Exotic invasive plant species increase primary productivity, but not in their native ranges

Ragan M. Callaway[1*], Robert W. Pal[2], Adrian Schaar[3], David Hooper[1‡], Harald Auge[4,5] Isabell Hensen[5,6], Kevin Kožić[5,6], Ylva Lekberg[7,8], Dávid U. Nagy[5,9], Julian A. Selke[10], Arpad E. Thoma[5,6], Sabrina Träger[5,6], Christoph Rosche[5,6]

[1] Division of Biological Sciences, University of Montana, Missoula, MT, USA. [2] Department of Biological Sciences, Montana Technological University, Butte, MT, USA. [3] State Office for Environmental Protection Saxony-Anhalt, Reideburger Straße 47, 06116 Halle, Germany. [4] Helmholtz-Centre for Environmental Research – UFZ, Theodor-Lieser-Straße 4, 06120 Halle, Germany. [5] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany [6] Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, 06108 Halle, Germany. [8] MPG Ranch Missoula, Florence, MT, USA. [9] Institute for Ecology, Evolution and Diversity, Faculty of Biological Sciences, Goethe University Frankfurt, Frankfurt am Main, Germany. [10] Faculty of Informatics and Data Science, University of Regensburg, Regensburg, Germany

‡ current affiliation - Ahtna Intertribal Resource Commission, Glennallen, AK, U.S.A.

* Corresponding author: ray.callaway@mso.umt.edu

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Abstract

Ecosystem net primary productivity is thought to occur near the maximum that abiotic constraints allow; but exotic invasive plants often correlate with increased productivity. However, field patterns and experimental evidence for this come only from the non-native ranges of exotic species. Thus, we do not know if this pattern is caused by exotic invasions *per se* or whether successful exotic species are disproportionately productive or colonize more productive microsites. We measured aboveground biomass in the field and in common gardens with five plant species in their native and non-native ranges. For all species combined, exotic invaders increased total plot productivity in their non-native ranges by 91% in the field, and by 107% in the common garden, but had much smaller or no such effects in their native ranges. Thus, exotic invaders appear to be a *driver* of increased productivity, not simply a passenger, but only in their non-native ranges.

Introduction

Global patterns of ecosystem net primary productivity (NPP) are controlled by variation in precipitation, temperature, and soil fertility (Leith, 1975; Chu, 2015). NPP is thought to occur near the maximum that these abiotic constraints allow (Running, 2012) and has been called the "basis for all ecosystem services" (Cherlet et al., 2018). The consistent and predictable effect of climate on NPP is a key to predicting the causes and effects of climate change (Chu et al., 2015) and setting predictable planetary boundaries for the biosphere (Running, 2012).

Plant communities invaded by exotic species appear to "break the climate rules" for global NPP as ecosystems dominated by exotic plants have much higher aboveground net primary productivity (ANPP) than the native communities they replace (Ehrenfeld, 2003; Rout & Callaway, 2009; see Vitousek, 1990). In a meta-analysis of field patterns, Liao et al. (2008) found that exotic plant invasions were associated with an 83% increase in ANPP across ecosystems and invader life histories. McLeod et al. (2016) found that exotic invasive plants produced 74% more ANPP in the field than intermixed native patches and caused a 57% increase in ANPP in experimental plots relative to native plots. It is not clear why exotics increase ANPP, but escape from consumers, including those in soil biota, is one possible mechanism (Lucero et al. 2020).

Nitrogen supply is inextricably connected to NPP (Elser et al., 2007; LeBauer & Treseder, 2008) and high plant productivity can increase soil N through increased cycling rates (Furey & Tilman, 2021). Increases in ANPP associated with exotic invasive species are also associated with increases in soil N supply. In Liao et al.'s (2008) review, invaded stands had 17% higher soil nitrate and 53% higher net nitrification rates (also see Castro-Diez 2014; Xu et al., 2020). McLeod et al. (2016) found that in the field, soil nitrate concentrations were 103% higher

in invaded as compared with native patches. Invasive species associated with nitrogen fixing bacteria may increase soil N, but McLeod et al. (2016) did not include legumes. Otherwise, it is not clear how exotic invasives might increase available soil N, but some exotic species accelerate nitrogen cycling through litter or roots with lower C:N ratios (Stark & Norton, 2015) and others by increasing ammonia-oxidizing bacteria (Hawkes et al., 2005; McLeod et al., 2016).

The evidence for exotic invasive species increasing ANPP and soil N is good, but several key gaps remain. Robust correlational evidence from field surveys do not exclude the possibility that invaders consistently colonize the most productive microhabitats on landscapes instead of driving increases in ANPP or soil fertility. In other words, we do not know if exotic invasives are drivers or passengers with respect to ANPP (see MacDougall & Turkington, 2005). Furthermore, all studies of the effects of invasions on ANPP so far have been conducted without biogeographical comparisons (see Hierro et al., 2004). Thus, we cannot discern if both field and experimental results are simply driven by the invasion of disproportionately large species, and that these species have the same effect on ANPP and soil N in their native ranges. Additionally, biogeographic differences in ANPP in common gardens might be due to different genotype distributions between the selected regions or populations sampled (e.g., Rosche et al., 2019; Lucas et al., 2024. This increases the potential for false positives in range differences in common gardens.

Better support for exotic invasives as the cause of increased ANPP and soil N needs the integration of several key questions. First, for which currently there is strong evidence, do exotic invaders correlate with higher productivity and soil N in their non-native ranges, relative to natives (e.g., Ehrenfeld, 2003; Liao et al., 2008)? Second, for which the evidence is currently limited to a single study in the non-native range (McLeod et al., 2016), do any differences

between non-native and native species in ANPP and soil N found in the field hold in controlled experiments? Third, for which there are hints from tree growth rates (Davis et al., 2019), are invasives more productive in their non-native ranges than in their native ranges? And fourth, for which there are clues from reciprocal transplants between native and non-native ranges (e.g., Pal et al., 2020), do plant accessions sourced from native vs. non-native populations perform differently or similarly under common conditions in either range? To tackle these questions, we studied five invasive species, integrating extensive field measurements of ANPP and available soil N with the same measurements and experiments conducted in common gardens, and both of these in the native and non-native ranges.

Methods

Field ANPP – We sampled the above ground biomass of four Eurasian natives, *Linaria vulgaris* Mill., *Hypericum perforatum* L., *Tanacetum vulgare* L., and *Leucanthemum vulgare* Lam., and one North American native, *Solidago canadensis* L, in their native and non-native ranges (all species are referred to by genus hereafter). None of these species are legumes and all species are considered to be invasive in some parts of their non-native ranges and are so in the areas where we studied them. For simplicity we refer to these species as "invasive", even though they are not invasive in their native ranges. Sampling was conducted at peak biomass of the target species, from the mid-to late summer. In western Montana, we sampled 17 *Linaria*, 13 *Hypericum*, 15 *Tanacetum*, 17 *Leucanthemum*, and 14 *Solidago* populations. In central Germany, we sampled 12 *Linaria*, 12 *Hypericum*, 14 *Tanacetum*, 11 *Leucanthemum*, and 14 *Solidago* populations. For each population, we chose one location, or patch, where the target invasive species was common, and at the center of each of these patches, we measured the total cover of all vegetation in a 1 m^2 plot. We located a second 1 m^2 plot at least four meters from the edge of the patch, where the

target invasive species was not present, and measured total cover. In each of these paired plots we harvested all aboveground biomass in a 50 × 25 cm quadrat located randomly within plots. The biomass was then dried at 60°C for 48 hours and weighed. We also collected seeds from the localities sampled.

Common garden - We conducted reciprocal common garden experiments at Bad Lauchstädt, Germany (51.3895, 11.8773, 120 m asl) and at Fort Missoula, Montana, USA (46.8386, -114.0567, 970 m asl). At Bad Lauchstädt, annual precipitation averages 486 mm, and the mean annual temperature is 8.9°C. Precipitation during the growing season (April to October), averages 346 mm, with no substantial dry periods during the year. Annual precipitation in Missoula is 358 mm, with a mean annual temperature of 6.8°C. From April to October, precipitation averages 219 mm, and during the two years of our experiment, annual precipitation averaged 316 mm.

In the German common garden, we grew plants of two ranges for the four European natives, eight different populations of *Hypericum*, *Linaria*, *Tanacetum*, and *Leucanthemum* seed-sourced from the native range (n=32 plots), and eight more populations of each of these seed-sourced from the non-native range (n=32 plots). In addition, we grew plants from eight different populations of *Solidago* seed-sourced from its non-native range (Europe, n=8 plots). Each of the eight (non-native species) or 16 plots (native species) per study species contained only plants that were sourced from a single unique population, thus minimizing the effects of restricting sampling to local genotypes. In Germany, the total number of plots with exotic invasives was 72 which were paired with 40 plots containing native communities (eight per study species). In particular, the eight native community plots corresponding to each of the target species were composed of five native species common to the habitat of the target species (Supplementary

Table S1). To do so, in Germany, we identified the ten most common native co-occurring herbaceous perennial plants in the respective area, based on information in the sPlot database (Bruelheide et al., 2019). From these ten species we randomly chose eight unique combinations of five species to use in the native community plots.

In the Montana garden, we grew plants sourced from eight different populations of the European species seed-sourced from the non-native range (North America, n=32), eight populations of *Solidago* seed-sourced from the native range (North America) and eight populations of *Solidago* seed-sourced from the non-native range (n=16 plots). In Montana, we used the plot data from our field surveys (described above) to select the five most common co-occurring native perennial species for constructing the native communities for each invasive species in the garden. Survival was much lower in the Montana garden, yielding a final total of 28 plots with exotics and 27 plots with natives.

