OIKOS

Research

The stronger, the better – trait hierarchy is driving alien species interaction

Editor's OIKOS Choice

Viktoria Ferenc and Christine S. Sheppard

V. Ferenc (https://orcid.org/0000-0003-4116-0089) ✉ *(viktoria.ferenc@uni-hohenheim.de) and C. S. Sheppard (https://orcid.org/0000-0002-7847-2310), Inst. of Landscape and Plant Ecology, Univ. of Hohenheim, DE-70593 Stuttgart, Germany.*

Multiple invaders commonly co-occur in native ecosystems and in some cases have been shown to facilitate each other thus exacerbating impacts on native species, while in other cases one invader may reduce the impact of another due to competition. We therefore aimed at identifying mechanisms driving alien species interactions. We conducted a common garden experiment investigating all pairwise combinations of 20 alien annual plant species in Germany. We first tested whether competition or facilitation occurred more often. Secondly, we determined whether individual traits, hierarchical or absolute trait distances, multivariate trait or phylogenetic distance explained alien plant interactions best. Thirdly, we assessed whether accounting for trait plasticity explains plant performance better than species-level trait averages. While the magnitude of interspecific competition compared to intraspecific competition was on average larger across the 190 alien species combinations, interspecific facilitation still occurred in 24% of cases. Interactions could be better explained by hierarchical trait distances which reflect competitive ability, compared to phylogenetic and multivariate trait distance (reflecting niche differences). This finding supports criticisms about the applicability of testing limiting similarity versus environmental filtering and the community phylogenetic approach. Specifically, when growing taller and having a lower specific leaf area than the co-occurring alien neighbour, biomass and seed number of individuals in mixture increased compared to growing alone. Effects of seed mass, root:shoot ratio and flowering time depended on the performance measure. In contrast to recent suggestions, accounting for trait plasticity did not necessarily explain plant performance better than models using species-level trait averages. These results advance our fundamental understanding of trait-interaction relationships, strengthening recent findings on the importance of competitive hierarchy in shaping interactions and community structure. In particular, applying these concepts to the novel case of alien-alien interactions, is crucial given the continuing accumulation of alien species around the globe.

Given the ongoing global accumulation of invasive species, it becomes crucial to better understand interactions among multiple alien species. Our experimental study, measuring growth, seed production and functional traits in 190 alien plant species combinations, shows that alien interactions are driven by hierarchical differences in functional traits reflecting competitive ability. While competition among two invaders was more prevalent, interspecific facilitation occurred in a quarter of cases, which could potentially exacerbate impacts on native species ('invasional meltdown'). Our findings advance the understanding of trait-interaction relationships, particularly by being applied to the novel case of alien-alien interactions.

Synthesis

NSO
NORDIC SOCIETY OIKOS

www.oikosjournal.org

Introduction

Biological invasions have various impacts on ecosystems and communities, posing major threats to biodiversity (Vilà et al. 2011) and are still increasing in number (Seebens et al. 2017). This increase is not only due to well-known reasons such as the invasion debt (Essl et al. 2011) or an increase of global trade and transport (Hulme 2009), but also due to newly accessible source pools (Seebens et al. 2018). Facing increasing accumulation of invasive species, it becomes apparent that more attention must be paid to interactions among invasive species which are especially important in terms of management decisions (Kuebbing et al. 2013). Whether species facilitate each other (which may lead to accelerated impacts, termed as 'invasional meltdown' by Simberloff and von Holle (1999)), interfere with each other or have a neutral interaction has rarely been studied. At least until recently, most studies focused on single invasive species: as the review of Kuebbing et al. (2013) showed, out of 153 studies less than 6% investigated interactions of multiple co-occurring plant invaders. These studies usually focus on few species and their interactions, whereas to identify underlying drivers of species interactions multi-species approaches should be employed, which are suitable for making generalisations across species on mechanisms of species coexistence (van Kleunen et al. 2014).

To achieve such generalisations, functional traits may be used to explain variation in species interaction. Indeed, combining functional trait-based approaches and demographic approaches is necessary to answer pending questions on trait variation (Salguero-Gómez et al. 2018). Trait-based approaches are also a powerful tool explaining community assembly, whereby functional traits influencing plant performance are employed to assess niche differences and species interactions (Violle et al. 2007). Niche differences, which may be reflected by differing trait combinations, enable species to coexist due to, for example, different demands in resource acquisition. Trait-based approaches were often employed in the context of native-alien species interactions (Ordonez et al. 2010), but rarely have studies looked at alien–alien interactions (but see Sheppard et al. 2018). There are two opposite theories predicting the outcome of community assembly in such approaches. The limiting similarity hypothesis suggests that individuals compete more strongly the more similar they are due to occupying similar niche space and competing for resources (MacArthur and Levins 1967), therefore more dissimilar species are more likely to coexist. Assuming the relevant functional traits are fixed in the phylogeny, the same patterns are expected when analysing phylogenetic relatedness as a proxy of niche similarity, which is the approach taken in phylogenetic community ecology (Webb et al. 2002). Conversely, the environmental filtering hypothesis predicts the occurrence of more similar (or related) species

in a given environment, as their traits would be best adapted to certain conditions (Keddy 1992). However, Mayfield and Levine (2010) outline that the phylogenetic approach is not a good predictor of interaction outcome as empirical evidence of many studies have not uniformly supported theory. They argue that focusing on trait-based niche description is neglecting competition between dissimilar species and therefore is also often erroneous in predicting interaction patterns. Thus, if niche differences are important, species dissimilarity (phylogenetic or trait-based) is promoted, while fitness differences (hierarchical trait differences related to competitive ability) would promote species similarity in a community (Chesson 2000, Kunstler et al. 2012).

Considering traits related to competitive ability, the plastic response of individuals to biotic or abiotic stress is a common driver of community assembly outcome (Violle et al. 2012) and is an important predictor of biological invasions (Richards et al. 2006). This would imply that to improve predictions of interaction outcome, not only species-level trait averages growing under ideal conditions without competition should be measured, but also traits of individuals growing under competition to account for competition-induced trait plasticity (Richards et al. 2006).

Our study aims to evaluate the previously mentioned hypotheses on trait-interaction relationships to identify which mechanisms determine alien plant species interactions. To this end, we performed a common garden experiment, investigating all inter- and intraspecific pairs of 20 alien plant species (giving 190 interspecific combinations) and additionally growing alone. To explain species interactions we considered five different models to investigate plant performance: I) individual functional traits of each plant individual (targets) to assess performance independent of neighbour traits; II) individual trait hierarchy (trait distances between target and neighbour) as recent studies showed that fitness differences are correlated with competitively superior traits; III) absolute trait distances to test the possibility that trait differences regardless of the direction are relevant (in which case the individual trait hierarchy model would show a quadratic relationship); IV) multivariate trait distance, as a measure to describe overall niche differences; and V) phylogenetic distance as another proxy for niche differences. In this study we aimed at answering 1) whether alien species are more likely to compete or facilitate each other when growing in interspecific pairs, as well as assessing whether inter- or intraspecific competition is stronger; 2) which of the above mentioned models explains alien plant interactions best, and consequently how the relative performance of aliens relates to phylogenetic or trait similarity and hierarchy; and 3) whether accounting for trait plasticity explains plant performance better compared to only employing species-level trait averages.

