

Competitive effects of plant invaders on and their responses to native species assemblages change over time

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Abstract

Alien plant invaders are often considered to be more competitive than natives, and species-rich plant communities are often considered to be more resistant to invaders than species-poor communities. However, the competitive interactions between invaders and assemblages of different species richness are unlikely to be static over time (e.g. during a growth season). To test this, we grew five alien and five native species as invaders in a total of 21 artificial assemblages of one, two or four native competitor species. To test for temporal changes in the reciprocal effects of invaders and the competitor assemblages on each other, and how these depend on the species richness of the assemblages, we harvested plants at three growth stages (weeks 4, 8 and 12). We found that the invaders and competitor assemblages had negative effects on each other. Aboveground biomass of invaders was reduced by the presence of a competitor assemblage, irrespective of its species richness, and this difference gradually increased over time. Alien invaders accumulated more aboveground biomass than the native invaders, but only after 12 weeks of growth. Meanwhile, the invaders also negatively affected the biomass of the competitor assemblages. For multi-species assemblages, the increase in the negative effect of the presence of the invader occurred mainly between weeks 4 and 8, whereas it happened mainly between weeks 8 and 12 for the one-species assemblages. Our results suggest that although alien invaders are more competitive than native invaders, the competitive effects of the invaders on and their responses to native competitor assemblages changed over time, irrespective of the origin of the invaders.

Keywords

Coexistence, community assembly, diversity-invasibility, exotic, native invader, plant invasion, resistance, species richness

Introduction

Biological invasions, as one of the major components of global change (Hobbs and Mooney 2005; Vilà et al. 2011; Essl et al. 2020), have become a matter of great concern in recent decades. More and more alien species have established populations outside their native ranges (Strayer 2010; Dawson et al. 2017), resulting in biotic homogenization (Yang et al. 2021). The accumulation of such naturalized alien species is still increasing globally and forecasted to continue increasing (Seebens et al. 2017; Seebens et al. 2021). Some naturalized alien plant species have become widespread and dominant, and are considered invasive as they seriously threaten native biodiversity and ecosystem functioning (Richardson et al. 2000; Vilà et al. 2011). The factors allowing alien species to establish, their impacts on the native species they compete with, and what allows communities to resist invaders have therefore become major research questions in ecology.

Although invasion biology focuses on alien species, the process of invasion is not restricted to alien species, as native species can also invade communities (Valéry et al. 2008, 2009; Carey et al. 2012). Actually, invasion (or colonization) by native species is an inherent part of community assembly and metacommunity dynamics, and invading native species can also impact the other species (Holyoak et al. 2005). However, as alien and native species differ in their eco-evolutionary experience with the other community members, their invasion dynamics might differ (Saul et al. 2013). Therefore, a major question is whether the establishment and impacts of alien species differ from those of native species.

The relationships between invaders and the species they interact with has been of high interest to biologists for a long time (Darwin 1859; Elton 1958; Fridley et al. 2007; Howeth 2017; Li et al. 2021). For example, Elton (1958) proposed that more diverse communities should be more resistant to invaders. This now classic diversity-invasibility hypothesis is based on the idea that more niches are already occupied in species-rich communities than in species-poor ones. This reduces the available resources in species-rich communities and thereby creates a more competitive environment. Consequently, it will be more difficult for invaders to establish when they have to compete with multiple species (Knops et al. 1999; Levine et al. 2004). While theoretical studies generally support the diversity-invasibility hypothesis, empirical studies have provided inconsistent results (Levine and D'Antonio 1999). In particular, studies at large spatial scales frequently find positive instead of negative relationships (Levine 2000; Shea and Chesson 2002). However, even in studies at small spatial scales, the diversity-invasibility relationship is not always negative, as it can depend on the environmental conditions (Naeem et al. 2000; Zeiter and Stampfli 2012) and community productivity (Davies et al. 2007). In more diverse communities, the growth of plants can be limited by resource availability (e.g. light and nutrients), and this may also affect the possibility of invasion (Mata et al. 2013; Kelso et al. 2020).

While invaders may impact the native community, and the latter might affect the establishment success of the invader, these competitive effects and responses are not static over time (Dostál et al. 2013; Yelenik and D'Antonio 2013). Some studies have shown that the negative effects of invaders on their competitors are more pronounced

at the early stages, that is, the superior competitiveness of invaders is more likely to provide advantages in the early stages of growth (Goldberg 1990; Golivets and Wallin 2018). Meanwhile, the change in reciprocal effects may also be related to the species richness of the community (i.e. the competitive environment; Clark and Johnston 2011; Clark et al. 2013). Studies have shown that species-richness effects can become important during later stages of establishment (Roscher et al. 2013; Nitschke et al. 2010). After a period of growth, a species-rich community can establish a more stable community structure (Cavieres and Badano 2009), so that invaders are more strongly suppressed than when competing in a species-poor community. However, it could also be that the often high competitive ability of alien invaders may be sufficient to overcome the competitive pressures (Ridenour et al. 2008; Golivets and Wallin 2018). In that case, the biomass of the competitors could decrease without obvious suppression of the invaders. Therefore, the competitive effects and responses of invaders need to be assessed at different time points during the growth period.