All species were started from seed in greenhouses. In the European common garden, seeds were sown in 120 mL pots in a greenhouse in Bad Lauchstädt, in April 2019. Seedlings were transplanted to the field in September 2019, with twenty-five seedlings transplanted into 1 × 1 m^2 plots in arrangements of 5 × 5 individuals per plot (for the target species 25 individuals from a single unique population, for the native communities: five randomly distributed seedlings per species). In September 2021, aboveground biomass was harvested. Plants for the North American common garden were initially grown in 120 mL pots in the greenhouse of Montana Technological University, in Butte, Montana, in March 2021. In October of 2021, the plants were transplanted to the common garden in Missoula. In August 2023, all aboveground biomass was harvested. *Linaria* did not survive the first transplanting in the Montana garden and new transplanted seedlings in six plots were grown from April to August 2024. In both gardens,

seedlings were watered thoroughly after planting but received no additional irrigation, and weeding was conducted twice per year. Also, after harvest on both continents, plants were dried for 48 hours at 60°C and weighed.

Soil nitrogen – Soil samples were collected from beneath all biomass samples in both the field and common garden experiments, with the exception of *Linaria*. A total of 50 g of soil from a depth of 0–10 cm was collected from the center of the four 50 × 50 cm subplots comprising the 1 m^2 plot. Samples were placed in Ziploc bags and refrigerated until gravimetric water content (GWC) determination and KCl extraction, both of which were performed within one week. GWC was determined by measuring 15 mL of wet soil, corresponding to a mass between 10–15 g. The soil was then dried at 105°C for 48 hours and reweighed to calculate moisture content.

For KCl extraction, approximately 8 g of soil were transferred into 50 mL sterile conical centrifuge tubes. To each tube, 35 mL of 2M KCl solution were added, with a KCl blank prepared for quality control. Samples were shaken on an orbital shaker for 1 hour, then allowed to settle at 4°C overnight followed by filtration of the supernatant through Whatman No. 1 filters. The filtered solution was collected in labeled scintillation vials and stored in a freezer until analysis. We quantified NO_3^- and NH_4^+ in extracts colorimetrically using a Synergy 2 Microplate Reader (BioTek, Winooski, VT, USA) as in Lekberg et al., 2024).

Statistics – All statistical analyses were conducted with linear mixed-effects models in R version 4.3.3 (R Core Team, 2024), using the lme4 package 1.1-35.1 (Bates et al., 2015). Model significance was evaluated using likelihood ratio tests.

To quantify differences in the field ANPP between the plots with the target invasive species vs. the adjacent native plots, we calculated log response ratios (LRR), determined as the natural logarithm of the ratio between the target invasive species' biomass and that of the

adjacent native plots within each sampling site. This approach allowed us to standardize the relative differences in ANPP between the target invasive species and the respective native community for each sampling site, providing an independent metric for comparison. Within each range, we tested whether the LRR was significantly different from zero using a one sample t-test, i.e., testing whether the plot types differed significantly from another within the range. The calculated LRR values were then used to evaluate differences between ranges (native vs. non-native), using range as a fixed factor and location and species as random factors.

To explore species-specific effects, we investigated whether ANPP differed between plot types (target plots with the invasive species vs. adjacent native community plots) for each species individually. Two separate linear mixed-effects models per species were fitted for the native and non-native ranges with plot type as a fixed factor and the sampling site as a random factor. We used two separate models rather than a single model with an interaction term because many of the response variables varied on different scales between the two ranges, meaning they were not independent of the range itself. Thus, interaction effects would not be reliable. Systematic differences between the ranges were especially apparent in the common garden experiment, where the garden in Germany was significantly more productive. Therefore, we considered pairwise comparisons to be more appropriate, as this accounted for range- specific (pair wise comparisons) or site-specific (LRRs) conditions in a standardized manner.

We used the same procedure for all other response variables, including vegetation cover, and NO_3^- and NH_4^+ concentrations in the field, and ANPP, NO_3^-, and NH_4^+ in the common garden. Transformation of variables depended on visual inspection of 'model-checking plots' in R for the models with transformed vs. untransformed variables. Plot biomass and nitrogen data

were $\log_e$-transformed, vegetation cover was logit-transformed, while the LRRs were not transformed.

Results

Field ANPP – In the native ranges, the mean ANPP across all species in patches with the invasive species was 596.5 ± 55.3 $g \cdot m^{-2}$ compared to 457.5 ± 37.4 $g \cdot m^{-2}$ in communities without the invasive species (31% increase, Fig. 1). This resulted, for all five species combined in the native ranges, in a positive log response ratio (LRR) for ANPP in plots with the target species vs. ANPP in adjacent plots without the target invasive species ($LRR_{native\ range}$=0.18 ± 0.06; one sample t-test: t_{61}=3.14, P=0.003). In the non-native ranges, the mean ANPP across all species was 846.3 ± 55.3 $g \cdot m^{-2}$ for plots with the target invaders vs. 443.5 ± 25.7 $g \cdot m^{-2}$ (91% increase) in communities without the invaders (Fig. 1). This resulted in a highly positive LRR for ANPP plots inside vs. outside of invaded patches ($LRR_{non\text{-}native\ range}$=0.59 ± 0.06; t_{58}=9.70, P<0.001). Importantly, the LRR was significantly higher in the non-native range than in the native range (χ^2=22.97; P<0.001; Fig. 1).

Breaking this down by species, ANPP in the native range was no different between plots with target invasive species and those without the target invaders for four of the five species: *Leucanthemum* (χ^2=0.003; P=0.956; Fig. 1), *Linaria* (χ^2=0.1; P=0.75), *Hypericum* (χ^2=1.01; P=0.315), and *Tanacetum* (χ^2=3.65; P=0.056). However, for *Solidago* (χ^2=5.87; P=0.015), ANPP was higher in the plots with the invader than without the invader in the native range. In the non-native ranges, ANPP was significantly higher in plots with the invasive species in all cases: *Leucanthemum* (χ^2=7.49; P=0.006), *Linaria* (χ^2=8.79; P=0.003), *Hypericum* (χ^2=16.59; P<0.001), *Tanacetum* (χ^2= 28.97; P<0.001) and *Solidago* (χ^2= 32.61; P<0.001). Between ranges, ANPP in the plots with the invasive species in the non-native range was on average 41.8% higher

196 than in the plots with the same species in the native range. In contrast, the ANPP of the
197 corresponding native communities was very similar in the native and non-native ranges; it was
198 on average 3.1% lower in the non-native ranges. In other words, our invasive target species
199 colonized regions with similar ANPP in both ranges but only correlated with the greater increase
200 in ANPP in the non-native ranges.

201 The results for total vegetation cover in the 1×1 m^2 plots were very similar to the
202 patterns for ANPP (Fig. S1) and ANPP and vegetation cover were highly correlated across
203 species and ranges (Fig. S7). For all species combined, the LRR in the native ranges indicated a
204 weak positive effect of the target invasive species ($LRR_{native\ range}$= 0.07±0.03; t_{62}=2.10, P=0.040),
205 but in the non-native ranges cover was much higher in plots with the invasive species (LRR_{non-}
206 $_{native\ range}$=0.44±006; t_{70}=6.99, P<0.001). As such, the LRR was significantly higher in the non-
207 native than native ranges (χ^2=14.84; P<0.001).

208 *Field nitrogen* - For all five species combined, the log response ratio (LRR) for soil NO_3^- in the
209 plots with the invasive species vs. the adjacent plots without the invasive species was greater in
210 the non-native ranges than the native ranges (χ^2=6.52; P=0.011; Fig. 2). The LRR did not differ
211 from zero in the native ranges ($LRR_{native\ range}$=0.001±0.114; t_{54}=0.01, P=0.989), but was positive
212 in the non-native ranges ($LRR_{non\text{-}native\ range}$=0.392±0.102; t_{60}=3.86, P<0.001). By species, *Linaria*
213 (χ^2=5.95; P=0.015), *Tanacetum* (χ^2=9.41; P=0.002), and *Solidago* (χ^2=5.74; P=0.017) had
214 significantly higher soil NO_3^- concentrations in invaded patches than patches without the
215 invaders in the non-native ranges, but not so in the native ranges (Fig. S2). For *Leucanthemum*
216 and *Hypericum* there were no differences between invaded and non-invaded plots in either range.

217 For all five species combined, the LRR for soil NH_4^+ in plots with invasive species vs. in
218 adjacent plots without the invasive species, was significantly higher in the non-native ranges than

in the native ranges (χ^2=6.03; P=0.014; Fig. 2). The LRR was not different from zero in the native ranges ($LRR_{native\ range}$=-0.123±0.11; t_{66}=-1.1121, P=0.2701), but higher than zero in the non-native ranges ($LRR_{non\text{-}native\ range}$=0.207±0.079; t_{73}=2.6197, P=0.0107). By species, only *Linaria* (χ^2=10.28; P=0.001) and *Leucanthemum* (χ^2=4.62; P=0.032) had significantly higher soil NH_4^+ concentrations in invaded patches than patches without the invaders in the non-native ranges, but not in the native ranges (Fig. S3). For *Hypericum*, *Tanacetum*, and *Solidago* there were no differences between invaded and non-invaded plots in either range.

Common garden ANPP – Consistent with the correlational patterns in the field, there was a significant difference in how the target species affected ANPP in the common garden (Fig. 3), with exotic invaders increasing ANPP by 107%, relative to the native community plots, in the non-native ranges vs. no effect in the native ranges. The LRR was close to zero in the native ranges ($LRR_{native\ range}$=-0.04±0.136; t_{37}=-0.30, P=0.7684) but positive in the non-native ranges ($LRR_{non\text{-}native\ range}$=0.563±0.118; t_{30}=4.77, P<0.001). In the native ranges, ANPP did not differ between monocultures of the target species and native community plots for three of the five species: *Leucanthemum* ($F_{1,14}$=1.69; P=0.215), *Hypericum* ($F_{1,14}$=2.48; P=0.138) and *Tanacetum* ($F_{1,14}$=0.002; P=0.962). In plots with *Solidago*, ANPP was higher than the constructed native community plots ($F_{1,12}$=3.615; P=0.08). In plots with *Linaria*, ANPP was significantly lower than the constructed native community plots ($F_{1,14}$=13.98; P=0.002). In contrast to the overall weak and inconsistent effects of the target species in their native ranges, all five invasive target species increased ANPP in their non-native ranges, relative to native plots: *Leucanthemum* ($F_{1,11}$=5.67; P=0.036), *Linaria* ($F_{1,10}$=21.01; P=0.001), *Hypericum* ($F_{1,14}$=8.0; P=0.013), *Tanacetum* ($F_{1,10}$=13.06; P=0.005) , and *Solidago* ($F_{1,14}$=9.47; P=0.008).