Methods

Study system

We selected 20 annual plant species from seven different plant families across three functional groups (2 legumes, 4 grasses, 14 forbs). The species occur in ruderal plant communities and were selected as they cover a wide phylogenetic range (phylogenetic tree in the Supplementary material Appendix 1 Fig. A1). The study comprises only annual species to reduce bias of different plant life forms and as it enables the measurement of an individual's fitness within one experimental season. We obtained seeds of most species from botanical gardens, the remaining from seed suppliers or monocultures of previous common garden experiments (Supplementary material Appendix 1 Table A1). All study species are considered established neophytes in Germany except for *Amaranthus tricolor*, *Bidens pilosa* and *Cosmos bipinnatus*, which are casual neophytes (Supplementary material Appendix 1 Table A1). On the scale of ca 11 × 11 km, species range size in Germany ranges from less than 1% to 47%, suggesting that some species are more likely to co-occur than others. Minimum residence time (years since first record in Germany) varied from 38 to 434 years (Supplementary material Appendix 1 Table A1).

Experimental set-up

We conducted the experiment during the growing season 2018 at a field station of the University of Hohenheim (48°42′45.2″N, 9°11′23.6″E) in Stuttgart, Germany (400 m a.s.l.; mean annual temperature 2018: 11.15 °C; annual precipitation 2018: 649.7 mm). In this common garden pot experiment, plants were growing either alone or with one neighbour plant. Specifically, all species were planted alone (control) and in all pairwise combinations (20 intraspecific [monoculture], 190 interspecific [mixture]) in a completely randomized design using four replicates for the pairwise pots. Overall, we used 926 pots with a volume of 10 l (28 cm diameter, 21 cm height) filled with field soil (total soil carbon content 1.8%; total soil nitrogen content 0.075%; 212 mg potassium (K_2O) kg^{-1}, 347 mg phosphate (P_2O_5) kg^{-1}; soil texture of 9.8% clay, 70.7% sand and 19.5% silt) and placed on concrete tiles to improve drainage. Seeds of the study species were sown in trays in a greenhouse on 20 April 2018. Five weeks later (22–30 May 2018) seedlings were transplanted into the experimental pots. Individuals in pairwise treatments were placed 5 cm apart, single individuals were placed in the centre of the pot. Due to low germination rates, *Amaranthus blitoides* and *Atriplex sagittata* could only be replicated three times and *Iva xanthiifolia* two times, resulting in a total of 698 mixture pots. Control individuals were planted in eight replicates (respectively six and four) to obtain more accurate trait measurements (see below) adding up to a total of 926 pots. Weeds emerging from the seedbank in the pots were removed before transplanting seedlings and continuously throughout the experiment. All pots were watered sufficiently by a drip watering system. Initial height was measured (longest leaf for species growing as rosettes, stem height for all others) after planting, to correct for initial differences that are not a result of varying neighbour treatment. Individuals which died from transplanting were replaced in the first two weeks of the experiment. We harvested all plants between 15 October and 7 November 2018 (21 weeks after the start of the experiment).

Trait selection and data collection

We measured the traits that are considered to be 'fundamental tradeoffs controlling plant strategies' according to Westoby (1998): specific leaf area (SLA), plant height and seed mass. Additionally, we measured flowering onset and root:shoot ratio. Relevant traits for resource acquisition and allocation were chosen and trait measurements followed standard protocols (for further information see Supplementary material Appendix 2). Each of these traits was measured on each individual plant except for root:shoot ratio, which, due to its labour intensiveness, was only measured for control pots. For the remaining traits we thus estimated both species-level trait averages in ideal conditions, that is on the individuals growing alone as well as traits at individual-level accounting for competition-induced plasticity in the various pairwise treatments. Additionally, we classified our species according to plant functional group (forb, grass and legume), which encompasses several traits and can thereby also incorporate traits which are more difficult to measure (Cornelissen et al. 2001). We note that while seed mass was higher for the legumes in our study, the other four quantitative traits greatly overlap across the three functional groups (Supplementary material Appendix 2 Fig. A2). We thus consider it likely that functional group adds other dimensions of plant ecological strategies and follow the methods of other studies that included both quantitative and categorical traits in analyses of trait effects (Carboni et al. 2016). As niche differences of species might be better represented in multidimensional space (Kraft et al. 2015), we also calculated multivariate trait distance from the species-level trait averages and plant functional group of control individuals, as well as calculating phylogenetic distances between species pairs (for details see Supplementary material Appendix 2).

To assess plant performance, we considered aboveground biomass as a proxy for competitive ability and total seed number as measure of fitness for such annual species. For biomass, we cut plants at ground level and dried them at 70 °C for 72 h. As seeds ripened during the season, a subset of ten intact flower heads was collected per plant. All seeds of the subsets were counted and weighed. At harvest we counted the total number of flower heads with ripe seeds to extrapolate the counted subset to total seed number. For species releasing whole flower heads which are not countable anymore afterwards (*Diplotaxis muralis*, *Eragrostis minor*, *Hirschfeldia incana*, *Medicago polymorpha* and *Vicia villosa*), all flower heads were collected throughout the season as they ripened (at least two times per week).

Of initially 926 pots with 1700 plants, we removed 59 pots from the dataset due to mortality, resulting in 1582 observations (1288 interspecific, 142 intraspecific, 152 single; for 32 of these individuals (26, 3 and 3, respectively) we could not assess biomass as it was ripped off in a storm just before harvest, but this did not affect neighbouring plants). For the seed number analysis *Berteroa incana* was removed as it did not produce seeds during the experimental period, resulting in 1438 observations (1160 interspecific, 134 intraspecific, 144 single; for 54 of these individuals (43, 7 and 4, respectively) we could not assess seed number because they were released before we could collect them).

Statistical analysis

To address aim 1) of finding out whether competition (interspecific versus intraspecific) or facilitation is more common, we first tested for general differences among treatments: single plants (control), intra- and interspecific pairs (split into respective neighbour plant functional group). We examined log-transformed aboveground biomass and log-transformed seed number +1 for each species separately with ANOVA using R ver. 3.5.3 (<www.r-project.org>). For pots with intraspecific pairs we used the mean performance of both individuals to account for non-independence within the pot.

For each performance measure (i.e. biomass and seed number) relative performance growing in interspecific pairs was calculated as the log response ratio (lnRR, which is the log(performance in mixture/performance in control, Weigelt and Jolliffe 2003) separately for each individual. As a measure for performance in the control, we used the mean of all control individuals of the respective species. These log response ratios (in the following referred to as lnRR_inter/control) represent the relative ability to tolerate a heterospecific individual compared to growing alone. Positive values indicate facilitation and negative values indicate competition. Analogously we calculated the relative performance in interspecific pairs compared to intraspecific pairs (i.e. log(performance in mixture/mean performance in monoculture; in the following referred to as lnRR_inter/intra), here, positive values indicate higher intraspecific competition and negative values indicate higher interspecific competition as compared to each other.

To address aim 2) of exploring whether species interaction is best explained by phylogenetic, multivariate trait based or hierarchical trait models; we built five models for each log response ratio, to investigate the response to I) a target individual's own traits (log SLA, log maximum height, log seed mass, log root:shoot ratio, flowering onset, plant functional group; in the following called target trait model); II) trait hierarchies between target and neighbour, which is the (except for flowering onset) logarithmized distance of each species-level trait average between the two species (target – neighbour) of a respective pot, plus the plant functional group of the neighbour (trait hierarchy model); III) absolute trait distances (the absolute values of the trait hierarchy model) and neighbour plant functional group (absolute trait distance model); IV) multivariate trait distance between the two species in the pot

(multivariate trait distance model); V) and phylogenetic distance (phylogenetic distance model). When calculating log response ratios, we considered all individuals as target individuals, while accounting for sources of non-independence in the random effects. We added log-transformed initial height as covariate to all models to account for potential differences in starting conditions. All numeric explanatory variables were scaled to a mean of zero and standard deviation of one.

To address aim 3) of examining whether models accounting for trait plasticity explain plant performance better that only considering species-level trait averages, we compared the three models using separate traits, with the respective individual-level trait based model for lnRR biomass and lnRR seed number. We ran the species-level trait average model again on a reduced dataset comprising only individuals with data for each individual-level trait. As root:shoot ratio could only be assessed for individuals growing alone, these models only consider SLA, height, seed mass and flowering onset (plus neighbour functional group).

