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REVIEW ARTICLE

Are alien plant species superior to natives, and is this determined by performance measure and study design? A meta-analysis

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ABSTRACT

Biological invasions are a major threat to biodiversity because of invasive alien species' high population growth rates and spread in new ranges. The inherent superiority hypothesis states that particular characteristics of alien species cause them to perform better than native species. Using a meta-analysis of 127 studies and more than 900 experimental observations comparing alien and native plant performance, we investigated, whether: (1) studies comparing alien and native performance generally support the inherent superiority hypothesis; (2) the direction and magnitude of superiority depend on the choice of performance measure; and (3) it depends on other aspects of the study design or species. We found that the inherent superiority hypothesis was overall supported, although the strength of this result depended on the chosen measure of effect size (a significant effect for the standardized mean difference SMD (Hedge's g) but not for the log response ratio LRR). Alien plant species were more likely to be found superior compared to natives if performance was measured in terms of growth, reproduction or response to natural enemies. Measuring survival or abundance was less likely to result in alien superiority, while for measurements of physiology and response to mutualists results were mixed. Furthermore, aspects of experimental design, selection and number of study species played an important role. We thus quantitatively showed across a broad range of conditions how choice of performance measure and experimental design affect the direction and magnitude of alien superiority found in small-scale studies. Furthermore, our review pointed out a lack of studies that assessed population growth as a direct determinant of true superiority. Conducting studies using performance measures relevant for superiority, while also considering other potentially important factors such as residence time, will shed more light on how common true alien superiority is and in which contexts it is to be expected.

Introduction

Biological invasions are a major threat to biodiversity, impacting native species and ecosystems in many ways (Pyšek et al., 2020; Simberloff et al., 2013). However, not all alien species that arrived in a new biogeographical region due to intentional or accidental human-mediated transport become invasive (showing rapid population growth and the potential to spread over large areas; Richardson et al., 2000). Despite considerable advances, even after a few decades of research on biological invasions, there is little general understanding on what makes an alien species invasive. Aspects such as legacy effects depending on introduction history, complex biotic interactions and general context-dependence (due to interactions between species and ecosystems as well as effects of time or invasion stage) have made robust predictions of invasions difficult (Gurevitch et al., 2011; Kueffer et al., 2013; Novoa et al., 2020; van Kleunen et al., 2018). Numerous hypotheses on what makes an alien species invasive have been proposed and tested, usually with variable results.

According to a systematic review by Lowry et al. (2013), the inherent superiority hypothesis is the most often tested hypothesis in invasion biology. This is an umbrella hypothesis (similar to the ideal weed hypothesis) stating that particular characteristics of alien species cause them to perform generally better than native species (but note that many studies do not necessarily refer to this hypothesis by name). This hypothesis thus addresses alien species invasiveness (rather than community invasibility, i.e. the susceptibility of a native community to

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invasions, which is determined by competitive abilities of the native species, the diversity of the community and the environment it is set in, e.g. disturbance, resource supply or climatic conditions, Lonsdale, 1999), regardless of the context or environmental conditions. There is a multitude of possible mechanisms for inherent superiority, such as competitive superiority, a broad tolerance of environmental conditions, high reproductive output, rapid growth rates, dispersal ability or vegetative or self-compatible reproduction systems (Lowry et al., 2013). Although this hypothesis is often tested, the overall support for the inherent superiority hypothesis remains unclear. While many studies find aliens perform generally better than natives (e.g. Guo et al., 2020; Kimball et al., 2014; Siemann & Rogers, 2003; Morrison & Mauck, 2007), there are also plenty of studies with mixed results, where performance advantages depend on factors such as the invasive species studied (e.g. Čuda et al., 2015; Verlinden et al., 2013), environmental conditions (e.g. Vallano et al., 2012) or biotic interactions (e.g. Heard & Sax, 2013). The latter results suggest that superiority may be context-dependent, especially as species invasiveness may interact with aspects of community invasibility (e.g., Catford et al., 2019; Novoa et al., 2020). Additionally, there are studies contradicting the inherent superiority hypothesis, showing that aliens did not perform better than natives (e.g. Domènech & Vilà, 2008; Funk & Zachary, 2010). Further, even if the hypothesis is supported, it is not clear if this is because of true superiority of alien species or because of various types of research bias. Such bias may arise from most studies focusing on a small set of highly invasive species or from a publishing bias, where studies that find strong evidence for invader superiority get published more often. Furthermore, there may be a bias towards easily measured proxies for superiority which may or may not strongly influence true superiority, that is higher population growth rates and spread across a broad range of conditions.

Here we define superiority as the higher performance of alien species compared to native species considering measures of individual size/growth, survival, reproduction, physiological traits and responses to natural enemies or mutualists as well as population size/growth. The demographic performance measures at the individual level thereby should be at least distantly related to population growth or spread (true superiority). We only considered performance measures with a clear expectation of whether higher or lower values are associated with superiority, such as higher growth rates or seedling establishment, but not morphological functional traits whereby higher or lower values may be (dis-)advantageous depending on context, such as specific leaf area or root-to-shoot ratio. We note however that considering the definition of an invasive species, a species should only really be considered superior, if it exhibits higher intrinsic population growth rates and/or spread rates compared to another species in the same environment, making demography central to the understanding of invasion success (Gurevitch et al., 2011). Yet, a broad variety of performance measures have been considered in empirical studies at small spatial scales. These measures are often collected over comparatively short timespans at the individual level, and may only be distantly related to demography, population growth and spread. Hence, it is unclear whether they can be used to test the superiority hypothesis.

The aim of this study is to quantitatively assess across many studies conducted under a broad range of conditions, whether experiments comparing alien and native performance are generally supportive of the inherent superiority hypothesis. Furthermore, we aim to explore how the methods used and the choice of performance measure as proxy for true superiority influence the conclusions drawn in the studies. Thus, we conducted a meta-analysis including 127 small-scale studies with more than 900 observations experimentally comparing performance of alien and native plant species to address the research questions: (1) Do studies comparing alien and native performance generally support the inherent superiority hypothesis? (2) Does the direction and magnitude of superiority reported in the studies depend on the choice of performance measure? (3) Does it depend on other aspects of the study design or study species, including the type of experiment (such as lab, greenhouse, common garden or field), the temporal or spatial scale, the number of alien and native species being compared, the life form of the species, the relatedness between alien and native species being compared, invasion status of the alien species (i.e. alien or invasive) or the competition environment used in the study?

Materials and methods

To address our research questions, we used a meta-analysis, which is a statistical tool that quantitatively synthesizes results across multiple studies (Koricheva & Gurevitch, 2014; Stewart, 2010).

Study selection

We searched for studies which contrasted performance of at least one alien and one native plant species in empirical small-scale studies, such as greenhouse, common garden, lab or field experiments. We focused on plants to make studies more comparable and because plants have been the focus of many such small-scale experiments in invasion biology. To be included, the studies needed to measure some aspect of performance that is at least distantly related to population growth or spread of the study species (alien or native, respectively). Furthermore, the studies had to conduct some type of manipulation of the study species or study environment, such as growing aliens and natives in an artificial environment, having a control versus environmental treatment design or a gradient treatment design (i.e. we excluded purely observational studies).