241 In the common garden experiment, unlike patterns in the field comparisons, ANPP in the
242 plots built with the suite of native species was 50.8% higher in Germany than in Montana,
243 demonstrating an overall higher productivity in the European common garden, mostly likely due
244 to higher soil N and precipitation. In contrast, ANPP in the plots with the invasive species in the
245 non-native range were similar; on average 4.2% higher in the non-native range than in the plots
246 with the same species in the common garden in the native range.
247 In an effort to eliminate potential error due to sampling different genotypes with respect
248 to their productivity in the two ranges (e.g., high performance genotypes sampled only within
249 one range; Lucas et al. 2024), we constructed plots in the common gardens using the invasive
250 species sourced from their non-native ranges and their native ranges (the former source is what
251 we compared to the corresponding constructed native communities). Note that we only did this
252 with the European natives in the European common garden, and *Solidago* in the North American
253 common garden to avoid introducing new genotypes to the non-native ranges of our target
254 species. For these comparisons, within the garden of the respective native range of each species,
255 ANPP in plots of *Linaria*, *Leucanthemum*, and *Hypericum* did not differ between their sources,
256 i.e., between native vs. non-native populations of the same species under the same garden
257 setting. *Tanacetum* sourced from the non-native range produced higher ANPP than when sourced
258 from the native range ($F_{1,14}$=3.94; P=0.067), whereas *Solidago* sourced from its non-native range
259 produced *less* ANPP than when sourced from its native range ($F_{1,12}$=7.33; P=0.019). In sum,
260 there were no systematic differences in productivity between native vs. non-native genotypes,
261 which suggests that our results were not affected by sampling different genotypes in different
262 source regions.

Common garden nitrogen – For all species combined, the log response ratio (LRR) for soil NO_3^- in patches of invasive species, vs. in adjacent plots without the invasive species, did not significantly differ between the ranges (χ^2=2.8; P=0.094; Fig. 4). More specifically, the LRRs did not differ from zero in the native ranges ($LRR_{native\ range}$=-0.084±0.17; t_{37}=-0.50, P=0.623) or the non-native ranges ($LRR_{non\text{-}native\ range}$=0.337±0.249; t_{18}=1.35, P=0.1926). Only *Tanacetum* ($F_{1,9}$=9.64; P=0.012) had significantly higher soil NO_3^- concentrations in the monocultures than in the plots with the corresponding native community in the non-native ranges, but not in the native ranges (Fig. S4). For *Leucanthemum*, *Hypericum*, and *Solidago*, there were no differences between the monocultures and the plots with the corresponding native community in either range. For *Linaria*, there were no differences in NO_3^- concentrations in the native ranges, but we did not have soil N data from the non-native ranges.

For all species combined, the LRR for soil NH_4^+ in monocultures of invasive species, vs. corresponding native communities did not differ between the ranges (Fig. S5; χ^2=0.07; P=0.789). The LRRs were negative in the native ranges ($LRR_{native\ range}$=-0.376±0.134; t_{37}=-2.82, P=0.007) but not different from zero in the non-native ranges ($LRR_{non\text{-}native\ range}$=-0.318±0.175; t_{21}=-1.82, P=0.084; Fig. S5). By species, in the non-native range, *Leucanthemum* decreased soil NH_4^+ compared to plots with native species ($F_{1,11}$=17.23; P=0.001; Fig. S5) but this difference was not apparent in the native range. *Hypericum* showed lower NH_4^+ concentrations in the monocultures than the corresponding native communities in both its non-native ($F_{1,13}$=6.58; P=0.024) and native ranges ($F_{1,14}$=8.5; P=0.011). For *Linaria*, there were no differences in NH_4^+ concentrations in the native ranges, but we did not have soil data from the non-native ranges. For *Solidago* and *Tanacetum*, there were no differences between the monocultures and their corresponding native communities in either range.

Discussion

Our biogeographical experimental results are consistent with a number of other studies, all in the non-native ranges of plant species, indicating that exotic invasive species increase ANPP (Ehrenfeld, 2003; Liao et al., 2008; Rout & Callaway, 2009). A meta-analysis of correlative patterns in non-native ranges by Liao et al. (2008) found a mean 83% increase in ANPP across all exotic species tested. In the field, we found a 91% increase in ANPP in plots with our five target species, relative to adjacent communities without the target species, but only in the non-native ranges. Correlative evidence cannot separate exotics as the cause from exotics disproportionately colonizing more productive microsites. However, the 107% increase in ANPP caused by the invaders in our common garden experiment strongly supported the field results and indicates that invaders are the drivers, not passengers, of increased ANPP. This was not due to invasive plants being inherently large, because our biogeographical comparisons—crucial for these type of questions (Hierro et al., 2005)—showed that invaders were not larger than native plants in their native range.

Because differences in ANPP in common gardens might be due to different genotype distributions between the selected regions (e.g., Lucas et al., 2024), when we compared accessions of each species sourced from both ranges, ANPP generated by three of the four European species in the European garden did not differ among the accessions (Fig. S6). *Tanacetum* sourced from the non-native range was larger than those sourced from its native range, consistent with the evolution of increased competitive ability (Callaway et al., 2022) or selection towards high performance genotypes (Matesanz & Sultan, 2013). *Solidago* accessions sourced from its native range were larger than those collected in the non-native range, consistent with Pal et al., (2020).

309 The results for inorganic nitrogen were not as convincing as those for ANPP. For all
310 species combined in the field in the non-native range, plots with exotic invaders averaged 41.3%
311 higher soil NO_3^- and 7.9% higher NH_4^+ than plots with adjacent native community. This was not
312 the case in the native range. However, for all species combined in the common garden, there
313 were no differences in form of nitrogen in plots with exotics vs. natives in either range. Thus, we
314 did not determine whether exotics cause increases in soil inorganic N, or simply preferentially
315 colonize more fertile microhabitats in the non-native range. However, the faster rates of nutrient
316 cycling described for some exotic species (Hawkes et al., 2005; Castro-Diez et al., 2014) may
317 take more than the two years of our experiment to materialize, particularly if increased inorganic
318 N is due to lower C:N ratios in tissues. Also, we did not account for soil inorganic N
319 incorporated into the increased biomass.
320 Our results must be interpreted with a crucial caveat – we measured peak standing
321 biomass a common proxy for ANPP, which can underestimate ANPP in some ecosystems by
322 missing turnover and the effects of consumers (Scurlock et al., 2002). However, most direct
323 estimates of ANPP in the literature are based on peak standing biomass or remotely sensed
324 measurement based on vegetation greenness and density, the latter representing perhaps proxies
325 for a proxy. Our field plots were not grazed by livestock, but were exposed to natural consumer
326 pressure, and our common gardens were fenced, but exposed to insect herbivory. Thus, our peak
327 biomass-based estimates are reasonable estimates of ANPP and were made under similar
328 conditions in both ranges. Furthermore, ANPP does not include belowground productivity, and if
329 allocation differs between ranges our results might not accurately reflect NPP. Belowground
330 productivity can be highly variable in grassland systems (e.g., Ridenour & Callaway, 2001;
331 Frank 2002; Liao et al., 2008; Wilsey et al. 2011), yet these studies do not suggest that exotic

invaders show strongly different belowground allocational patterns than natives, which would be necessary to affect our conclusions. A final caveat is that all of the invasive species we studied are forbs, limiting generalization this to plant species with other life histories. However, Liao et al. (2008) reported increased productivity across forbs, grasses, and woody perennials.

What might explain the apparent increase in ANPP in the non-native ranges of exotic invasive plant species? First, and relevant to differences in the effects of generalist insects and soil biota, increased growth may be due to escaping herbivores in the non-native ranges of exotics (Agrawal et al., 2005; Blumenthal, 2006; Brian & Catford, 2023; but see Colautti et al., 2004; Chun et al., 2010). Escape from soil biota or more beneficial mutualistic interactions (Sheng et al., 2022) have received less attention than herbivores, but plant-soil feedbacks can be far more inhibitory in soils from the native ranges than the non-native ranges of invaders (Callaway et al., 2004; Kulmatiski et al., 2008; Maron et al., 2014). While such novel biotic interactions may promote peak standing biomass in the nonnative range, exotic invaders may also rapidly evolve greater individual size (Joshi & Vrieling, 2005; Callaway et al., 2022; Villasor et al. 2024).

Increased ANPP may either drive faster rates of nutrient cycling (Castro-Díez et al., 2014) or the release of more carbon belowground, promoting bacteria involved in nitrogen cycling. For example, McLeod et al. (2016) found very large and consistent increases in ammonia oxidizing bacteria associated with four different exotic invasive species in the field, and this could contribute to higher levels of soil NO_3^- (also see Hawkes 2005) however, unlike McLeod et al. (2016), we only found higher levels of soil NO_3^- in the field and in the common garden for *Tanacetum*. Increased soil N might be caused by invaders that have tissues or litter with lower C:N ratios than natives. In a meta-analysis, Lee et al. (2016) found that invasive

355 species with greater litter N content and lower litter C:N ratios corresponded with the largest
356 increases in soil N. Finally, is it possible that the uptake rates of invasive species were lower than
357 that of natives.

358 Not all exotic species are invasive (Simberloff, 2013), thus, studies of exotic invasion
359 should focus on species that at least appear to be invasive, for example those that become hyper-
360 abundant or displace natives. Certainly, some species classified as invasive behave quite
361 differently in their non-native ranges than native species (Wilsey et al., 2009; Graebner et al.,
362 2012; Callaway et al., 2011; Kaur et al., 2012; Shah et al., 2014; Montesinos et al., 2019), likely
363 due to their eco-evolutionary novelty (Pearse et al., 2019; Davis et al., 2019). Thus, it is
364 important to note that all five of our species are considered to be invasive (Pauchard et al., 2003;
365 Clements et al., 2004; Wilke & Irwin, 2010; Bauer, 2006; Ledger et al., 2015). Whether ANPP is
366 affected by species not classified as invasive is less clear. Furthermore, invasive species can
367 disrupt ecosystems in ways that are unrelated to ANPP, for example through allelopathy (Hierro
368 & Callaway 2023) or intense shade (Reinhart et al. 2006) and thus increased ANPP is not
369 requisite for invader impact.