For all models analysing the log response ratios of each target individual, we used the Markov chain Monte Carlo method in the MCMCglmm package (Hadfield 2010) in R ver. 3.5.3 (<www.r-project.org>) to account for phylogenetic correlation between species. We calculated the correlation as the inverse phylogenetic covariance, using the function inverse in the MCMCglmm package. Besides phylogenetic correlation, target species identity was included as a random effect, as well as unique combination of species to account for lower differences between same combinations than between different combinations. To account for non-independence of individuals in the same pot, pot identity nested in combination was further included as a random effect. We defined priors for each random effect corresponding to Gaussian inverse-Gamma distribution with a variance of one and shape and scale parameters set to 0.01 (Hadfield 2010). We ran the models with 1 000 000 iterations, using a burn-in phase of 100 000 and a thinning interval of 200, resulting in 4500 observations. We assumed convergence after visually checking trace plots of all models. To estimate the phylogenetic signal we used Pagel's lambda (Freckleton et al. 2002). We considered fixed effects as relevant for plant performance if their respective 95% credible interval of the effect size did not overlap zero. The variance explained by each model (R^2) was calculated following Nakagawa and Schielzeth (2013). Since the R^2 value only takes into account posteriori model output, we relied on the deviance information criterion (DIC) to compare model fit, a measure which is commonly employed for model selection in Bayesian statistics (Spiegelhalter et al. 2002).

Results

Alien species competition versus facilitation

We found species-specific variation concerning whether alien species benefitted or suffered from growing in mixture compared to growing alone or with conspecifics
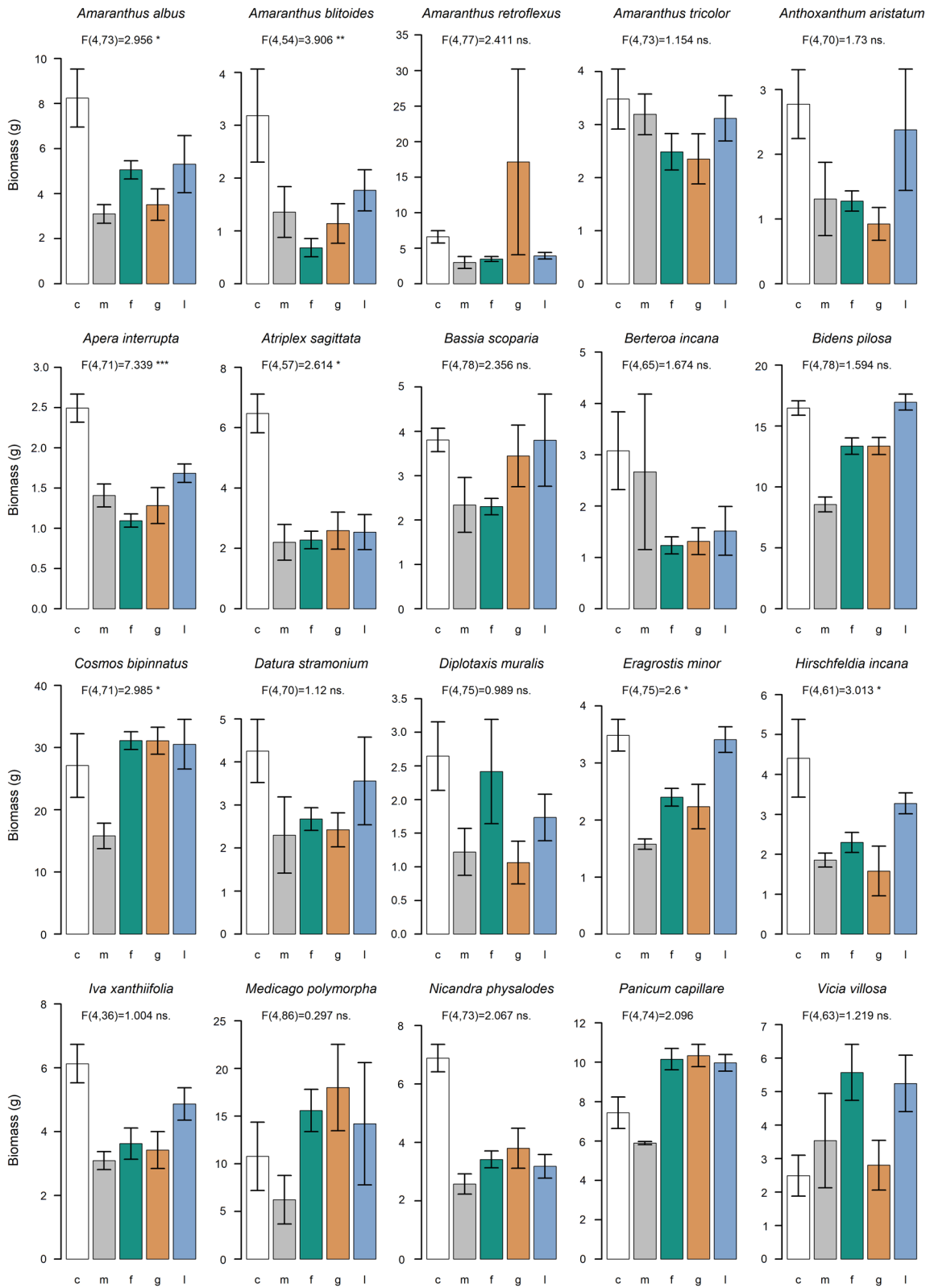
Figure 1. Mean biomass production in g (±1 SE) per species depending on competition treatment. White bars represent the control (plants growing alone in the pot, 'c'); grey bars the monoculture treatment (plants grow with a conspecific individual, 'm'); coloured bars represent the mixture treatment with the neighbour being a forb (green, 'f'), a grass (orange, 'g') or a legume (blue, 'l'). Significance of competition treatment effect on log-transformed biomass was tested using ANOVA. F-statistics and significance of p-values (indicated by asterisk; *=p < 0.05; **=p < 0.01; ***=p < 0.001; ns. indicates no significance) are displayed.

Table 1. Model overview of the five different models for each response variable (log response ratios of individuals in interspecific competition compared to control individuals or compared to individuals in intraspecific competition, for biomass and seed number); showing the results of the target trait model; trait hierarchy model; absolute trait distance model; multivariate trait distance model; phylogenetic distance model. Marginal R^2 and conditional R^2 are reported as well as the delta DIC (deviance information criterion) value (difference between the respective model and the model with lowest DIC for each response variable). The phylogenetic signal was calculated as Pagel's lambda.

