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RESEARCH ARTICLE

Exotic success following disturbance explained by weak native resilience and ruderal exotic bias

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Abstract

1. Disturbance is a primary driver of exotic plant invasions, but why disturbance commonly favours exotics over natives is unresolved.
2. To address this question, we conducted the first biogeographic study of disturbance across multiple plant species. We experimentally disturbed grasslands and added seeds of 34 plant species to plots in their native range and in two introduced ranges that differed in invasibility (susceptibility to invasion) to evaluate recruitment while examining potential influences of resource availability, native community recovery from disturbance (resilience) and life-history traits in local species pools.
3. Species pools in the native (donor) range were more strongly skewed towards ruderal taxa than species pools in the introduced ranges. This bias in the donor pool was exacerbated by introduction filters that further selected for ruderal traits, strongly skewing exotic species pools in the introduced ranges towards ruderals. Sown species, which reflected these trait patterns, benefited from disturbance universally, but their disturbance response was 10-fold greater in the more invasible introduced range. This result was not explained by nutrient availability, which responded similar to disturbance across ranges. Nor was it driven by background propagule pressure, which was minimal. Rather, the exaggerated disturbance effect in the more invasible introduced range appeared to be driven by weak recovery of the native plant community that allowed ruderal-biased exotics to proliferate.
4. Overall, disturbance appeared to favoured exotics because they were much more likely than natives to be ruderal. However, this trait bias only corresponded with an invader advantage in the more invasible range where weak community resilience was linked to slow-growing, stress-tolerant natives that failed to rapidly recover space and resources. In contrast, in the less invasible introduced range,

highly competitive native perennials quickly filled the disturbance gap, demonstrating high community resilience that appeared to limit invader recruitment.
5. *Synthesis*: Biogeographic influences on local species pools can facilitate invader success following disturbance, but final invasion outcomes are conditioned by native community resilience.

KEYWORDS
biogeography, community assembly, context dependence, disturbance, ecological resilience, introduction filters, invasibility, invasion, propagule pressure, species pools

1 | INTRODUCTION

Disturbance has long been recognized as a principal driver of plant invasions (Davis et al., 2000; Hobbs & Huenneke, 1992; Jauni et al., 2015). Yet, the specific role that disturbance plays in facilitating invasions remains unclear. Disturbance can increase a community's susceptibility to invasion, that is, its invasibility (sensu Lonsdale, 1999), by reducing competition and increasing resource availability (Davis et al., 2000). Hence, ecological resilience, the degree and rate of recovery of a community from a perturbation (Beisner et al., 2003), provides a valuable metric for evaluating how disturbance-driven changes in competition and resource uptake may influence invasibility. However, these factors alone are insufficient to explain why exotics are commonly more successful than natives at exploiting disturbances (Hierro et al., 2005; Jauni et al., 2015; Seabloom et al., 2015). Disturbances are endemic to most native communities, and, in the absence of exotics, most native communities recover from disturbances through processes of succession (Pickett et al., 1987). Why then do exotics so often gain the upper hand following disturbance?

It was recently proposed that community assembly theory could provide a framework for understanding this exotic disturbance advantage as a function of biogeographic processes (Pearson, Ortega, Eren, & Hierro, 2018). These authors posited that if species pools in the donor range are better represented by traits adapted to disturbed conditions, for example, ruderal traits (sensu Grime, 1974; Kotanen, 1997), than are native species pools in the recipient range, and/or if introduction filters favour species with more ruderal traits arriving from donor pools (e.g. Colautti et al., 2006), these processes could generate higher proportions of ruderals in local exotic versus native species pools. Such a provenance bias sets up a scenario where disturbance is likely to favour introduced over native species via numerical or qualitative sampling effects, that is, the local species pool is numerically dominated by exotic ruderals and/or has a greater likelihood of superior exotic ruderal species being present (Huston, 1997). Alternatively, exotics may gain a general advantage over natives through other biogeographic processes like release from natural enemies (Keane & Crawley, 2002) that could be exacerbated by disturbances. For example, increased resource availability and/or reduced competition may interact with enemy release (e.g. Blumenthal, 2006). Testing these hypotheses requires biogeographic disturbance studies in the native and introduced range for multiple invaders that ideally account for the composition of ruderal traits in species pools in both ranges. Despite calls for such studies made over 15 years ago (Hierro et al., 2005), surprisingly few biogeographic disturbance studies have been conducted to date (e.g. Hierro et al., 2006; Maron et al., 2013; Williams et al., 2010), and none have addressed multiple invaders and the functional trait composition of donor and recipient species pools necessary to test these hypotheses.

