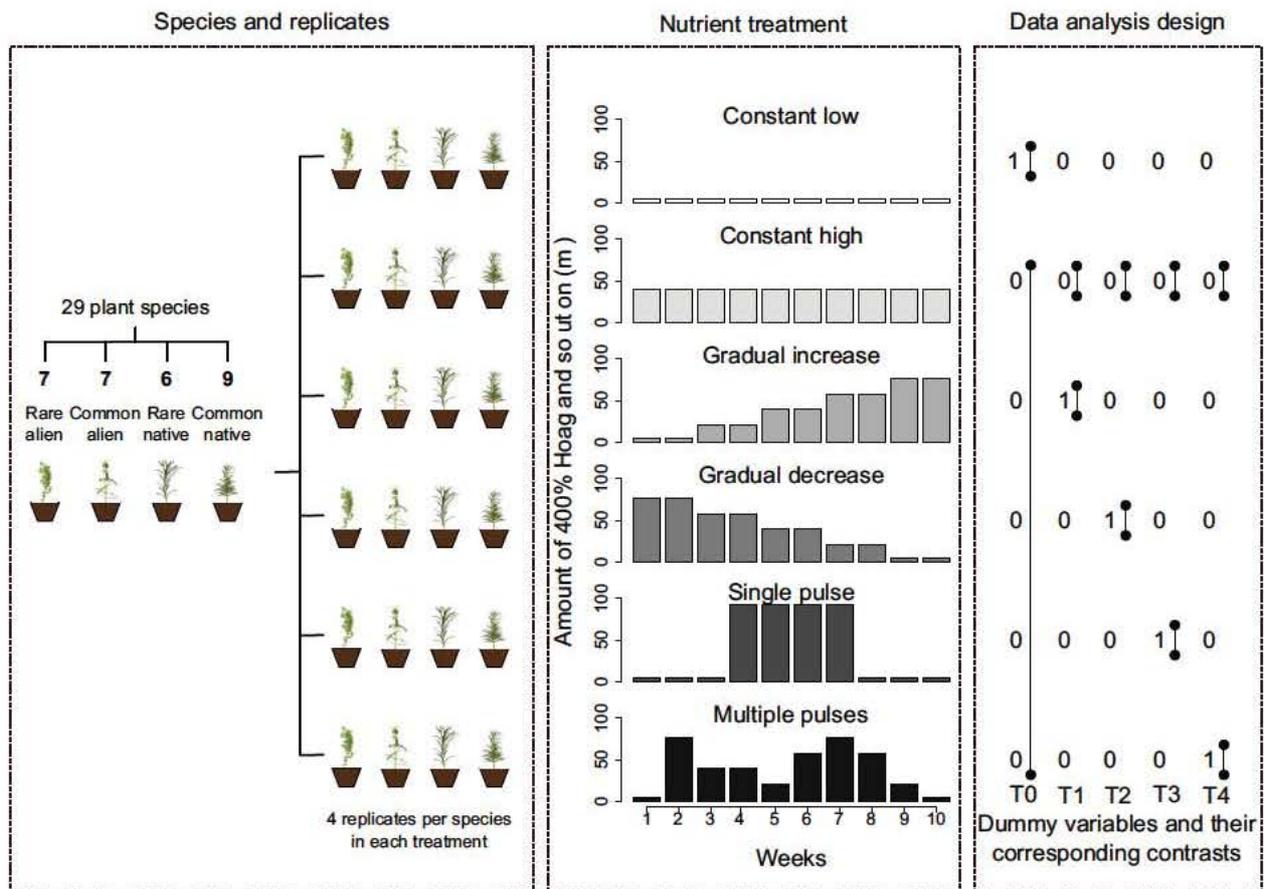


Fig. 1. Graphical illustration of the experimental design (number of species per group, nutrient treatments and number of replicates per species and nutrient treatment combinations) and data analysis design for the effects of the nutrient treatments (i.e. dummy variables and their corresponding contrasts). Each bar represents the amount of nutrient solution supplied each week during the 10 weeks of the experiment. The total amount of nutrients is the same in all high mean treatments. In the data analysis design, dummy variable coding for the scenarios of nutrient supply was used to test the effects of the mean level of nutrient supply (constant low treatment vs. the average across the five high treatments; T0), and the effects of different temporal patterns of high nutrient supply vs. the constant high supply (T1–T4). For the latter, each contrast of interest was made by fitting the corresponding dummy variable after all other dummy variables (for details on model comparisons, see Methods S4). The two lines next to each dummy coding indicate the contrasts of interest. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

above ground biomass harvest in order to halt growth or decay of the plants and thus to avoid introducing a potential bias due to different harvesting times. After washing all the roots clean of substrate, we randomly took a representative subsample from each replicate root system, and stored it in a plastic 20 mL tube filled with distilled water in a cold room at 4 °C. The remaining root mass and the above ground biomass of each plant were dried for at least 72 hours at 80 °C, and weighed. We stained the root subsamples in a neutral red solution for 30 minutes. We then determined the total root length, and the mean root diameter of each subsample using a flatbed scanner specifically modified for root scanning (Epson Expression 10000 XL; Regent Instruments, Ville de Québec, QC, Canada) and WinRhizo software (2012; Regent Instruments Inc.). All root subsamples were then dried for at least 72 hours at 80 °C, and weighed.