To test how alien and native plant invaders and native competitor assemblages of different species richness affect each other over time, we conducted a mesocosm experiment using five alien and five native invader species and 21 competitor assemblages of three species-richness levels (1, 2 or 4 native species). To test if competitive effects and responses of invaders changed over time, we had three harvesting times (4, 8 and 12 weeks after the start of the experiment). We addressed the following specific questions: (1) How does the presence of a competitor assemblage (i.e. a community) affect growth of the invader, and does it depend on the origin of the invader and species richness of the competitor assemblage? (2) How do invaders affect the productivity of the plants they compete with, and does it depend on the origin of the invader and species richness of the competitor assemblage? (3) Do the competitive effects and responses of the invader change over time?

Materials and methods

Study species

To test the effects of alien and native invaders on competitor assemblages of different diversities, we selected five pairs of taxonomically related species to be used as invaders. Each pair consisted of one species that is a naturalized alien and one species that is native to Germany. The five pairs of species are from four families, as we chose two pairs of Poaceae so that the numbers of grasses and forbs were relatively balanced (Suppl. material 1: Table S1). To test the effects of competitor assemblages of different diversities on the invaders, we chose a native species pool of seven species (five grasses and two forbs) that frequently coexist in German grasslands (Suppl. material 1: Table S2A). The alien-native classification of all species used in the experiment was based on the FloraWeb database (www.floraweb.de). Seeds of six species were from the Botanical Garden of the University of Konstanz, and seeds of the other 11 species were ordered from Rieger-Hofmann GmbH (Suppl. material 1: Tables S1, S2A).

Experimental set up

From 10 to 17 February 2020, we sowed the invader and competitor species in trays (18 cm × 14 cm × 5 cm) filled with potting soil (Einheitserde, Gebr. Patzer GmbH & Co. KG, Sinnatal, Germany). This was done on different dates (Suppl. material 1: Tables S1, S2A), based on prior knowledge about the time required for germination, so that the seedlings would be in a similar growth stage at transplanting. Seedling cultivation was done in a greenhouse of the Botanical Garden of the University of Konstanz (47°41'33"N, 9°10'35"E) with a temperature maintained between 18 °C and 25 °C.

For the experiment, we filled 3L pots ($\Phi = 16$ cm, H = 12 cm) with a soil substrate consisting of a mixture of field soil, sand and vermiculite (v:v:v = 1:1.5:1.5). The field soil, which served as inoculum of a natural soil microbiome, was dug up from a native grassland patch in the Botanical Garden of the University of Konstanz and was sieved using a 1-cm metal mesh to remove large plant fragments and pebbles. On 3 and 4 March 2020, we transplanted the seedlings into the pots. We used the pool of seven native species to create a total of 21 competitor assemblages that had different species-richness levels (Suppl. material 1: Table S2B): one, two and four species. For each of the three species-richness levels, we had seven different assemblages. We first transplanted into each pot four individuals of the competitor assemblage. Specifically, we planted four seedlings of the same species in the one-species pots, two seedlings from each of the two species in the two-species pots, and one seedling from each of the four species in the four-species pots. After planting the competitors, we transplanted one of the ten invaders in the center of each pot (Fig. 1). To assess the effect of the presence of a competitor assemblage on the invader, we also had pots in which we only planted a single invader individual (i.e. without competitors; zero-species assemblage). Furthermore, to assess the effect of the invader on the competitors, we also had pots for each competitor assemblage in which we only planted the four individuals of the competitors (i.e. without an invader). Seedlings that died within two weeks after transplanting were replaced. For the two control treatments (i.e. only with invader, only with competitors), we replicated each invader species or competitor assemblage three times, resulting in 909 pots in total ([21 assemblages × 10 invaders + 21 assemblages × 3 replicates + 10 invaders × 3 replicates] × 3 harvest times). All pots were placed on plastic dishes ($\Phi = 20$ cm) and randomly allocated to positions in three greenhouse compartments (24 °C/18 °C day/night temperature, 16h/8h day/night light). We watered the plants every 1–2 days, and fertilized them six times (1, 3, 5, 7, 9 and 11 weeks after the start of the experiment) with a water-soluble fertilizer (1‰ m/v, Universol Blue).