Propagule pressure has the capacity to override many ecological processes when strong (Colautti et al., 2006; Lockwood et al., 2005; Simberloff, 2009). Hence, it is necessary to account for propagule pressure while quantifying other factors to disentangle their independent effects. Although historical interest in propagule pressure has emphasized its influence on processes acting at continental and regional scales, that is, the likelihood of introduced species establishing in a new range (Colautti et al., 2006; Lockwood et al., 2005, 2009), these concepts also apply at local scales where propagule pressure can influence invader establishment, spread and population density (e.g. Rouget & Richardson, 2003; Von Holle & Simberloff, 2005). Within a system, total propagule pressure may arise from intrinsic processes like seed rain that derive from inherent invader traits such as fecundity in addition to extrinsic anthropogenic inputs deriving from sources like nearby roads or agricultural fields (Lockwood et al., 2009; Pearson, 2022). While it can be very difficult to distinguish between intrinsic versus extrinsic sources of propagule inputs, quantifying recruitment in the presence and absence of controlled seed additions in the native and introduced ranges can provide a metric for evaluating the extent to which propagule pressure may drive invader success in new ranges.

Herein, we conducted experimental disturbances and seed additions (full factorial design) of 34 grassland plant species in their native and two introduced ranges that differ in invasibility in order to evaluate the effects of disturbance on plant invasions in a biogeographic context. We quantified recruitment of focal invaders in 1 m^2 disturbed and undisturbed plots with and without seeds added. This allowed us to both control propagule inputs and account for the effects of background propagule pressure. To evaluate how key aspects of disturbance influence invasion, we quantified the recovery of the native plant communities (resilience) and soil nutrient levels following experimental disturbances.

Finally, we evaluated the functional composition of the native communities relative to the exotics to determine whether provenance differences in the representation of ruderal traits might influence responses to disturbance.

2 | METHODS

2.1 | Study areas

We conducted experiments on 34 herbaceous plant species (Table S1) at grassland sites in their native range of Turkey ($n=10$; centroid latitude = 38.0° and longitude = 29.1°) and two introduced ranges: Montana, United States (hereafter MT; $n=9$; in MT; centroid latitude = 47.0° and longitude = 113.5°) and La Pampa, Argentina (hereafter LP; $n=10$; centroid latitude = −37.3° and longitude = −64.6°). Sites were located in natural bunchgrass communities that were untransformed by agriculture or severe domestic grazing and were dominated by native plant species with very low cover of exotics. Within each range, sites were spaced 12.5 km apart on average (±SD of 17.1), with Turkey sites somewhat more clustered because higher human populations have isolated natural grasslands more so there (Figure S1). The Turkey grasslands were dominated by perennial grasses in the genera: *Festuca*, *Koeleria*, *Bromus*, *Stipa*, *Elymus* and *Poa*. MT grasslands represented the bluebunch wheatgrass (*Pseudoroegneria spicata*) habitat type (Mueggler & Stewart, 1980) dominated by the genera: *Pseudoroegneria*, *Festuca*, *Koeleria* and *Stipa*. LP grasslands were dominated by the perennial grasses in the genera: *Piptochaetiun*, *Nassella* (aka *Stipa*) and *Poa*. Hence, the ranges all reflect bunchgrass systems and share several dominant genera.

