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Negative competitive effects of invasive plants change with time since invasion

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Abstract. Competitive impacts of invasive species may vary across invaded ranges, owing to spatio-temporal gradients in adapted traits and abundance levels. Higher levels of interspecific competition in recently invaded areas may lead invaders to be more competitive. Here, using meta-analysis and home range estimation techniques, we examine how negative competitive effects of invasive species vary across different spatio-temporal invasion contexts. We conducted a meta-analysis of 26 studies that used greenhouse microcosm and common garden pairwise experiments to measure the growth response of native plants in the presence of terrestrial plant invaders (totaling 36 species), and compared this to the time since invasion at the collection site (number of years between the estimated year of initial invasion, by spread of the invader, and the time of collection for the study). We show that negative competitive effects decline across sites that had been invaded for longer periods of time, with effects of invasive grasses declining more rapidly over time than forbs, herbs and shrubs. To our knowledge, only two studies have directly measured competitive or consumptive effects of invaders across a gradient of time since invasion; our study is the first to identify a general pattern of temporal variation of competitive effects that may be attributed to intraspecific trait differences. Management efforts may be guided by such spatio-temporal patterns of invader impact, particularly for grasses.

Key words: competition; home range estimation; impact; invasive species; meta-analysis; plant; spatio-temporal gradient; time since invasion; trait variation.

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INTRODUCTION

Impacts of invasive species on recipient communities are highly dynamic and can vary spatio-temporally. Intraspecific trait differences of an invasive species across its invaded range may create differences in impact with time since invasion. As an invader spreads, it moves from an established source population, where intraspecific competition is relatively high, to an invasion front where interspecific competition dominates (hereafter our use of the terms "invasive" and "invader" requires that the non-native population has actively spread from the site of introduction) (Lankau et al. 2009, Phillips et al. 2010*b*). Invasive species may adapt to the gradient in intra/interspecific interactions by becoming more competitive at invasion fronts (Lankau et al. 2009, Lankau 2012), as interspecific competition is one of the primary factors limiting the spread and abundance of an invader, particularly for plants (Crawley 1990, Vilà and Weiner 2004). Lankau et al. (2009) found that the competitive impact of an invasive plant was negatively correlated with time since invasion owing to reduced production of allelopathic chemicals in established individuals. Invading birds have also been found to be highly aggressive upon recent invasion, and this behavioral trait declines rapidly as interspecific competition diminishes over time (Duckworth and Badyaev 2007). Though spatio-temporal changes in physical and behavioral traits of invasive species have been documented (Phillips et al. 2010*a*, Llewellyn et al. 2011, Lopez et al. 2012), it is still unclear how trait variation across invaded ranges may influence invader ecological impacts. To our knowledge, only two studies have compared the competitive (Lankau et al. 2009) and consumptive per capita effects (Iacarella et al. 2015) of invaders across spatio-temporal gradients of invasion; a general pattern of variation in invader impacts across time since invasion remains to be tested.

Impacts of invasive species may also change over time in response to local adaptations and shifts in community composition (Strayer et al. 2006). A community that is evolutionarily naïve to an invader may take time to develop appropriate competitive (Callaway and Aschehoug 2000), consumptive (Pimm 1987) or avoidance responses (Cox and Lima 2006). For instance, invasive plant growth has been found to be more suppressed by negative soil feedbacks with time since invasion (Diez et al. 2010). Abundance of the invader will also change over time, though the relationship between invader abundance and impact may increase (Thomsen et al. 2011) or decrease linearly (Kornis et al. 2014), or have a non-linear relationship, depending on the response being measured (Yokomizo et al. 2009, Jackson et al. 2015). Changes in impacts over time are not well understood as most impact studies are conducted for less than a year, and 40% of studies do not report the time since invasion of their study organism (Strayer et al. 2006).

The overall ecological impact of an invasion is a function of the per capita effect, abundance and range of the invader (Parker et al. 1999). Measurements of per capita effect provide a mechanistic understanding of the impact of an invader and, moreover, are necessary to detect trait-based differences between and within invasive populations (Parker et al. 1999, Dick et al. 2014). For instance, predatory and behavioral responses of invasive crayfishes have been found to differ across native and introduced ranges, which may explain variation in field impacts (Pintor et al. 2008, Pintor and Sih 2009). Ecological impacts are highly context dependent, and per capita effects measured across different abiotic (Hwang and Lauenroth 2008, Verlinden et al. 2013) and biotic contexts (Ellrott et al. 2007, Haddaway et al. 2012) can aid in the prediction of field impacts (Ricciardi et al. 2013). Predictions of when and where impacts of invasive species will be highest can enable prioritization of management efforts.

