Commonness and rarity of alien and native plant species – the relative roles of intraspecific competition and plant–soil feedback

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The success of invasive alien and common native species may be explained by the same underlying mechanisms. Differences in intraspecific competition as well as differences in plant–soil feedback have been put forward as potential determinants of plant success. We teased apart the relative roles of competition and plant–soil feedback in a greenhouse experiment with 30 common and rare alien and native species from nine plant families. We tested whether plant biomass decreased less for common than rare species, regardless of origin, when grown at higher relative frequencies (1, 3 or 6 out of 9 plants per pot) in a community and in soil previously conditioned by the same species at different frequencies (0, 1, 3 or 6 out of 9 plants per pot) in an orthogonal design for these two factors. Plant survival decreased slightly, but non-significantly, for all species when grown in soil previously occupied by conspecifics. Among surviving plants, we found a decrease in biomass with increasing intraspecific competition across all species (regardless of origin or commonness), and alien species were more negatively affected by previous high plant frequency than native species, but only marginally significantly so. Our findings suggest that, while intraspecific competition limits individual biomass in a density-dependent manner, these effects do not depend on species origin or commonness. Notably, alien species but not natives showed a decrease in performance when grown in soil pre-conditioned with a higher frequency of conspecifics. In conclusion, soil-borne pathogen accumulation might be weak in its effects on plant performance compared to intraspecific competition, with neither being clearly linked to species commonness.

Why are some species common while others are rare? This short question has puzzled ecologists for decades (Preston 1948). With the emergence of invasion ecology in times of globalization (Mack et al. 2000, Bradley et al. 2010), the question ‘what determines species commonness’ has gained further interest. Numerous theories and approaches that tackle this challenging question have been developed (Kunin and Gaston 1993, Mitchell et al. 2006, Gaston 2011). However, general rules and the driving mechanisms behind sometimes striking differences in species success have not been clearly identified. The mechanisms explaining why some alien species successfully spread and occupy large areas at high abundances in the introduced range might be the same as those explaining high abundance in their native range or that similarly allow some native species to obtain a wide distribution and a high abundance. This possibility has recently received growing attention by ecologists (Thompson et al. 1995, van Kleunen et al. 2010). Thus, commonness and rarity of alien and native species might represent ‘two sides of the same coin’ (Jeschke and Strayer 2008).

Differences in density-dependent enemy attack or resource partitioning have been put forward to explain plant species success (Adler et al. 2007, MacDougall et al. 2009). We specifically focus on two processes in our study;

plant–soil feedback and intraspecific competition, and potential interactions between the two processes. Plant–soil feedback has recently been proposed as a potential mechanism that could explain plant species commonness and rarity (Klironomos 2002, MacDougall et al. 2011, van der Putten et al. 2013). Since plants influence their community of soil biota and these in turn influence plant performance, such host-specific plant–soil feedback may be an important regulator of plant species abundance. In particular, differences among species in accumulation of soil-borne pathogens, or a low susceptibility to or even the absence of such pathogens could lead to the dominance or high abundance of common native and alien species. Especially invasive alien species might have left their soil pathogens behind, allowing them to gain advantage over resident native species. An absence of soil-borne pathogens would be in line with the enemy release hypothesis (ERH) (Keane and Crawley 2002), which so far has mainly been tested with regard to aboveground enemies (Mitchell and Power 2003, Liu and Stiling 2006).

Based on the theoretical framework of species coexistence, self-limitation of species by intraspecific competition should be stronger than limitation by interspecific competition providing a stabilizing mechanism that allows for species coexistence as lined out by (Chesson 2000). However, species

might differ in the magnitude of the difference between self-limitation and limitation by other competitors (Comita et al. 2010). In other words, common species might be less self-limited in terms of intraspecific competition than rare species.