All study sites were located within continental climate zones in each region. Mean annual precipitation and temperature, respectively, are 61 cm and 11°C in Turkey, 32 cm and 8°C in MT and 63 cm and 15°C in LP, with most precipitation coming as snow and rain during winter and spring in Turkey and MT and as rain in spring and summer in LP. Sites in Turkey and MT are mountainous with an average elevation of 1391 m (±160 m) and 1277 m (±233 m), respectively, whereas sites in LP are relatively flat and lower elevation (280 ± 48 m). All ranges experience grazing by large and small native herbivores and domestic grazers, mostly cows and sheep. Turkey and MT have open ranges that experience periodic, haphazard grazing pressure, so they were not fenced. Plots were fenced in LP (standard barbed wire cattle fencing) during the experiment to protect seedlings from trampling because the private grasslands there are heavily grazed. However, comparison of cover estimates in plots prior to the experiments with those late in the experiment indicated that fencing did not affect native cover, an outcome we attribute to the high resilience of this system to grazing and other disturbances (Appendix S1). Finally, extensive grassland surveys which encapsulated and extended well beyond the study areas but reflected the representative community types for each range (400 1 m^2 plots from 20 locations in each system) indicated that the proportion of total plant cover represented by exotics averaged >13 times higher in MT ($\bar{x}=0.27 \pm$ SE of 0.26) versus LP ($\bar{x}=0.02 \pm 0.009$) even though the incidence of local-scale disturbance followed the opposite pattern (Appendix S2), suggesting MT is more susceptible to invasion, that is, more invasible, than LP (see also Pearson et al., 2016; Pearson, Ortega, Villarreal, et al., 2018). Note, while MT does have higher invasion levels across the region, the proportion of exotic species in local pools associated with the study sites was similar in MT versus LP (23% vs. 26% of species were exotic, respectively; $\chi^2=0.3$, $p=0.6$), as MT had higher richness of both native and exotic species relative to LP (see Section 3). The study area in Turkey had very low representation of introduced species.

Permissions for conducting this research were as follows: Turkey, Gıda, Tarım ve Hayvancılık Bakanlığı, Tarımsal Araştırmalar ve Politikalar Genel Müdürlüğü (permit number: 50955690-335.01/48883); Montana, Bitterroot National Forest (permit number: BIT 201307); Confederated Salish and Kootenai Tribes (permit number: TLD-CP-2013-1); Bureau of Land Management (no permit number); National Bison Range (no permit number); Lee Metcalf National Wildlife Refuge (no permit number). Additional permissions were granted verbally by private ranch owners in Montana and Argentina.

2.2 | Experimental design

At each site in the introduced ranges, we established three blocks in native-dominated grasslands with minimal invasion, each consisting of four 1 m^2 plots spaced 1 m apart and randomly assigned to receive disturbance (±) and/or seed addition (±) in a full-factorial design. Disturbance consisted of digging up and breaking the soil to a depth of approximately 15 cm and removing plant biomass including roots and shoots. These treatments were meant to mimic the small-scale disturbances that dominate these systems, which are commonly created by rodent and mesocarnivore digging and ungulate trampling. Seed addition in the introduced ranges involved adding seeds of 19 exotic plant species to each seed addition plot. The set ('cohort') of 'focal invaders' added in each introduced range were species native to Turkey and present within the corresponding introduced range, but species differed between MT and LP with the exception of six overlapping species (Table S1). The chosen invaders represented 20% of the exotic species found in extensive grassland surveys conducted MT in and 26% of those in LP. To reflect the fact that larger seeded species produce fewer seeds (e.g. Westoby et al., 1996), we varied the number of seeds added per species according to seed size, with the total number of seeds added to each plot differing minimally between introduced ranges (MT: $n=4500$ per plot; LP: $n=4200$ per plot; Table S1).

We followed a parallel design in Turkey, with each site consisting of three blocks in native-dominated grasslands but with six 1 m^2 plots randomly assigned to receive disturbance (±) crossed with addition of seeds of either MT invaders, LP invaders, or none. In each of these blocks, MT invaders were added to one disturbed and one undisturbed plot and LP invaders were added to a separate disturbed and undisturbed plot, with the total number of seeds

added per plot matching the number added in the corresponding introduced range. Each block in Turkey also included one pair of disturbed/undisturbed plots with no seeds added to represent the unseeded controls. Seeds were collected locally from ≥3 populations in each system. Experimental treatments were initiated at the end of the respective growing seasons in each range: Turkey and MT 2011 and LP 2012. Treatments were repeated the following year (Turkey and MT 2012 and LP 2013) using new +disturbance +seed addition, +disturbance −seed addition and −disturbance +seed addition plots, but keeping the same −disturbance −seed addition control plots in both years. Note that two focal invaders in the La Pampa cohort were replaced in year 2 due to insufficient seed source such that the total number of seeds added to each plot differed slightly in year 2 ($n = 4300$ per plot; Table S1). Focal exotics in seed addition plots were not allowed to reproduce during the study and were removed after sampling in MT.