Based on the initial size measurements, we calculated an estimate of initial leaf area as the length × width of the largest leaf × the number of true leaves. Based on the final biomass and root morphology measurements, we calculated total below ground biomass (biomass of subsample used for root morphology measurements + biomass of the rest of the root system), total biomass (above ground biomass + below ground biomass), root mass fraction

(below ground biomass/total biomass), total root length (root length of subsample × total below ground biomass/subsample mass) and specific root length (total root length/total below ground biomass).

ANALYSES

To test for differences in growth performance, and root morphology and allocation among common alien, rare alien, common native and rare native plant species, we fitted linear mixed effect models using the *lme* function in the R package *NLME* (Pinheiro *et al.* 2015) in R 3.1.3 (R Core Team 2015). Total biomass, root mass fraction, total root length, root average diameter and specific root length of the plants were the response variables in the models. To meet the assumption of normality, we tried different transformations; and achieved the best residual distributions with a square root transformation of total biomass and root mass fraction, and a natural log transformation of the three root morphological traits. We included species origin (alien vs. native), commonness (rare vs. common), nutrient level (low vs. high), nutrient variability (constant high vs. each of the four scenarios of nutrient pulse), and their interactions, as fixed effects in all models. Because nutrient variability was nested within

the high nutrient level, we coded the nutrient supply patterns as dummy variables T0–T4 (Fig. 1) in all models to obtain the different treatment contrasts required (Schielzeth 2010). Because initial variation in plant size might contribute to differences in final biomass and biomass allocation, we also added initial plant leaf area and initial plant height as scaled natural log transformed covariates in the models for total biomass and root mass fraction. To account for phylogenetic non independence of species and for non independence of replicates of the same species, we included species nested within family as random effects in all models.

As the homoscedasticity assumption was violated, we also included variance structures modelling different variances per species in all models using the *varIdent* function in the R package NLME (Pinheiro *et al.* 2015; see also Zuur *et al.* 2009). As species within each of the four groups of different origin and commonness might vary in their responses to the nutrient treatments, we also ran models with random slopes for family and species with respect to nutrient treatment. However, because this decreased the AIC values (i.e. increased model fit) only for the total biomass model, we did not consider the random slopes models for the other traits. In the linear mixed models described above, we assessed the significance of fixed effects (i.e. species origin, commonness, nutrient level and nutrient variability) and their interactions with likelihood ratio tests (Zuur *et al.* 2009; for details, see Methods S4).

Plastic changes in root allocation and morphology in response to nutrient availability are frequently implicitly assumed to constitute adaptive plasticity (i.e. to result in high performance of plants across different nutrient conditions). Ideally, the adaptive value of plasticity should be tested explicitly (van Kleunen & Fischer 2005). Although there are ways of testing whether plasticity is adaptive based on selection gradient analysis (see Dudley & Schmitt 1996; van Kleunen & Fischer 2001 for one approach, and Keser *et al.* 2015 for another), these approaches cannot be applied in a straight forward way to a multispecies data set with few replicates per species. Instead, we tested how the change in biomass across two nutrient conditions (i.e. log response ratios of biomass) relates to plasticity in the trait of interest across the same two nutrient conditions, using the 29 species as replicates (see Liu *et al.* 2016a). These analyses revealed some significant relationships between plastic responses of some of the root traits and the plant performance response to nutrients (see Methods S5). However, as we have only 29 species (i.e. data points), which does not provide enough degrees of freedom to include multiple traits and their plasticities in one and the same regression model, this approach is not very powerful and informative. Therefore, we did not interpret these results.

## Results

### MEAN VALUES ACCORDING TO ORIGIN AND COMMONNESS OF PLANT SPECIES

Averaged across all six nutrient treatments, common alien, rare alien, common native and rare native plants did not differ in total biomass, root mass fraction (Table 1 and Fig. S1) and root morphological traits (root length, root diameter and specific root length; Table 1 and Fig. S1). In other words, there were no significant main effects of origin and commonness, and no significant interaction between both for any of the measured traits (Table 1).

### RESPONSES TO MEAN NUTRIENT AVAILABILITY

Averaged across all 29 species, plants produced significantly more biomass (+160.3%), and had a significantly lower root mass fraction (–18.5%) when growing under high nutrient conditions (i.e. averaged across the treatments constant high, gradual increase, gradual decrease, single pulse and multiple pulses) than under constant low nutrient conditions (Table 1 and Fig. 2). The decrease in root mass fraction was stronger for native species (–22.8%) than for alien species (–14.6%; significant  $O \times T0$  interaction in Table 1; Fig. 2).

Averaged across all 29 species, plants produced significantly longer roots (+90.1%) when growing under high nutrient conditions than under constant low nutrient conditions (Table 1 and Fig. 2). Root diameter and specific root length, on the other hand, were not significantly affected by the mean level of nutrient availability (Table 1 and Fig. 2). However, while for alien species the root diameter slightly increased (+6.5%) and the specific root length decreased (–12.5%) with increasing nutrient availability, the reverse tended to be the case for native species (root diameter decreased by 0.4% and specific root length increased by 3.6%; significant  $O \times T0$  interactions in Table 1; Fig. S2). The slight decrease in root diameter for native species was driven by the common ones (–3.5%) as the rare native species, just like the rare (+3.6%) and common alien species (+9.9%), also showed a slight increase (+4.2%; Fig. 2). This was reflected in a significant  $O \times C \times T0$  interaction in Table 1.