If plant–soil feedback acts in a density-dependent manner, with more negative effects of soil biota when conspecifics grow at high density, then plant–soil feedback and self-limitation might operate simultaneously and may interact to determine plant performance. The relative importance of the two mechanisms in explaining success of alien and native species has yet to be tested. Consequently, testing both factors simultaneously may shed light on whether an interaction between plant–soil feedback and intraspecific competition takes place. For example Petermann et al. (2008) stated that negative plant–soil feedback might hamper the competitive ability of plants (see also Kardol et al. 2007) leading to the possibility that plant–soil-feedback effects become more important than self-limitation by intraspecific competition in regulating plant species abundances.

To test the roles of plant–soil feedback and intraspecific competition in explaining species success, we used a greenhouse experiment with 30 herbaceous plant species, including 13 native and 17 alien species, respectively, that vary in commonness within Germany. We grew the species at different intraspecific frequencies and in soils previously occupied by the same species at differing frequencies, and analysed individual plant performance. We asked the following questions: 1) Are common species less negatively affected by density-dependent plant–soil feedback than rare species, irrespective of origin? 2) Are common species less self-limited by intraspecific competition than rare species, irrespective of origin? 3) Do plant–soil feedbacks and intraspecific competition interact synergistically

and thus increase the negative impact on per capita plant performance?

Material and methods

In order to be able to generalize results beyond a few study species (van Kleunen et al. 2014) we conducted a multi-species greenhouse experiment using 30 different target species from nine different families (Table 1). The chosen target species represented taxonomic groups, which ideally contained at least one common native, one rare native, one common alien and one rare alien plant species. As a proxy for the degree of commonness of each species, we used the number of 130-km² grid cells occupied by the species in Germany (maximum 3000) extracted from the FloraWeb database (FloraWeb, Bundesamt für Naturschutz). We also aimed to choose species that occur in similar habitats, excluding habitat specialists (excluding also woodland and riverine species), and which are not simply rare due to their geographic distribution overlapping only marginally with the borders of Germany. Alien species were defined as being introduced to Germany after 1492. Another three species from families different to the ones of the target species, *Phleum pratense* (2558 grid cells), *Galium album* (2463 grid cells), and *Ranunculus acris* (2985 grid cells), were selected to represent a common background community typical for grasslands in Germany. The experiment consisted of two growing phases. Phase one was used as a soil-conditioning phase to build up a potentially species-specific microbial community. Phase two was then used for testing the effect of increasing intraspecific competition under simultaneous influence of the pre-trained soil microbial community at different frequencies, allowing for an orthogonal study design with respect to phase 1

Table 1. The 30 study species and their respective commonness (measured as number of ~130 km² grid cells occupied in Germany (out of 3000 maximum), (FloraWeb, Bundesamt für Naturschutz)) listed by family and origin. Year of introduction of alien species in Germany as found in Krausch (2003) and year of naturalization (FloraWeb, Bundesamt für Naturschutz) are displayed. The percentage of pots per species (out of 36 pots maximum) that was not affected by mortality in phase 2 is also shown. Species in bold font were represented in all treatment combinations.

Family	Species	Alien			Species	Native	
		Grid cells	Year introduced (naturalized)	% of pots		Grid cells	% of pots
Apiaceae	Anethum graveolens	576	– (–)	94.4%	Daucus carota	2942	88.8%
	Foeniculum vulgare	297	– (–)	86.1%	<i>Oenanthe lachenalii</i>	104	75%
Asteraceae	<i>Artemisia verlotiorum</i>	168	– (1920)	33.3%	Achillea millefolium	2741	80.5%
	Aster novi-belgii	1530	1686 (18th cent.)	88.9%	<i>Gnaphalium luteoalbum</i>	562	44.4%
	Solidago canadensis	2660	1648 (1736)	83.3%	Lactuca saligna	119	88.8%
					Senecio jacobaea	2773	61.1%
Brassicaceae	<i>Cardaria draba</i>	1513	– (1728)	36.1%	<i>Cardamine pratensis</i>	2923	41.6%
	Lepidium heterophyllum	98	– (–)	86.1%	Lepidium graminifolium	86	88.8%
Caryophyllaceae	Cerastium tomentosum	1296	1594 (16th cent.)	80.5%	Silene latifolia	2893	80.5%
	Gypsophila paniculata	122	1757 (–)	86.1%			
Geraniaceae	<i>Geranium macrorrhizum</i>	146	1588 (–)	27.7%	Geranium lucidum	103	80.5%
	Geranium pyrenaicum	2134	17th cent. (1800)	91.6%	Geranium pratense	1844	66.6%
Lamiaceae					<i>Salvia pratensis</i>	1694	41.6%
Plantaginaceae	<i>Linaria dalmatica</i>	21	– (–)	63.8%	<i>Pseudolysimachion spicatum</i>	559	63.8%
	Veronica persica	2863	– (1805)	91.6%	Veronica chamaedrys	2913	80.5%
					<i>Digitalis lutea</i>	127	47.2%
Scrophulariaceae	Scrophularia vernalis	105	18th cent. (1768)	58.3%			
Phrymaceae	<i>Mimulus guttatus</i>	694	1812 (1830)	36.1%			