Measurements

At the start of the experiment, we counted on each invader seedling the number of leaves, and measured the length and width of the largest leaf. From these measurements, we calculated the initial leaf area as number of leaves × length of largest leaf × width

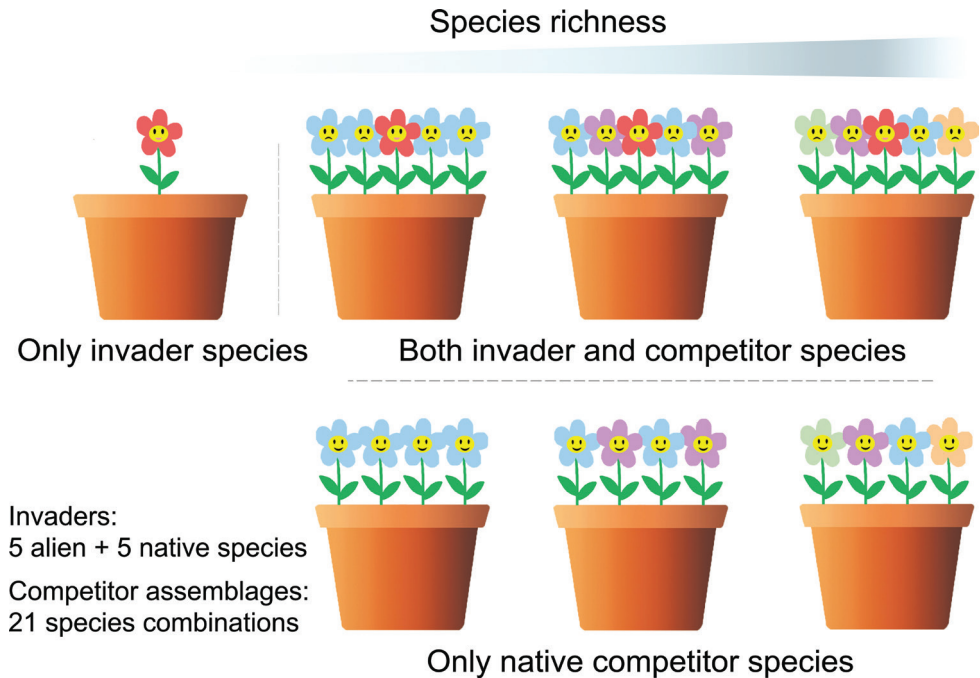


Figure 1. Overview of the experimental design. For the treatments with both an invader and competitors, five seedlings (one invader and four competitor seedlings) were planted into each pot. There was one control treatment with only plants of the native competitor assemblage (four seedlings per pot). The competitor assemblages were created with three species-richness levels: one, two and four native species. Another control treatment had only the invader species (without the competitors; one seedling per pot). All treatment combinations were replicated three times, and one replicate was harvested at each of the three time points (weeks 4, 8 and 12).

of largest leaf. In order to test the reciprocal effects of invaders and competitors over time, we selected three time points for harvesting: week 4, week 8 and week 12. These time points were chosen to represent the early, mid and late growth stages of the species during a season. On 15 April, 13 May and 10 June 2020, we harvested one third of the plants in each treatment combination. After each harvest, the remaining pots were re-randomized to reduce potential effects of environmental heterogeneity in the greenhouse compartments. We separately harvested the aboveground biomass of each individual plant. The belowground biomass, we only harvested at week 4, because it was impossible to separate the roots of the different species at weeks 8 and 12. The biomass of each individual was dried to constant weight at 70 °C, and then weighed with an accuracy of 0.001g. To compare differences in biomass between treatments, we calculated the percentage of change in biomass, using the raw data, as $(\text{Mean of biomass in the focal treatment} - \text{Mean of biomass in reference treatment}) / \text{Mean of biomass in reference treatment}$.

Statistical analysis

To test the effects of origin of the invader and species richness of the competitor assemblage on invader performance over time, we fitted a linear mixed model with the *lme* function in the R package ‘nlme’ (Pinheiro et al. 2019). This was done for the subset of pots with invaders, and aboveground biomass of the invaders was the main response variable. In addition, to test whether the dominance of the invader relative to the competitors depended on origin of the invader, species richness of the competitor assemblage and time, we also analyzed the proportional invader biomass (i.e. aboveground biomass of the invader / [aboveground biomass of the invader + aboveground biomass of the competitors]) as the response variable. The latter was done for the subset of pots with both invader and competitor plants. Invader origin (alien or native), species richness of the competitor assemblage (0, 1, 2 and 4 species or 1, 2 and 4 species when pots without competitors were excluded), harvesting time (weeks 4, 8 and 12) and their interactions were included as fixed effects in the models. For species richness of the competitor assemblage, we also ran orthogonal hierarchical contrasts to test the effect of the presence of the competitors (i.e. without competitors vs. the average of one-, two- and four-species competitor assemblages; this contrast was not included for proportional aboveground biomass), the effect of having multiple species as competitors (i.e. one-species assemblages vs. the average of two- and four-species assemblages), and the effect of having more species in the multi-species competitor assemblages (i.e. two-species assemblages vs. four-species assemblages). To account for variation in initial size of the invaders, we included the initial leaf area of the invaders as a covariate.