### GRADUAL CHANGES IN NUTRIENT SUPPLY OVER TIME

When nutrients were gradually increased over time, total biomass and root mass fraction were significantly lower than when nutrients were supplied at a constant high rate (total biomass: –11.3%; root mass fraction: –10.8%; significant T1 effect in Table 1; Fig. 3 and Fig. S1). On the other hand, when nutrients were gradually decreased over time, root mass fraction was significantly higher than when nutrients were supplied at a constant high rate (+9.0%; significant T2 effect in Table 1; Fig. 3). Root diameter was significantly larger when nutrients were gradually decreased instead of supplied at a constant high rate (+4.8%; Table 1, Fig. 3 and Fig. S1). On the other hand, specific root length was significantly lower when nutrient were gradually decreased instead of supplied at a constant high rate (–14.8%; Table 1, Fig. 3 and Fig. S1). Root length was not affected by gradual changes in nutrient supply for any of the four groups of plant species (Table 1; Fig. 3 and Fig. S1). For alien plants, root diameter was slightly higher (+4.7%) when nutrients gradually increased than when they were supplied at a constant high rate, whereas the reverse was true for the native species (–3.2%; significant  $O \times T1$  interaction in Table 1; Fig. 3 and Fig. S3). Moreover, root diameter tended to be increased more for alien species (+7.5%) than for native species (+2.0%) when nutrients were gradually decreased instead of supplied at a constant high rate (marginal significant  $O \times T2$  interaction in Table 1; Fig. 3 and Fig. S3).

**Table 1.** Results of linear mixed effects models testing the effects of species origin, species commonness, changes in mean nutrient availability (T0) and temporal patterns of variability in nutrient availability (T1–T4), and all interactions thereof, on total biomass, root mass fraction, root length, root diameter and specific root length of experimental plants

Fixed effects	Total biomass			Root mass fraction			Root length			Root diameter			Specific root length		
	d.f.	$\chi^2$	<i>P</i>	d.f.	$\chi^2$	<i>P</i>	d.f.	$\chi^2$	<i>P</i>	d.f.	$\chi^2$	<i>P</i>	d.f.	$\chi^2$	<i>P</i>
Initial leaf area	1	19.77	<b>&lt;0.0001</b>	1	5.43	<b>0.0198</b>									
Initial height	1	3.79	<b>0.0515</b>	1	0.51	0.4741									
Origin (O)	1	0.79	0.3737	1	0.59	0.4421	1	0.14	0.7090	1	1.30	0.2550	1	2.54	0.1107
Commonness (C)	1	2.03	0.1538	1	1.55	0.2129	1	0.16	0.6863	1	3.01	<b>0.0827</b>	1	0.96	0.3267
Low vs. High (T0)	1	12.43	<b>&lt;0.0001</b>	1	73.00	<b>&lt;0.0001</b>	1	92.98	<b>&lt;0.0001</b>	1	1.72	0.1893	1	0.46	0.4996
Constant high vs. Gradual increase (T1)	1	6.18	<b>0.0129</b>	1	15.10	<b>0.0001</b>	1	2.09	0.1487	1	0.14	0.7114	1	0.08	0.7834
Constant high vs. Gradual decrease (T2)	1	0.34	0.5628	1	7.95	<b>0.0048</b>	1	0.64	0.4254	1	4.43	<b>0.0354</b>	1	9.86	<b>0.0017</b>
Constant high vs. Single pulse (T3)	1	0.85	0.3554	1	0.94	0.3328	1	1.59	0.2071	1	0.22	0.6354	1	0.16	0.6906
Constant high vs. Multiple pulses (T4)	1	0.12	0.7309	1	0.03	0.8630	1	0.03	0.8623	1	2.09	0.1479	1	1.37	0.2426
O × C	1	1.44	0.2297	1	1.56	0.2118	1	0.20	0.6547	1	0.08	0.7708	1	1.70	0.1928
O × T0	1	0.92	0.3374	1	4.21	<b>0.0402</b>	1	0.08	0.7796	1	6.69	<b>0.0097</b>	1	3.90	<b>0.0484</b>
O × T1	1	0.23	0.6308	1	1.61	0.2042	1	0.33	0.5634	1	5.84	<b>0.0157</b>	1	1.72	0.1893
O × T2	1	0.03	0.8530	1	0.01	0.9116	1	0.25	0.6179	1	2.96	<b>0.0856</b>	1	0.43	0.5105
O × T3	1	3.28	<b>0.0703</b>	1	8.04	<b>0.0046</b>	1	2.08	0.1491	1	3.75	<b>0.0527</b>	1	2.07	0.1502
O × T4	1	0.93	0.3352	1	0.00	0.9544	1	0.11	0.7397	1	6.49	<b>0.0108</b>	1	2.88	<b>0.0899</b>
C × T0	1	0.48	0.4907	1	0.78	0.3762	1	0.55	0.4592	1	0.66	0.4165	1	1.02	0.3123
C × T1	1	0.33	0.5634	1	0.44	0.5062	1	1.21	0.2704	1	1.39	0.2387	1	0.03	0.8649
C × T2	1	2.38	0.1232	1	0.25	0.6173	1	0.37	0.5434	1	0.36	0.5475	1	3.74	<b>0.0533</b>
C × T3	1	0.29	0.5921	1	1.15	0.2841	1	0.75	0.3874	1	0.08	0.7751	1	0.29	0.5889
C × T4	1	0.78	0.3782	1	0.66	0.4161	1	0.09	0.7609	1	0.25	0.6172	1	0.03	0.8570
O × C × T0	1	0.79	0.3726	1	1.83	0.1756	1	0.06	0.8108	1	7.02	<b>0.0081</b>	1	1.69	0.1932
O × C × T1	1	0.51	0.4756	1	0.31	0.5768	1	0.15	0.6952	1	0.00	0.9848	1	0.22	0.6372
O × C × T2	1	0.13	0.7173	1	0.08	0.7834	1	2.02	0.1548	1	0.22	0.6428	1	0.63	0.4287
O × C × T3	1	1.56	0.2111	1	1.54	0.2142	1	0.20	0.6548	1	0.60	0.4380	1	0.04	0.8435
O × C × T4	1	0.34	0.5591	1	1.72	0.1895	1	1.41	0.2348	1	6.94	<b>0.0084</b>	1	0.54	0.4637
Random effects		SD			SD			SD			SD			SD	
Family		0.4019*			0.0567			0.9084			0.2742			0.0002	
Species within Family		0.5052*			0.1255			0.9611			0.1807			0.5596	
Residual		0.3120			0.0606			0.8856			0.1593			0.4496	
<i>R</i> <sup>2</sup> of the model															
Marginal <i>R</i> <sup>2</sup>		0.2052			0.1215			0.0316			0.0469			0.1132	
Conditional <i>R</i> <sup>2</sup>		0.9484			0.8577			0.6998			0.8184			0.6521	