frequencies (i.e. plant–soil feedback) and phase 2 frequencies (i.e. intraspecific competition).

Experimental setup phase 1

We planted a total of nine plants per pot in a 3×3 square (Fig. 1). For the target species we planted zero, one, three or six plants per pot. The remaining plants planted were the three community species. These were planted using the following frequencies: pots with zero target plants contained six *Phleum pratense*, two *Galium album* and one *Ranunculus acris* plants; pots with one target plant contained five *Phleum pratense*, two *Galium album* and one *Ranunculus acris* plants; pots with three target plants contained four *Phleum pratense*, one *Galium album* and one *Ranunculus acris* plants; pots with six target plants contained two *Phleum pratense*, and either one *Galium album* or one *Ranunculus acris* plants chosen at random. We chose these frequencies in order to maintain a ratio of approximately 1:2 of forbs to grasses among the community species. We replicated each frequency level nine times in the first phase resulting in 36 pots for each target species including the nine ‘community’ pots, which did not contain a target plant. The total number of pots in the first phase consequently was 1080.

Prior to the start of the first growing phase, we collected approximately 250 l of soil from six grassland areas in the vicinity of the Univ. of Konstanz (list of species occurring at the site is given in Supplementary material Appendix 1 Table A1). We systematically took 5–15 samples (10 cm deep) per area along transects with a spacing of approximately 10 m between each sampling point. We pooled the samples and homogenised the soil by sieving through a 5 mm mesh to remove roots, stones and other plant material. This soil was then used as a soil inoculum for each pot.

The species were germinated in a growth chamber (temperature = $15^{\circ}\text{C}/20^{\circ}\text{C}$, 12 h/12 h darkness/light, light level = $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, relative humidity = 90%) on a 1:1 sand:vermiculite substrate. The substrate was not sterilized prior to the germination of seedlings, however, incubated

agar plates that were inoculated with the substrate showed no visible signs of contamination. We planted the species in 4.2-l square pots ($16 \times 16 \times 16.4$ cm) filled with ~ 4 l mixed substrate. The substrate consisted of 250 ml field soil inoculum, mixed with 1:1 vermiculite:sterile sand and 20 g 8–9 month slow release fertiliser pellets (NPK = 18:6:12). Because of the large size of the experiment, we planted the species over a staggered period between 27 August and 7 September 2012. We replaced dead plants within a period of two weeks after initial planting. The pots were blocked into the three greenhouses (one replicate in each) and were randomized within the greenhouses. We set the mean temperature to 21°C during the day and 16°C at night. Lights were switched on for 14 h per day but only if natural light levels fell below $100 \mu\text{mol s}^{-1} \text{m}^{-2}$. After six weeks, we moved a randomly chosen subset of the pots into a fourth greenhouse compartment with the same growing conditions in order to provide sufficient space for continued growth. We watered the plants once every three days to levels that ensured no lack of water availability.

We harvested the aboveground biomass of plants of the first phase after a growing period of eight weeks. We then dried (72 h at 80°C), and weighed the biomass and calculated the per capita aboveground biomass (total target biomass divided by number of target plants in the pot). After the harvest, we sieved and homogenised the substrate in the pots through a 5 mm mesh, removed roots and rhizomes from the soil, and put the substrate back in its original pot. All pots were then returned to their original greenhouse compartments and stored at an air temperature of $5\text{--}8^{\circ}\text{C}$ until they were required for the second phase of the experiment.