370 In sum, exotic invasions appear to be the drivers of increased ANPP, not simply
371 passengers (i.e., MacDougall & Turkington, 2005), as evidenced by biogeographically explicit
372 field patterns, experiments, and comparisons of accessions. This was not the case for field-based
373 increases in soil inorganic N concentrations, for which we could not separate the driver from the
374 passenger (but see McLeod et al., 2016). This effect of invasive species on ANPP suggests that
375 biotic factors, such as consumers, may play a much greater role in determining global patterns of
376 productivity than currently thought, and that the evolutionary history of plants, herbivores, and
377 soil biota may determine the magnitude of their roles.

Acknowledgements

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Figure legends

Figure 1. Differences in aboveground net primary productivity (ANPP) between field plots dominated by the target invasive species, and adjacent plots with native species, in both the native (blue) and non-native (red) ranges of the invaders. The log-response ratio plot is standardized across the five study species for different ANPPs across species (plot biomass). Positive LRRs indicate an increase in ANPP in invaded plots vs. that in adjacent native plots, whereas negative LRRs indicate a decrease in ANPP in invaded plots vs. that in adjacent native plots. For individual species, estimated differences are based on pair-wise comparisons between plots with the target species (orange) and the adjacent community (purple) within both ranges and denoted as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s. = non-significant. ANPP data are presented on a $\log_e$-scaled axis as they were logged in the statistical analyses.

Figure 2. Differences in NO_3^- and NH_4^+ between field plots dominated by the target invasive species and adjacent plots with native species, in both the native (blue) and non-native (red) ranges of the invaders. LRR plots are standardized across the five study species using the log-response ratios (LRRs) for NO_3^- and NH_4^+. Positive LRRs indicate an increase in NO_3^- or NH_4^+ in invaded plots vs. that in adjacent native plots, whereas negative LRRs indicate a decrease in NO_3^- or NH_4^+ in invaded plots vs. that in adjacent native plots. For both NO_3^- and NH_4^+, the LRRs in the nonnative range were significantly higher than those in the native range, as denoted by an * for the respective pair-wise comparison between plots with the target species (orange) and the adjacent community (purple) within both ranges.

Figure 3. Differences in aboveground net primary productivity (ANPP) between common garden plots dominated by the invasive species, and adjacent plots with native species, in both the native (blue) and non-native (red) ranges of the invaders. For gardens in both ranges only the local genotypes were used in this comparison – both for the native and the non-native species – ensuring that the sample size remained consistent. The LRR plot is standardized across the five study species using the log-response ratios (LRRs) for plot biomass. Positive LRRs indicate an increase in ANPP in invaded plots vs. that in adjacent native plots, whereas negative LRRs indicate a decrease in ANPP in invaded plots vs. that in adjacent native plots. For individual species, estimated differences are based on pair-wise comparisons between plots with the target species (orange) and the adjacent community (purple) within both ranges and denoted as follows:

581 *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s. = non-significant. ANPP data are presented on a
582 $\log_e$-scaled axis as they were logged in the statistical analyses.

583 **Figure 4**. Differences in NO_3^- and NH_4^+ between common garden plots dominated by the target
584 invasive species and adjacent plots with only native species, in both the native (blue) and non-
585 native (red) ranges of the invaders. For gardens in both ranges only the local genotypes were
586 used in this comparison – both for the native and the non-native species – ensuring that the
587 sample size remained consistent. LRR plots are standardized across the five study species using
588 the log-response ratios (LRRs) for NO_3^- and NH_4^+. Positive LRRs indicate an increase in NO_3^- or
589 NH_4^+ in invaded plots vs. that in adjacent native plots, whereas negative LRRs indicate a
590 decrease in NO_3^- or NH_4^+ in invaded plots vs. that in adjacent native plots. For both, NO_3^- and
591 NH_4^+, the LRRs in the nonnative range were not significantly different from those in the native
592 range, as indicated by an "n.s." for the respective pair-wise comparison between plots with the
593 target species (orange) and the adjacent community (purple) within both ranges.