To test the effects of the presence of the invader and its origin, and of the species richness of the competitor assemblages on performance of the assemblages over time, we fitted again a linear mixed model. This was done for the subset of pots with competitors, and aboveground biomass of the competitor assemblage and total aboveground biomass per pot (i.e. cumulative biomass of the invader and competitors) were used as response variables. Invader treatment (without invader, with alien invader or with native invader), species richness of the competitor assemblage (1, 2 and 4 species), harvesting time (weeks 4, 8 and 12) and their interactions were included as fixed effects. For the invader treatment, we generated two orthogonal contrasts: without vs. with invader, and alien vs. native invader. We also generated two orthogonal contrasts for species richness of the competitor assemblage: one-species assemblages vs. the average of two- and four-species assemblages, and two-species assemblages vs. four-species assemblages.

To test whether the belowground parts of plants show a similar response as the aboveground parts, we also fitted two linear mixed effects models to analyze the belowground biomass of the invaders and competitor assemblages, respectively, at the first harvest time (i.e. week 4). For the invaders, this was done for the subset of pots with invaders in week 4, and belowground biomass and root weight ratio of the invaders were the response variables. Invader origin (alien or native), species richness of the competitor assemblages (included as three orthogonal contrasts: without competitors vs. the average of one-, two- and four-species assemblages, one-species assemblages vs. the average of two- and four-species assemblages, and two-species assemblages vs.

four-species assemblages) and their interactions were included as fixed effects. We also included initial leaf area of the invaders as a covariate in the model. For the competitor assemblages, belowground biomass and root weight ratio (i.e. belowground biomass allocation) for the subset of pots with competitors in week 4 were used as response variables. Invader treatment (two orthogonal contrasts: without vs. with invader, and alien vs. native invader), species richness of the competitor assemblage (included as two orthogonal contrasts: one-species assemblages vs. the average of two- and four-species assemblages, and two-species assemblages vs. four species assemblages) and their interactions were included as fixed effects.

In all models, to account for phylogenetic non-independence of species, and non-independence of plants belonging to the same species, we included species identity and family of the invader plants as random effects. To account for non-independence of measurements in pots with the same competitor assemblage, we also included assemblage identity as a random effect. To meet the assumption of normality, aboveground biomasses of invaders and competitor assemblages were cubic-root-transformed. To improve homoscedasticity of residuals of the models, we allowed the variance to vary among invader species and/or the assemblage identity (Suppl. material 1: Table S6) by using the *varComb* and/or *varIdent* functions of 'nlme' package. For all models, we used log-likelihood ratios, which are approximately χ^2 distributed, to assess the significances of the fixed effects by comparing models with and without the effect of interest (Zuur et al. 2009). All analyses were conducted with R 3.6.2 (R Core Team 2019). An effect was considered significant if $P < 0.05$.

Results

Effects of competitor presence and species richness on invaders at different times

Across all competitor-assemblage treatments, the aboveground biomass of alien and native invaders did not differ significantly after four and eight weeks of growth (Table 1, Fig. 2A). However, after 12 weeks of growth, the alien invaders had produced significantly more aboveground biomass than the native ones (+16.3%; Table 1, Fig. 2A). Compared to the treatment without competitors (i.e. 0-species assemblage), aboveground biomass of invaders was significantly lower in the presence of competitors, and this difference gradually increased over time (-35.5% in week 4, -53.1% in week 8, and -55.5% in week 12; Table 1, Fig. 2B). Belowground biomass of the invader, which was only measured at week 4, was also significantly reduced by the presence of competitors (-45.3%), while the root weight ratio was not significantly affected (Suppl. material 1: Table S4, Fig. S1).

Among the pots with competitors, aboveground biomass of the invader was not significantly affected by the species richness of the competitor assemblage (one-species vs. multi-species assemblages, and two-species vs. four-species assemblages; Table 1, Fig. 2B). The proportional biomass of the invaders relative to the competitors was not significantly affected by the origin of the invader, species richness of the competitor assemblage and time (Fig. 3C, Suppl. material 1: Table S3).

Table 1. Effects of invader origins (alien or native), presence and species richness of the native competitor assemblage (0, 1, 2 or 4 species), harvesting time (week 4, week 8 or week 12) and their interactions on aboveground biomass of invader plants. For the factor Species richness, we created three orthogonal contrasts ($R_{\text{Without/With}}$: without competitors vs. average of one-, two- and four species assemblages, $R_{\text{One-/Multi-species}}$: one-species assemblages vs. average of two- and four-species assemblages, $R_{\text{Two-/Four-species}}$: two-species assemblages vs. four-species assemblages).

	df	Aboveground biomass	
		χ^2	P
Fixed effects			
Initial leaf area of invader	1	15.542	<0.001
Origin of invader (O)	1	0.339	0.560
Species richness of assemblage (R)	3	18.319	<0.001
$R_{\text{Without/With}}$	1	17.643	<0.001
$R_{\text{One-/Multi-species}}$	1	0.750	0.387
$R_{\text{Two-/Four-species}}$	1	0.868	0.352
Time of harvest (T)	2	479.275	<0.001
O × R	3	0.950	0.813
O × $R_{\text{Without/With}}$	1	0.179	0.672
O × $R_{\text{One-/Multi-species}}$	1	0.780	0.377
O × $R_{\text{Two-/Four-species}}$	1	0.006	0.936
O × T	2	8.655	0.013
R × T	6	83.415	<0.001
$R_{\text{Without/With}} \times T$	2	79.256	<0.001
$R_{\text{One-/Multi-species}} \times T$	2	4.435	0.109
$R_{\text{Two-/Four-species}} \times T$	2	0.614	0.736
O × R × T	6	1.921	0.927
O × $R_{\text{Without/With}} \times T$	2	0.492	0.782
O × $R_{\text{One-/Multi-species}} \times T$	2	1.034	0.596
O × $R_{\text{Two-/Four-species}} \times T$	2	0.380	0.827
Random effects		SD	
Invader family		0.206	
Invader species †		0.314	
Assemblage identity		0.068	
Residual		0.166	