Experimental set-up phase 2

We germinated the plants for the second phase in January 2013 under similar growth conditions as the seedlings for phase 1, and planted them again staggered from 28 January to 10 February 2013. We planted the target species always in pots that previously contained the same species or only

Figure 1. Schematic illustration of the experimental setup. Phase 1 represents the soil conditioning phase. Phase 2 represents varying intraspecific competition levels in preconditioned soil of phase 1. (Replicated three times for each species).

community plants in the following manner: target species in frequencies of one, three and six out of nine were planted in pots previously containing zero, one, three, or six conspecific plants (i.e. in phase 1). This resulted in three pots per target species for each combination of planting frequency in the second phase and planting frequency of the first phase (Fig. 1). Thus, we achieved a fully orthogonal design. We filled the remaining positions in the pots again with community species in the same way as in phase 1. Because of variation in substrate volumes due to loss from pots during sieving, we placed 1 l of 1:1 vermiculite and sterile sand mixture at the bottom of each pot and refilled the remainder with the substrate of phase 1.

Since *Oenanthe lachenalii* germinated in insufficient numbers, we only planted this species at phase 2 frequencies of one and six out of nine plants in pots with soil of one and six plants in phase 1. Thus we finally had a set of 29 species with 36 pots each, representing three replicates of all respective combinations of phase 1 and phase 2, and one species with twelve pots, making a total of 1056 pots in phase 2. We kept the plants under the same greenhouse conditions as in phase 1, and applied the same watering regime. To reduce mortality after planting, we delayed additional lighting until 25 February. We then increased lighting from five to eight and finally to 14 h in a two-day stepwise interval. We replaced dead plants within a period of two weeks from initial planting.

After a growth period of 10 weeks, we harvested the plants, again in a staggered manner following their planting sequence (8–19 April 2013). We dried and weighed the aboveground biomass of all plants following the same procedure as in phase 1. We counted and recorded the number of surviving plants one week before the harvest.

Analyses

Due to high mortality of target plants in phase 2, we split the statistical analysis into an analysis of survival, and, for the subset of plants that survived, an analysis of aboveground biomass. We used the proportional data on survival of target plants per pot to analyse probability of survival per target. Survival was analysed using a generalised linear mixed model with binomial error distribution in the lme4 package (Bates et al. 2014) in the software R ver. 3.1.1. We used the optimizer 'bobyqa' and set the maximum number of iterations to 100 000 to achieve model convergence. Species nested in family and greenhouse compartment were included as random effects. Initial phase 1 planting frequency (0, 1, 3, 6 out of 9 plants per pot, i.e. plant–soil feedback effect), initial phase 2 planting frequency (1, 3, 6 out of 9 plants per pot, i.e. intraspecific competition), commonness as a continuous variable (number of grid cells occupied by the species in Germany; centred on the mean and scaled by the standard deviation), origin and all respective interactions were included as fixed effects in a four-way interaction model. We also added total biomass per pot in phase 1 as a covariate (centred to the mean and scaled by the standard deviation). We used stepwise backward model selection via likelihood-ratio tests to obtain a minimum model and to test for significance of interactions. We performed multiple pairwise comparisons to test for differences among levels of

planting frequency in phase 2 using the 'multcomp' package (Hothorn et al. 2008).

For the biomass analysis, we only used the subset of pots in which all target plants survived, which resulted in a data set of 719 pots (out of 1056 pots). All 30 species were represented in this subset. We used linear mixed effect models in the lme4 package to analyse per capita aboveground biomass. Per capita aboveground biomass (in grams) was natural log-transformed prior to analysis to achieve normality of the residuals. The fixed and random effects were the same as in the model used for the analysis of survival. Similarly we used stepwise backward model selection via likelihood-ratio tests to assess significance of the model terms. The 'multcomp' package was used to test for differences among levels of phase 1 and phase 2 planting frequencies. Furthermore, to ensure that our results were not affected by species that were absent in some treatment combinations, we analysed a subset of the data excluding those species (Table 1). The analysis was performed in the same way as for the complete data set. To assess whether relationships between per capita biomass and commonness were non-linear, we also performed the same analysis with a discretized commonness variable (rare; intermediate; common – based on clear groupings evident in the Supplementary material Appendix 1 Fig. A4). However, per capita performance was not significantly explained by this discrete measure of commonness and hence, the minimum model remained the same (data not shown).