Response variable (sample size)	Model	R^2 marginal (95% credible interval)	R^2 conditional (95% credible interval)	ΔDIC	Mean phylogenetic signal (95% credible interval)
Facilitation versus Competition –lnRR_ inter/control biomass (n = 1262)	Target trait	0.22 (0.077 – 0.362)	0.64 (0.484 – 0.818)	17.2	0.23 (<0.001 – 0.586)
	Trait hierarchy	0.20 (0.136 – 0.263)	0.48 (0.353 – 0.608)	0	0.17 (0.002 – 0.424)
	Absolute trait distance	0.05 (0.023 – 0.086)	0.54 (0.368 – 0.703)	18	0.17 (0.001 – 0.528)
	Multivariate trait distance	0.03 (0.009 – 0.061)	0.54 (0.397 – 0.711)	20.1	0.16 (0.001 – 0.511)
	Phylogenetic distance	0.03 (0.005 – 0.048)	0.53 (0.392 – 0.709)	21.3	0.16 (0.001 – 0.515)
Facilitation versus Competition –lnRR_ inter/control seed number (n = 1117)	Target trait	0.17 (0.038 – 0.344)	0.46 (0.328 – 0.790)	60.6	0.18 (<0.001 – 0.598)
	Trait hierarchy	0.12 (0.076 – 0.172)	0.47 (0.342 – 0.624)	0	0.07 (<0.001 – 0.264)
	Absolute trait distance	0.04 (0.016 – 0.064)	0.36 (0.238 – 0.492)	52.7	0.04 (<0.001 – 0.158)
	Multivariate trait distance	0.02 (<0.001 – 0.036)	0.36 (0.229 – 0.495)	57.7	0.04 (<0.001 – 0.141)
	Phylogenetic distance	0.01 (<0.001 – 0.032)	0.35 (0.233 – 0.499)	59.6	0.04 (<0.001 – 0.149)
Inter- versus Intraspecific competition –lnRR_ inter/intra biomass (n = 1262)	Target trait	0.22 (0.088 – 0.372)	0.62 (0.463 – 0.803)	17.6	0.24 (0.002 – 0.547)
	Trait hierarchy	0.19 (0.140 – 0.260)	0.44 (0.325 – 0.573)	0	0.11 (0.002 – 0.348)
	Absolute trait distance	0.06 (0.025 – 0.086)	0.51 (0.371 – 0.667)	17.4	0.13 (0.001 – 0.454)
	Multivariate trait distance	0.03 (0.007 – 0.058)	0.52 (0.363 – 0.669)	20	0.14 (0.001 – 0.462)
	Phylogenetic distance	0.02 (0.004 – 0.046)	0.51 (0.364 – 0.665)	21.4	0.13 (0.001 – 0.438)
Inter- versus Intraspecific competition –lnRR_ inter/intra seed number (n = 1117)	Target trait	0.15 (0.030 – 0.291)	0.52 (0.319 – 0.776)	61.2	0.11 (<0.001 – 0.490)
	Trait hierarchy	0.12 (0.076 – 0.170)	0.49 (0.348 – 0.631)	0	0.07 (<0.001 – 0.267)
	Absolute trait distance	0.04 (0.016 – 0.065)	0.35 (0.231 – 0.486)	52.2	0.03 (<0.001 – 0.148)
	Multivariate trait distance	0.02 (<0.001 – 0.034)	0.35 (0.233 – 0.494)	57.3	0.03 (<0.001 – 0.128)
	Phylogenetic distance	0.01 (<0.001 – 0.029)	0.35 (0.225 – 0.493)	59.1	0.04 (<0.001 – 0.130)

(Fig. 1). Legumes (*M. polymorpha* and *V. villosa*) and three other species we observed to be more dominant in the pots (*B. pilosa*, *C. bipinnatus*, *Panicum capillare*, i.e. those with highest biomass production) grew equally good or better in interspecific pairs compared to growing alone. Although performance generally varied more within treatment, this trend was also found for seed number in the same species except for *C. bipinnatus* (Supplementary material Appendix 3 Fig. A3).

Comparing biomass production over all interspecific pairs, we found competition more often than facilitation (958 versus 304 cases). Thus, interspecific facilitation occurred in 24% of all observations and was more common among plants growing with a legume than with a grass or forb (31% versus 23% of cases). Intraspecific facilitation, on the other hand, was rare (ca 10%, i.e. 14 versus 128 observations). Comparing interspecific competition with intraspecific competition, higher intraspecific competition was more common than higher interspecific competition (730 versus 532 cases). Nevertheless, although instances of higher interspecific competition were less common, interspecific competition was on average stronger as the mean lnRR_inter/intra across all species is negative for all response values. Mean (±1 SE) values for the four log response ratios considered were: −0.75 ± 0.033 (n = 1262) for lnRR_inter/control biomass; −1.24 ± 0.051 (n = 1117) for lnRR_inter/control total seeds; −0.15 ± 0.033 (n = 1262) for lnRR_inter/intra biomass; and −0.45 ± 0.051 (n = 1117) for lnRR_inter/intra total seeds.

Niche differences (phylogenetic or multivariate) versus functional trait hierarchies

While the target trait model and trait hierarchy model explained more variance in the data than the other models, we found the best model fit using DIC with the hierarchical trait model for all response variables (Table 1). The phylogenetic signal Pagel's lambda differed between models, being highest for the target trait models. For all models the random effects phylogeny, target species identity and species combination explain more variation than pot identity. For the target trait model species combination explains more variation than for the trait hierarchy model which already includes information on species combination in fixed effects (Supplementary material Appendix 4 Table A2). Concerning the fixed effects of this target trait model, maximum height was the only significant trait, with a strong positive effect on relative biomass, while none of the measured focal traits were significant for seed number (Supplementary material Appendix 3 Fig. A4).

For the best model (based on DIC, trait hierarchy model), maximum height and seed mass had a strong positive effect on relative biomass, meaning growing taller and growing from heavier seeds than the neighbour, increases biomass in mixture compared to growing alone (Fig. 2a, 3a, b). Root:shoot ratio had a positive effect as well, meaning species which are potentially better belowground competitors have a competitive advantage over the neighbour (Fig. 3c). SLA had a negative effect, meaning species with lower SLA than their neighbour increased relative performance in mixture compared to growing alone (Fig. 3d). Flowering onset had no effect on relative
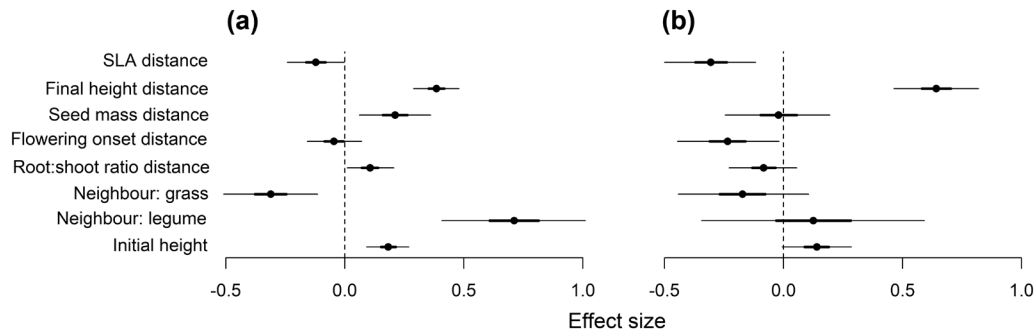
Figure 2. Results of the trait hierarchy model to explain relative performance in interspecific competition compared to growing alone (lnRR_inter/control): effects of specific leaf area (SLA) distance, final height distance, seed mass distance, flowering onset distance, root:shoot ratio distance and the effect of having a grass or a legume as neighbour (relative to a forb) and initial height of the individual on log response ratio biomass (a) and log response ratio seed number (b). All numerical traits are log-transformed and scaled to a mean of 0 and standard deviation of 1 (except for flowering onset which is only scaled). Positive effects indicate that a higher value of the respective trait leads to more biomass (respectively seeds) in interspecific competition (compared to control single individuals). Effects are considered relevant if the 95% credible interval does not overlap zero. Dots show the posterior mean, wide lines indicating one standard deviation (68% credible interval), while narrow lines indicate the 95% credible interval.

biomass, whereas the functional group of the neighbour plant had a strong effect. Growing next to a legume increased relative performance, whereas growing next to a grass decreased performance compared to growing with a forb (Fig. 2a).

For seed number the effects of height, SLA and having a grass as neighbour pointed in similar directions (Fig. 2b, 4a, b). In contrast to lnRR biomass, for lnRR seed number flowering onset had a negative effect, meaning the relative number of produced seeds increased when flowering earlier than the neighbour plant (Fig. 4c). Seed mass, root:shoot ratio and having a leguminous neighbour did not have an effect on lnRR total seed number (Fig. 2b).