Here, we present a meta-analysis combined with home range estimation for measurements of time since invasion to test a global temporal trend in negative competitive effects of invasive terrestrial plants. Invasive plants tend to be superior competitors (Vilà and Weiner 2004, Simberloff et al. 2012) and have higher impacts on resident species in the invaded range than in the invader's native range (Callaway and Aschehoug 2000). However, it is generally unknown how competitive effects of invasive species vary temporally across invaded ranges. Our meta-analysis uses pairwise experiments that test competition between invasive and native plants in different density combinations (i.e., additive and substitutive designs), and thus does not directly compare per capita effects; most importantly, we remove the potential influence of invader abundance changing with time since invasion by only including experiments with controlled initial invader densities. This is different from correlative field studies which cannot distinguish between the contribution of per capita effects and abundance to measures of impact. It is necessary to assess competitive and consumptive effects in controlled settings to develop a mechanistic understanding of impact variation across spatio-temporal gradients. We test the hypothesis that negative competitive effects of invasive plants decline with time since invasion.

METHODS

Impact data collection

Study selection criteria.—Through the Web of Science database, we searched for studies published during the period from 1970 to 2013 on experimentally measured changes in native populations attributable to impacts of invasive species. Papers were selected from the literature search based on the following criteria: (1) the invasive species had spread from its original site of introduction (i.e., recent time since invasion does not correspond with recent introduction); (2) a control treatment was run simultaneously to measure the performance of native species without the invader present; (3) the abundance of the invasive species was controlled, thus excluding removal experiments and surveys; (4) the collection location of the invader was stated and different collection locations were not combined in experiments; and (5) the time since invasion at the collection location was reported in the paper or could potentially be derived from georeferenced observations of the invader (using home range estimation methods, see *Methods: Time since invasion data collection*) made available on open access databases (e.g., Global Biodiversity Information Facility, GBIF [http://www.gbif.org] and Early Detection and Distribution Mapping System, EDDMapS [http://www.eddmaps.org]). Our initial selection criteria yielded 51 papers on impacts of invasive terrestrial plants, 20 papers on invasive terrestrial animals and 35 papers on invasive aquatic animals. Further screening of papers for required information to conduct the meta-analysis and home range estimation greatly reduced available data on animals. Thus, we focused on greenhouse microcosm and common garden experiments that measured the competitive effects of invasive terrestrial plants on the growth of native plants; this standardized impact comparisons and maximized the number of usable studies.

Data selection criteria.—Additional selection criteria were needed to ensure that impact measures between studies were comparable. We preferentially selected data from experimental conditions that had no additional manipulation (e.g., nitrogen added), or secondarily, most closely reflected field conditions. In the studies that manipulated emergence time, we used data from treatments that began the competition experiment with invasive and native plants at the same developmental stage. We used data only from experiments that involved the presence of the invasive plant directly (e.g., not merely its leaf litter or soil, as in some allelopathic studies) and preferentially chose results that provided biomass metrics for the entire native plant, rather than for components of the plant. Furthermore, we sought to keep impacts on different native species separate, but took combined data on native species when necessary. Data were collected for all possible density combinations of invader:native pairs, excluding experimental densities that did not match control densities of the native based on an additive (no. native in control = no. native in treatment) or substitutive design (no. native in control = no. native + no. invader in treatment). The ability of substitutive, or replacement-series, designs to distinguish mechanisms of competitive effects (Jolliffe 2000) and predict field dynamics (Connolly 1986) is widely debated; however, they provide a metric for competitive advantage and have been used for comparing competitive effects between invasive and native species (Vilà and Weiner 2004). We recorded whether the experiment used an additive or substitutive design, as well as whether the invasive and native plant had the same life cycle (annual, perennial or biennial; "life cycle difference") and growth form (grass or forb/herb/shrub; "growth form difference") using the PLANTS Database (http://plants.usda.gov).

The final dataset included 27 pairwise competition studies that measured the impact (resource competition and interference competition through allelopathy) of invasive terrestrial plants on native plants (see Appendix: Table A1 for all data sources and values). When raw data were not provided, we used Data Thief (datathief.org) to extract values from figures, and authors were contacted for further information if necessary. Mean biomass metrics of native populations with ($\bar{X}_I$) and without the invader ($\bar{X}_{NI}$) were used to calculate a log response ratio (*LR*; Hedges et al. 1999) for comparing competitive impacts of the invader on the native species, where $LR = \ln(\bar{X}_I) - \ln(\bar{X}_{NI})$.

Time since invasion data collection

For each impact study, the time since invasion of the invasive plant at the collection site was obtained in the following ways, listed in preferential order: (1) taken directly from the study (1/27 studies), (2) calculated using home range estimation (18/27), (3) taken from other published sources or government websites when observations for home range estimation were too sparse (5/27) and (4) provided by the authors of the study when observations were too sparse and other sources could not be found (3/27) (see Appendix: Table A1 for time since invasion data sources). *Time since invasion* was calculated as the number of years between the estimated year of initial invasion at the collection site (by spread of the invader, not by intentional introduction) and the time of collection for the impact study.