Results

Survival response

Analysis of survival showed that none of the model terms was significant (Supplementary material Appendix 1 Table A2). Increasing phase 1 planting frequency resulted in slightly lower survival for all plant species, however, this effect was only marginally significant and accounted only for a 3% lower survival probability between the different planting frequencies (Fig. 2).

Biomass responses

The minimum model for per capita biomass retained phase 2 planting frequency as a significant main effect and a significant interaction between species origin and phase 1 planting frequency (Table 2, Supplementary material Appendix 1 Table A3). Per capita biomass of the target species was reduced by increasing intraspecific plant frequency in phase 2 (Fig. 3). Multiple comparisons between phase 2 planting frequencies revealed that pots with six target plants in phase 2 showed a significant reduction in per capita biomass compared to pots with one target plant in phase 2 (mean difference = -0.209 , 95% CI = -0.376 ; -0.041 , $p = 0.004$, Fig. 3). Reductions in per capita biomass of pots with six target plants compared to pots with three target plants in phase 2 (mean difference = -0.150 , 95% CI = -0.324 ; 0.017 , $p = 0.146$, Fig. 3) and of pots with three targets compared to pots with one target in phase 2 were not significant (mean difference = -0.058 , 95% CI = -0.214 ; 0.097 , $p = 0.956$, Fig. 3).

Figure 2. Probability of survival of target plants ($\pm$ SE) of 30 species grown in soils of target plant frequencies of 0, 1, 3 and 6 out of 9 plants in phase 1 (averaged across phase 2 frequencies). Black dots display means across 30 species. Grey dots indicate means for each of the 30 species.

Multiple comparisons between levels of phase 1 planting frequencies showed a marginally non-significant reduction in per capita biomass of alien species when grown on phase 1 soils containing six target plants compared to phase 1 soils containing no target plants (mean difference = -0.249 , 95% CI = -0.518 ; 0.01 , $p = 0.092$, Fig. 4a). Notably, native species showed no significant reduction of per capita biomass when grown in soils previously occupied by six conspecifics compared to pots with no conspecifics in phase 1 (mean difference = -0.028 , 95% CI = -0.304 ; 0.247 , $p = 1.000$, Fig. 4b). Comparisons between the control and one, three or six plants in phase 1 were not significant for either aliens or natives (Supplementary material Appendix 1

Figure 3. Least-square mean per capita biomass ($\pm$ SE) of 30 species grown at target plant frequencies of 1, 3 and 6 out of 9 plants (averaged across phase 1 frequencies). Black dots indicate means across the 30 target species. Grey dots display means for each of the 30 target species. Letters indicate significant differences between planting frequencies. (y-axis is displayed on natural log scale).

Fig. A5). The covariate of total biomass per pot in phase 1 had no significant effect on per capita biomass in phase 2 (Table 2). Our analysis showed that the relationship between species commonness and per capita plant performance did not significantly differ according to phase 1 planting frequency (Table 2; Supplementary material Appendix 1 Fig. A4), suggesting that density-dependent plant–soil feedback effects are not related to species commonness. The results for the analysis of the species that were represented in all treatments led to the same minimum model as for when all 30 species were included (Supplementary material Appendix 1 Table A6), indicating that our findings were

Table 2. Results for each step of the stepwise backward model selection via likelihood-ratio tests for the linear mixed effects model of per capita aboveground biomass. The main effects 'Origin' and 'Phase 1 frequency' were not tested, as the interaction of both terms was significant and therefore was retained in the minimum model.