We carried out a literature search with the search platform Scopus using the following search term: (native OR indigenous) AND (alien OR introduced OR invas* OR invad* OR exotic OR non-indig* OR non-native) AND (greenhouse OR common garden OR field) AND (experiment*). Studies were considered from all years up to and including year 2020. Additionally, we screened studies included in a meta-analysis on the benefits of global environmental change on alien plant species by Liu et al. (2017). Although Scopus generally provides better coverage than Web of Science and has been shown to be suitable as a principal source for systematic literature reviews (Gusenbauer & Haddaway, 2020), we acknowledge that our search is likely not fully comprehensive. Abstracts were checked for suitability of the studies, and if they matched our criteria the publications were then read in full to extract the relevant information (Appendix A: Fig. A1).

Data extraction and moderators

If a study fitted the criteria above, the following information was extracted: general information on the publication, publication year and information on where the study was conducted (i.e. country and continent). We extracted various parameters on the type of study (for the different categorizations, see Table 1), including information on study type in regards to whether it is a greenhouse, field, common garden or lab experiment (note that the last category was only later included, as we did not specifically search for lab experiments with the search term above), spatial and temporal scales and various information on the study species (Table 1). Furthermore, information on the experimental manipulation was documented: we noted whether the experimental design involved competition (intra- or interspecific) or not, as well as the manipulation of other factors, for which effects on alien and native species were tested (e.g. a nutrient addition treatment). Finally, information on the performance measures was extracted, whereby we initially came up with eight performance categories to categorize the different types of measurements (Table 1). However, the category "population growth" had to be excluded as none of the studies in our literature search assessed this performance measure.

For many studies, multiple performance comparisons between alien and native species were extracted. This was the case if several performance measures were included, various experimental manipulations

Table 1
List of moderators. Description of moderators shown with their respective categories (for factors) or unit of measurement (for continuous variables), number of studies and observations included in the meta-analysis using the standardized mean difference (SMD) or the log response ratio (LRR). Note that the number of studies sometimes exceeds 127 as studies may have included several experiments, performance categories etc.

Moderator	Description	Categories or unit of measurement	# studies SMD/ LRR	# observations SMD/ LRR
Study type	Type of empirical small-scale experiment, from which data was measured	Common garden experiment	37/37	270/268
		Field experiment	34/33	165/157
		Greenhouse experiment	62/62	455/448
		Laboratory experiment	9/9	55/52
Performance category	Type of performance under which measurement could be categorized	Growth	96/96	511/503
		Survival	7/7	35/35
		Reproduction	23/22	131/122
		Abundance	10/10	54/54
		Physiology	20/20	133/134
		Natural enemies	19/19	54/51
		Mutualists	8/8	27/26
Relatedness	Taxonomic level of relatedness between the alien and native species	Confamilial	37/37	224/214
		Congener	28/28	179/175
		Other	65/65	542/536
Invasion status	Stage of invasion of the alien species as stated in the study[*]	Alien	52/52	285/281
		Invasive	76/76	660/644
Life form	Lifespan category of the study species	Annual	17/17	135/134
		Short-lived perennial	62/62	444/428
		Long-lived perennial	29/29	207/204
		Mixed[†]	13/13	61/61
		Different life form	15/15	98/98
Competition	Type of competition that was used in the experiment	Interspecific competition	51/51	322/317
		Intraspecific competition	27/27	120/118
		Without competition	76/76	503/490
No. alien species	Number of alien species used in the experiment	#	127/127	945/925
No. native species	Number of native species used in the experiment	#	127/127	945/925
Spatial extent	Distance between sites if there are multiple and they are not adjacent[§]	km	127/127	945/925
Spatial scale	Surface area/plot size	m^2	127/127	945/925
Temporal scale	Duration of the experiment	weeks	127/127	945/925
Total	–	–	127/127	945/925

[*] Other distinct invasion stages such as "casual" or "naturalized" were categorised as "alien", since only two studies used this distinction.
[†] If there were several species from different life forms within both the alien and native study species group, they were documented as "mixed". Conversely, if the alien and native species came from different life forms or plant types, it was documented as "different life form".
[§] if there was only one site or sites were adjacent, the spatial extent was set to zero.

were conducted (since we aimed to gain a broad assessment whether superiority holds across a wide range of environmental conditions), or if several pairs of alien-native species were included. If more than one performance measure was given in the study (e.g. various measures such as survival, biomass and photosynthesis rate were collected), each performance measure that fitted the criteria was included as a separate observation (with this non-independence accounted for by the random effect of study identity, see 'Data analysis'). Similarly, if the study contained multiple experiments (e.g. one common garden and one lab experiment) or if within an experiment there were multiple manipulations of the study environment (such as control – environmental treatment, different treatment combinations, or a gradient design), each individual experiment or experimental manipulation was recorded as a separate observation, if the information provided in the study fitted the criteria above. In case of a gradient design, such as if there were four different concentrations of nutrient addition, the highest and lowest concentration were recorded to focus on the highest contrast and avoid recording similar data.

We extracted details on the performance measure and the measurement unit, as well as the observed mean and measure of variation (standard deviation, standard error or confidence interval) for the alien and native species. For those studies where data was only reported graphically, the Web Plot Digitizer (Rohatgi, 2020) was used to extract information from figures. Before data analysis, standard errors and confidence intervals were converted into standard deviations. Finally, the number of alien and native species as well as respective sample sizes (number of observations) of alien and native species were extracted. Thereby, ideally comparisons of alien versus native performance were extracted at species-level for specific pairs of species (i.e. one alien species versus one native species), or group-level (i.e. several alien species versus the same number of native species) if the species included in the group shared the same life form. However, in case of unclear pairing or unbalanced study design (e.g. one alien species being compared to ten native species), weighted means and standard errors were calculated manually (Appendix A.1). If species were compared within a study that had different life forms, subgrouping by life form was done if possible.

Calculation of effect sizes

As measures of effect size, both the standardized mean difference (SMD), also known as Hedge's g, and the log response ratio (LRR), also known as the log transformed ratio of means, were calculated (Hedges, 1981; Hedges et al., 1999). Both measures are suitable for data comparing two groups (here alien and natives) with respect to the same type of outcome (i.e. superiority), but different measurement methods were used (here various quantitative measures such as survival, biomass, photosynthetic rate) (Borenstein et al., 2009). Because both measures are frequently used in ecological meta-analyses and each measure may have its own (dis-)advantages (Crystal-Ornelas, 2020; Hedges et al., 1999; Koricheva & Gurevitch, 2014; Lajeunesse, 2015) we compared whether the outcome of our analyses would differ if using SMD vs LRR. Means and standard deviations for both alien and native species, as well as the respective sample sizes of individuals for both groups, were used to calculate the effect sizes SMD and LRR using the escalc-function of the metafor-package in R (Viechtbauer, 2010). This results in effect sizes, which estimate the magnitude and direction of the difference between observations of the alien and the native species. For most characteristics measured, the alien species was considered superior to a native species, if it has a larger mean value. However, in some cases a smaller mean was identified as superior performance, for example lower mortality of the individual or a lower fraction of leaf damage by herbivores. In these cases, we inverted the algebraic sign for SMD (Higgins et al., 2019) and for LRR by taking the logarithm of the inverse of the LRR. Variance was not changed, as it is not affected by the direction of the effect size (Higgins et al., 2019). A few observations had to be excluded as effect sizes could not be calculated (e.g. if variance was zero or log of zero). Further, one of the SMD effect sizes appeared to be disproportionally large (-558.62) and was also excluded. Similarly, an effect size with a disproportionally large variance ($9 \times 10\hat{}4$) was excluded for LRR (Appendix A: Fig. A1).