594

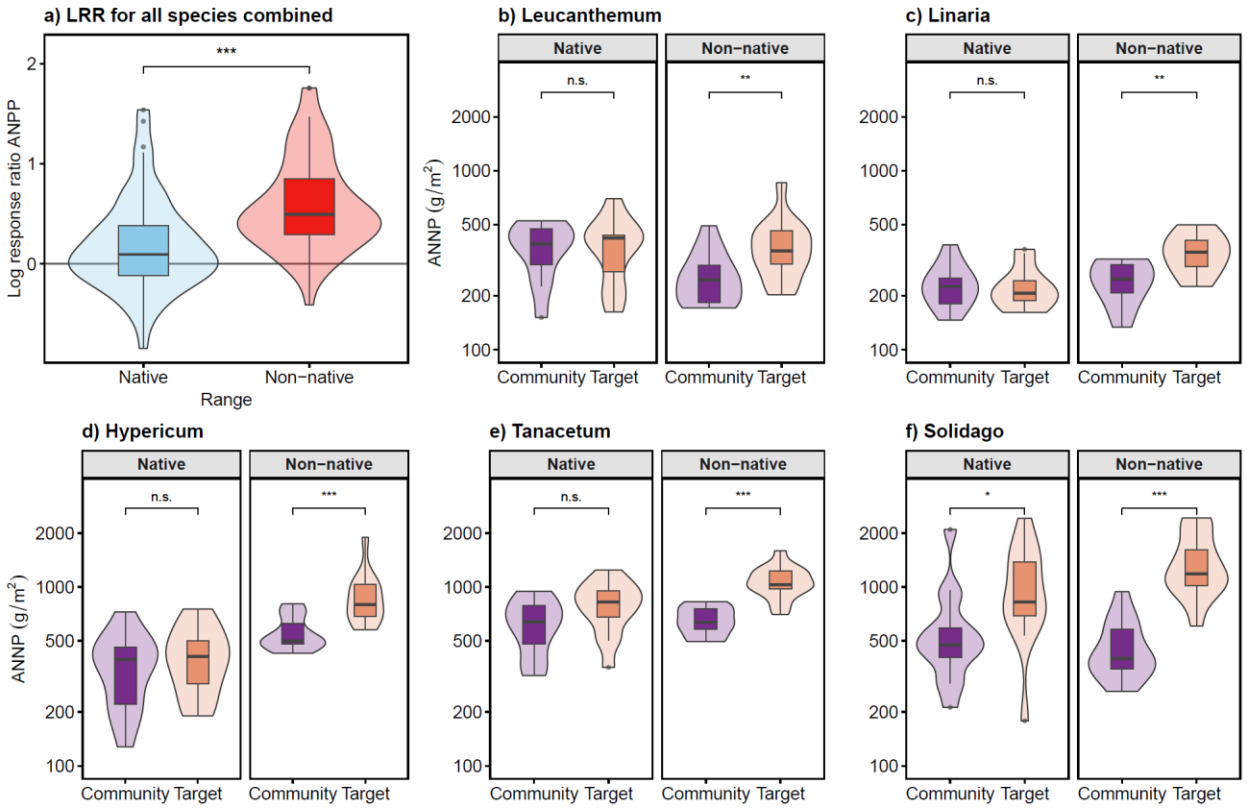


Figure 1

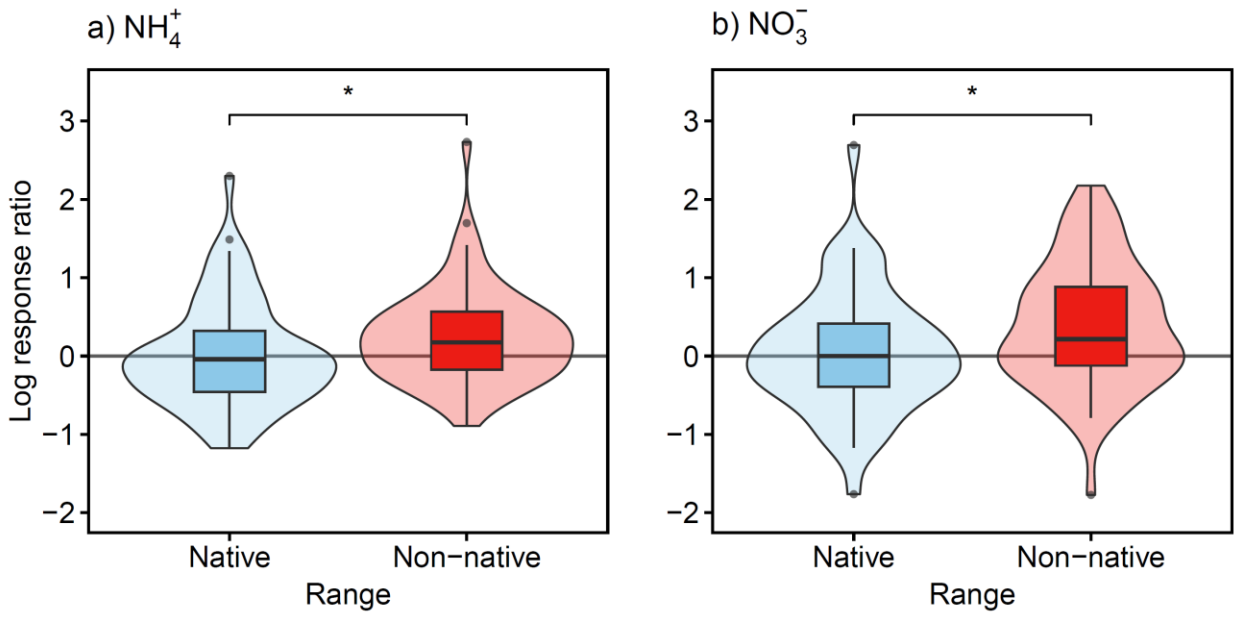


Figure 2

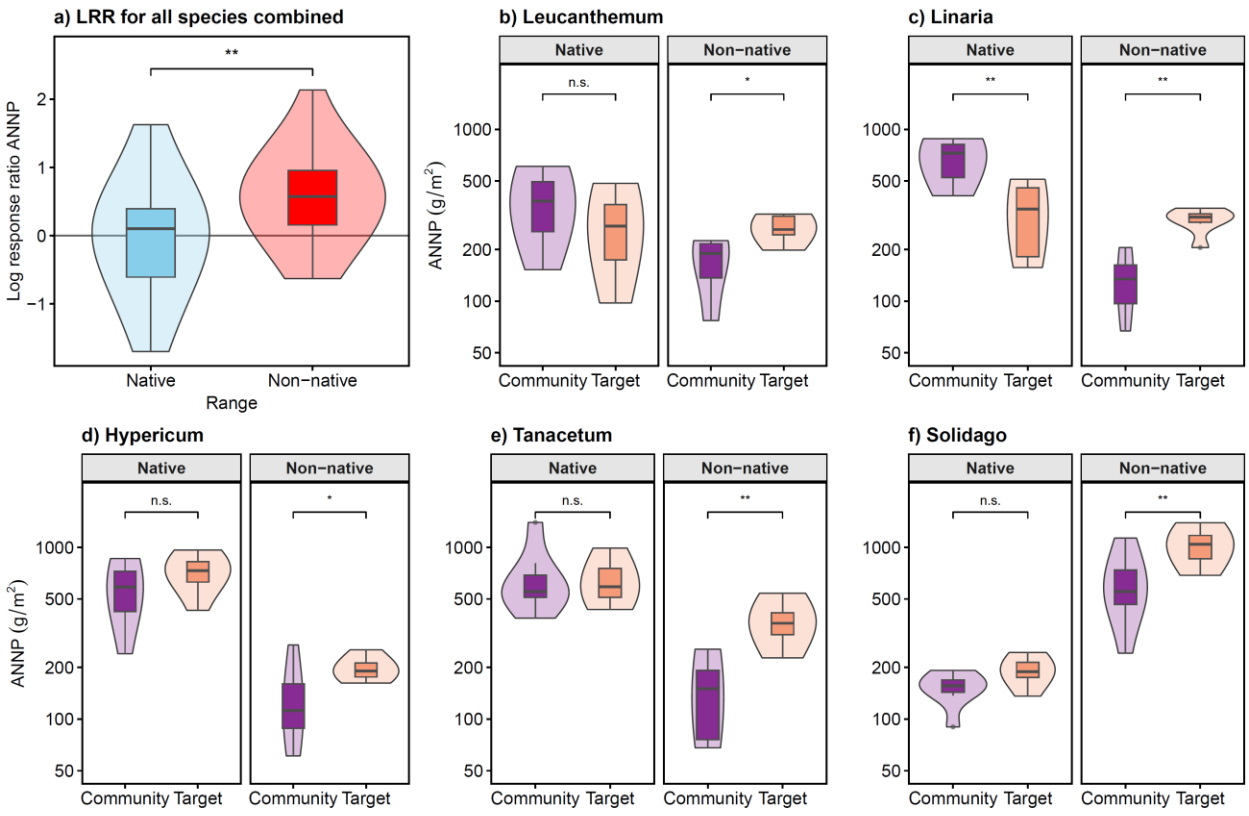


Figure 3

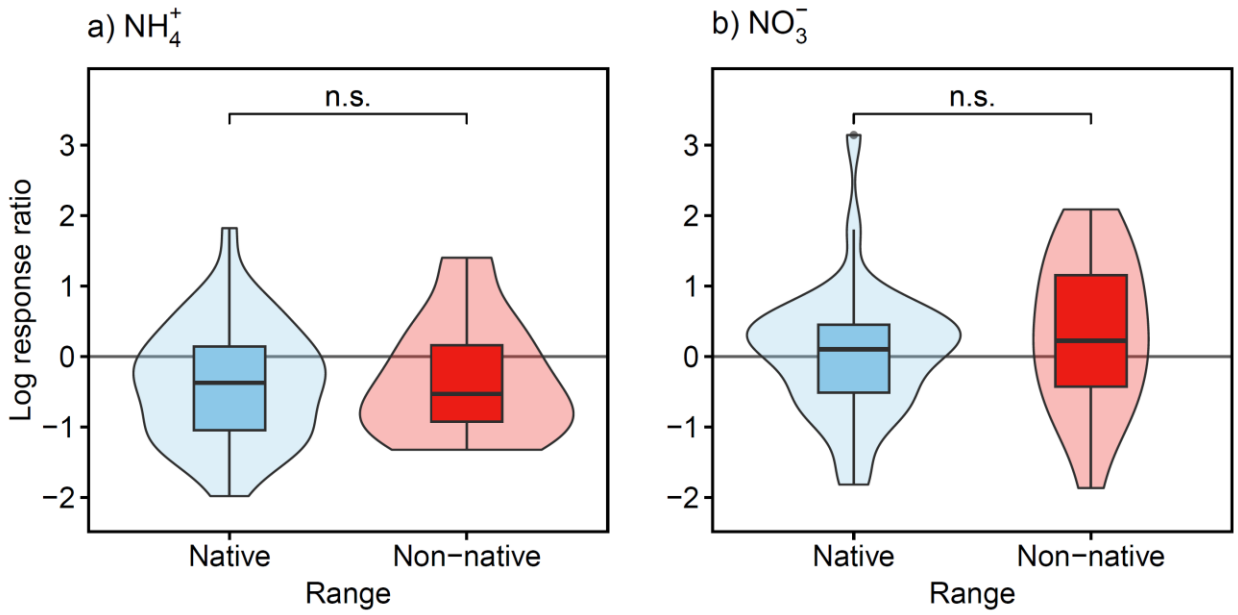
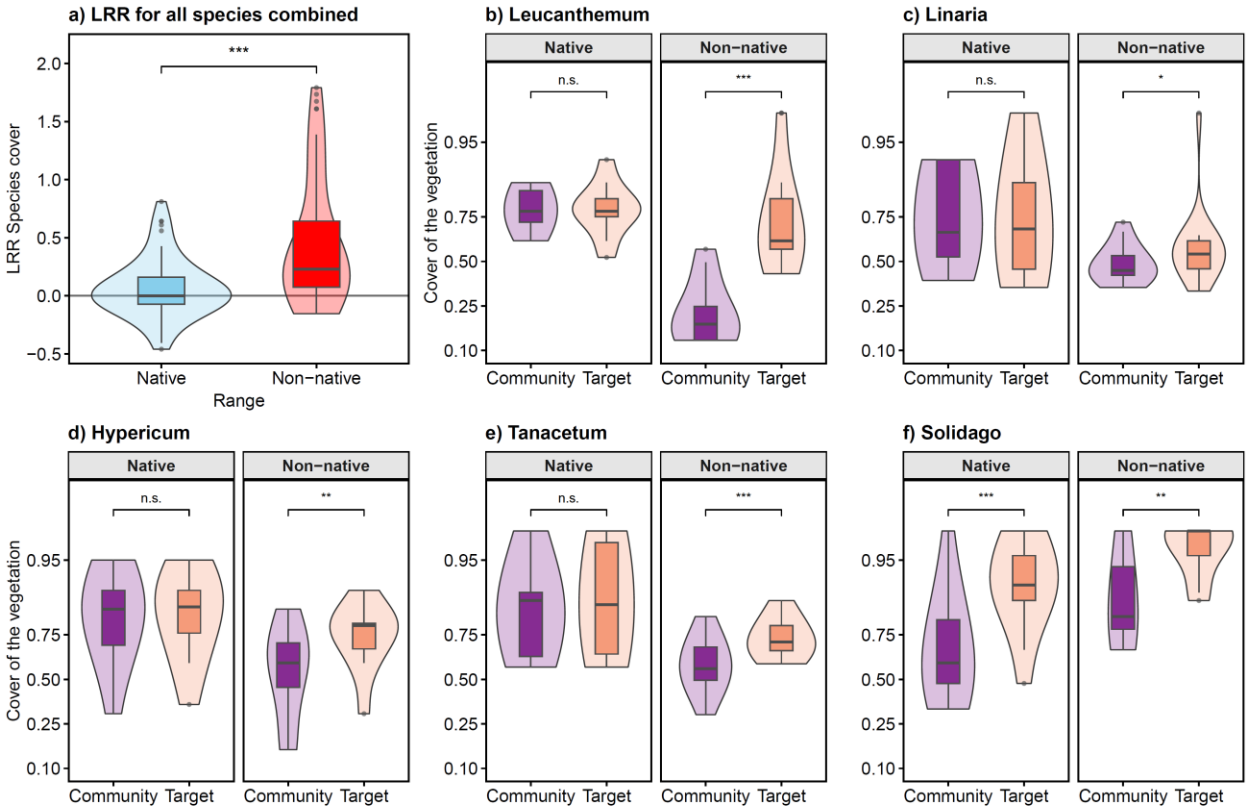


Figure 4

Supplementary Information



595 **Figure S1.** Differences in total vegetation cover between field plots dominated by the target
596 invasive species and adjacent plots with only native species, in both the native and non-native
597 ranges of the invaders. The LRR plot is standardized across the five study species using the log-
598 response ratios (LRRs) for plot cover. Positive LRRs, denoted by an *, indicate an increase in
599 cover in invaded plots vs. adjacent native plots, whereas negative LRRs indicate a decrease in
600 cover in invaded plots vs. adjacent native plots. For individual species, estimated differences are
601 based on pair-wise comparisons within the ranges and denoted as follows: *, $P < 0.05$; **, $P <$
602 0.01; ***, $P < 0.001$; n.s. = non-significant. Data are presented on a logit-scaled axis as they
603 were logit transformed in statistical analyses.