Term	χ^2	DF	p
Four-way-interaction			
Phase1 frequency $\times$ Phase2 frequency $\times$ Origin $\times$ Commonness	1.006	6	0.985
Three-way-interactions			
Phase1 frequency $\times$ Phase2 frequency $\times$ Origin	2.350	6	0.884
Phase2 frequency $\times$ Origin $\times$ Commonness	1.169	2	0.557
Phase2 frequency $\times$ Phase2 frequency $\times$ Commonness	5.439	6	0.488
Phase1 frequency $\times$ Origin $\times$ Commonness	6.622	3	0.084
Two-way-interactions			
Origin $\times$ Commonness	0.000	1	0.993
Phase1 frequency $\times$ Phase2 frequency	1.263	6	0.973
Phase2 frequency $\times$ Origin	0.589	2	0.744
Phase2 frequency $\times$ Commonness	0.555	2	0.757
Phase1 frequency $\times$ Commonness	2.121	3	0.547
Phase1 frequency $\times$ Origin	9.309	3	0.025
Main effects			
Commonness	0.029	1	0.864
Total biomass Phase1	0.947	1	0.330
Phase2 frequency	11.862	1	<0.001
Phase1 frequency	–	–	–
Origin	–	–	–

Figure 4. Panel (a) displays least-square mean per capita biomass ($\pm$ SE) of 17 alien species grown in soil previously occupied by 0, 1, 3 or 6 target plants of the same species in phase 1 (averaged across target plant frequencies in phase 2). Black dots display means across the 17 target species. Grey dots indicate the respective means for each of the 17 target species. Panel (b) displays least-square mean per capita biomass ($\pm$ SE) of 13 native species grown in soil previously occupied by 0, 1, 3 or 6 target plants of the same species in phase 1 (averaged across target plant frequencies in phase 2). Filled white dots display means across the 13 target species. Grey dots indicate the respective means for each of the 13 target species. (y-axis is displayed on natural log scale in both panels).

not driven by underrepresented species in our data set. To the contrary, this analysis revealed a more significant effect of phase 1 planting frequencies for alien species, and non-significant effects for native species (Supplementary material Appendix 1 Fig. A7).

Discussion

In this study, we tested if differences in intraspecific competition and plant–soil feedback could explain commonness of alien and native species. We found that per capita plant performance declined with increasing intraspecific plant frequency, regardless of origin and commonness, which suggests that alien and native, and rare and common species are affected similarly by intraspecific competition. Negative plant–soil feedback effects were relatively weak, and alien but not native species showed a reduction of performance when grown in soils previously occupied by the same species at high frequencies. Furthermore, we did not find evidence for interactions between density-dependent soil effects and intraspecific competition.

In contrast to expectations, our study shows that growing plants in soil previously occupied by the same species at increasing frequencies did not lead to a stronger reduction of performance of rare species compared to common species. However, alien plant species showed reduced per capita biomass when grown in soil conditioned by the highest conspecific plant frequency compared to control community soil, whereas native species were generally not affected by phase-1 planting frequencies. In a previous study Klironomos (2002) found evidence for consistently positive plant–soil feedback for common alien species compared to a consistently negative feedback of rare native species. In a comparable experiment, Reinhart (2012) found

a prevalence of negative plant–soil feedbacks for the focal species in semiarid grasslands, but did not find a clear pattern explaining species abundances with regard to effects of soil biota. Our findings similarly point towards a limited role of plant–soil feedback in explaining species commonness, and plant–soil feedback effects may rather be largely context dependent (Bezemer et al. 2006, Reinhart 2012). An explanation for our findings, specifically the absence of a significant and concordant pattern in reduction of plant performance by plant–soil interactions, likely lies in the experimental approach that we used. We did not test plant performance in pre-trained soils in comparison to sterilized soils, which is an often-used method in plant–soil feedback experiments and which leads to stronger feedback effects (van der Putten and Peters 1997, van der Putten et al. 2007, MacDougall et al. 2011, but see Brinkman et al. 2010). Instead we used a set of common grassland species as a neutral community, creating a much more realistic soil-microbiome control. Consequently, the ‘neutral’ community could have accumulated already a high density of pathogens so that native species experienced a ‘ceiling-effect’, such that an increase in frequency of a target species does not lead to a substantial further reduction of biomass due to the presence of pathogens. Similarly, Maron et al. (2014) found that negative soil effects for species grown in soil with their native soil biota seem to develop largely independently of study species presence. This would indicate that generalists among soil pathogens might play an important role. We also found a marginally non-significant trend that phase 1 planting frequencies cause mortality in phase 2, albeit with a very small effect size that cannot fully explain greater mortality rate observed in the second phase of the experiment compared to the first. Mortality also did not differ according to species origin or commonness. This, combined with the overall greater mortality in the second