\*The standard deviation (SD) was only given for the intercept of family and species here (for the random slopes of all treatments, please, see Table S1). Significant or marginal significant effects ( $P < 0.1$ ) are in bold.

[Correction added after online publication on 22 February 2017: *P* values for Total biomass Initial height and for Root diameter Commonness (C) were changed to bold. Footnote changed to ( $P < 0.1$ )].

## NUTRIENT PULSES

When nutrients were supplied as a single large pulse in the middle of the 10 week growth period instead of at a constant high rate, alien species increased their biomass (+7.5%) and root mass fraction (+5.7%), while native species did the opposite (biomass: -13.8%, root mass fraction: -11.5%; significant O × T3 interaction in Table 1; Fig. 4 and Fig. S4). Root diameter of alien species was also slightly higher (+3.2%) when nutrients were supplied as a single large pulse instead of at a constant high rate, whereas the reverse was true for the native species (-3.5%; marginal significant O × T3 interaction in Table 1; Fig. 4 and Fig. S4). Biomass

production and root mass fraction were not affected by whether the nutrients were supplied as multiple pulses or at a constant rate (Table 1 and Fig. 4).

Root length and specific root length were neither affected by a single nutrient pulse nor by multiple nutrient pulses compared to a constant high supply rate for any of the four groups of plants (Table 1, Fig. 4 and Fig. S1). Root diameter was also not affected by the single nutrient pulse (Table 1, Fig. 4 and Fig. S1). However, root diameter was differently affected by multiple nutrient pulses for the four groups of plant species. Root diameter was strongly increased (+14.2%) for common alien species, while it was only slightly increased for rare alien (+2.4%) and rare native species (+3.1%), and even slightly