604

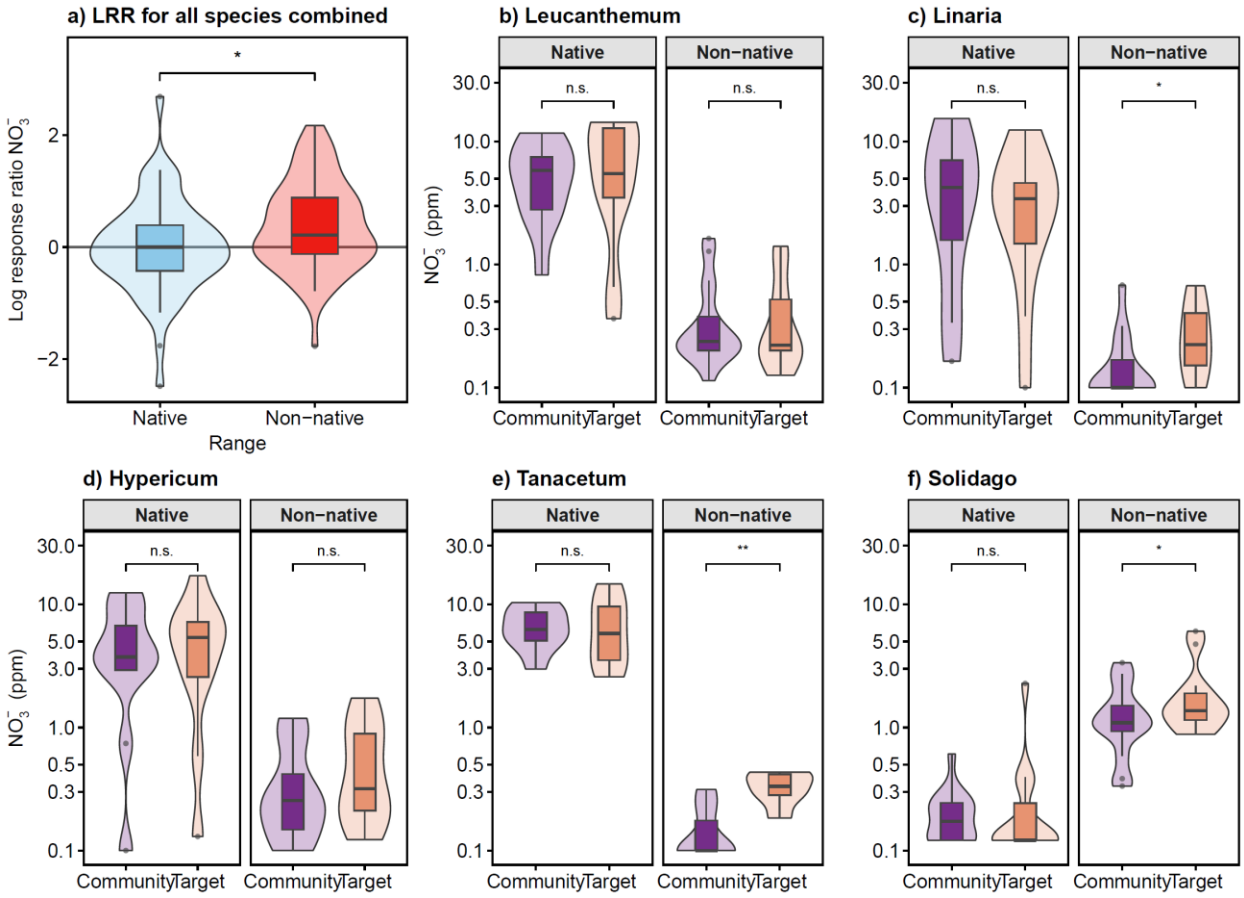


Figure S2. Differences in NO_3^- between field plots dominated by the target invasive species and adjacent plots with only native species, in both the native and non-native ranges of the invaders. The LRR plot is standardized across the five study species using the log-response ratios (LRRs) for plot cover. Positive LRRs, denoted by an *, indicate an increase in NO_3^- in invaded plots vs. adjacent native plots, whereas negative LRRs indicate a decrease in NO_3^- in invaded plots vs. adjacent native plots. For individual species, estimated differences are based on pair-wise comparisons within the ranges and denoted as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s. = non-significant. Data are presented on a $\log_e$-scaled axis as they were logged in statistical analyses.

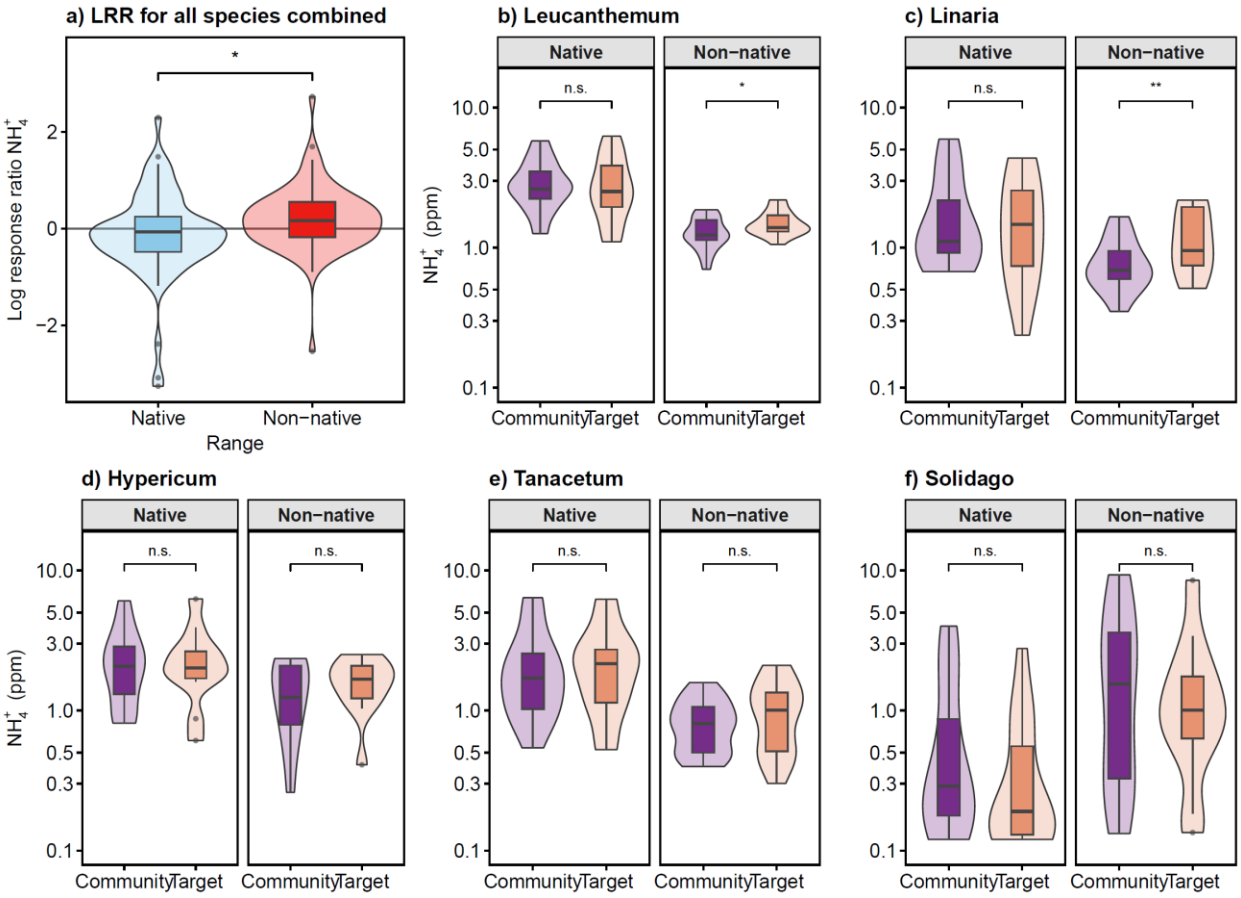


Figure S3. Differences in NH_4^+ between field plots dominated by the target invasive species and adjacent plots with only native species, in both the native and non-native ranges of the invaders. The LRR plot is standardized across the five study species using the log-response ratios (LRRs) for plot cover. Positive LRRs, denoted by an *, indicate an increase in NH_4^+ in invaded plots vs. adjacent native plots, whereas negative LRRs indicate a decrease in NH_4^+ in invaded plots vs. adjacent native plots. For individual species, estimated differences are based on pair-wise comparisons within the ranges and denoted as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s. = non-significant. Data are presented on a $\log_e$-scaled axis as they were logged in statistical analyses.