Values are in bold when $P < 0.05$. † Shown is the standard deviation (SD) of *Lepidium virginicum*. The SDs of all invader species are shown in Suppl. material 1: Table S6.

Effects of invaders on competitors and overall productivity at different times

After four weeks of growth, the aboveground biomass of the competitor assemblage, irrespective of its species richness, was not affected by the presence of the invader. The same was true for belowground biomass and the root weight ratio of the competitor assemblages (Suppl. material 1: Table S5, Fig. S2). After 8 and 12 weeks of growth, however, the presence of the invader had a significant negative effect on the aboveground biomass of the competitors (Table 2, Fig. 3A). Moreover, while the increase in the negative effect of the presence of the invader happened mainly between weeks 4 and 8 for the multi-species competitor assemblages (two-species assemblages: -8.4% in week

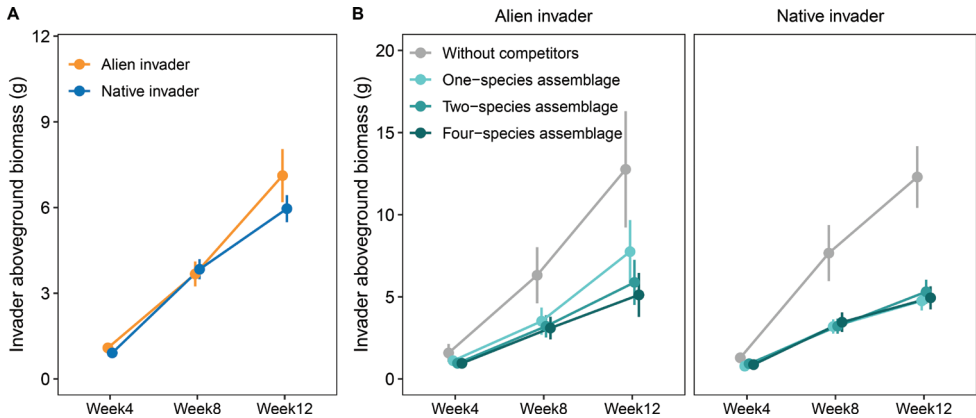


Figure 2. **A** aboveground biomass of alien and native invaders at each of the three harvests, **B** aboveground biomass of alien and native invaders in the absence or presence of native competitor assemblages of different species richness at each of the three harvests. Shown are means (\pm SEs) of the raw data.

4, -28.7% in week 8 and -15.7% in week 12; four-species assemblages: -0.2% in week 4, -20.6% in week 8 and -11.0% in week 12), it happened mainly between weeks 8 and 12 for the one-species assemblages (-2.7% in week 4, -12.5% in week 8 and -27.1% in week 12; Table 2, Fig. 3A). The origin of the invader did not have a significant effect on the aboveground biomass of the competitor assemblage (Table 2, Fig. 3A).

The total aboveground biomass per pot was not significantly affected by the species richness of the competitor assemblage (Table 2, Fig. 3B). However, having an invader plant, in addition to the competitors, increased biomass for the one-species assemblages after week 4, whereas, for the multi-species assemblages, it only increased biomass at week 12 (significant $I_{\text{Without/With}} \times R_{\text{One-/Multi-species}} \times T$ in Table 2, Fig. 3B). There was no significant effect of the origin of the invader (Table 2, Fig. 3B).

Discussion

In our experiment on competitive effects and responses of native and alien invaders over time, we found that the invaders had strongly reduced biomass in the presence of the competitors. This negative effect of the competitors on the invaders strongly increased during the growth period, but did not significantly depend on the species richness of the competitor assemblage. The alien and native invaders produced similar amounts of biomass during the first eight weeks, but after 12 weeks, the alien invaders had produced more biomass than the native ones. Similarly, addition of single invader plants also suppressed the biomass production of the competitor assemblage, and this effect also increased over time. In the multi-species competitor assemblages (two- and four-species assemblages), this effect was already pronounced after eight weeks, whereas in the one-species assemblages, it became most obvious after twelve weeks and then