phase may further indicate the accumulation of generalist pathogens within the whole experiment.

The limited role of plant–soil feedback that we find in our study does not mean that for a particular species in a particular context, plant–soil-feedback effects are not important. There are a number of studies that find negative feedback effects on plant performance (Kulmatiski et al. 2008) that are likely driven by species-specific pathogens (Bezemer et al. 2006, Kardol et al. 2007, Petermann et al. 2008, Reinhart 2012). However, the complexity of plant–soil interactions and their dependence on multiple factors (i.e. soil type, soil-legacy history, presence of competitors) often results in large variation among species and study systems (Kulmatiski et al. 2008), thus preventing clear, general patterns from being observed among species.

An alternative explanation for our results may be that pot limitation (Poorter et al. 2012) has magnified the effect of competition relative to plant–soil-feedback effects, so that effects of the soil biota were overridden by competition for root space. However, growing plants in larger pots would have reduced the potential for plants to compete, and plants may also experience intense belowground competition in natural communities (Casper and Jackson 1997). Thus, we consider the conditions under which competition and plant–soil feedback can be detected in our experiment to be reasonably realistic.

Nevertheless, alien species in our study showed a reduction in performance when grown in soil previously occupied by conspecifics at high frequencies. These findings may be explained by the nature of the interactions between alien species and their new soil biota. Alien species might on the one hand not be affected by some of the soil-borne pathogens of their new range and might even have left some of their co-evolved enemies of their native range behind. On the other hand they might be naïve towards some of their soil-borne enemies in the new range resulting in accordingly strong detrimental effects (Parker et al. 2006, Parker and Gilbert 2007, Verhoeven et al. 2009). Verhoeven et al. (2009) argue that ‘novelty’ can be claimed for both sides of the interaction, the plant as well as the pathogen. Consequently there can be a mismatch that leads to enemy release, but also a mismatch that leads to biotic resistance, which may explain the unexpected divergent plant–soil feedback effects on alien and native species in our study.

However, since the selected species in our experiment have been present in Germany for at least two centuries, alien species and their respective pathogens might have already adapted, resulting in the reduced performance of the alien species that we observe in our experiment. For example, Diez et al. (2010) found that the negative plant–soil-feedback effect of alien species in New Zealand increased with increasing residence time. In contrast, Speek et al. (2015) did not find such a pattern among alien species in a multi-species study in the Netherlands. These contrasting findings reflect the complexity of plant–pathogen interactions, such that changes in the effects of interactions over time are unlikely to be consistent.

We found that an increase in current conspecific frequency led to a strong reduction in per capita biomass. This finding is in line with the predictions of coexistence theory, namely that intraspecific competition should affect species