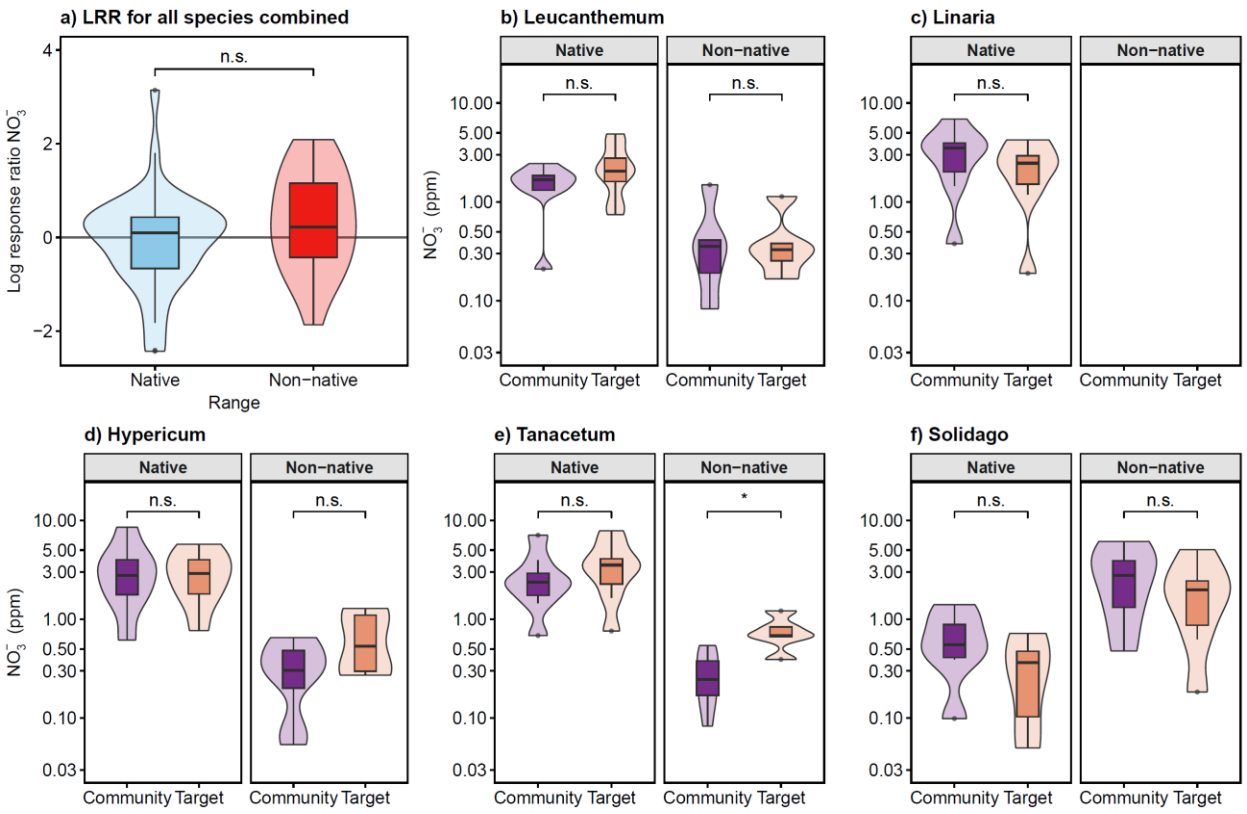


Figure S4. Differences in NO_3^- between common garden plots dominated by the target invasive species and adjacent plots with only native species, in both the native and non-native ranges of the invaders. The LRR plot is standardized across the five study species using the log-response ratios (LRRs) for plot cover. Positive LRRs, denoted by an *, indicate an increase in NO_3^- in invaded plots vs. adjacent native plots, whereas negative LRRs indicate a decrease in NO_3^- in invaded plots vs. adjacent native plots. For individual species, estimated differences are based on pair-wise comparisons within the ranges and denoted as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s. = non-significant. Data are presented on a $\log_e$-scaled axis as they were logged in statistical analyses.

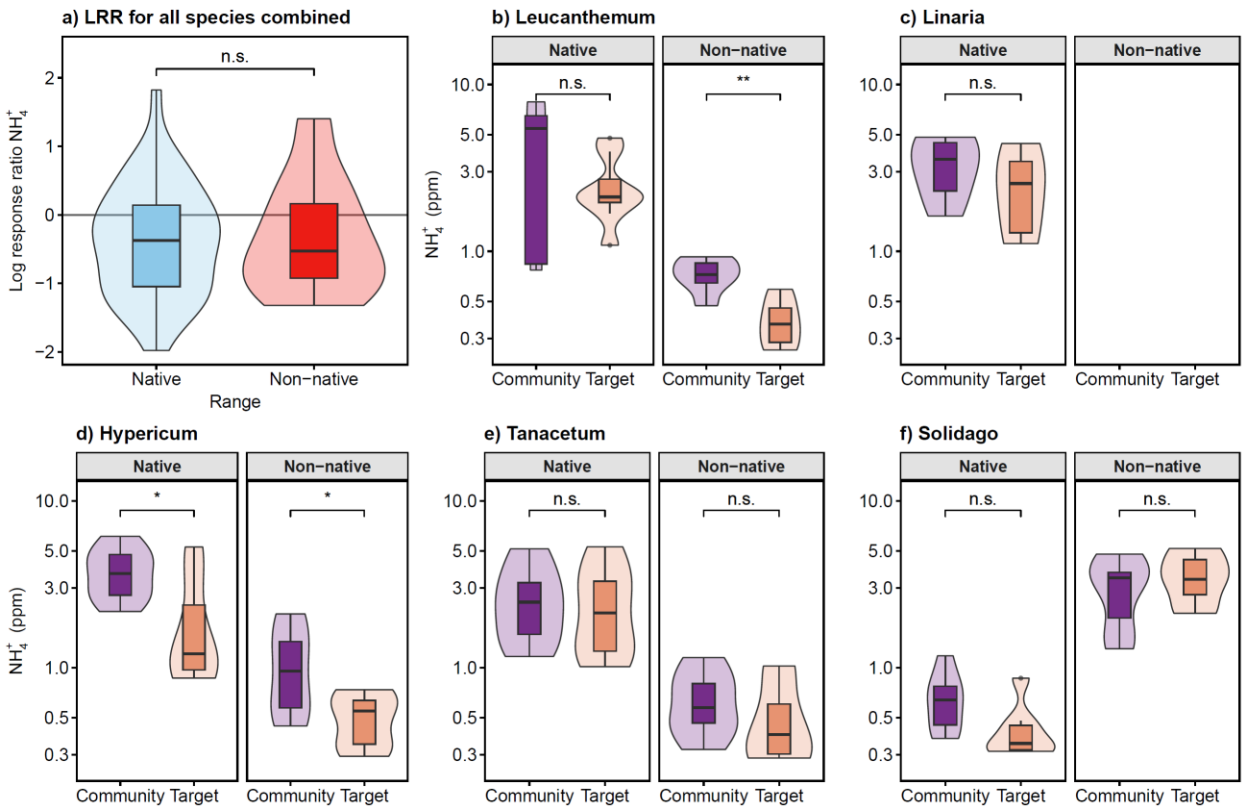


Figure S5. Differences in NH_4^+ between field plots dominated by the target invasive species and adjacent plots with only native species, in both the native and non-native ranges of the invaders. The LRR plot is standardized across the five study species using the log-response ratios (LRRs) for plot cover. Positive LRRs, denoted by an *, indicate an increase in NH_4^+ in invaded plots vs. adjacent native plots, whereas negative LRRs indicate a decrease in NH_4^+ in invaded plots vs. adjacent native plots. For individual species, estimated differences are based on pair-wise comparisons within the ranges and denoted as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s. = non-significant. Data are presented on a $\log_e$-scaled axis as they were logged in statistical analyses.

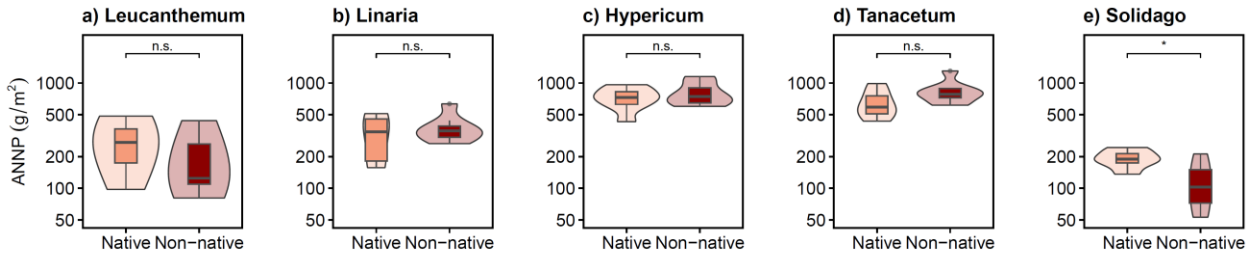


Figure S6. ANPP of the accessions/genotypes collected in the native vs. non-native ranges. *Leucanthemum*, *Linaria*, *Hypericum*, and *Tanacetum* were grown in the European common garden, whereas *Solidago* was grown in the North American common garden. This was to avoid introducing new genotypes to non-native ranges.

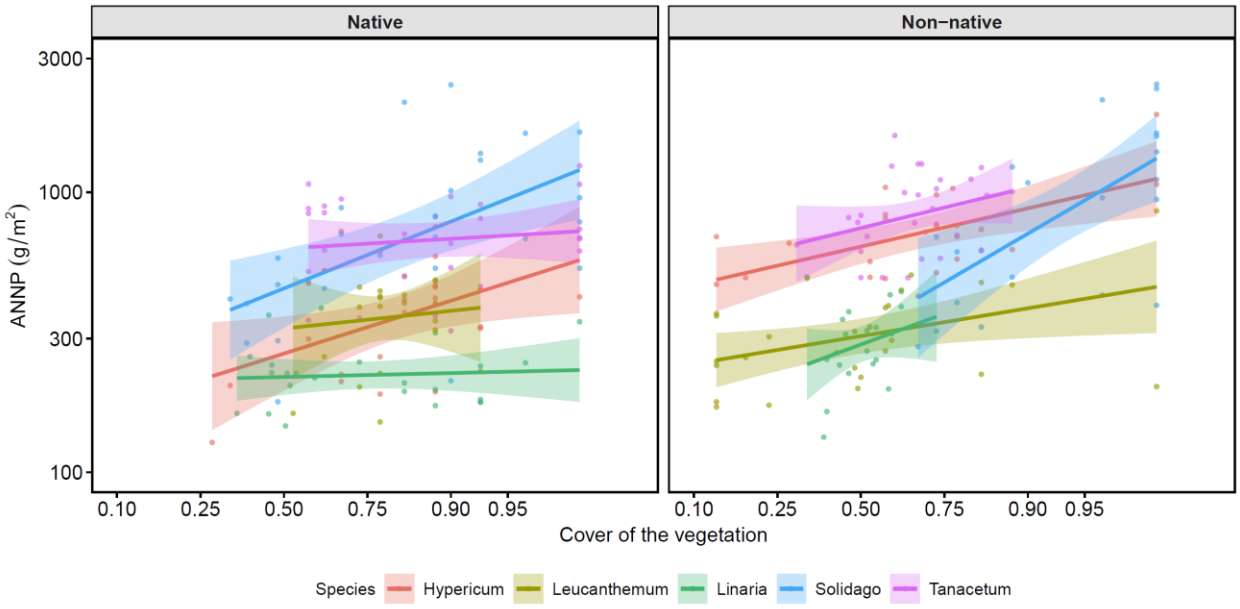


Figure S7. Regressions between ANPP and vegetation cover for each target species in their native and nonnative ranges. Shaded regions show 95% confidence limits. Linear mixed-effects models accounting for sampling location and species identity as random effects yielded significant relationships for productivity and vegetation cover across all species combined in both the native range (χ^2=15.07; P<0.001) and the non-native range (χ^2=31.71; P<0.001).