Home range estimation was used to calculate time since invasion by first obtaining georeferenced observations of invasive plant species from open access databases (GBIF and EDDMapS). We calculated the home range using Kernel Density Estimation ("KDE") in Geospatial Modeling Environment (GME) (Beyer 2012) with bivariate plug-in bandwidth selection. KDE with the plug-in estimator results in more conservative smoothing and is best suited for less mobile species in small geographic areas (Walter et al. 2011). The home range of the invasive plant was calculated for each year for which there were observations, with each successive year including the observations from the previous years; thus we assumed that the plant remained established in areas that it had previously invaded. This provided probability estimates of the home range of the invasive plant for each year. We then drew 95% confidence intervals (CI) around the probability estimates, resulting in isopleths for each year of observations ("Isopleth" in GME). Finally, we recorded the estimated year of invasion using ArcGIS 10.1 (ESRI 2011) to visually determine which isopleth was the first to enclose the collection site of the impact study.

Data analysis

We assessed how the negative competitive effects of invasive plants change with time since invasion. We excluded positive *LR*s (11/118 data points) from the analysis, because none of the six studies containing these data attributed increased growth of natives to positive interactions with the invasive plant; therefore, we could not distinguish whether in these cases the invaders were in fact having positive effects or if it was an artifact of the study design. For instance, positive *LR*s were attributed to differences in optimal conditions for the invader and native (Firn et al. 2010, Verlinden et al. 2013) or inadequate duration to detect full impacts (Miklovic and Galatowitsch 2005, Murrell et al. 2011). Furthermore, all studies that measured a positive effect of an invader also measured a negative effect with a different native pairing, except for Verlinden et al. (2013), who measured invaders' effects with only one native plant pairing. All studies that measured non-significant or low *negative* competitive effects were included in the meta-analysis.

Average effect sizes were calculated for all invader:native pairs within a study in which they were measured more than once (i.e., different density combinations of the same species), to reduce non-independence of effect sizes within studies. One study was removed from the analysis (Abraham et al. 2009) because it used an average invader:native density ratio (12:1) much higher than all other studies ($\leq$4:1), resulting in outlying high impacts. Intraclass correlation coefficients ("ICC" in R; Wolak et al. 2012) revealed moderate correlation (0.35) of effect sizes of invasive plants paired with multiple native plant species within a study.

We applied a maximum likelihood mixed-effects regression model with the random effect of invasive species within studies to account for moderate non-independence of *LR*s ("lme4" in R; Bates et al. 2014). Along with the fixed effect of time since invasion, we assessed the main effects of life cycle difference (yes or no) and growth form difference (yes or no) between the invasive and native plant competitors, growth form of the invader, experimental design (additive or substitutive) and competition type (resource or allelopathic). We could not test for all interactive effects between model terms owing to overparameterization of the model; thus, we first reduced main effects using backwards stepwise multiple regression with analysis of variance likelihood ratio tests to determine variable retention ($\alpha = 0.05$). We then tested for interactions between the remaining main effect (time since invasion) and all other effects. We verified the selection of our final model using Akaike information criterion for small sample sizes (AIC_c) to find the best fit model (Bolker et al. 2009) by testing all possible combinations of main effects and the interaction term that was

Table 1. Model values for the best fit model (time since invasion × growth form of invader) and separate main effect models. The best fit model was determined by likelihood ratio tests (χ^2 and p-values shown here are comparisons with the random effect only model) and Akaike information criterion for small sample sizes (AIC_c; $\Delta AIC_c = AIC_c$ [mixed model] − AIC_c [random only model]). Confidence intervals (95%) are provided for each model term.

Fixed effects	95% CI	χ^2	p-value	ΔAIC_c
1a. Time since invasion: growth form of invader	<−0.001 to 0.008			
1b. Time since invasion	<−0.001 to 0.003	12.14	0.007	−5.25
1c. Growth form of invader	−0.887 to −0.124			
2. Time since invasion	<0.001 to 0.004	5.60	0.018	−3.37
3. Growth form of invader	−0.482 to 0.012	3.53	0.060	−1.30

retained using the likelihood ratio comparisons (time since invasion × growth form of the invader) ("MuMIn" in R; Bartoń 2015). Significance of the model terms were also determined when 95% CIs did not overlap zero. All analyses were done in R (R Development Core Team 2012).