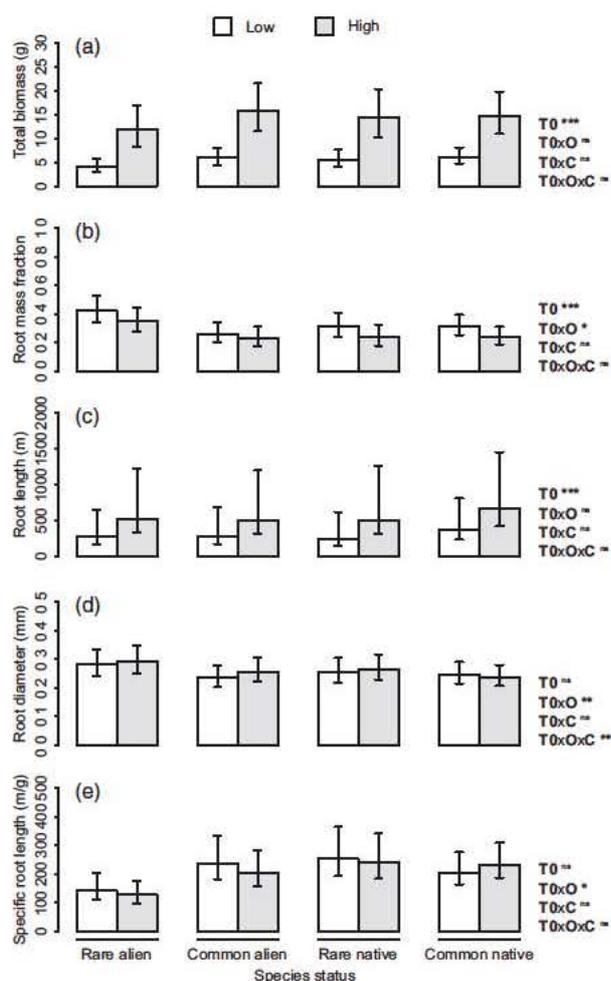


Fig. 2. Modelled means of (a) total biomass, (b) root mass fraction, (c) root length, (d) root diameter and (e) specific root length of the seven rare alien and seven common alien, six rare native and nine common native plant species growing under low and high (averaged across five different temporal patterns; corresponding to contrast T0 in Table 1, also see Fig. 1) nutrient conditions. Error bars represent SEs of the means. Significant effects are presented as follows:  $0.05 < P < 0.1$  ('),  $0.01 < P < 0.05$  (\*),  $0.001 < P < 0.01$  (\*\*),  $P < 0.001$  (\*\*\*).

decreased for common native species (2.6%; significant  $O \times T4$  and  $O \times C \times T4$  interactions in Table 1; Fig. 4).

## Discussion

### SIMILAR RESPONSES TO MEAN NUTRIENT AVAILABILITY AMONG ALIEN RARE, ALIEN COMMON, NATIVE RARE AND NATIVE COMMON SPECIES

As expected, all plants produced more biomass under high mean nutrient supply than under low mean nutrient supply. This coincided with a decrease in the relative allocation of biomass to the root system, which is in line with predications of resource limitation theory, posing that plants should allocate biomass to structures that help them acquire more of the most limiting resource (Bloom, Chapin & Mooney 1985; Poorter & Nagel 2000). Although both native and alien plant

species allocated relatively less biomass to the root system under high nutrient conditions, this decrease was weaker for aliens. However, alien plant species produced thinner roots under low than under high nutrient conditions, whereas native plant species showed the opposite pattern. As thin roots partly result from plants producing more root length with a given amount of dry weight (Pearson  $r = 0.451$ ,  $n = 679$ ,  $P < 0.0001$  for root diameter and specific root length), an opposite pattern was found for specific root length. Together, these results suggest that natives and aliens follow partly different strategies in response to low nutrient conditions; natives more strongly increase the allocation of biomass to the roots, whereas aliens do so to a lesser degree but compensate this by producing thinner roots.

Despite these apparently different strategies of native and alien plants, we found similar responses in biomass production to changes in mean nutrient availability among the four groups of species. In another multispecies experiment, Dawson, Fischer & van Kleunen (2012) compared responses to nutrient addition among the same four types of species in Switzerland, and found that common alien plant species did not differ in their performance response to nutrient addition from common native plant species, but that, irrespective of origin, common species exhibited stronger responses to nutrient addition than rare species. Although we did not find that common species took more advantage of increased nutrient availability, we found, just like Dawson, Fischer & van Kleunen (2012), that there was no overall difference in biomass production response between natives and aliens. The latter is also supported by findings of Godoy, Valladares & Castro Díez (2011), who compared 20 invasive alien and 20 widespread native congeners in Spain across nutrient gradients, and found that both groups responded to environmental variation with similar levels of plasticity. The consistency of these findings might indicate that the aliens and natives in both studies come from habitats with similar variation in mean nutrient levels, suggesting that species origin does not drive differences of plant performance in response to changes in mean nutrient availability.

It has previously been shown that common alien plant species tend to have stronger adaptive root foraging responses than rare alien species, which could help common alien plant species capture more nutrients (Keser *et al.* 2014, 2015). Additionally, common species, irrespective of whether alien or native, appear to frequently occur in widespread nutrient rich habitats (Thompson, Hodgson & Rich 1995; Dawson *et al.* 2012; Dostál *et al.* 2013). There is also evidence that rare species tend to disappear from communities after nutrient enrichment (Suding *et al.* 2005). Thus, common species usually benefit more strongly from nutrient addition than rare species. Although this was also found by Dawson, Fischer & van Kleunen (2012), our multispecies experiment does not show this. Flores Moreno *et al.* (2016) found that nutrient addition controlled the abundance (percentage cover) of native and alien species, and that the nutrient addition effect on species richness, in particular for native species, was mediated by climatic conditions. In that study, alien species are likely