Supplementary Table S1. Species composition of the 40 native community plots in common garden at Bad Lauchstädt, Germany. The plots were designed to compare to monoculture plots of the target species and were composed of five native species common to the habitat of the target species. Ten species were chosen from the sPlot database (Bruelheide et al., 2019) and randomly selected to create eight unique combinations.

Hypericum perforatum

Brachypodium pinnatum	*Dactylis glomerata*	*Brachypodium pinnatum*	*Plantago lanceolata*
Plantago lanceolata	*Arrhenatherum elatius*	*Dactylis glomerata*	*Achillea millefolium*
Hieracium pilosella	*Achillea millefolium*	*Arrhenatherum elatius*	*Hieracium pilosella*
Briza media	*Lotus corniculatus*	*Lotus corniculatus*	*Koeleria pyramidata*
Sanguisorba minor	*Koeleria pyramidata*	*Briza media*	*Sanguisorba minor*

Brachypodium pinnatum	*Plantago lanceolata*	*Brachypodium pinnatum*	*Plantago lanceolata*
Achillea millefolium	*Dactylis glomerata*	*Arrhenatherum elatius*	*Dactylis glomerata*
Hieracium pilosella	*Arrhenatherum elatius*	*Hieracium pilosella*	*Achillea millefolium*
Lotus corniculatus	*Koeleria pyramidata*	*Lotus corniculatus*	*Briza media*
Briza media	*Sanguisorba minor*	*Koeleria pyramidata*	*Sanguisorba minor*

Tanacetum vulgare

Urtica dioica	*Arrhenatherum elatius*	*Urtica dioica*	*Vicia cracca*
Vicia cracca	*Dactylis glomerata*	*Arrhenatherum elatius*	*Achillea millefolium*
Rumex acetosa	*Achillea millefolium*	*Dactylis glomerata*	*Rumex acetosa*
Elymus repens	*Agrostis capillaris*	*Agrostis capillaris*	*Artemisia vulgaris*
Rumex acetosa	*Artemisia vulgaris*	*Elymus repens*	*Rumex acetosa*

Urtica dioica	*Vicia cracca*	*Urtica dioica*	*Vicia cracca*
Achillea millefolium	*Arrhenatherum elatius*	*Dactylis glomerata*	*Arrhenatherum elatius*
Rumex acetosa	*Dactylis glomerata*	*Rumex acetosa*	*Achillea millefolium*
Agrostis capillaris	*Artemisia vulgaris*	*Agrostis capillaris*	*Elymus repens*
Elymus repens	*Rumex acetosa*	*Artemisia vulgaris*	*Rumex acetosa*

Linaria vulgaris

Achillea millefolium	*Holcus lanatus*	*Achillea millefolium*	*Artemisia vulgaris*
Artemisia vulgaris	*Arrhenatherum elatius*	*Holcus lanatus*	*Poa pratensis*
Agrostis capillaris	*Poa pratensis*	*Arrhenatherum elatius*	*Agrostis capillaris*
Dactylis glomerata	*Hypericum perforatum*	*Hypericum perforatum*	*Rumex acetosella*
Elymus repens	*Rumex acetosella*	*Dactylis glomerata*	*Elymus repens*

Achillea millefolium	*Artemisia vulgaris*	*Achillea millefolium*	*Artemisia vulgaris*
Poa pratensis	*Holcus lanatus*	*Arrhenatherum elatius*	*Holcus lanatus*
Agrostis capillaris	*Arrhenatherum elatius*	*Agrostis capillaris*	*Poa pratensis*
Hypericum perforatum	*Rumex acetosella*	*Hypericum perforatum*	*Dactylis glomerata*
Dactylis glomerata	*Elymus repens*	*Rumex acetosella*	*Elymus repens*

Leucanthemum vulgare

Rumex acetosa	*Plantago lanceolata*	*Rumex acetosa*	*Festuca rubra*
Festuca rubra	*Briza media*	*Plantago lanceolata*	*Festuca pratensis*
Cerastium holosteoides	*Festuca pratensis*	*Briza media*	*Cerastium holosteoides*
Holcus lanatus	*Trisetum flavescens*	*Trisetum flavescens*	*Lotus corniculatus*
Achillea millefolium	*Lotus corniculatus*	*Holcus lanatus*	*Achillea millefolium*

Rumex acetosa	*Festuca rubra*	*Rumex acetosa*	*Festuca rubra*
Festuca pratensis	*Plantago lanceolata*	*Briza media*	*Plantago lanceolata*
Cerastium holosteoides	*Briza media*	*Cerastium holosteoides*	*Festuca pratensis*
Trisetum flavescens	*Lotus corniculatus*	*Trisetum flavescens*	*Holcus lanatus*
Holcus lanatus	*Achillea millefolium*	*Lotus corniculatus*	*Achillea millefolium*

Solidago canadensis

Plantago lanceolata	*Poa angustifolia*	*Plantago lanceolata*	*Arrhenatherum elatius*
Arrhenatherum elatius	*Urtica dioica*	*Poa angustifolia*	*Hypericum perforatum*
Poa trivialis	*Hypericum perforatum*	*Urtica dioica*	*Poa trivialis*
Taraxacum officinale	*Achillea millefolium*	*Achillea millefolium*	*Artemisia vulgaris*
Cerastium holosteoides	*Artemisia vulgaris*	*Taraxacum officinale*	*Cerastium holosteoides*

Plantago lanceolata	*Arrhenatherum elatius*	*Plantago lanceolata*	*Arrhenatherum elatius*
Hypericum perforatum	*Poa angustifolia*	*Urtica dioica*	*Poa angustifolia*
Poa trivialis	*Urtica dioica*	*Poa trivialis*	*Hypericum perforatum*
Achillea millefolium	*Artemisia vulgaris*	*Achillea millefolium*	*Taraxacum officinale*
Taraxacum officinale	*Cerastium holosteoides*	*Artemisia vulgaris*	*Cerastium holosteoides*

Species composition of the 40 native community plots in common garden at Fort Missoula, Montana. The plots were designed to compare to monoculture plots of the target species and were sourced from eight different populations in the non-native range. In Montana, we used the plot data from our field surveys to select the five most common co-occurring native perennial species for constructing the native communities for each invasive species in the garden.

Solidago & Tanacetum

Leymus cynereus	*Deschampsia cespitosa*	*Leymus cynereus*	*Deschampsia cespitosa*
Agropyron dasystachyum	*Spirea betulifolia*	*Deschampsia cespitosa*	*Achillea millefolium*
Achillea millefolium	*Symphyotrichum spathulatum*	*Spirea betulifolia*	*Artemisia ludoviciana*
Gaillardia aristata	*Artemisia ludoviciana*	*Artemisia ludoviciana*	*Geranium viscosissimum*
Solidago gigantea	*Geranium viscosissimum*	*Gaillardia aristata*	*Solidago gigantea*

Leymus cynereus	*Agropyron dasystachyum*	*Leymus cynereus*	*Agropyron dasystachyum*
Symphyotrichum spathulatum	*Deschampsia cespitosa*	*Spirea betulifolia*	*Symphyotrichum spathulatum*
Achillea millefolium	*Spirea betulifolia*	*Achillea millefolium*	*Achillea millefolium*
Artemisia ludoviciana	*Geranium viscosissimum*	*Artemisia ludoviciana*	*Solidago gigantea*
Gaillardia aristata	*Solidago gigantea*	*Geranium viscosissimum*	*Epilobium angustifolium*

Hypericum & Linaria

Artemisia frigida	*Astragalus adsurgens*	*Artemisia frigida*	*Artemisia ludoviciana*
Artemisia ludoviciana	*Gaillardia aristata*	*Astragalus adsurgens*	*Grindelia squarrosa*
Heterotheca villosa	*Grindelia squarrosa*	*Gaillardia aristata*	*Heterotheca villosa*
Pseudoroegneria spicata	*Lupinus serriceus*	*Lupinus serriceus*	*Symphyotrichum spathulatum*
Koeleria cristata	*Symphyotrichum spathulatum*	*Pseudoroegneria spicata*	*Koeleria cristata*

Artemisia frigida	*Artemisia ludoviciana*	*Artemisia frigida*	*Artemisia ludoviciana*
Grindelia squarrosa	*Astragalus adsurgens*	*Gaillardia aristata*	*Astragalus adsurgens*
Heterotheca villosa	*Gaillardia aristata*	*Heterotheca villosa*	*Grindelia squarrosa*
Lupinus serriceus	*Symphyotrichum spathulatum*	*Lupinus serriceus*	*Pseudoroegneria spicata*
Pseudoroegneria spicata	*Coeleria cristata*	*Symphyotrichum spathulatum*	*Koeleria cristata*

Leucanthemum

Leymus cynereus	*Lupinus serriceus*	*Symphyotrichum spathulatum*	*Artemisia frigida*
Heterotheca villosa	*Spirea betulifolia*	*Geranium viscosissimum*	*Pseudoroegneria spicata*
Achillea millefolium	*Gaillardia aristata*	*Epilobium angustifolium*	*Achillea millefolium*
Koeleria cristata	*Artemisia ludoviciana*	*Artemisia ludoviciana*	*Poa secunda*
Solidago gigantea	*Geranium viscosissimum*	*Gaillardia aristata*	*Astragalus adsurgens*
Symphyotrichum spathulatum	*Epilobium angustifolium*	*Heterotheca villosa*	*Gaillardia aristata*
Koeleria cristata	*Grindelia squarrosa*	*Spirea betulifolia*	*Symphyotrichum spathulatum*
Artemisia frigida	*Geranium viscosissimum*	*Agropyron dasystachyum*	*Pseudoroegneria spicata*
Artemisia ludoviciana	*Lupinus serriceus*	*Artemisia ludoviciana*	*Grindelia squarrosa*
Gaillardia aristata	*Achillea millefolium*	*Astragalus adsurgensniculatus*	*Solidago gigantea*