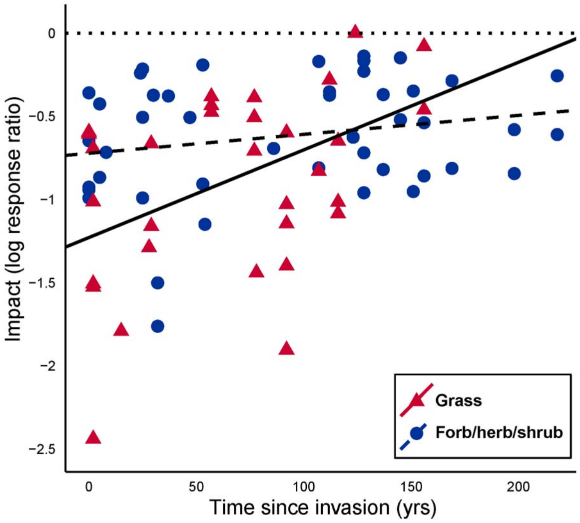

Fig. 1. Negative competitive effects (log response ratios; *LR*) of invasive terrestrial grasses (red triangles) and forbs, herbs and shrubs (blue circles) declined with time since invasion across invaded ranges. The competitive effects of invasive grasses (solid line, $LR = -1.227 + 0.005 \times$ [time since invasion]) declined more rapidly than for forbs, herbs and shrubs (dashed line, $LR = -0.722 + 0.001 \times$ [time since invasion]). Impacts on the growth of native plants in pairwise experiments were fit with a mixed-effects regression model.

RESULTS

Negative competitive effects of invasive plants declined over time, with an interaction between time since invasion and the growth form of the invader (Table 1, Fig. 1). The competitive effects of invasive grasses (slope = 0.005) declined with time since invasion more rapidly than for forbs, herbs and shrubs (slope = 0.001). Time since invasion was also a significant predictor of competitive effects when included as the only main effect. Invasive grasses tended to have higher impacts (mean *LR* ± 1SE: −0.91 ± 0.10) than forbs, herbs and shrubs (−0.62 ± 0.05), though growth form was only a significant predictor when included as an interaction term with time since invasion. No other tested effects were included in the best fit model.

From the 26 studies included in the meta-analysis, impacts were recorded on 12 invasive grasses and 24 invasive forbs, herbs and shrubs. Of the grasses, seven were perennial, two were annual and three could exhibit either life cycle. Of the forbs, herbs and shrubs, 12 were perennial, five were annual and seven were biennial or a combination of the three life cycles. Competition studies were conducted in the USA (n = 16), Australia (n = 4), as well as the following countries (n = 1): Belgium, Canada, Czech Republic, France, Mexico and Switzerland. While the studies provided conditions for potential resource competition, 11 of the 36 invasive plants may have also caused interference competition through the production of allopathic chemicals (allelopathic potential is indicated with an asterisk in Appendix: Table A1).

Discussion

Our meta-analysis reveals that the negative competitive effects of invasive terrestrial plants decline with time since invasion across invaded ranges, and at different rates depending on the growth form. Diminished per capita effects over time have previously been observed in spatio-temporal comparisons of a single invasive plant (Lankau et al. 2009) and animal (Iacarella et al. 2015). A gradient in invader abundance can develop during dispersal, with lower abundance at invasion fronts (Crooks 2005, Phillips et al. 2010*b*). The reduction in intraspecific competition and simultaneous increase in interspecific competition upon recent invasion may select for adaptive traits that lead to higher competitive (Lankau et al. 2009, Lankau 2012) and consumptive effects (Brown et al. 2013). Several studies have shown adaptive trait differences across spatio-temporal invasion gradients (e.g., Phillips et al. 2010*a*, Llewellyn et al. 2011, Lopez et al. 2012), whereas ours provides evidence of a general temporal trend in competitive effects across invaded ranges.

The competitive effects of invasive grasses declined more rapidly with time since invasion and tended to be higher than invasive forbs, herbs and shrubs. Superior competitive ability may be associated with phenotypic plasticity (Callaway et al. 2003), such that more competitive plants at recent time since invasion may also respond quicker to spatio-temporal shifts in intra/interspecific competition. A previous meta-analysis revealed that invasive grasses, and also herbs, were more phenotypically plastic than their native counterparts, but that invasive shrubs were similar to natives (Davidson et al. 2011). Invasive annual grasses have also been found to be more likely to exert a significant impact on native species abundance and diversity than other growth forms, including herbs and shrubs (Pyšek et al. 2012). Invasive annual grasses are particularly competitive against native perennials as a result of both faster aboveground growth that blocks sunlight and shallower root systems that deplete moisture in the upper soil layers (Dyer and Rice 1999). However, we did not find any influence of life cycle or growth form differences between the invader and native pair on the competitive outcome. Our results indicate that the rate of decline in competitive effects across a spatio-temporal invasion gradient is partially dependent on the life-history traits of the invader.