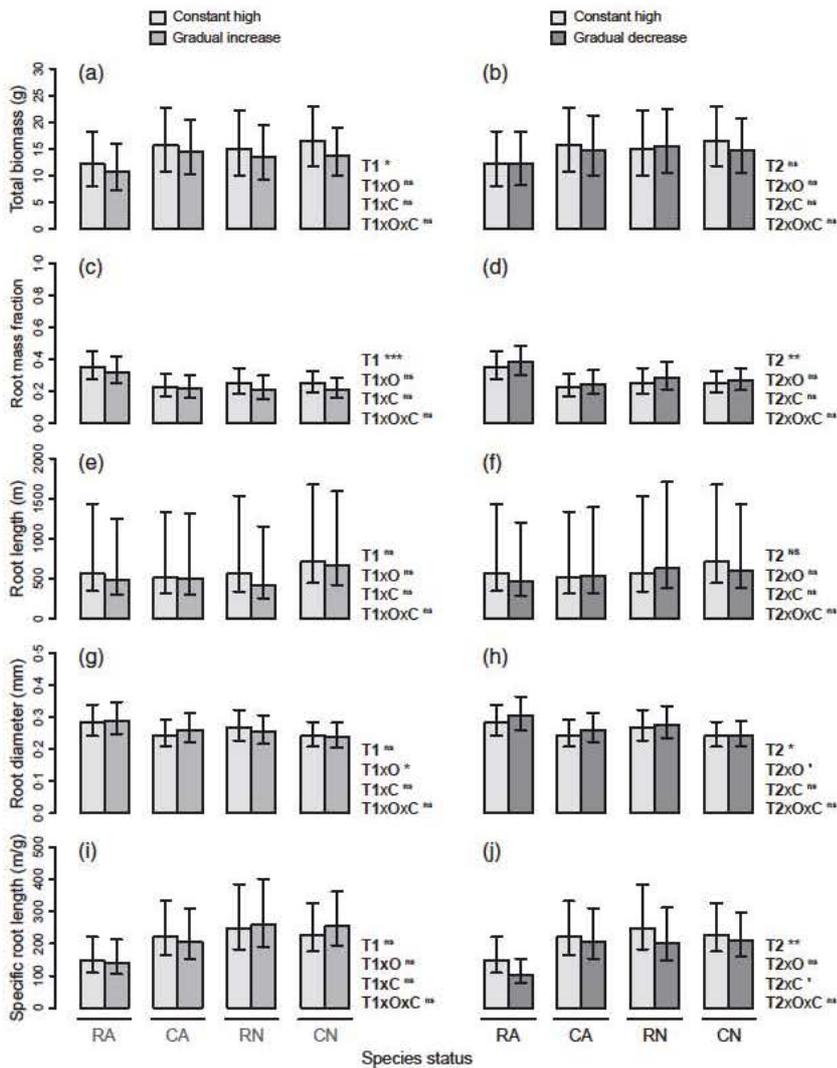


Fig. 3. Modelled means of (a, b) total biomass, (c, d) root mass fraction, (e, f) root length, (g, h) root diameter, and (i, j) specific root length of the seven rare alien (RA) and seven common alien (CA), six rare native (RN) and nine common native (CN) plant species growing under conditions of constant high vs. a gradual increase (a, c, e, g, i; corresponding to contrast T1 in Table 1, also see Fig. 1) and a gradual decrease (b, d, f, h, j; corresponding to contrast T2 in Table 1, also see Fig. 1) in nutrient supply over time. Note that the constant high treatment is shown twice (in a, c, e, g, i and in b, d, f, h, j) for clarity. Error bars represent SEs of the means. Significant effects are presented as follows:  $0.05 < P < 0.1$  (\*),  $0.01 < P < 0.05$  (\*\*),  $P < 0.001$  (\*\*\*)

to be common (invasive) rather than rare; whereas the natives included both common and rare species. Their result that native species declined in abundance but not in richness in response to nutrient addition might indicate a reduction of common rather than rare native species when competing with common alien species. Therefore, the question whether differences in performance to changes in mean environmental conditions could drive commonness of species still needs further research.

#### GRADUAL CHANGES IN NUTRIENT SUPPLY OVER TIME INFLUENCE PLANT PERFORMANCE

Under an equally high cumulative nutrient supply during the 10 week growth period, plants produced less biomass when they grew initially under low nutrient supply that gradually increased than when they grew under constant nutrient supply. This could be because under a gradual increase in nutrient supply over time, nutrient availability was insufficient at the early growth stage when plants needed nutrients the most. There was, on the other hand, no difference in biomass production between when plants grew under gradually decreased

nutrient supply and when they grew under constant nutrient supply. Possibly, while nutrient supply decreased over time in this treatment, the nutrient availability might have decreased to a lesser extent due to storage of nutrients in the substrate and/or plant. Alternatively, a possible growth disadvantage at the end of the experiment might not have compensated for the initial growth advantage yet.

Plants allocated more biomass to roots under a gradually decreased nutrient supply than under constant nutrient supply, whereas they showed the opposite pattern in response to a gradually increased nutrient supply compared to a constant nutrient supply. We found that the final root mass fraction was higher in the decreasing treatment, where plants had the lowest nutrient supply at the end of the experiment, than in the constant treatment. Useche & Shipley (2009) found evidence among 14 plant species that those that increased root mass fraction more strongly under decreasing nutrient availability were less affected in their relative growth rate, suggesting that a plastic increase of root mass fraction under decreasing nutrient availability is adaptive. According to an optimal growth model developed by Iwasa & Roughgarden (1984), when a plant grows in a constant environment, once