Table 2. Effects of invader treatment (without invader, with alien or native invader), species richness of competitor assemblage (1, 2 or 4 species), harvesting time (week 4, week 8 or week 12) and their interactions on aboveground biomass of the competitor assemblage and the total aboveground biomass per pot. For the factor Invader, we created two orthogonal contrasts ($I_{\text{Without/With}}$: without vs. with invader, $I_{\text{Alien/Native}}$: with alien vs. with native invader). For the factor Species richness, we created two orthogonal contrasts ($R_{\text{One-/Multi-species}}$: one-species assemblages vs. average of two- and four species assemblages, $R_{\text{Two-/Four-species}}$: two-species assemblages vs. four-species assemblages).

	df	Aboveground biomass of competitors		Total aboveground biomass per pot	
		χ^2	P	χ^2	P
Fixed effects					
Invader treatment (I)	2	2.870	0.238	0.505	0.777
$I_{\text{Without/With}}$	1	2.559	0.110	0.505	0.477
$I_{\text{Alien/Native}}$	1	0.368	0.544	0.000	0.997
Species richness of assemblage (R)	2	1.507	0.471	1.351	0.509
$R_{\text{One-/Multi-species}}$	1	1.506	0.220	1.011	0.315
$R_{\text{Two-/Four-species}}$	1	0.001	0.978	0.368	0.544
Time of harvest (T)	2	1877.817	<0.001	1888.372	<0.001
I × R	4	7.421	0.115	1.860	0.761
$I_{\text{Without/With}} \times R_{\text{One-/Multi-species}}$	1	0.003	0.954	0.020	0.889
$I_{\text{Without/With}} \times R_{\text{Two-/Four-species}}$	1	5.053	0.025	0.842	0.359
$I_{\text{Alien/Native}} \times R_{\text{One-/Multi-species}}$	1	0.006	0.938	1.041	0.308
$I_{\text{Alien/Native}} \times R_{\text{Two-/Four-species}}$	1	2.375	0.123	0.032	0.858
I × T	4	29.829	<0.001	5.454	0.244
$I_{\text{Without/With}} \times T$	2	29.675	<0.001	4.026	0.134
$I_{\text{Alien/Native}} \times T$	2	0.197	0.906	1.534	0.464
R × T	4	5.760	0.218	0.874	0.928
$R_{\text{One-/Multi-species}} \times T$	2	0.068	0.967	0.103	0.950
$R_{\text{Two-/Four-species}} \times T$	2	5.593	0.061	0.795	0.672
I × R × T	8	14.863	0.062	11.242	0.188
$I_{\text{Without/With}} \times R_{\text{One-/Multi-species}} \times T$	2	11.933	0.003	8.667	0.013
$I_{\text{Without/With}} \times R_{\text{Two-/Four-species}} \times T$	2	0.885	0.643	0.491	0.782
$I_{\text{Alien/Native}} \times R_{\text{One-/Multi-species}} \times T$	2	0.049	0.976	0.650	0.723
$I_{\text{Alien/Native}} \times R_{\text{Two-/Four-species}} \times T$	2	2.115	0.347	1.529	0.466
Random effects		SD		SD	
Invader family		0.001		0.073	
Invader species		0.056		0.141	
Assemblage identity [†]		0.083		0.048	
Residual		0.099		0.105	

Values are in bold when $P < 0.05$. [†] Shown is the standard deviation (SD) of the one-species assemblage of *Lolium perenne*. The SDs of all assemblage identities are shown in Suppl. material 1: Table S6.

even more pronounced than in the multi-species assemblages. So, although our results did not indicate major roles of the origin of the invader and the species richness of the competitor assemblage, we found that the invader and competitors reciprocally suppressed one another, and that these interactions became more intense over time.

The alien invaders only produced more biomass than the native invaders by week 12. As invasive alien plants are frequently characterized by fast early growth (Grotkopp

et al. 2010; Dawson et al. 2011), and frequently produce more biomass than native species (van Kleunen et al. 2010), it is surprising that the difference in biomass did not appear earlier. It could be that the delay is due to the resistance provided by the competitors, which slowed down the overall growth rates of the invaders. Meanwhile, all the seedlings per pot were transplanted at the beginning of the experiment, which may eliminate the effect of differences in the phenological niche between the competitor species, and between the competitor assemblage and the invader in the growth stages (Wolkovich and Cleland 2011; Godoy and Levine 2014). Furthermore, it could reflect that not all naturalized alien species in our study are highly invasive and that the native invaders themselves are also very common. The fact that the alien invaders nevertheless produced more biomass than the native invaders at the end of the experiment may reflect that many naturalized alien species are more competitive than natives (Vilà and Weiner 2004; Kuebbing and Nuñez 2016; Golivets and Wallin 2018; Zhang and van Kleunen 2019). Another reason why alien invaders ultimately performed better than native invaders may be that they have escaped from the co-evolved enemies in their native ranges (Keane and Crawley 2002). As we did our experiment in a greenhouse environment, it is likely that both the aliens and natives were released from aboveground herbivores. However, as we provided all pots with an inoculum of field soil, it is likely that the soil contained root herbivores and pathogens that might have preferentially attacked the native plants. The differences in competitive ability among the native plants can have been equalized by the native soil pathogens (Albornoz et al. 2017). Despite the difference in biomass between the alien and native invaders at the end of the experiment, they did not have different effects on the biomass production of the competitor assemblages. Moreover, the proportional biomass of the alien and native invaders in the presence of competitors was not significantly different (Fig. 3C). In other words, the slight superiority in biomass production of the alien invaders did not result in a larger dominance, at least not during the 12 weeks of our experiment.