performance more negatively than interspecific competition (Chesson 2000). Despite its clear theoretical underpinning, empirical proof of this concept has been equivocal (Goldberg and Barton 1992, Gurevitch et al. 1992, but see Levin and HilleRisLambers 2009). Our study supports the idea of stronger self-limitation, but we did not find evidence for any differences in density-dependent intraspecific competition between alien and native species, or in relation to commonness. However, it is important to note that interspecific effects could have an influence on the performance of the focal species in species mixtures, as other studies show (Bezemer et al. 2006, Kardol et al. 2007). Kardol et al. (2007) for example reported that a selection of early successional plant species showed differential responses towards heterospecific soil inocula, ranging from positive to negative. In our case this specifically means that interspecific effects of the community species, e.g. *Phleum pratense*, may influence our results besides intraspecific effects of the targets. Due to the design of our study, which aimed to entail a realistic grassland background community, we cannot fully assess this role of interspecific effects. Nonetheless, Blank (2010) also reports on stronger effects of intraspecific competition compared to interspecific competition for a set of native and alien species, but highlights that alien species might gain advantage over natives by better capitalizing on nutrients in highly fertile soils (see also Dawson et al. 2012). This may also explain the higher per capita performance of aliens compared to natives in our study, since plants were grown with addition of slow-release fertilizer and should therefore not have been limited in nutrient supply. Furthermore, Duralia and Reader (1993) tested if abundance of three prairie grasses is explained by competitive ability in a replacement series experiment, and found only weak evidence for a relationship between commonness and competitive ability. Despite the theoretical importance of density-dependent self-limitation in regulating species abundance and coexistence, we found no evidence that it covaries with commonness of either alien or native species.

Although plant–soil feedback has been proposed as a mechanism that could drive species success (Klironomos 2002, van der Putten et al. 2013), we found no evidence that commonness is explained by differences in density-dependent plant–soil feedback. A meta-analysis on the effects of plant–soil feedback by Kulmatiski et al. (2008) showed that there is a general signal for a reduction in plant performance due to plant–soil feedback. However, Kulmatiski et al. (2008) as well as van de Voorde et al. (2012) and Brinkmann et al. (2010) raise the point that varying experimental protocols and a bias towards simplified greenhouse studies, each with a limited but different set of target species and life forms, may account for a considerable amount of variation in study outcomes. Another aspect in studies on plant–soil feedback is that only net outcomes of plant–soil interactions are measured (e.g. biomass), however, this overall performance results from potentially multiple antagonistic (e.g. pathogens) and mutualistic (e.g. mycorrhiza) interactions and physical properties of the soil (Reinhart and Callaway 2006, van der Putten et al. 2013). Disentangling the relative contributions of antagonistic and mutualistic soil organisms under controlled conditions will provide important insights into the underlying mechanisms. Moreover, transferring

these insights to manipulative experiments under realistic field conditions with a focus on population dynamics covering the whole life cycle of a study organism (Maron et al. 2010, Flory and Clay 2013) may lead the way to a better understanding of plant–soil interactions.

A specific aspect that arises by studying the role of plant–soil interactions in driving species commonness is the two-way nature of species commonness in this relationship. On the one hand, commonness may be the outcome or in part be influenced by plant–soil interactions, while on the other hand the commonness of a species is also a factor that determines the chances for pathogens and other soil biota to encounter (and potentially adapt to) their host or vice versa. Hence, commonness is a dependent and independent variable at the same time. Furthermore the chances of encountering a pathogen (or a host) also depend on dispersal abilities of both parts of the pathogen–plant interaction, which adds spatial and temporal dimensions to plant–soil interactions (Adler and Muller-Landau 2005). Considering these spatial and temporal dimensions may help to improve our understanding of whether plant–soil feedbacks drive the patterns of commonness we observe in both alien and native plant species.

Conclusions

Our study suggests that plant–soil feedback plays little role in determining the success of common native and alien species compared to rare natives and aliens, at least for a number of species from several families in central Europe. Furthermore, species responses to increasing intraspecific frequency are not linked to commonness and origin, suggesting that intraspecific competitive ability does not in general drive alien and native plant species commonness or rarity. Contrary to the notion of enemy release, we also found that alien species suffer more from plant–soil feedback than native species. Rather than being released from soil-borne pathogens, alien species may suffer more from novel belowground interactions; alternatively, adaptation of pathogens to the alien species may have already taken place, resulting in negative feedback. Thus, enemy release needs to be interpreted as a potentially dynamic process since a static interpretation may not capture the evolutionary aspects in the plant–pathogen interaction. While we found no clear role for plant–soil feedback in explaining current commonness of alien and native species, future studies should consider whether plant–soil feedback is linked to dynamic changes in species commonness over time.

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