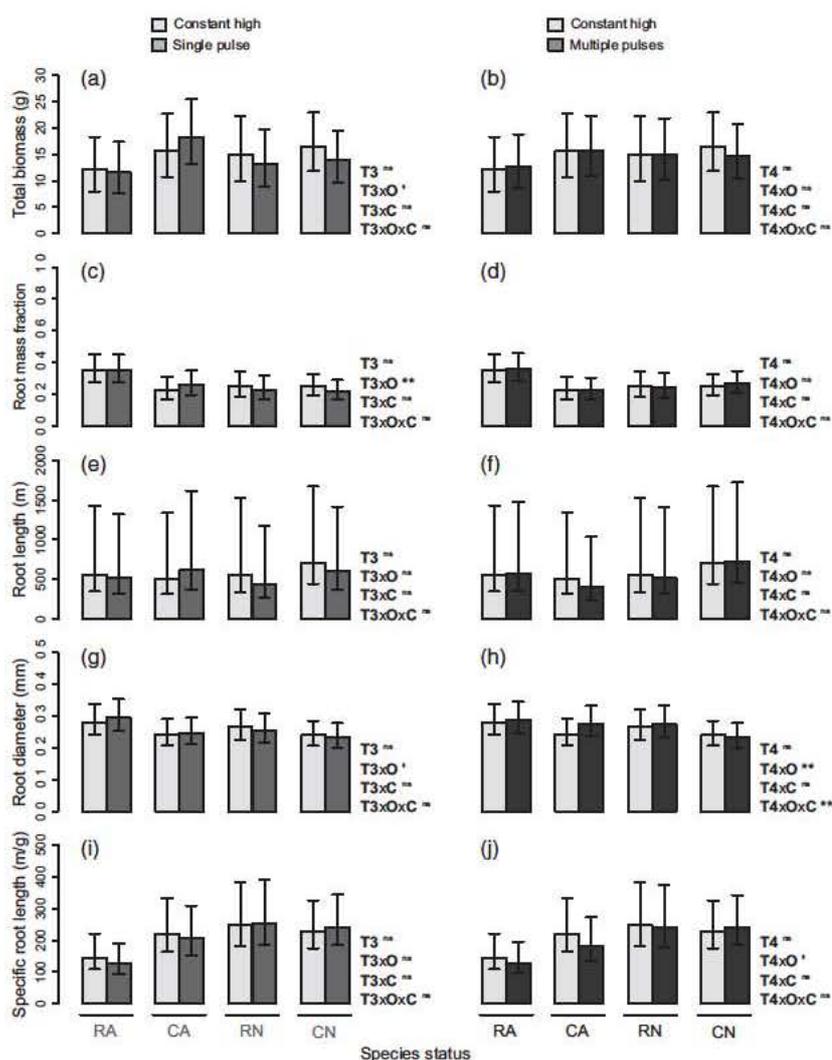


Fig. 4. Modelled means of (a, b) total biomass, (c, d) root mass fraction, (e, f) root length, (g, h) root diameter, and (i, j) specific root length of the seven rare alien (RA), seven common alien (CA), six rare native (RN) and nine common native (CN) plant species growing under conditions of constant high vs. single pulse (a, c, e, g, i; corresponding to contrast T3 in Table 1, also see Fig. 1) and multiple pulses (b, d, f, h, j; corresponding to contrast T4 in Table 1, also see Fig. 1) in nutrient supply. Note that the constant high treatment is shown twice (in a, c, e, g, i and in b, d, f, h, j) for clarity. Error bars represent SEs of the means. Significant effects are presented as follows:  $0.05 < P < 0.1$  (\*),  $0.01 < P < 0.05$  (\*\*),  $0.001 < P < 0.01$  (\*\*\*),  $P < 0.001$  (\*\*\*).

both the roots and shoots have begun to grow simultaneously, their balanced growth will continue until the end of the vegetative growth. However, this root shoot balance is likely to change when nutrient availability changes (Iwasa & Roughgarden 1984). Our results for the patterns in root allocation, as measured at the end of the experiment, are in line with the predictions of Iwasa & Roughgarden (1984), and with the predictions of the resource limitation theory (Bloom, Chapin & Mooney 1985), suggesting that plants continuously adjust biomass allocation depending on the actual nutrient availability. This might also happen with regard to the thickness of roots produced. However, at the end of the experiment, plants under a gradually decreased nutrient supply had thicker instead of thinner roots. Possibly, this reflects a legacy of the thick roots produced at the beginning of the experiment when nutrient availability was very high in the decreasing treatment. It would thus be interesting to assess how the thickness of newly produced roots changes over time under changing nutrient supplies.

Root traits of alien and native plants responded overall in a similar way to gradual changes in nutrient supply. However, whereas under a gradual increase in nutrient supply, native

plants had in the end slightly thinner roots than under a constant nutrient supply, alien plants had slightly thicker roots. These differences in root thickness responses were apparently not large enough to result in significantly different biomass responses of alien and native plants to gradual changes in nutrient supply. On the other hand, rare plants produced slightly more biomass when nutrient supply gradually decreased instead of remained constant, whereas common plants produced slightly less biomass. Under the scenario of a gradual decrease in nutrient supply over time, nutrient availability was sufficient at the beginning, whereas it was likely insufficient at the end. Rare plants might be better able to deal with a decrease in nutrients as they often have adaptations suited for resource conservation rather than acquisition (Reich *et al.* 1999).