Data analysis

All data was analysed in R v 4.1.0 (R Core Team, 2021) using the metafor-package (Viechtbauer, 2010). To first test whether our set of studies overall support or contradict superiority of aliens (addressing our first research question), a random effects model was run using the rma.mv-function of the metafor-package. Such a model accounts for the heterogeneity (between study variance) arising from dealing with multiple studies, that do not have the same methods or study characteristics. Given that we had multiple observations for most studies, the study identity was added as a random effect. We ran two separate models to analyze the full data set, one model using SMD and one using LRR.

To reveal possible publication bias, we checked funnel plots plotting the standard error against the effect size estimate for the random effect models (Viechtbauer, 2010). In the absence of publication bias, studies with low standard error should be located near the estimated effect size, while studies with high standard error should be symmetrically spread on both sides. The funnel plots indicated some asymmetry mostly from the growth performance category (Appendix A: Fig. A2-A3). Furthermore, Egger's test for funnel plot asymmetry (Egger et al., 1997) was conducted by modifying the original random effects model to include the sampling variance of the effect sizes as a moderator. If the intercept of this regression test was significantly different from zero, the data is considered asymmetrical and hence biased. This test indicated no significant publication bias ($z = 1.24$, $p = 0.214$ for SMD; $z = 0.88$, $p = 0.376$ for LRR). However, when running the tests for subsets of each performance category separately, the test was (marginally) significant for growth, indicating skewedness to the right ($z = 1.93$, $p = 0.053$ for SMD; $z = 2.28$, $p = 0.023$ for LRR), as also visible in the funnel plot (Appendix A: Fig. A2-A3). Additionally, for LRR there was a marginally significant left-skewedness for the category response to natural enemies ($z = -1.78$, $p = 0.074$).

To address the second and third research questions, we conducted mixed effect models using the rma.mv-function of the metafor-package to examine whether study conclusions were dependent on various aspects of the study. Keeping the study identity as a random effect, various categorical and continuous variables were included as moderators (Table 1). The categorical moderators included study type, performance measure, relatedness, invasion status, life form and competition. The continuous moderators spatial extent, spatial scale, temporal scale, number of alien and number of native species were log-transformed (log+1 in case of spatial scale due to many zero-values) and scaled to a mean of zero and standard deviation of one. Again, we ran two separate models, one using SMD as the response variable and one using LRR.

To investigate which moderators are relevant to explain variation in alien superiority, a model selection approach was used to find the best supported model out of the combinations of moderators that are possible from the full mixed effects model above. We compared all $2\hat{}11 = 2048$ combinations of the full mixed effects model using eleven moderators. The models were fitted via maximum likelihood estimation and examined with the dredge-function in the MuMIn package (Barton, 2020), whereby model weights and the small-sample corrected Akaike Information Criterion (AICc) were used to determine the best model. To follow best-practice, when conducting the meta-analysis the checklist of quality criteria by Koricheva and Gurevitch (2014) was considered (Appendix A: Table A2).

Results

Studies included in the meta-analysis

127 studies were included in our meta-analysis, most with several observations, totalling 945 observations for SMD and 925 for LRR respectively (Table 1; Appendix A: Table A1; a considerably higher sample size compared to the median sample size in ecological meta-analyses of 64 effect size observations from 24 studies, Costella & Fox, 2022). All except two studies (from year 1982 and 1994) were published between 2001 and 2020 (Appendix A: Fig. A4 and A5). The largest number of studies were published between 2011 and 2015. Greenhouse experiments (49 % of studies included a greenhouse experiment, amounting to 48 % of the observations) and measurements in the performance category growth (76 % of studies included at least one growth measurement, amounting to 54 % of the observations) were most common (Table 1). There were no clear trends of how (study type) and what (performance category) is being studied over time (Appendix A: Fig. A4 and A5). Most studies were conducted in North America (56 %), followed by Asia (18 %) and Europe (15 %). Africa, Antarctica, Australia and South America each had only 1–5 studies (Appendix A: Table A1). Overall, the mean effect size for SMD was 0.91 ± 4.99 SD, with a median of 0.22, minimum of -22.14 and a maximum of 72.10 (Appendix A: Fig. A6). Mean effect size for LRR was 0.27 ± 1.07 SD, with a median of 0.21, minimum of -5.27 and a maximum of 4.40 (Appendix A: Fig. A7).

Results of the meta-analysis

In answer to our first research question of whether the inherent superiority hypothesis was generally supported, aliens were overall superior to natives across all studies considering the effect size measure SMD, but not LRR. The estimated average effect from the random effect model was 0.30 (95 % confidence interval: 0.05, 0.55, $p = 0.020$) for SMD and 0.09 for LRR (95 % confidence interval: -0.05, 0.22, $p = 0.197$). The Q-test for heterogeneity among true effects is highly significant for both effect size measures (SMD: Q (df=944) = 15,779, $p < 0.001$, LRR: Q (df=924) = 504,823, $p < 0.001$).

All, or almost all, moderators were relevant to explain variance in alien superiority (Table 2, Fig. 1 and 2). The model selection for SMD indicated that the full model was the best with a weight of 88.4 % and difference in AICc of 4.39 lower than the second-best model (one without temporal scale, with a weight of 9.8 %). For LRR there were two best models (differing only in AICc of 0.13), the full model and one without the moderator log number of alien species. These two models had weights of 51.7 and 48.3 % and a difference in AICc of 33.6 lower than all other models. Thus, in answer to our second research question, the direction and magnitude of superiority reported in the studies indeed depended on the performance measure. Considering SMD, alien species were most likely to be considered superior to natives if performance was measured in terms of growth, reproduction, physiology or response to natural enemies (Fig. 1, Table 2). For LRR, response to mutualists also more likely resulted in alien superiority, whereas in contrast to SMD studying physiology was less likely to result in superiority (Fig. 2). For both measures, alien superiority was also less likely to be found when considering survival or abundance.

In answer to our third research question, the direction and magnitude of superiority reported in studies also depended on various other

Table 2
Model parameters with their estimates and 95 % confidence intervals (CI) for the meta-analysis using the standardized mean difference (SMD) and the log response ratio (LRR). Note that the following levels of the moderators are included in the intercept: study type = common garden experiment, performance category = growth, life form = annual, relatedness = confamilial, invasion status = alien, competition = interspecific.

Moderator	Estimate SMD	95 % CI SMD	Estimate LRR	95 % CI LRR
Intercept	2.15	1.64, 2.67	2.46	2.02, 2.90
Study type (field experiment)	0.25	0.03, 0.48	−0.75	−0.96, −0.53
Study type (greenhouse experiment)	−0.93	−1.14, −0.73	−2.70	−2.91, −2.49
Study type (lab experiment)	−0.17	−0.46, 0.13	−2.01	−2.36, −1.67
Performance category (survival)	−1.00	−1.12, −0.88	−0.21	−0.21, −0.20
Performance category (reproduction)	0.19	0.11, 0.26	0.02	−0.03, 0.06
Performance category (abundance)	−0.43	−0.55, −0.32	−0.43	−0.51, −0.35
Performance category (physiology)	−0.0005	−0.13, 0.13	−0.28	−0.32, −0.24
Performance category (natural enemies)	0.06	−0.008, 0.12	0.12	0.05, 0.20
Performance category (mutualists)	−0.56	−0.70, −0.42	0.22	0.15, 0.30
Life form (different life forms)	0.28	−0.06, 0.63	0.39	0.23, 0.55
Life form (long-lived perennial)	0.37	−0.02, 0.77	2.49	2.28, 2.69
Life form (mixed)	0.19	−0.21, 0.59	0.02	−0.31, 0.35
Life form (short-lived perennial)	−0.70	−1.05, −0.36	0.47	0.33, 0.61
Relatedness (congener)	−0.77	−1.23, −0.31	−0.43	−0.56, −0.31
Relatedness (other)	−0.41	−0.81, −0.002	−0.50	−0.61, −0.38
Invasion status (invasive)	−1.54	−1.81, −1.28	−2.61	−2.95, −2.26
Competition (intraspecific)	0.09	0.01, 0.18	−0.22	−0.22, −0.21
Competition (without)	0.20	0.11, 0.28	0.80	0.77, 0.82
Log (spatial extent [km] + 1)	−0.11	−0.12, −0.09	−0.21	−0.23, −0.20
Log (spatial scale [m^2])	−0.18	−0.23, −0.12	−0.30	−0.34, −0.26
Log (temporal scale [weeks])	−0.10	−0.18, −0.02	−0.24	−0.30, −0.18
Log (number of alien species)	−0.55	−0.74, −0.36	−0.09	−0.23, 0.04
Log (number of native species)	0.32	0.15, 0. 49	−0.27	−0.35, −0.18