All plots were read for recruitment during peak growing season the year following treatment by counting seedlings of each focal species. To represent focal invader recruitment in each seed addition plot, (1) seedling counts for each species were adjusted for background recruitment by subtracting the number of seedlings recorded in the unseeded plot from the same block, disturbance treatment and year, and (2) adjusted counts were summed across species. We also estimated cover and species richness of all plant taxa (both focal and non-focal taxa) to assess community responses to disturbance, including (1) resilience, defined as the rate and degree of native community recovery from disturbance and (2) the success of exotic versus native species in establishing following disturbance. Although our primary analysis of community responses focused on unseeded plots (see Section 2.4 for details), we also used data from seeded plots for follow-up analyses (see Section 3). Cover was visually estimated by species to the nearest 5% except for species with <10% cover, which were estimated to the nearest 1%, and those with <1% cover, which were recorded as 0.1% cover. Cover was also estimated pretreatment, and in the second post-treatment year for plots initiated in year 1 of the study. For analysis of community responses to disturbance, cover per plot and year was summed across species by provenance category (i.e. native vs. exotic). Similarly, the number of species per plot and year was tallied by provenance category to represent richness. To consider the role of functional groups, we further split both cover and richness between perennial species and shorter lived species (annuals and biennials), with the latter representing ruderal life-history strategies (sensu Grime, 1974).

2.3 | Soil sampling

Soils were sampled coincident with vegetation sampling in the first growing season after treatment year 1 by collecting two soil cores (5 cm dia. × 10 cm deep) from each unseeded disturbed plot and from the adjacent undisturbed grassland (to avoid disturbing control plots) and then pooling the samples by disturbance treatment for each site. Soils were sent to Ward Laboratories (Kearny, Nebraska) for standard nutrient analyses. We focused on available nitrogen (NO_3^-), phosphorus (P, Mehlich 3) and potassium (K) as key limiting nutrients for plants (per Davis et al., 2000). Soil data are presented by site in Table S2.

2.4 | Statistical analyses

Analyses were conducted using generalized linear mixed models in SAS (version 9.4, PROC GLIMMIX, SAS Institute 2013) with two exceptions described below. Response variables were fit to the most appropriate distribution, as assessed by examining scatterplots of residuals against predicted values (negative binomial distribution for number of seeded invaders and species richness; lognormal distribution for cover, NO_3^-, P and K). We present least squares means and SEs backtransformed from the scale used in analysis.

For analysis of focal invader recruitment, the response variable was the number of target species plants tallied per seed addition plot 1 year after treatment, as adjusted for background recruitment in unseeded plots. Plots seeded in each of 2 years were analysed in the same model to assess the collective response across years, with the inclusion of random factors to account for potential covariance linked to spatial (site, block within site) and spatiotemporal aggregation (site within year, and block within site and year). Disturbance (±), range (native or introduced), invader cohort (sown species representing MT vs. LP exotics) and their interactions were treated as fixed factors in the model. We used this same model structure to evaluate background recruitment patterns of focal invaders in unseeded plots.

To assess community responses to disturbance in unseeded plots, including resilience of native taxa and the success of exotics in the absence of seed addition, we ran a separate model for each cover and species richness variable defined by provenance category and by functional group, with each post-treatment year tested separately. Fixed factors in these models were disturbance (±), range (Turkey, MT or LP) and their interaction; and random factors were site and block within site. We were able to take this simple approach to evaluating community responses to disturbance given that in all cases, cover and richness variables did not differ by disturbance treatment prior to treatment ($p > 0.1$; Tables S3–S5). Hence, as our measure of community recovery, we considered the degree to which native cover and richness metrics in disturbed plots matched levels measured in adjacent undisturbed plots in each post-treatment year, with the latter representing pretreatment conditions as adjusted for background temporal fluctuations. Exotic success was assessed via cover and not richness metrics, as the latter models would not converge given that values were almost always zero in Turkey (99% of 180 cases across years). However, we note that exotic richness was highly correlated with exotic cover ($r = 0.95$, $p < 0.001$), and hence, the latter sufficed to represent status of exotic taxa in communities. Soil nutrient variables were analysed individually in models that included disturbance (±), range

(Turkey, MT or LP) and their interaction as fixed factors, and site as a random factor. To evaluate significant ($p < 0.05$) disturbance x range effects obtained in these analyses, we tested for post hoc differences between disturbed and undisturbed plots in each context using multiple comparisons wherein the p-value was adjusted for the number of comparisons via the Bonferroni method.