#### A NUTRIENT PULSE FAVOURS ALIEN, BUT NOT NATIVE PLANT SPECIES

The responses to the nutrient pulse treatments differed among the four groups of plant species. In response to a single large nutrient pulse, alien plant species showed an increase in total

biomass, whereas native plant species showed a decrease. This coincided with an increase and decrease in root allocation for alien and native species, respectively, in response to an increase in the mean nutrient level. Based on the resource limitation theory (Bloom, Chapin & Mooney 1985), one would expect that a decrease in root allocation in response to an increase in nutrients would be beneficial. However, in case of an ephemeral increase in nutrient availability, as during a pulse, having a large root mass fraction has the advantage that it allows a plant to take immediate advantage of the temporary surplus of nutrients. Our finding that a large nutrient pulse favours alien but not native plants is in line with the finding of Parepa, Fischer & Bossdorf (2013) that the biomass of the highly invasive Japanese knotweed (*Fallopia* spp.) was 2 to 4 fold increased when nutrients were supplied pulse wise instead of at a constant rate in experimental plant communities.

When nutrients were supplied in multiple pulses instead of at a constant rate, common alien plants increased their root diameter, whereas the other groups showed negligible changes. These differences in root diameter responses, however, did not appear to affect biomass responses of the four groups of species. Possibly, the effects of the multiple nutrient pulses treatment were overall small because this treatment is quite similar to the constant nutrient supply treatment, which in effect consists of multiple pulses of the same magnitude. Nevertheless, our finding contrasts with the results of Parepa, Fischer & Bossdorf (2013), who found that invasive Japanese knotweed did not just benefit from a single large pulse but even more so from multiple pulses of smaller magnitude. A possible explanation for this is that the plants in our study grew without competition, whereas Parepa, Fischer & Bossdorf (2013) grew the invasive alien in competition with natives. The ability of alien plant species to rapidly take advantage of available resources (Richards *et al.* 2006) could help them outperform native plants when they compete with native plants.

In a community setting, coexistence of plant species, and thus invasion, is more likely when the species differ in their phenology (Wolkovich & Cleland 2011; Godoy & Levine 2014). With fluctuating nutrient availability, it is likely that the degree to which nutrient peaks coincide with a species main growth period might determine which species is likely to survive. The competitive advantages resulting from differences in nutrient uptake ability or phenology between alien and native plants might be less apparent when plants are grown individually. Although our results suggest that it is not a general phenomenon that common alien plants take more advantage of multiple nutrient pulses than native plants do, future studies should also consider competitive environments, like Parepa, Fischer & Bossdorf (2013) did, and species with different phenologies.

## Conclusion

Irrespective of their origin and commonness, all species in our study produced more biomass under high nutrient conditions than under low nutrient conditions. In addition, plants

produced longer roots under high nutrient conditions despite allocating less biomass to roots. Among the five high nutrient treatments, the temporal pattern of nutrient supply also influenced biomass production, root allocation and root thickness, but the magnitude and/or direction of these responses varied among the four groups of species. Particularly, we found that alien plant species, irrespective of whether they are common or rare, produced more biomass, and had a higher root mass fraction when nutrients were supplied as a single pulse in the middle of the growth period instead of supplied at a constant rate, whereas the reverse was true for the native species. This suggests that alien plant species, possibly as a consequence of an increased biomass allocation to the root system, could, in contrast to native plant species, benefit from large nutrient pulses.

## Authors' contributions

Y.L. conceived the experiment. Y.L. and M.v.K designed the experiment. Y.L. performed the experiment and collected the data. Y.L. and M.v.K performed data analyses and wrote the manuscript.

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## Data accessibility

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dp24m> (Liu & van Kleunen 2017).

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Methods S1.** Information on status, commonness, number of grid cells, native continent(s), seed source, sowing date, transplanting date

and mortality of the 29 study species in Germany. The species are grouped per family.

**Methods S2.** Recipe for 400% strength Hoagland's Complete Nutrient Solution.

**Methods S3.** Pilot experiment to determine nutrient concentrations to be used in main experiment.

**Methods S4.** Details of the models compared in likelihood ratio tests to assess the significance of fixed effects (i.e. initial size covariates, species origin, commonness, nutrient level [T0] and temporal patterns in nutrient supply [T1–T4]) and their interactions.

**Methods S5.** Results of analyses testing for adaptive plasticity of root mass fraction (RMF), root length (RL), root diameter (RD) and specific root length (SRL).

**Table S1.** The standard deviation (SD) for random effects of the total biomass model, which included random slopes for family and species with respect to nutrient treatment (i.e. constant low, constant high, gradual increase, gradual decrease, single pulse and multiple pulses).

**Fig. S1.** Modelled means of (a) total biomass and (b) root mass fraction, (c) root length, (d) root diameter, and (e) specific root length of the seven rare alien, seven common alien, six rare native and nine common native plant species growing under six different patterns of nutrient supply.

**Fig. S2.** Modelled means of (a) root mass fraction, (b) root diameter, and (c) specific root length of the 14 alien and 15 native plant species, irrespective of commonness, growing under low and high (averaged across the five patterns of resource supply) nutrient supply.

**Fig. S3.** Modelled means of root diameter of the 14 alien and 15 native plant species, irrespective of commonness, growing under a constant high and a gradually changed nutrient supply.

**Fig. S4.** Modelled means of (a) total biomass and (b) root mass fraction of the 14 alien and 15 native plant species, irrespective of commonness, growing under a constant high and a single pulse nutrient supply.