aspects of the study design and study species. In fact, most of these methodological aspects led to larger differences in superiority compared to the performance measure used. Specifically, common garden and field experiments resulted in the largest positive effect sizes for both SMD and LRR (Fig. 1 and 2, Table 2). Studying long-lived perennials most likely resulted in superior effects, with this finding being much more distinct for LRR. Comparing aliens and natives of the same family (but not genus) more likely resulted in superiority. Interestingly, for both SMD and LRR effect sizes were large and positive when studying alien species in general, but not invasives. For LRR superior effects were more likely found in studies using no competition whereas for SMD, differences in competition environment played a smaller role (Fig. 1 and 2, Table 2). The continuous moderators (spatial extent, spatial and temporal scale, number of alien and native species) all had negative effects on superiority, except for SMD where the number of native species studied increased the chance of finding alien superiority (Table 2). Overall, for SMD, the inherent superiority hypothesis was thus most likely to be supported in a shorter, smaller field experiment considering reproduction of long-lived perennials, comparing few alien-non-invasive species with many confamilial native species in an environment without competition. For LRR, superiority was most likely found in a shorter, smaller common garden experiment considering mutualists of long-lived perennials, comparing few alien non-invasive species with few confamilial native species in an environment without competition.

Discussion

Our meta-analysis of 127 experimental studies with more than 900 effect sizes revealed some support of the inherent superiority hypothesis, showing higher performance of aliens compared to natives across a broad range of environmental conditions (although mostly limited to studies in the Northern hemisphere) at least for SMD. However, across studies and observations, we found large variation in the direction and magnitude of effect sizes, showing that superiority of alien species is also context-dependent. Effect sizes were highly influenced by the performance measure, characteristics of study species and other aspects of the study design, but the exact nature of these effects also depended on the choice of effect size measure.

Is the inherent superiority hypothesis generally supported across studies?

Overall, both effect size measures (SMD and LRR) were positive across the many different studies, environmental conditions and performance observations we considered, indicating that aliens were generally superior to natives, but this effect was only significant for SMD. In line with supporting inherent superiority of alien species, in a previous meta-analysis invasive species were shown to have higher values compared to natives in traits related to fitness, size, growth rates, allocation patterns and physiology (van Kleunen et al., 2010). Similarly, another meta-analysis showed that alien plants were more tolerant to competition than natives (Golivets & Wallin, 2018). Such superior performance of alien species may then result in negative impacts on native species. One may argue that invasive species by definition should be superior, however, the classification as "invasive" is often subjective and invasive species may only be superior in certain contexts (under specific environmental conditions or depending on community invasibility) and superiority may also change with invasion stage or over time (Catford et al., 2019). Our study included also alien species in general rather than just those species specifically pointed out as invasive. Nevertheless, several authors have argued that the field of invasion biology is biased towards reporting negative effects of a few particularly harmful invasive species, ignoring neutral or positive effects (Charlebois & Sargent, 2017; Davis et al., 2011; Davis & Chew, 2017; Thomas & Palmer, 2015). Such a bias in study species or in reporting of negative effects could contribute to an overall positive effect size regarding alien superiority (particularly in the growth category, where there was tendency towards publication bias of positive results). Given the large variation in the direction (61 % of individual effect sizes being positive) and magnitude (Appendix A: Fig. A6-A7) of effect sizes we found, alien superiority clearly is not universal. Furthermore, superiority also depends on many other aspects, some of which we discuss below. Finally, as seen by comparing the results from SMD and LRR, the calculation of the effect size measure to compare means and variance (and with it the weighing) can strongly influence results.