Invader per capita effects may decrease over time owing to adaptive trait changes in the invader and in the native community, particularly if the native community has no evolutionary experience with a functionally-similar species (Pimm 1987, Blossey and Nötzold 1995, Ricciardi and Atkinson 2004). There is mixed evidence (Bossdorf et al. 2005, Blumenthal 2006, Strayer et al. 2006) for invasive plants to reallocate resources from chemical defenses towards competition in recently invaded areas where evolutionarily-adapted enemies, such as herbivores, are absent (Evolution of Increased Competitive Ability hypothesis; Blossey and Nötzold 1995). Evolution of increased competitive ability may partly explain the superior competitive effects of recent invaders, including interference competition through allelopathy (Lankau et al. 2009). Over time, the native community may reduce the impact of an invader by adapting to exploit the invasive population through consumption, parasitism and disease (Strayer et al. 2006, Diez et al. 2010). In addition, changing selection pressures on the invader owing to increased abundances, as well as gene flow from individuals following the invasion front, should eventually erode differences in traits with time since invasion (Phillips et al. 2010*b*).

Invader per capita effects may also be higher on competitors or prey until sufficient time has passed for adaptations to novel interactions, such as allelopathy (Callaway and Aschehoug 2000) and predation (Cox and Lima 2006, Desurmont et al. 2011). We were unable to assess the evolutionary naïveté of native plants in our meta-analysis, given a lack of information on the history of native seeds obtained from commercial distributors (8/26 studies) and on the presence of functionally-similar plants in the invaded ranges (Ricciardi and Atkinson 2004). Our meta-analysis, combined with published genetic studies of adaptive trait differences across invaded ranges (Duckworth and Badyaev 2007, Lankau et al. 2009, Phillips et al. 2010*a*), provides evidence for negative competitive effects decreasing with time since invasion owing in part to the traits of the invader.

Table 2. Studies that have tested the effect of time since invasion (TSI) on impacts of invasive species across their invaded ranges. Drivers of the measured impacts were per capita effects (PE; experimental study) or both PE and abundance (A; correlative study).

Group, species, common name	Impact driver, type	Impact metric	TSI span (years)	Change in impact with TSI	Change in abundance across TSI comparisons	Source
Plants						
Alliaria petiolata, garlic mustard	PE, allelopathy	plant biomass	1 to 140	declined	none, controlled experiment	1
Heracleum mantegazzianum, giant hogweed	PE + A, resource competition	plant density	0, 11 to 48	unimodal	decreased	2
Typha × *glauca*, cattail hybrid	PE + A, resource competition	microbial diversity	0, 13 to 40	increased	none	3
Typha × *glauca*, cattail hybrid	PE + A, resource competition	plant richness	0, ≤ 10 to ≥ 35	increased	increased	4
Animals						
Hemimysis anomala, bloody-red shrimp	PE, predation	zooplankton density	3, 5	declined	none, controlled experiment	5
Hemimysis anomala, bloody-red shrimp	PE + A, predation	zooplankton diversity	0, 3, 5	increased	not measured	5
Neogobius melanostomus, round goby	PE + A, predation	invertebrate catch/unit effort	≤ 1 to ≥ 3	increased	increased	6
Odocoileus hemionus sitkensis, black-tailed deer	PE + A, herbivory	plant richness	0, <20, >50	increased	not measured	7

Sources are: 1, Lankau et al. (2009); 2, Dostál et al. (2013); 3, Geddes et al. (2014); 4, Mitchell et al. (2011); 5, Iacarella et al. (2015); 6, Brandner et al. (2013); 7, Martin et al. (2010).

A few correlative field studies—those including both per capita effect and abundance metrics—have also directly tested ecological impact variation across invaded ranges. These studies show higher impacts with time since invasion, with the exception of one study that found the impact of an invasive plant was eroded over time by soil pathogens (Dostál et al. 2013) (Table 2). Higher ecological impacts over time may be attributable to a lag time in observed effects in recently invaded areas (Crooks 2005) or legacy effects of early invaders at older, more established sites (Grove et al. 2012, Jordan et al. 2012). In addition, subtle ecosystem-level impacts such as changes to soil characteristics may accrue over time, such that the extent of the impact may not be observed for decades; such long-term cumulative impacts are generally caused by ecosystem engineers (see Crooks 2002, Strayer et al. 2006). Higher abundance levels may also contribute to higher impacts measured at more established sites; however, only two of the six correlative studies reported higher abundances with time since invasion (Mitchell et al. 2011, Brandner et al. 2013). Furthermore, high abundances of an invader can, in some cases, lead to reduced ecological impacts owing to interference competition (Kornis et al. 2014). Long-term studies measuring invader abundance and community responses over time are required to tease apart the contribution of per capita effects and abundance to overall ecological impact.

High competitive and consumptive impacts of invasive species spreading into new habitats, combined with the potential naïveté of the community, may magnify ecological impacts and cause shifts in native species composition towards those that are more resistant (Strayer et al. 2006). Management of invader impacts requires a better understanding of whether efforts should prioritize preventing the spread of invaders or mitigating impacts of already established invaders. The economic cost of invasive species management has been shown to be reduced when focused on prevention of high-impact invasions rather than spread across the mitigation of many invasions (Leung et al. 2002). Our finding that competitive effects are higher in more recently invaded areas also suggests that preventing the further spread of invaders may be more beneficial for maintaining native communities, though this should be considered on a taxonomic or life-history basis.