While the presence of competitors significantly reduced the biomass of the invader, the effect of species richness of the competitor assemblage was not significant. In other words, we did not find support for Elton (1958)'s diversity-invasibility hypothesis. Other studies found that invader species could be strongly limited by nutrient and light availability when they competed with more diverse species assemblages (Roscher et al. 2009; Mata et al. 2013), whereas other studies found also no significant relationship (Smith and Côté 2019) or actually found a positive one (Jiang and Morin 2004; Zeiter and Stampfli 2012). It has, however, also been reported that the diversity-invasibility relationship can change with time (Clark and Johnston 2011). Actually, at week 12 (i.e. at the end of our experiment), there was a slight, though non-significant, trend that the invader aboveground biomass was lowest in four-species competitor assemblages and highest in one-species assemblages (Fig. 2B). So, possibly if the experiment would have lasted longer, the effect might have become significant. This would be particularly likely, if complementarity effects increase with time (Fargione et al. 2007). It could also be that diversity effects on resistance against invaders require higher species-richness levels than we used. Therefore, we recommend that future invasion experiments use

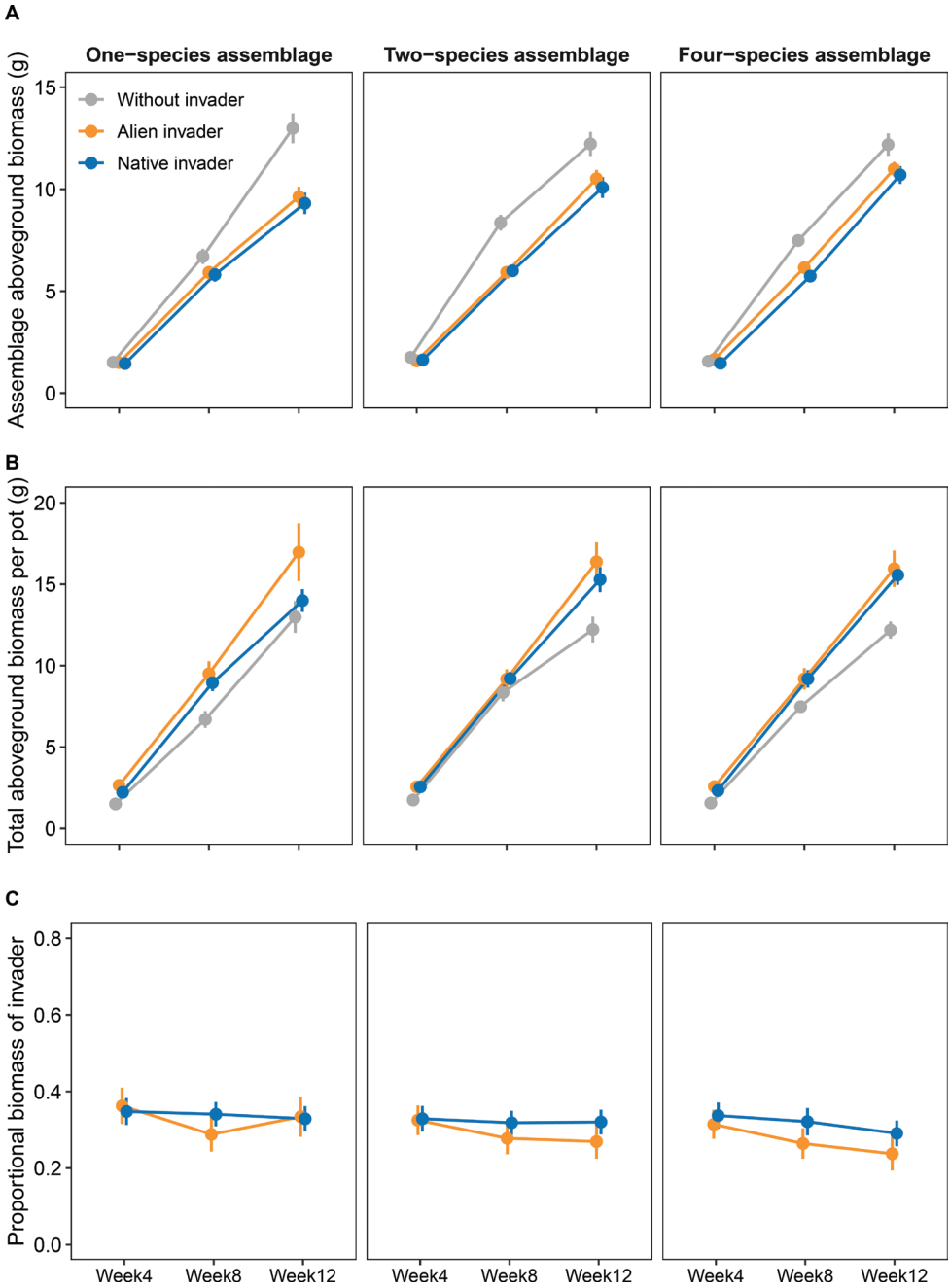


Figure 3. Aboveground biomass of native competitor assemblages (A) and total aboveground biomass per pot (B) for different competitor assemblages of different species richness and in the absence or presence of alien and native invaders at each of the three harvests, C proportional aboveground biomass per pot of alien and native invaders in competitor assemblages of different species richness at each of the three harvests. Shown are means (\pm SEs) of the raw data.

species assemblages that are older and have higher maximum species-richness values than the ones we used.

A potential limitation of our study is that the species pool that we used to create the competitor assemblages was relatively small ($n = 7$). As a consequence, some of the two-species assemblages shared species with one another, and this sharing was even stronger for the four-species assemblages (each species was present in 4 of the 7 four-species assemblages). In other words, with increasing species richness, the assemblages became more similar to each other. In our study this confounding most likely had no major consequences as there were no significant effects of species richness. Visual inspection of the biomass development of each of the competitor assemblages (Suppl. material 1: Fig. S3) also did not reveal clear indications that the presence of a particular species drove the differences in biomass among the assemblages. Nevertheless, we recommend that future experimental studies on the diversity-invasibility hypothesis use larger species pools to avoid such effects.

Like the presence of competitors reduced the biomass of the invader, so did reciprocally the presence of the invader reduce the biomass of the competitors. This most likely reflects that the addition of the invader increased the density of plants per pot, and that this resulted in more intense competition among the plants (Callaway and Walker 1997; Zhang and Tielbörger 2020). Moreover, the effect of the invader on the biomass of the competitor assemblage increased over time, but the pattern of this increase depended on whether the assemblage consisted of one or multiple species (Fig. 3A). Surprisingly, although we had expected that already early on in the experiment the one-species competitor assemblages would suffer more from the invader than the multi-species assemblages, the one-species assemblages