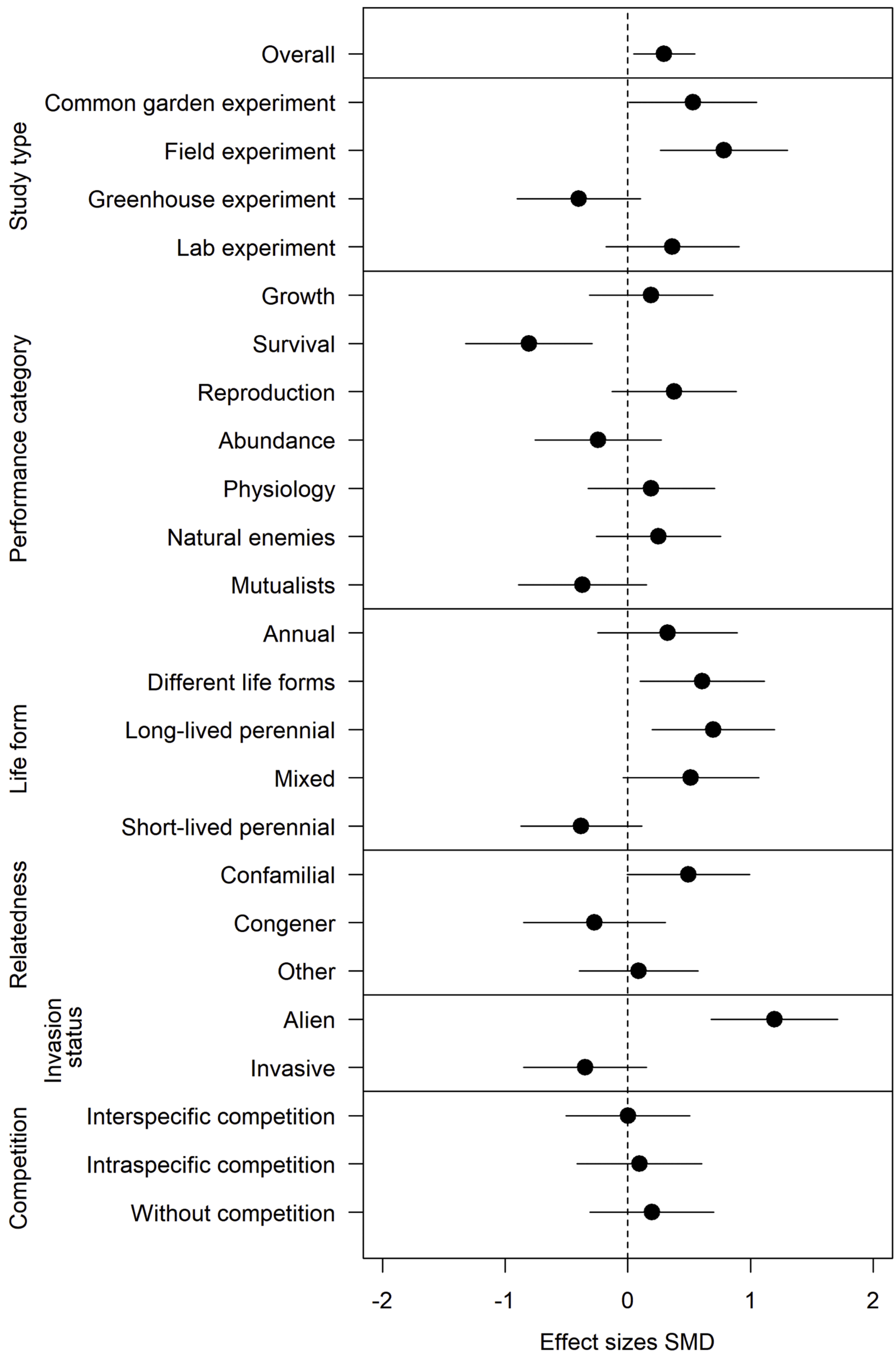

Fig. 1. Predicted effect sizes with 95 % confidence intervals for the meta-analysis using the standardized mean difference (SMD). The overall effect shows the result of the random effects model. The effects shown for the various levels of each moderator originate from the full mixed-effects model. Thereby, the predicted values for each moderator were calculated separately by creating predictions across the dataset when fixing each level of interest (945 predictions for each observation, then taking the mean and mean confidence interval), thus resulting in a mean prediction for each level weighted by frequency of the levels of the other moderators.

Both SMD and LRR are commonly used for meta-analyses in ecology and evolution (Koricheva & Gurevitch, 2014). Hedge's g (SMD), as a standardized measure, allows data to be synthesized that were measured on different scales, such as the various performance measures considered here. Log response ratios quantify the proportional change and when back-transformed are easily interpretable (Crystal-Ornelas, 2020). In our study, SMD might be more appropriate, as Hedge's g (SMD) statistically corrects for variance due to small sample sizes, whereas the variance estimate for LRR may be biased for small sample sizes or when one of the sample means is close to zero (Lajeunesse, 2015). Ecological

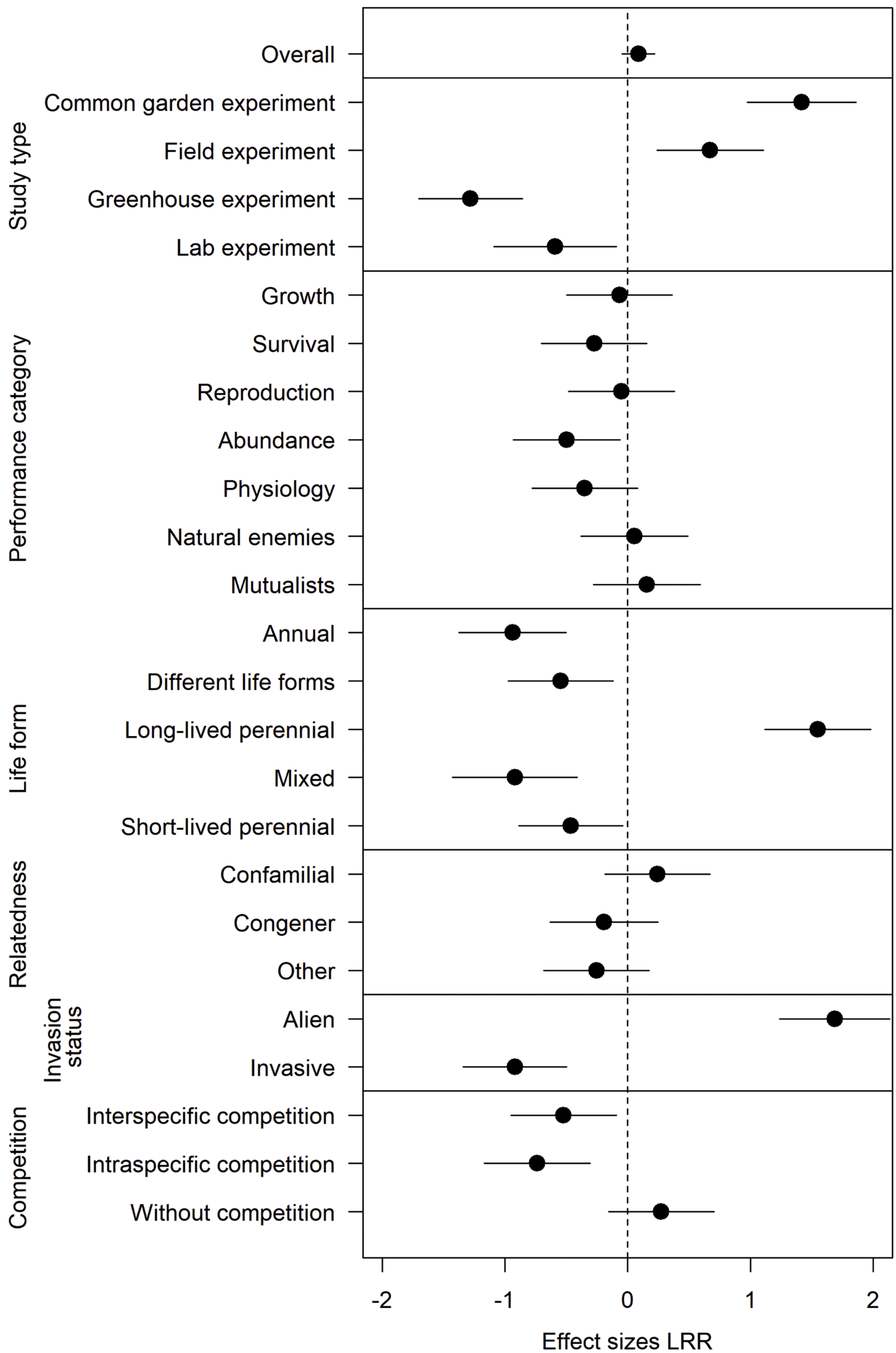

Fig. 2. Predicted effect sizes with 95 % confidence intervals for the meta-analysis using the log response ratio (LRR). The overall effect shows the result of the random effects model. The effects shown for the various levels of each moderator originate from the full mixed-effects model. Thereby, the predicted values for each moderator were calculated separately by creating predictions across the dataset when fixing each level of interest (925 predictions for each observation, then taking the mean and mean confidence interval), thus resulting in a mean prediction for each level weighted by frequency of the levels of the other moderators.

studies often have small sample sizes, for instance in our data set samples had a median of 18–20 (with a range of 2–1280) observations. Furthermore, when means are close to zero, the weights in LRR will be disproportionally small (Lajeunesse, 2015) – indeed in our data set, the ratio of largest to smallest variance was very large. Bias is also higher when there are larger differences between the means (Lajeunesse, 2015), which might be particularly the case as we were comparing two (or several) different species that are not always closely related. Because LRR can also show greater heterogeneity than SMD (which minimizes individual sampling error of the alien vs native group by homogenizing and pooling the standard deviations from these two groups) this can result in different outcomes of meta-analyses on the same data set (Lajeunesse, 2015). In our study, the performance measures included in a single analysis were rather broad, which may also have contributed to these differences. The most appropriate choice of effect size or rather the limitations with each one and how to overcome them is an issue that should be further explored in future studies.

Do the direction and magnitude of superiority depend on performance measure?