For the log response ratios comparing performance in mixture to intraspecific pairs (lnRR_inter/intra), results were qualitatively similar for all traits for relative biomass and seed number measures respectively (except that the effect of root:shoot ratio on relative biomass showed only a positive trend but was not significant) (Supplementary material Appendix 4 Fig. A5–A7).

Individual-level traits versus species-level trait averages

We compared our models using separate traits with models using trait measures at an individual-level (accounting for competition-induced plasticity) instead of traits measured as species-level trait averages (for comparison only SLA, height, seed mass and flowering onset were included as for root:shoot ratios only control individuals could be assessed) (Table 2; Figures for the two best models in Supplementary material Appendix 5 Fig. A8 and A9). For both, lnRR_inter/control biomass and lnRR_inter/control seed number the datasets were reduced, excluding all individuals where one of the measures was missing (Table 2). While the trait hierarchy model is still the best model for this reduced dataset when using species-level trait averages (but with weaker effect

sizes for some traits), the target trait model has the lowest DIC when comparing individual-level traits. Furthermore, when considering only traits of the target plant relative performance (both biomass and seed number) were explained better when using individual-level traits, whereas when considering trait hierarchies, species-level trait averages explained performance better (Table 2). Height was by far the most important trait influencing species performance for the individual-level model, showing a strong positive effect for lnRR biomass as well as lnRR seed number (Supplementary material Appendix 5 Fig. A9).

Discussion

Although individual species varied in their response to neighbouring species, overall competition was more commonly found than facilitation in terms of biomass production. Higher intraspecific competition was slightly more common, though on average weaker, than higher interspecific competition. Hierarchical trait differences between target and neighbour explained interactions between alien species best (even though the target trait model also explained considerable variation in relative performance). Specifically, relative performance advantages (i.e. seed number and aboveground biomass) were greater for species having lower SLA values, growing taller, producing larger seeds, investing into roots compared to shoots and flowering earlier than the respective neighbour. Notably, using traits measured at individual-level, thereby accounting for plasticity, did not explain relative performance better than using species-level trait averages when looking at species differences (trait hierarchy model). However, for models focusing only on target traits, individual-level traits explained species performance better. Specifically, relative aboveground biomass and seed production was larger, the taller the species grew.
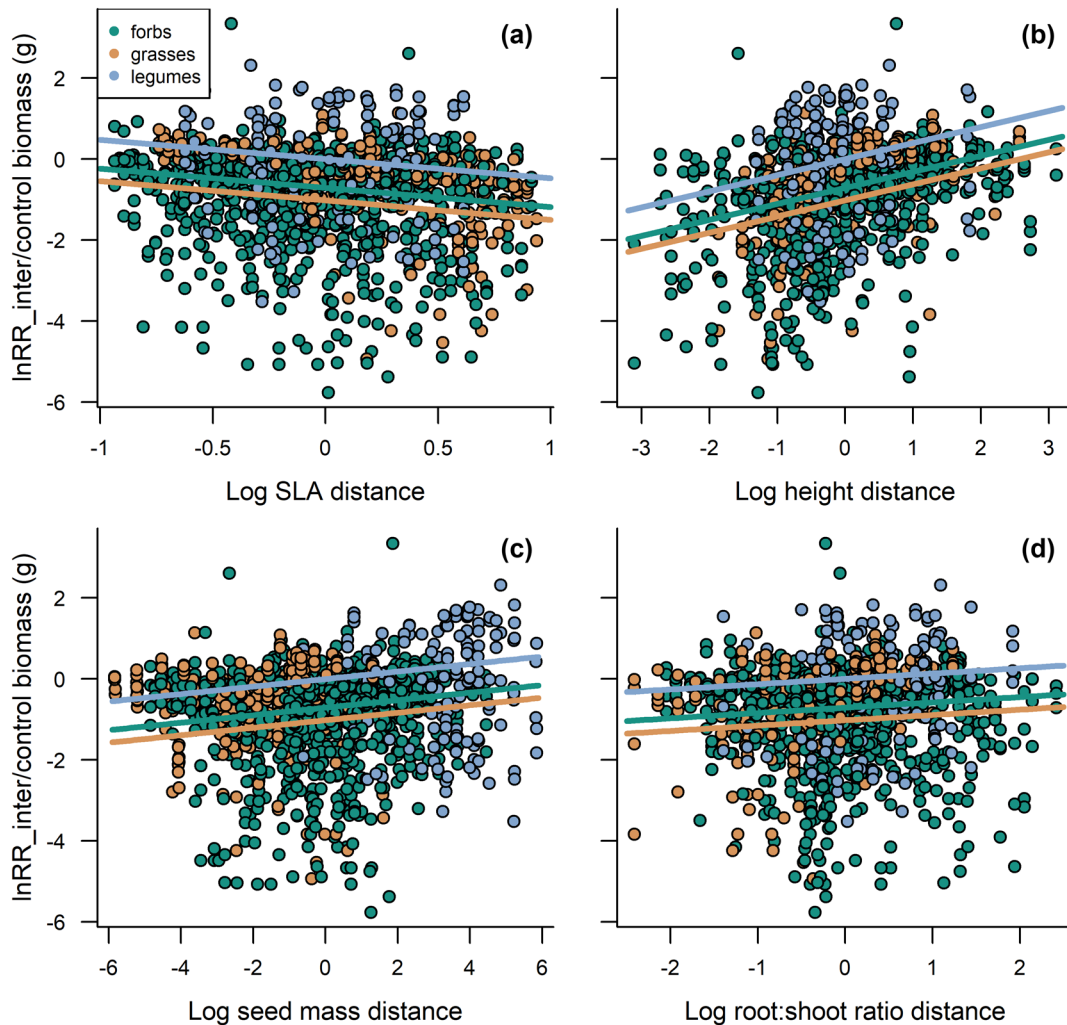
Figure 3. Predictions of trait effects on the log response ratio biomass of alien plants growing in interspecific competition compared to growing alone (lnRR_inter/control). Displayed are the predicted effects of the four relevant traits from the trait hierarchy model: specific leaf area (SLA) distance (a), maximum height distance (b), seed mass distance (c) and root:shoot ratio distance (d) (all log-transformed and scaled to a mean of 0 and standard deviation of 1; predictions for each trait effect shown with the other numeric traits fixed at their mean). Different colours depict the different functional groups: forbs (green), grasses (orange) and legumes (blue). Positive effects indicate that a higher value of the respective trait of the target individual compared to its neighbour leads to more biomass in interspecific competition (compared to control single individuals).

Alien species competition versus facilitation

When addressing aim 1), that is comparing individuals growing in mixture versus growing alone, we find competition to be more common than facilitation (76% of the cases). Comparisons to previous studies are difficult, as few studies to date have examined interactions among invasive species (Kuebbing et al. 2013) and even less studies have used a multi-species approach to empirically test pairwise interactions among alien species (but see Sheppard 2019). Nevertheless, so far mostly evidence of competition was found for alien plants but also other taxa (Kuebbing and Nuñez 2014, Jackson 2015), which is in line with our results. These predominantly negative interactions among several