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Supplemental Material

Appendix

Table A1. Details of the studies and data included in the meta-analysis: Impact and time since invasion (TSI, in years) data for 36 invasive terrestrial plants within 27 studies on competition with native plants. Competitive effects were calculated with the log response ratio (*LR*) and included resource and interference competition (allelopathic potential indicated by "*" next to the name of the invader). Treatments that measured competition at different densities of the invasive and native plants are indicated as the number of invaders: number of natives. Parentheses around *LR*s indicate the study that was excluded as an outlier.

Growth form, invasive species	TSI	Native species impacted	Effect size: *LR*	Treatment	Collection location†	Effect size origin (*LR*, TSI source)‡
Forb/herb/shrub						
*Bidens frondosa**	107	*Bidens alba* var. *radiata*	−0.17	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Lycopus europaeus	−0.81	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
*Bunias orientalis**	151	*Berteroa incana*	−0.95	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Centaurea jacea	−0.35	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
*Conyza canadensis**	218	*Daucus carota*	−0.61	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Erigeron acer	−0.26	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
Epilobium ciliatum	47	*Achillea millefolium*	−0.51	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
*Erigeron annuus**	123	*Geum urbanum*	−0.63	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
*Impatiens parviflora**	137	*Galeopsis speciosa*	−0.82	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Impatiens noli-tangere	−0.37	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
*Lupinus polyphyllus**	112	*Heracleum sphondylium*	−0.37	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Lotus corniculatus	−0.35	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
Matricaria discoidea	156	*Galeopsis bifida*	−0.54	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Matricaria chamomilla	−0.86	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
Sedum hispanicum	53	*Arenaria serpyllifolia*	−0.19	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Sedum acre	−0.91	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
*Solidago altissima**	169	*Barbarea vulgaris*	−0.29	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Solidago virgaurea	−0.81	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
Trifolium hybridum	198	*Plantago lanceolata*	−0.58	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Trifolium repens	−0.84	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
Centaurea solstitialis	128	*Elymus multisetus*	−0.96	"new" microcosms	Palo Alto, CA, USA	Fig. 7a, 8a (2, 3)
		Hemizonia congesta spp. *luzulifolia*	−0.17	"new" microcosm	Palo Alto, CA, USA	Fig. 7a, 8a (2, 3)
		Lasthenia californica	−0.14	"new" microcosm	Palo Alto, CA, USA	Fig. 7a, 8a (2, 3)
		Lessingia hololeuca	−0.72	"new" microcosm	Palo Alto, CA, USA	Fig. 7a, 8a (2, 3)
		Plantago erecta	−0.23	"new" microcosm	Palo Alto, CA, USA	Fig. 7a, 8a (2, 3)
*Acroptilon repens**	0	*Agropyron smithii*	−0.36	trials combined	Mead, CO, USA	Table 4 (4, 5)
		Bouteloua gracilis	−1.41	invader root mass: 3.8 g/pot	Mead, CO, USA	Table 3 (4, 5)
			−0.48	1.9 g/pot	Mead, CO, USA	Table 3 (4, 5)
		Koelaria cristata	−1.27	3.8 g/pot	Mead, CO, USA	Table 3 (4, 5)
			−0.71	1.9 g/pot	Mead, CO, USA	Table 3 (4, 5)
		Sporobolus cryptandrus	−1.14	3.8 g/pot	Mead, CO, USA	Table 3 (4, 5)
			−0.71	1.9 g/pot	Mead, CO, USA	Table 3 (4, 5)
Elodea nuttallii	8	*Elodea canadensis*	−0.88	"small-mixed"	Lyon, FR	Fig. 3 (6, PBA)
			−0.41	"small-aggregated"	Lyon, FR	Fig. 3 (6, PBA)
Hesperis matronalis	32	*Campanula rotundifolia*	−1.49	1:1	Estes Park, CO, USA	Fig. 1c, 3c (7, 8)
			−1.90	3:1	Estes Park, CO, USA	Fig. 1c, 3c (7, 8)
			−1.90	5:1	Estes Park, CO, USA	Fig. 1c, 3c (7, 8)
		Muhlenbergia montana	−1.17	1:1	Estes Park, CO, USA	Fig. 1c, 3c (7, 8)
			−1.76	3:1	Estes Park, CO, USA	Fig. 1c, 3c (7, 8)
			−1.58	5:1	Estes Park, CO, USA	Fig. 1c, 3c (7, 8)

Table A1. Continued.