The direction and magnitude of alien superiority depended on what aspect of performance was measured. We divided the different measures of superiority into several performance categories, some of which influence population growth and/or spread rates directly (i.e. growth, survival, reproduction and abundance) and some more indirectly (physiology and interactions with natural enemies or mutualists), to assess any bias in choice of performance measure on findings of superiority. Population growth and spread of alien species necessarily arise from variation in reproduction, survival (mortality) and dispersal (Gurevitch et al., 2011; Sakai et al., 2001; Schurr et al., 2012). This demographic variation in turn is determined by the abiotic and biotic environment (such as interactions with natural enemies and mutualists). Comparing the demographic rates, studies measuring growth and reproduction more likely resulted in positive effect sizes, whereas for survival effect sizes were negative. The finding that alien species were superior in growth and reproduction compared to aliens may directly influence their invasion success: elasticity analyses of matrix population models of 21 invasive and 179 native plant species showed that growth and fecundity had a larger effect on population growth of invaders whereas survival was more important for native species (Ramula et al., 2008). Also, in our meta-analysis most study species were short-lived perennials (i.e. herbs), for which growth and reproduction have higher elasticities than in trees (Franco & Silvertown, 2004).

The finding that studies on response to natural enemies resulted on average in positive effect sizes may not be surprising, given that the enemy release hypothesis is one main explanation for invader superiority (Keane & Crawley, 2002). Nevertheless, the performance measures considered in this category may not always be highly relevant for true superiority, that is population growth and spread rates. For example, statistically significant differences between native and alien species in levels of damage from herbivory (as a frequently used performance measure) are taken as support of the enemy release hypothesis, but such differences need not translate into differences in growth, reproduction or survival (Chun et al., 2010). Compared to responses to natural enemies, less is known on the role of mutualists for invasions, although it is thought that because many mutualists are generalists, lack of mutualism is unlikely to prevent invasion success (Richardson et al., 2000). The direction of effect we found in this category differed depending on the effect size measure (this category, however, also had the fewest observations). Our results regarding physiology also depended on the effect size measure. This category included various traits (e.g. related to photosynthesis rates or nutrient uptake) for which effects on population growth may be ambiguous and more dependent on the manner in which effect sizes were calculated.

Given that within our search term we did not find any studies measuring population growth, it is difficult to determine whether the overall positive effect size (for SMD) is due to true inherent superiority of alien species or due to a research bias. With a more targeted search for studies considering population growth in Scopus (using the search term: (native OR indigenous) AND (alien OR introduced OR invas* OR invad* OR exotic OR non-indig* OR non-native) AND (plant) AND ("population growth")) we found 263 studies from all years up to and including year 2020. We screened the Abstracts to check if these studies truly investigated population growth and found only 16 studies (published 2000–2017) in which population growth of both alien and native species were compared. In these studies, population growth was modelled from demographic rates such as survival and reproduction (rather than directly measured in the field, and thus likely not picked up or included by our search term including experiment*). For instance, Merow et al. (2017) investigated population growth of invasive *Alliaria petiolata* and *Berberis thunbergii* compared to native species and forecasted range changes under climate change in England. Demographic rates were measured in transplant plots and then used in structured population models. In another study, population growth rates of invasive *Cynoglossum officinale* and native *Hackelia micrantha* were studied in response to a biocontrol agent, using an experimental field study measuring demographic rates combined with matrix population models (Catton et al., 2016). Such a bottom-up approach that integrates small-scale data with demographic analyses that measure the sensitivity of population growth to the small-scale performance measures (Caswell et al., 2011) may help to more conclusively answer the question of inherent superiority of alien species. For short-lived species, population growth can also be directly measured in experimental settings (such as measured for alien and native Asteraceae over two years; Brendel et al., 2021).

Do the direction and magnitude of superiority depend on other aspects of study species and design?

All moderators we considered were important determinants of effect size as they were included in at least one best model. Choice of study design and type and number of study species thus influenced the likelihood of finding alien superiority. Experiments under more natural conditions (common garden, field) were more likely to find alien superiority, hinting that the alien superiority we found may indeed be due to true superiority rather than due to superiority found only under certain artificial conditions. In contrast, the negative effects of the continuous moderators suggested that superiority may be more likely due to a research bias than true superiority, as the likelihood of finding superiority generally decreased with spatial and temporal extent and number of study species. Long-term experiments are however crucial to better understand invasions (Catford et al., 2019).

Regarding life forms, we found the strongest positive effect for long-lived perennials (an effect which was much more distinct for LRR), as although fewer trees and shrubs are invasive, this group includes some of the most invasive species (Richardson & Rejmánek, 2011). Comparing species of the same family but not genus, that is native species chosen to be similar but not too similar, resulted in the largest superiority. One possible explanation for this finding is that there might be a bias in choosing poorly competitive, rare native species for comparison (Vilà & Weiner, 2004; Zhang & van Kleunen, 2019). When not restricted to choose species from the same genus, this bias might be exacerbated, whereas choosing entirely different species may result in higher variance (and thus lower weight in the meta-analysis). We also found that alien superiority was most likely found in experimental settings without competition. This is in line with what is expected from the typical alien species characteristics and the habitats they are found in. Alien species most commonly dominate in disturbed, ruderal sites (Chytrý et al., 2008), and being ruderal (i.e. R-strategists following Grime's CSR) increases the probability of alien plant establishment (Guo et al., 2018).

Finally, the most distinct effect we found (consistent across both SMD and LRR) was the counterintuitive finding that alien species (non-invasive according to the authors; ca. 40 % of the studies) were more likely to be found superior compared to alien invasive species. Several factors combined may explain this finding. The classification as "invasive" if not based on rapid population growth and spread (Richardson et al., 2000) is often based on impact (ecological, economic or human well-being) (International Union for Conservation of Nature, www.iucn.org). Our finding may suggest that this classification is too subjective and thus not based on actual superior performance. However, alien rather than invasive superiority may also be a result of certain characteristics of our data set. A far higher proportion of 78 % of studies on aliens compared to studies on invasives (54 %) measured growth or reproduction (which tended to have positive effect sizes). More importantly, although mean and median effect sizes for the two categories were not widely different (and for SMD in fact higher for invasives with a mean = 1.02 and median = 0.36, compared to aliens with a mean = 0.65 and median = 0.11), similar effect sizes tended to have lower variance in the alien category and thus likely resulted in a stronger effect, as large SMD values can result not only from a large difference in means but also from a small pooled variance (Koricheva et al., 2013).

Beyond the moderators we considered, there may be other factors important in determining alien superiority, such as the environmental conditions. In our study we specifically wished to assess superiority across a broad range of conditions, and hence included where possible also multiple experimental treatments that varied the abiotic environment. The meta-analysis by Stotz et al. (2016) found that temperature and precipitation influenced biotic resistance, that is the strength by which native communities inhibited alien plant species emergence, survival, reproduction or size. Furthermore, alien success has been shown to be higher in disturbed, nutrient-rich conditions; for instance, another meta-analysis showed that those alien species that responded more strongly to increased resources were more widespread globally (Dawson et al., 2012). Thus, the effect of abiotic conditions should be additionally evaluated in future studies. Furthermore, another aspect that is less often considered is the influence of residence time on whether alien species are superior to natives. The outcome of eco-evolutionary processes during an invasion depends on the time since introduction to a new area: longer residence time may lead to adaptation to a new climate or adaptation of native species to the alien (Brendel et al., 2021; Sheppard & Schurr, 2019), and thus alien superiority may change over time.