alien species rather contradict the proposed 'invasional melt-down' hypothesis (Simberloff and von Holle 1999). Yet in 24% of the interspecific and 10% of the intraspecific instances we observed facilitation. This was more often – but not exclusively – the case for growing with a legume compared to growing with a forb or a grass species, which is in line with the positive effect of legume neighbours also found in our models. To date very few studies have found facilitating effects among invasive plants (but see Cushman et al. 2011) whereas more commonly it has been demonstrated that native species can facilitate aliens (Abella and Chiquoine 2019, Lucero et al. 2019). Our results thus highlight that attention has to be raised to facilitative interactions among aliens, especially since they are not limited to benefitting
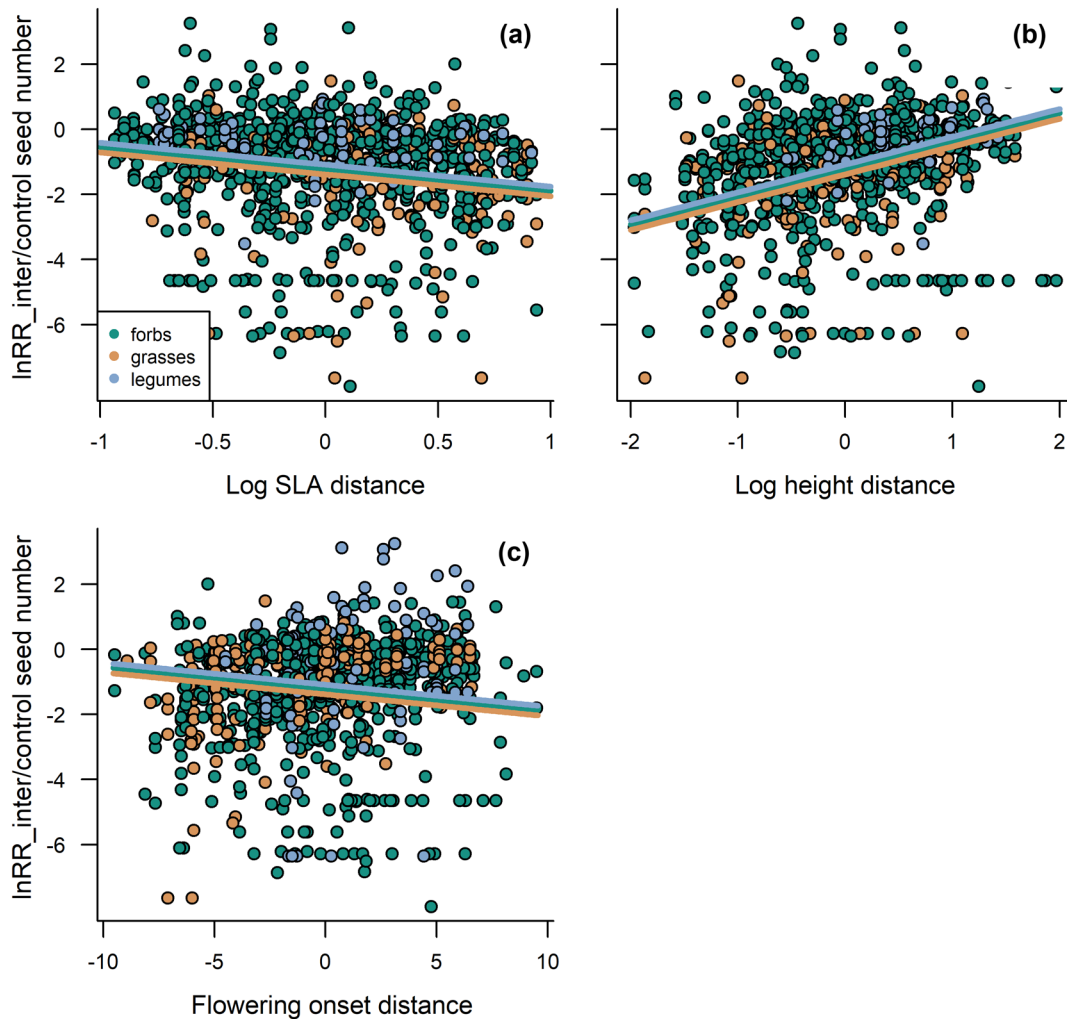
Figure 4. Predictions of trait effects on the log response ratio seed number of alien plants growing in interspecific competition compared to growing alone (lnRR_inter/control). Displayed are the three relevant traits from the trait hierarchy model: specific leaf area (SLA) distance (a), maximum height distance (b) and flowering onset distance (c) (all log-transformed and scaled to a mean of 0 and standard deviation of 1, except for flowering onset which is only scaled; predictions for each trait effect shown with the other numeric traits fixed at their mean). Different colours depict the different functional groups: forbs (green) grasses (orange) and legumes (blue). Positive effects indicate that a higher value of the respective trait of the target individual leads to higher seed number in interspecific competition (compared to control single individuals).

from legumes and occur also in casual neophytes. Such positive interactions may thus be highly relevant for invasion management (Kuebbing et al. 2013).

When comparing species growing in mixture with growing in monoculture, we found higher intraspecific competition to be slightly more common (58% of the cases) than higher interspecific competition. However, interspecific competition was on average stronger than intraspecific competition over all species (as also found by Sheppard 2019). Although a recent meta-analysis showed higher intraspecific competition among plants generally to be more common than higher interspecific competition (Adler et al. 2018), another meta-analysis showed differences for native and alien species in intensity of inter- and intraspecific competition

(Golivets and Wallin 2018). They found that while native species suffer more from interspecific competition, regardless of whether competing with alien or native species, alien species equally often suffer from intra- and interspecific competition. Past reviews (Goldberg and Barton 1992 and cited therein) found mainly contradicting results of empirically testing the strength of inter- versus intraspecific competition. Other mechanisms such as competitive hierarchy may be more important for shaping species coexistence rather than niche differentiation. Considering niche theory one would expect higher intraspecific competition whereas under the importance of fitness differences, interspecific competition may be higher depending on the species pair. This can explain the fact that species greatly differ in individual responses

Table 2. Model overview comparing the species-level trait average model; with the corresponding individual-level trait model for the models testing the effects of target traits, trait hierarchy and absolute trait distance on the log response ratios of individuals in interspecific competition compared to control individuals (lnRR_inter/control), for biomass and seed number; marginal R^2 and conditional R^2 are reported as well as the DIC (deviance information criterion) value. The phylogenetic signal was calculated as Pagel's lambda.

Response variable (sample size)	Model		R^2 marginal (95% credible interval)	R^2 conditional (95% credible interval)	DIC	Mean phylogenetic signal (95% credible interval)
Facilitation versus Competition lnRR_inter/control biomass (n=571)	Target trait	Average traits	0.14 (0.029 – 0.264)	0.43 (0.221 – 0.665)	448.38	0.17 (0.002 – 0.461)
		Individual traits	0.35 (0.152 – 0.535)	0.95 (0.912 – 0.988)	0	0.42 (0.001 – 0.962)
	Trait hierarchy	Average traits	0.12 (0.060 – 0.180)	0.39 (0.243 – 0.552)	423.03	0.17 (0.003 – 0.403)
		Individual traits	0.08 (0.038 – 0.134)	0.35 (0.209 – 0.524)	428.02	0.14 (0.002 – 0.390)
	Absolute trait distance	Average traits	0.04 (0.012 – 0.079)	0.35 (0.186 – 0.527)	449.70	0.12 (0.002 – 0.366)
		Individual traits	0.08 (0.039 – 0.133)	0.35 (0.204 – 0.515)	428.03	0.14 (0.002 – 0.380)
Facilitation versus Competition lnRR_inter/control seed number (n=565)	Target trait	Average traits	0.20 (0.063 – 0.351)	0.54 (0.330 – 0.768)	266.54	0.19 (0.001 – 0.572)
		Individual traits	0.46 (0.319 – 0.581)	0.80 (0.713 – 0.892)	0	0.14 (<0.001 – 0.607)
	Trait hierarchy	Average traits	0.15 (0.079 – 0.227)	0.50 (0.348 – 0.671)	222.28	0.23 (0.002 – 0.535)
		Individual traits	0.05 (0.015 – 0.081)	0.46 (0.276 – 0.675)	257.18	0.16 (0.001 – 0.534)
	Absolute trait distance	Average traits	0.04 (0.010 – 0.066)	0.48 (0.288 – 0.687)	263.15	0.17 (0.002 – 0.540)
		Individual traits	0.05 (0.015 – 0.080)	0.46 (0.272 – 0.670)	257.26	0.16 (0.001 – 0.522)

to intra- and interspecific competition in our experiment. Indeed, Stoll and Prati (2001) found that less competitive plants perform better growing with conspecifics whereas more competitive plants tend to perform better growing with heterospecific neighbours (also found in our experiment e.g. for *B. pillosa*, *C. bipinnatus*, *M. polymorpha*, *P. capillare* or *V. villosa* which were the species reaching highest absolute biomass, notably the first two are considered to be casual neophytes in Germany).