only showed a clear effect of the invader at week 12, whereas the multi-species assemblages showed it already at week 8. Possibly, early on, at week 4, the plants were still so small that they hardly interacted with one another. At week 8, the plants in the one-species assemblages without invaders were still relatively small, while in the multi-species assemblages the plants were larger, as intraspecific competition is usually more intense than interspecific competition (Adler et al. 2018). Consequently, in the presence of the invader, the one-species competitor assemblages still hardly interacted with the invader, whereas the multi-species assemblages had to share their resources with the invader, and therefore produced less biomass. Indeed, the joint invader and competitor biomass at week 8 differed less between the invaded and non-invaded multi-species assemblages than between the invaded and non-invaded one-species assemblages (Fig. 3B). Whatever the exact reason is for these different patterns over time, at the last census the negative effect of the invader was, as expected, larger for the one-species competitor assemblages than for the multi-species ones. Again this effect might have become even stronger if the experiment would have lasted longer.

In conclusion, we found reciprocal effects of invaders and competitors, and that these effects became stronger over time. Although the alien invaders produced more biomass than the native invaders by the end of the experiment, they were not yet

differently affected by the presence and species richness of the competitor assemblages. The effects of the invader on the competitors also did not yet depend on whether the invader was an alien or a native. However, at the end of the experiment, the one-species competitor assemblages were more strongly affected by the invader than the multi-species ones. So, even though our results did not support the diversity-invasibility hypothesis, if the effects that we found continue to increase over time the hypothesis might hold.

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Supplementary material I

Table S1–S6, Figs S1–S3

Authors: Duo Chen, Mark van Kleunen

Data type: PDF file

Explanation note: **Table S1.** Alien and native invader species used in the experiment.

Table S2. Competitor species used in the experiment and combinations of species to produce seven native competitor assemblages for each of the three species-richness levels. **Table S3.** Effects of invader origins, species richness of the competitor assemblage, harvesting time and their interactions on proportional aboveground biomass of invader plants. **Table S4.** Effects of invader origins, presence and species richness of the competitor assemblage and their interactions on belowground biomass and root weight ratio of invader plants at the first harvest time. **Table S5.** Effects of invader types treatment, species richness of competitor assemblage and their interactions on belowground biomass and root weight ratio of the native competitor assemblage at the first harvest time. **Table S6.** The SDs of the ten invader species and/or 21 assemblage identities from the models shown in Tables 1, 2, S3, S4 and S5. **Fig. S1.** Belowground biomass and root weight ratio of invaders in the absence or presence of native competitor assemblages of different species richness at the first harvest. **Fig. S2.** Belowground biomass and root weight ratio of the competitor assemblage in the absence or presence of alien and native invader species at the first harvest. **Fig. S3.** Aboveground biomass of each of 21 native competitor-assemblage combinations in the absence or presence of alien and native invaders at each of the three harvests.

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