Conclusions

Although overall alien species may indeed more likely be superior than natives, more importantly, the likelihood of superiority depends on many factors, including performance measure, aspects of experimental design, selection and number of study species, and choice of measures for statistical analysis. We here quantitatively showed across a broad range of studies and environmental conditions how these aspects affect the direction and magnitude of superiority found in small-scale studies. Thus, authors of future studies on alien superiority should carefully consider how their experimental choices may affect the conclusions drawn from their study. Besides providing a quantitative synthesis on the research findings so far, the conclusions from meta-analyses are meant to provide guidance for future primary studies to follow up on its results (Koricheva & Gurevitch, 2014). The partially conflicting results in our meta-analysis between effects of SMD and LRR highlight one important avenue for future research, investigating the causes of these differences. Furthermore, our review pointed out a lack of studies considering population growth as a direct measure of true superiority. Compiling studies on population growth would allow a future meta-analysis to shed light on how common true alien superiority is, and thus also provide information on which other performance measures might be biased towards superiority. Conducting studies using performance measures relevant for superiority, while also considering potentially confounding effects such as varying abiotic conditions and effects of residence time should clarify results on the contexts in which alien superiority is expected.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.04.002.

References

Barton, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. Https://CRAN.R-project.org/package=MuMIn.

Borenstein, M., Hedges, L. V., Higgins, J. P. T., & Rothstein, H. R. (2009). *Introduction to meta-analysis*. John Wiley & Sons.

Brendel, M. R., Schurr, F. M., & Sheppard, C. S. (2021). Inter- and intraspecific selection in alien plants: How population growth, functional traits and climate responses change with residence time. *Global Ecology and Biogeography, 30*(2), 429–442. https://doi.org/10.1111/geb.13228

Costello, L., & Fox, J. W. (2022). Decline effects are rare in ecology. *Ecology, 103*(6), e3680. https://doi.org/10.1002/ecy.3680

Catford, J. A., Smith, A. L., Wragg, P. D., Clark, A. T., Kosmala, M., Cavender-Bares, J., Reich, P. B., & Tilman, D. (2019). Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. *Ecology Letters, 22*(4), 593–604. https://doi.org/10.1111/ele.13220

Caswell, H., Neubert, M. G., & Hunter, C. M. (2011). Demography and dispersal: Invasion speeds and sensitivity analysis in periodic and stochastic environments. *Theoretical Ecology, 4*(4), 407–421. https://doi.org/10.1007/s12080-010-0091-z

Catton, H. A., Lalonde, R. G., Buckley, Y. M., & De Clerck-Floate, R. A. (2016). Biocontrol insect impacts population growth of its target plant species but not an incidentally used nontarget. *Ecosphere (Washington, D.C), 7*(5), e01280. https://doi.org/10.1002/ecs2.1280

Charlebois, J. A., & Sargent, R. D. (2017). No consistent pollinator-mediated impacts of alien plants on natives. *Ecology Letters, 20*(11), 1479–1490. https://doi.org/10.1111/ele.12831

Chun, Y. J., van Kleunen, M., & Dawson, W. (2010). The role of enemy release, tolerance and resistance in plant invasions: Linking damage to performance. *Ecology Letters, 13*(8), 937–946. https://doi.org/10.1111/j.1461-0248.2010.01498.x

Chytrý, M., Maskell, L. C., Pino, J., Pyšek, P., Vilà, M., Font, X., & Smart, S. M. (2008). Habitat invasions by alien plants: A quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology, 45*(2), 448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x

Crystal-Ornelas, R. (2020). robcrystalornelas/meta-analysis_of_ecological_data: First release (Version v0.1.0). *Zenodo*. https://doi.org/10.5281/zenodo.4320107

Čuda, J., Skálová, H., Janovský, Z., & Pyšek, P. (2015). Competition among native and invasive Impatiens species: The roles of environmental factors, population density and life stage. *AoB PLANTS, 7*, plv033. https://doi.org/10.1093/aobpla/plv033

Davis, M. A., & Chew, M. K. (2017). 'The denialists are coming!' Well, not exactly: A response to Russell and Blackburn. *Trends in Ecology & Evolution, 32*(4), 229–230. https://doi.org/10.1016/j.tree.2017.02.008

Davis, M. A., Chew, M. K., Hobbs, R. J., Lugo, A. E., Ewel, J. J., Vermeij, G. J., Brown, J. H., Rosenzweig, M. L., Gardener, M. R., Carroll, S. P., Thompson, K., Pickett, S. T. A., Stromberg, J. C., Tredici, P. D., Suding, K. N., Ehrenfeld, J. G., Philip Grime, J., Mascaro, J., & Briggs, J. C. (2011). Don't judge species on their origins. *Nature, 474*(7350), 153–154. https://doi.org/10.1038/474153a

Dawson, W., Rohr, R. P., van Kleunen, M., & Fischer, M. (2012). Alien plant species with a wider global distribution are better able to capitalize on increased resource availability. *New Phytologist, 194*(3), 859–867. https://doi.org/10.1111/j.1469-8137.2012.04104.x

Domènech, R., & Vilà, M. (2008). Response of the invader *Cortaderia selloana* and two coexisting natives to competition and water stress. *Biological Invasions, 10*(6), 903–912.

Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *BMJ (Clinical research ed.), 315*(7109), 629–634. https://doi.org/10.1136/bmj.315.7109.629

Franco, M., & Silvertown, J. (2004). A comparative demography of plants based upon elasticities of vital rates. *Ecology, 85*(2), 531–538. https://doi.org/10.1890/02-0651

Funk, J. L., & Zachary, V. A. (2010). Physiological responses to short-term water and light stress in native and invasive plant species in southern California. *Biological Invasions, 12*(6), 1685–1694. https://doi.org/10.1007/s10530-009-9581-6

Golivets, M., & Wallin, K. F. (2018). Neighbour tolerance, not suppression, provides competitive advantage to non-native plants. *Ecology Letters, 21*(5), 745–759. https://doi.org/10.1111/ele.12934

Guo, W. Y., Kleunen, M.van, Winter, M., Weigelt, P., Stein, A., Pierce, S., Pergl, J., Moser, D., Maurel, N., Lenzner, B., Kreft, H., Essl, F., Dawson, W., & Pyšek, P. (2018). The role of adaptive strategies in plant naturalization. *Ecology Letters, 21*(9), 1380–1389. https://doi.org/10.1111/ele.13104

Guo, X., Xu, Z. W., Li, M. Y., Ren, X. H., Liu, J., & Guo, W. H. (2020). Increased soil moisture aggravated the competitive effects of the invasive tree *Rhus typhina* on the native tree *Cotinus coggygria*. *BMC Ecology, 20*(1), 17. https://doi.org/10.1186/s12898-020-00284-9

Gurevitch, J., Fox, G. A., Wardle, G. M., Inderjit, & Taub, D (2011). Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters, 14*(4), 407–418. https://doi.org/10.1111/j.1461-0248.2011.01594.x

Gusenbauer, M., & Haddaway, N. R. (2020). Which academic search systems are suitable for systematic reviews or meta-analyses? Evaluating retrieval qualities of Google Scholar, PubMed, and 26 other resources. *Research Synthesis Methods, 11*(2), 181–217. https://doi.org/10.1002/jrsm.1378

Heard, M. J., & Sax, D. F. (2013). Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and susceptibility to herbivores. *Ecology Letters, 16*(2), 206–213.