Relative performance in competition with other aliens is not related to phylogenetic or functional similarity

Considering aim 2), the results generally showed that hierarchical traits related to competitive ability predict alien species interactions best, explaining 12–20% of the variance in relative performance. Additionally, the actual traits of the target individuals, irrespective of their neighbour, also explained considerable variance. Conversely, phylogenetic distance or overall trait distance only explained 1–3% of variance and thus cannot generally explain relative performance of aliens. While the 'limiting similarity' hypothesis states that species with more similar traits would compete more strongly and that more dissimilar species are more likely to coexist (MacArthur and Levins 1967), several authors questioned this hypothesis and pointed out the importance of fitness differences (described by 'trait hierarchy') rather than niche differences (described by multivariate trait distance or phylogenetic distance) (Chesson 2000, Mayfield and Levine 2010). Indeed, our results also support the argument that fitness differences may be more important in explaining alien species interactions than niche differences. Most recent studies found that phylogenetic distance is not a good predictor of species interactions (Kunstler et al. 2012, Golivets and Wallin 2018), whereas a trait-based approach may be more relevant. For instance, Feng et al. (2019) introduced alien

species into native communities of different diversity levels and found that the effect of multivariate trait distance was stronger than phylogenetic distance. Few studies compared multivariate trait distance approaches with trait hierarchy, but Funk and Wolf (2016) studied competition between 47 native species and an alien invader and found that species interaction could only be explained by trait hierarchy, not by a multivariate trait distance approach nor by phylogenetic relatedness. Kraft et al. (2014) found trait hierarchies to best explain interactions of eight studied native species in pairwise competition and Kunstler et al. (2012) compared the effects on competitive response between trait hierarchy and phylogenetic or functional similarity for 22 native tree species and found that only trait hierarchy could explain species interaction. A recent study by Carmona et al. (2019) with a set-up of pairwise competition involving six native species found more support for trait hierarchies determining species competition than for absolute trait distances. The importance of considering hierarchical trait differences has thus recently gained more attention and for the specific case of alien–alien interactions is in line with previous findings of Sheppard (2019).

Which traits determine alien species interactions?

From the five quantitative traits we considered, plant height had the strongest effect; consistently with previous studies, taller individuals had a competitive advantage over their neighbours (Kraft et al. 2015) which reflects an advantage in competition for light (Westoby 1998). When considering only target traits irrespective of the neighbour traits, height was in fact the only significant trait (and only affecting biomass production). Having lower SLA values compared to the neighbour resulted in relatively more aboveground biomass and more seeds and therefore in higher fitness, consistent with previous studies that showed higher competitive ability for individuals with low SLA (Kraft et al. 2015, Conti et al.

2018). High initial seed mass had a positive effect on biomass, because seedlings from heavier seeds tend to have more resources and are more robust facing environmental stress (Westoby 1998). However, we note that seed mass was correlated with plant functional group (Supplementary material Appendix 2 Fig. A2); and therefore has to be carefully interpreted. Because root:shoot ratio is a labour intensive measure empirical results are scarce compared to the previously discussed traits. Competition for nutrients may be more relevant than for light in our experimental set up with only two individuals per pot. We found higher root investment to result in higher biomass production, while it did not benefit seed production but rather tended to reduce it. This hints at a tradeoff between resource investment in competitive ability (hence biomass) and reproduction (seed number). Our results revealed a negative effect of flowering onset on seed number, meaning the earlier a plant flowers, compared to its neighbour, the more seeds it will produce relative to growing alone. Similarly a meta-analysis showed higher fitness for earlier flowering plants (Munguía-Rosas et al. 2011) which have a higher likelihood to finish seed set within the season.

Besides the quantitative traits we investigated, neighbour functional group played an important role. Having a legume as a neighbour is beneficial for biomass production, but has no effect on seed number. The facilitative effect of legumes due to their symbiosis with nitrogen fixing bacteria (Tate 1995) is well-known, experimental studies showed that the presence of legumes increases productivity (Temperton et al. 2007). However, given that the effect on seed number was not relevant in our study, positive fitness consequences may actually be low. Contrastingly growing next to a grass has a negative effect on biomass and seed number, as also found by Bloor et al. (2008), potentially due to altered soil microbiome or nutrient depletion by a dominant grass neighbour. However, we note that given the unbalanced number of species in each functional group in our study (and particularly the low number of legumes), our results may also reflect species-specific effects.

Generally, the same traits determined species interactions for the comparisons between growing in intraspecific and interspecific pairs. Although all traits point in the same directions the effects are less strong than for comparing individuals in competition with individuals growing alone. Comparing our results to similar studies is difficult as few studies so far have investigated alien species interactions (Kuebbing et al. 2013). While our results on the importance of trait hierarchies and the particular traits relevant for alien interactions match recent findings on native–native or native–alien interactions, certain differences between alien species interactions and native species interactions are nevertheless likely. Alien species are not a random subsample but biased due to species with certain characteristics being more commonly introduced by humans (Maurel et al. 2016). Invasive species in particular are often highly competitive and more dominant in various aspects of performance than native species (van

Kleunen et al. 2010). Thus, as aliens represent different trait variation compared to native species, they may be adapted to different abiotic conditions in their native range, and as most alien species did not coexist before introduction to the shared new range, the traits shaping species coexistence may differ for alien–alien interactions. As alien species can have severe impacts when invading new areas, we emphasise the importance of further investigating alien interactions, especially in the light of the high proportion of facilitative interactions found in our study. In fact, we here greatly extend previous work on alien species interactions by Sheppard (2019) who used a similar but smaller set of species and traits (as well as a shorter experimental duration, resulting in less data on seed production as the most important fitness measure for annual species). Importantly, while our results are generally in line with what was previously found by Sheppard (2019) (who however did not compare interspecific competition to growing alone), in the present study we can now distinguish between facilitation and competition, and add insight into the relevance of competition-induced trait plasticity, as unlike Sheppard (2019) we measured traits for every single individual.

Individual-level traits versus species-level trait averages

Regarding aim 3), using traits measured at an individual-level instead of species-level did not improve the fit of our trait hierarchy model. This result contradicts the general idea that a high degree of intraspecific variation (genetically or plastic) which can be explained with individual-based traits, captures niche differences better than by species-level trait averages (Kraft et al. 2014). For example Kraft et al. (2014) found individual-level trait hierarchies to explain competition among species in vernal pool habitats better than species-level trait averages. Conti et al. (2018) also underlined the importance of investigating traits at an individual-level, as they found that individuals could respond to competition by trait shifts, which increased their competitive ability and resulted in a positive feedback. Similarly, Carmona et al. (2019) concluded, individual trait expression can ameliorate the effect of lower trait hierarchical position. Bennett et al. (2016) found competition to induce changes in expressed traits and concluded that the environment where the sampled plant grows can affect the outcome of trait patterns. Such trait–environment effects may indeed be one reason that the species-level trait averages in our study performed well: while studies often use traits from databases (Kunstler et al. 2012, Carboni et al. 2016), which can come from various environments and populations, our species-level trait averages were grown and measured in the same abiotic conditions from the same populations as individuals in competition. The extent of intraspecific trait variation in our study depended on species, trait and competition treatment (Supplementary material Appendix 5 Fig. A11–A14), with height showing

the greatest variation within species, although notably for the grasses height hardly differed between competition treatments (Supplementary material Appendix 5 Fig. A12). The finding that for the target trait model the individual-level model performed better than the species-level trait average model is thus hardly surprising, given that this result appears to be highly driven by the effect of height, which generally is strongly correlated with biomass. Such circularity between explanatory and response variable, combined with the fact that it is often unrealistic to measure traits on each individual, may present arguments against using individual-level traits.