Growth form, invasive species	TSI	Native species impacted	Effect size: *LR*	Treatment	Collection location†	Effect size origin (*LR*, TSI source)‡
Achillea millefolium	37	*Poa fawcettiae*	−0.06	1:10	KNP, NSW, AU	Fig. 2a (9, 8)
			−0.38	1:1	KNP, NSW, AU	Fig. 2a (9, 8)
			−0.69	10:1	KNP, NSW, AU	Fig. 2a (9, 8)
Hyoscyamus niger	145	*Pascopyron smithii*	−0.52	seedling experiment	Laramie, WY, USA	Fig. 3 (10, 11–13)
		Poa secunda	−0.15	seedling experiment	Laramie, WY, USA	Fig. 3 (10, 11–13)
Typha angustifolia	25	*Alisma triviale*	−0.51	0 mg/L NaCl	Minneapolis, MN, USA	Table 1 (14, 5)
		Scirpus validus	−0.99	0 mg/L NaCl	Minneapolis, MN, USA	Table 1 (14, 5)
		Sium suave	−0.22	0 mg/L NaCl	Minneapolis, MN, USA	Table 1 (14, 5)
Fallopia × *bohemica**	54	native forbs	−1.15	no activated carbon	Delémont, CH	Fig. 2 (15, 16)
*Centaurea diffusa**	5	*Artemisia frigida*	−0.87	no herbivory	Boulder County, CO, USA	Fig. 3 (17, 5)
		Bouteloua gracilis	−0.43	no herbivory	Boulder County, CO, USA	Fig. 3 (17, 5)
Centaurea stoebe	86	*Pseudoroegneria spicata*	−0.69	no herbivory	Missoula, MT, USA	Fig. 4a (18, 19)
Phyla canescens	8	*Paspalum distichum*	−0.42	“dry soil”, 2:2	Gwydir Wetlands, NSW, AU	Fig. 1c (20, 8)
			−1.02	4:2	Gwydir Wetlands, NSW, AU	Fig. 1c (20, 8)
Myriophyllum spicatum L.	30	*Myriophyllum sibiricum*	−0.41	37.5:37.5/m^2	Minneapolis, MN, USA	Fig. 3 (21, 8)
			−0.34	75:75/m^2	Minneapolis, MN, USA	Fig. 3 (21, 8)
Senecio inaequidens	24	*Plantago lanceolata*	−0.24	“unheated”	Wilrijk, BE	Fig. 1 (22, 8)
Grass						
Bromus diandrus	112	*Holcus lanatus*	(−1.71)	20:3	TPP, CA, USA	raw data PBA (23, 8)
			(−3.57)	50:3	TPP, CA, USA	raw data PBA (23, 8)
		Festuca rubra	(−2.50)	20:3	TPP, CA, USA	raw data PBA (23, 8)
			(−2.67)	50:3	TPP, CA, USA	raw data PBA (23, 8)
		Nassella pulchra	(−2.87)	20:3	TPP, CA, USA	raw data PBA (23, 8)
			(−3.41)	50:3	TPP, CA, USA	raw data PBA (23, 8)
Holcus lanatus	124	*Erigeron glaucus*	0	uninvaded background soil, seed added	BMR, CA, USA	Fig. 2b (24, 8)
Juncus tenuis	156	*Juncus effusus*	−0.46	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
		Plantago major	−0.08	no activated carbon	Benešov, CZ	raw data PBA (1, 1)
Eragrostis curvula	78	*Bothriochloa decipiens*	−1.37	continuous water, low nutrients, 2:1	Millmerran, Qld, AU	Fig. 2a (25, 8)
			−1.51	6:1	Millmerran, Qld, AU	Fig. 2a (25, 8)
Microstegium vimineum	15	mixed trees	−0.59	first time point in repeat measures (2006)	Bloomington, IN, USA	Fig. 4 (26, PBA)
Bromus diandrus	107	*Bromus carinatus*	−0.83	“no stress”	Bodega Head, CA, USA	Fig. 2a, c (27, 8)
Microstegium vimineum	15	mixed forbs, grasses & hedges	−0.61	no nitrogen added	Bloomington, IN, USA	Fig. 3b (28, PBA)
Echinochloa pyramidalis	29	*Sagittaria lancifolia*	−0.44	“normal” hydroperiod, 1:3	LMCRC, Veracruz, MX	Fig. 3 (29, 8)
			−0.54	2:2	LMCRC, Veracruz, MX	Fig. 3 (29, 8)
			−1.02	3:1	LMCRC, Veracruz, MX	Fig. 3 (29, 8)
		Typha domingensis	−1.58	1:3	LMCRC, Veracruz, MX	Fig. 3 (29, 8)
			−0.86	2:2	LMCRC, Veracruz, MX	Fig. 3 (29, 8)
			−1.04	3:1	LMCRC, Veracruz, MX	Fig. 3 (29, 8)

Table A1. Continued.