Hedges, L. V. (1981). Distribution theory for Glass's estimator of effect size and related estimators. *Journal of Educational Statistics, 6*(2), 107–128. https://doi.org/10.2307/1164588

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology, 80*(4), 1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

Higgins, J. P. T., Thomas, J., Chandler, J., Cumpston, M., Li, T., Page, M., & Welch, V. (2019). *Cochrane handbook for systematic reviews of interventions* (2nd ed.). John Wiley & Sons.

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution, 17*(4), 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Kimball, S., Gremer, J. R., Barron-Gafford, G. A., Angert, A. L., Huxman, T. E., & Venable, D. L. (2014). High water-use efficiency and growth contribute to success of non-native *Erodium cicutarium* in a Sonoran Desert winter annual community. *Conservation Physiology, 2*(1). https://doi.org/10.1093/conphys/cou006

Koricheva, J., & Gurevitch, J. (2014). Uses and misuses of meta-analysis in plant ecology. *Journal of Ecology, 102*(4), 828–844. https://doi.org/10.1111/1365-2745.12224. Scopus.

Koricheva, J., Gurevitch, J., & Mengersen, K. (2013). *Handbook of meta-analysis in ecology and evolution*. Princeton University Press.

Kueffer, C., Pyšek, P., & Richardson, D. M. (2013). Integrative invasion science: Model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist, 200*(3), 615–633. https://doi.org/10.1111/nph.12415

Lajeunesse, M. J. (2015). Bias and correction for the log response ratio in ecological meta-analysis. *Ecology, 96*(8), 2056–2063. https://doi.org/10.1890/14-2402.1

Liu, Y., Oduor, A. M. O., Zhang, Z., Manea, A., Tooth, I. M., Leishman, M. R., Xu, X., & van Kleunen, M. (2017). Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology, 23*(8), 3363–3370. https://doi.org/10.1111/gcb.13579

Lonsdale, W. M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology, 80*(5), 1522–1536. https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2

Lowry, E., Rollinson, E. J., Laybourn, A. J., Scott, T. E., Aiello-Lammens, M. E., Gray, S. M., Mickley, J., & Gurevitch, J. (2013). Biological invasions: A field synopsis, systematic review, and database of the literature. *Ecology and Evolution, 3*(1), 182–196. https://doi.org/10.1002/ece3.431. Scopus.

Merow, C., Bois, S. T., Allen, J. M., Xie, Y., & Silander, J. A. (2017). Climate change both facilitates and inhibits invasive plant ranges in New England. *Proceedings of the National Academy of Sciences, 114*(16), E3276–E3284. https://doi.org/10.1073/pnas.1609633114

Morrison, J. A., & Mauck, K. (2007). Experimental field comparison of native and non-native maple seedlings: Natural enemies, ecophysiology, growth and survival. *Journal of Ecology, 95*(5), 1036–1049. https://doi.org/10.1111/j.1365-2745.2007.01270.x

Novoa, A., Richardson, D. M., Pyšek, P., Meyerson, L. A., Bacher, S., Canavan, S., Catford, J. A., Čuda, J., Essl, F., Foxcroft, L. C., Genovesi, P., Hirsch, H., Hui, C., Jackson, M. C., Kueffer, C., Le Roux, J. J., Measey, J., Mohanty, N. P., Moodley, D., … Wilson, J. R. U. (2020). Invasion syndromes: A systematic approach for predicting biological invasions and facilitating effective management. *Biological Invasions, 22*(5), 1801–1820. https://doi.org/10.1007/s10530-020-02220-w

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., … Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews,, 95*(6), 1511–1534. https://doi.org/10.1111/brv.12627

R Core Team. (2021). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org/.

Ramula, S., Knight, T. M., Burns, J. H., & Buckley, Y. M. (2008). General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. *Journal of Applied Ecology, 45*(4), 1124–1133. https://doi.org/10.1111/j.1365-2664.2008.01502.x. Scopus.

Richardson, D. M., Allsopp, N., D'antonio, C. M., Milton, S. J., & Rejmánek, M (2000a). Plant invasions—The role of mutualisms. *Biological Reviews, 75*(1), 65–93. https://doi.org/10.1111/j.1469-185X.1999.tb00041.x

Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Dane Panetta, F., & West, C. J. (2000b). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions, 6*(2), 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Richardson, D. M., & Rejmánek, M. (2011). Trees and shrubs as invasive alien species – A global review. *Diversity and Distributions, 17*(5), 788–809. https://doi.org/10.1111/j.1472-4642.2011.00782.x

Rohatgi, A. (2020). WebPlotDigitizer (4.4) [Computer software]. Https://automeris.io/WebPlotDigitizer.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., & Weller, S. G. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics, 32*(1), 305–332. https://doi.org/10.1146/annurev.ecolsys.32.081501.114037

Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., Hartig, F., Kissling, W. D., Linder, H. P., Midgley, G. F., Schröder, B., Singer, A., & Zimmermann, N. E. (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography, 39*(12), 2146–2162. https://doi.org/10.1111/j.1365-2699.2012.02737.x

Sheppard, C. S., & Schurr, F. M. (2019). Biotic resistance or introduction bias? Immigrant plant performance decreases with residence times over millennia. *Global Ecology and Biogeography, 28*(2), 222–237. https://doi.org/10.1111/geb.12844

Siemann, E., & Rogers, W. E. (2003). Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. *Journal of Ecology, 91*(6), 923–931. https://doi.org/10.1046/j.1365-2745.2003.00822.x

Simberloff, D., Martin, J. L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology and Evolution, 28*(1), 58–66.

Stewart, G. (2010). Meta-analysis in applied ecology. *Biology Letters, 6*(1), 78–81. https://doi.org/10.1098/rsbl.2009.0546

Stotz, G. C., Pec, G. J., & Cahill, J. F. (2016). Is biotic resistance to invaders dependent upon local environmental conditions or primary productivity? A meta-analysis. *Basic and Applied Ecology, 17*(5), 377–387. https://doi.org/10.1016/j.baae.2016.04.001

Thomas, C. D., & Palmer, G. (2015). Non-native plants add to the British flora without negative consequences for native diversity. *Proceedings of the National Academy of Sciences, 112*(14), 4387–4392. https://doi.org/10.1073/pnas.1423995112

Vallano, D. M., Selmants, P. C., & Zavaleta, E. S. (2012). Simulated nitrogen deposition enhances the performance of an exotic grass relative to native serpentine grassland competitors. *Plant Ecology, 213*(6), 1015–1026. https://doi.org/10.1007/s11258-012-0061-1

van Kleunen, M., Bossdorf, O., & Dawson, W. (2018). The ecology and evolution of alien plants. *Annual Review of Ecology, Evolution, and Systematics, 49*, 25–47. https://doi.org/10.1146/annurev-ecolsys-110617-062654

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters, 13*(2), 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Verlinden, M., Van Kerkhove, A., & Nijs, I. (2013). Effects of experimental climate warming and associated soil drought on the competition between three highly invasive West European alien plant species and native counterparts. *Plant Ecology, 214*, 243–254.

Viechtbauer, W. (2010). Conducting meta-analysis in R with the metafor package. *Journal of Statistical Software, 36*(3), 1–48.

Vilà, M., & Weiner, J. (2004). Are invasive plant species better competitors than native plant species? - Evidence from pair-wise experiments. *Oikos (Copenhagen, Denmark), 105*(2), 229–238.

Zhang, Z., & van Kleunen, M.van. (2019). Common alien plants are more competitive than rare natives but not than common natives. *Ecology Letters, 22*(9), 1378–1386. https://doi.org/10.1111/ele.13320