Conclusion

This study showed for a range of alien species in Germany that competition is the predominant type of interaction in pairwise settings, although in a quarter of cases aliens experienced facilitation by other aliens, which may have important management implications. We also showed that alien interactions were better explained by hierarchical traits related to competitive ability rather than by multivariate trait distance or phylogenetic relatedness, supporting recent criticism about the applicability of testing limiting similarity versus environmental filtering and the community phylogenetic approach. Contrasting recent suggestions, traits measured at individual-level did not necessarily explain species interaction better. With the continuing accumulation of alien species around the globe, such a better understanding of interactions among invaders is urgently needed. As a next step, interactions among co-occurring alien plants should be studied in a community context, thereby accounting for more direct and indirect biotic interactions in a more natural environment. Furthermore, as it is unlikely that several alien species arrive at the exact same moment in a certain location, studies should also investigate priority effects among alien species and not only between native and alien species.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.xksn02vcv> (Ferenc and Sheppard 2020).

References

Abella, S. R. and Chiquoine, L. P. 2019. The good with the bad: when ecological restoration facilitates native and non-native species. – Restor. Ecol. 27: 343–351.

Adler, P. B. et al. 2018. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. – Ecol. Lett. 21: 1319–1329.

Bennett, J. A. et al. 2016. The reciprocal relationship between competition and intraspecific trait variation. – J. Ecol. 104: 1410–1420.

Bloor, J. M. G. et al. 2008. Responses of *Fraxinus excelsior* seedlings to grass-induced above- and below-ground competition. – Plant Ecol. 194: 293–304.

Carboni, M. et al. 2016. What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. – Ecol. Lett. 19: 219–229.

Carmona, C. P. et al. 2019. Trait hierarchies and intraspecific variability drive competitive interactions in Mediterranean annual plants. – J. Ecol. 107: 2078–2089.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. – Annu. Rev. Ecol. Syst. 31: 343–366.

Conti, L. et al. 2018. Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. – J. Ecol. 106: 1607–1620.

Cornelissen, J. H. C. et al. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. – Oecologia 129: 611–619.

Cushman, J. H. et al. 2011. Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. – J. Ecol. 99: 524–531.

Essl, F. et al. 2011. Socioeconomic legacy yields an invasion debt. – Proc. Natl. Acad. Sci. USA 108: 203–207.

Feng, Y. et al. 2019. Linking Darwin's naturalisation hypothesis and Elton's diversity – invasibility hypothesis in experimental grassland communities. – J. Ecol. 107: 794–805.

Ferenc, V. and Sheppard, C. S. 2020. Data from: the stronger, the better – trait hierarchy is driving alien species interaction. – Dryad Digital Repository, doi:10.5061/dryad.xksn02vcv.

Freckleton, R. P. et al. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. – Am. Nat. 160: 712–726.

Funk, J. L. and Wolf, A. A. 2016. Testing the trait-based community framework: do functional traits predict competitive outcomes? – Ecology 97: 2206–2211.

Goldberg, D. E. and Barton, A. M. 1992. Patterns and consequences of interspecific competition in natural communities : a review of field experiments with plants. – Am. Nat. 139: 771–801.

Golivets, M. and Wallin, K. F. 2018. Neighbour tolerance, not suppression, provides competitive advantage to non-native plants. – Ecol. Lett. 21: 745–759.

Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. – J. Stat. Softw. 33: 1–22.

Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. – J. Appl. Ecol. 46: 10–18.

Jackson, M. C. 2015. Interactions among multiple invasive animals. – Ecology 96: 2035–2041.

Keddy, P. A. 1992. Assembly and response rules : two goals for predictive community ecology. – J. Veg. Sci. 3: 157–164.

Kraft, N. J. B. et al. 2014. Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. – Oikos 123: 1391–1399.

Kraft, N. J. B. et al. 2015. Plant functional traits and the multidimensional nature of species coexistence. – Proc. Natl. Acad. Sci. 112: 797–802.

Kuebbing, S. E. and Nuñez, M. A. 2014. Negative, neutral, and positive interactions among nonnative plants: patterns, processes, and management implications. – Global Change Biol. 21: 926–934.

Kuebbing, S. E. et al. 2013. Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. – Biol. Conserv. 160: 121–129.

Kunstler, G. et al. 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity : implications for forest community assembly. – Ecol. Lett. 15: 831–840.

Lucero, J. E. et al. 2019. The dark side of facilitation: native shrubs facilitate exotic annuals more strongly than native annuals. – NeoBiota 44: 75–93.

MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. – Am. Nat. 101: 377–385.

Maurel, N. et al. 2016. Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. – Global Ecol. Biogeogr. 25: 1500–1509.

Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – Ecol. Lett. 13: 1085–1093.

Munguía-Rosas, M. A. et al. 2011. Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. – Ecol. Lett. 14: 511–521.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. – Methods Ecol. Evol. 4: 133–142.

Ordonez, A. et al. 2010. Functional differences between native and alien species: a global-scale comparison. – Funct. Ecol. 24: 1353–1361.

Richards, C. L. et al. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. – Ecol. Lett. 9: 981–993.

Salguero-Gómez, R. et al. 2018. Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. – Funct. Ecol. 32: 1424–1435.

Seebens, H. et al. 2017. No saturation in the accumulation of alien species worldwide. – Nat. Commun. 8: 14435.

Seebens, H. et al. 2018. Global rise in emerging alien species results from increased accessibility of new source pools. – Proc. Natl Acad. Sci. USA 115: 2264–2273.

Sheppard, C. S. 2019. Relative performance of co-occurring alien plant invaders depends on traits related to competitive ability more than niche differences. – Biol. Invas. 21: 1101–1114.

Sheppard, C. S. et al. 2018. It takes one to know one: similarity to resident alien species increases establishment success of new invaders. – Divers. Distrib. 24: 680–691.

Simberloff, D. and von Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? – Biol. Invas. 1: 21–32.

Spiegelhalter, D. J. et al. 2002. Bayesian measures of model complexity and fit. – J. R. Stat. Soc. Ser. C. Appl. Stat. 64: 583–639.

Stoll, P. and Prati, D. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. – Ecology 82: 319–327.

Tate, R. L. 1995. Soil microbiology. – Wiley.

Temperton, V. M. et al. 2007. Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. – Oecologia 151: 190–205.

van Kleunen, M. et al. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. – Ecol. Lett. 13: 235–245.

van Kleunen, M. et al. 2014. The more the merrier: multi-species experiments in ecology. – Basic Appl. Ecol. 15: 1–9.

Vilà, M. et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. – Ecol. Lett. 14: 702–708.

Violle, C. et al. 2007. Let the concept of trait be functional! – Oikos 116: 882–892.

Violle, C. et al. 2012. The return of the variance: intraspecific variability in community ecology. – Trends Ecol. Evol. 27: 244–252.

Webb, C. O. et al. 2002. Phylogenies and community ecology. – Annu. Rev. Ecol. Syst. 33: 475–505.

Weigelt, A. and Jolliffe, P. 2003. Indices of plant competition. – J. Ecol. 91: 707–720.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. – Plant Soil 199: 213–227.

Supplementary material (available online as Appendix oik-07338 at <www.oikosjournal.org/appendix/oik-07338>). Appendix 1–5.