Growth form, invasive species	TSI	Native species impacted	Effect size: *LR*	Treatment	Collection location†	Effect size origin (*LR*, TSI source)‡
Bromus inermis	92	*Agropyron dasysdachyum*	−1.15	"moist" water regime	LMLNWA, SK, CA	Fig. 2 (30, 8)
		Agropyron trachyaulum	−1.03	"moist" water regime	LMLNWA, SK, CA	Fig. 2 (30, 8)
		Stipa comata	−1.40	"moist" water regime	LMLNWA, SK, CA	Fig. 2 (30, 8)
		Stipa curtiseta	−1.90	"moist" water regime	LMLNWA, SK, CA	Fig. 2 (30, 8)
		Stipa viridula	−0.60	"moist" water regime	LMLNWA, SK, CA	Fig. 2 (30, 8)
*Lolium perenne**	15	*Austrodanthonia eriantha*	−1.79	no phosphorous added	Broadford, VIC, AU	Fig. 5a shoot mass (31, 8)
Bromus tectorum	28	*Pseudoroegneria spicata*	−1.68	concurrent sowing, low nitrogen, 5:2	Norris, MT, USA	raw data PBA (32, 33)
			−0.95	5:12	Norris, MT, USA	raw data PBA (32, 33)
Bromus tectorum	28	*Pseudoroegneria spicata*	−1.56	10:2	Norris, MT, USA	raw data PBA (32, 33)
			0.00	10:6	Norris, MT, USA	raw data PBA (32, 33)
			−1.46	10:12	Norris, MT, USA	raw data PBA (32, 33)
			−2.77	20:2	Norris, MT, USA	raw data PBA (32, 33)
			−0.35	20:6	Norris, MT, USA	raw data PBA (32, 33)
			−1.55	20:12	Norris, MT, USA	raw data PBA (32, 33)
Bromus tectorum	2	*Eriogonum umbellatum*	−1.53	none	Boise, ID, USA	Table 4 (34, 5)
		Lomatium macrocarpum	−0.69	none	Boise, ID, USA	Table 4 (34, 5)
		Machaeranthera canescens	−1.51	none	Boise, ID, USA	Table 4 (34, 5)
		Penstemon speciosus	−2.44	none	Boise, ID, USA	Table 4 (34, 5)
		Sphaeralcea munroana	−1.01	none	Boise, ID, USA	Table 4 (34, 5)
Festuca arundinacea	57	*Agrostis oregonensis*	−0.47	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
		Festuca rubra	−0.38	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
		Nassella pulchra	−0.43	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
Holcus lanatus	116	*Agrostis oregonensis*	−1.02	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
		Festuca rubra	−1.09	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
		Nassella pulchra	−0.65	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
Phalaris aquatica	77	*Agrostis oregonensis*	−0.51	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
		Festuca rubra	−0.39	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
		Nassella pulchra	−0.71	unfertilized soil	TPP, CA, USA	raw data PBA (35, 8)
Lolium multiflorum	112	*Hemizonia pungens*	−0.28	non-alkali soil	AGR, CA, USA	Fig. 2a (36, 8)

† Location abbreviations are: KNP, Kosciuszko National Park; TPP, Tom's Point Preserve, Marin County; BMR, Bodega Marine Reserve; LMCRC, La Mancha Coastal Research Center; LMLNWA, Last Mountain Lake National Wildlife Area; AGR, Alkali Grasslands Reserve, Yolo County.

‡ "Raw data PBA" indicates raw data were provided by the author(s). Sources are: 1, Dostál (2011); 2, Dukes (2002); 3, Zouhar (2002); 4, Grant et al. (2003); 5, Early Detection and Distribution Mapping System (http://www.eddmaps.org); 6, Barrat-Segretain (2005); 7, Hwang and Lauenroth (2008); 8, Global Biodiversity Information Facility (http://www.gbif.org); 9, Johnston and Pickering (2007); 10, LaFantasie and Enloe (2011); 11, Hocking (1947); 12, Mack (2003); 13, Mitich (1992); 14, Miklovic and Galatowitsch (2005); 15, Murrell et al. (2011); 16, Bailey and Wisskirchen (2006); 17, Norton et al. (2008); 18, Ortega et al. (2012); 19, Duncan et al. (2001); 20, Price et al. (2011); 21, Valley and Newman (1998); 22, Verlinden et al. (2013); 23, Abraham et al. (2009); 24, Bennett et al. (2011); 25, Firn et al. (2010); 26, Flory and Clay (2010); 27, Kolb and Alpert (2003); 28, Lee et al. (2012); 29, Lopez-Rosas and Moreno-Casasola (2012); 30, Nernberg and Dale (1997); 31, O'Dwyer and Attiwill (1999); 32, Orloff et al. (2013); 33, Menalled et al. (2008); 34, Parkinson et al. (2013); 35, Thomsen et al. (2006); 36, Veblen and Young (2009).