To examine whether sown species generally responded similar to treatments in seed addition plots versus particular taxa driving overall patterns, we also examined recruitment of individual focal species while accounting for interdependencies of multiple taxa in the same plot using MANOVA (PROC GLM, SAS Institute 2013). Each invader cohort (sown species representing MT vs. LP exotics) was analysed in a separate model. The response was the mean number of plants per focal species, site and disturbance treatment across years, calculated on the log scale to account for positive skewness. Model factors included disturbance (±), range (native or introduced) and their interaction.

To examine how the proportional representation of ruderal traits within local species pools might influence responses to disturbance in each range, we compiled lists of all species recorded in plots across sampling years. Sown species were excluded from lists if recorded only in seed addition plots. We then used χ^2 tests for homogeneity of variance to test for differences in the proportion of ruderal versus perennial species (1) in the native pool of Turkey relative to the native pool in each introduced range, (2) in native versus exotic pools in each introduced range and (3) in the native pool of Turkey compared to the exotic pool in each introduced range consisting specifically of species native to Turkey.

3 | RESULTS

Disturbance consistently increased recruitment of sown focal invaders ($p < 0.001$), but this effect was >10 stronger in the introduced range of MT than in other ranges (disturbance × range × invader cohort: $p = 0.002$; Figure 1; Table S6). More focal plants generally recruited in their introduced relative to native range (i.e. MT vs. Turkey and LP vs. Turkey; $p < 0.001$), especially in MT (range × invader cohort: $p = 0.003$) as promoted by disturbance (disturbance × range × invader cohort: $p = 0.002$; Figure 1; Table S6). MANOVA generated parallel results to those described above, indicating that individual focal species within each invader cohort responded similar to disturbance and range shifts (Figure 2; Appendix S3; Table S7). Recruitment of focal invaders in unseeded plots was low relative to levels in seeded plots, signifying that effects of background propagule inputs were relatively minor. Disturbance increased background recruitment only in MT (disturbance × range × invader cohort: $p = 0.002$; Figure 1 inset; Table S6). MT invaders tended to recruit better in unseeded plots than LP invaders (invader cohort: $p < 0.001$), but this pattern was stronger in the native range (range × invader cohort: $p = 0.003$), where the advantage of MT invaders depended on disturbance (disturbance × range × invader cohort: $p = 0.002$).

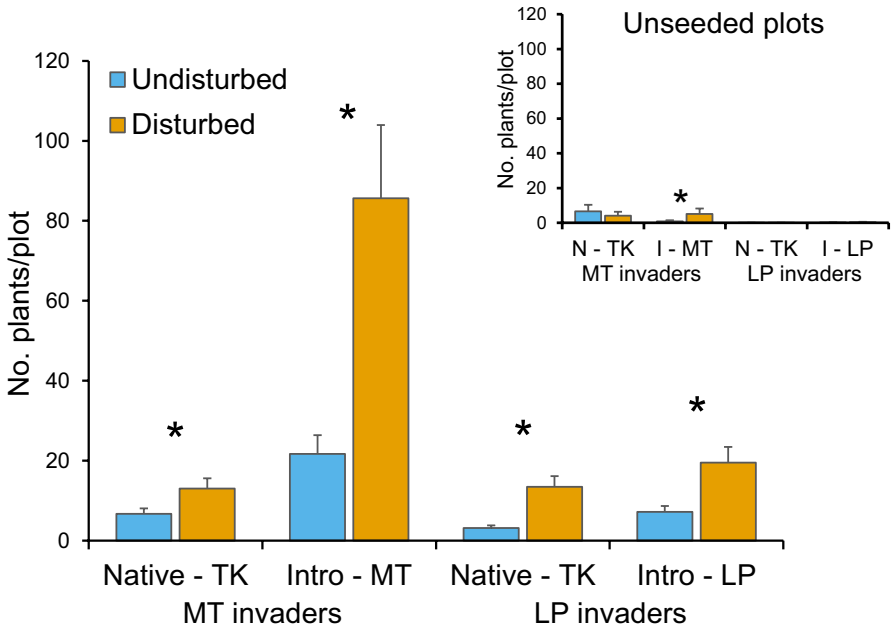

FIGURE 1 Mean (+SE) recruitment of focal invaders in disturbed versus undisturbed plots in their native range of Turkey and introduced ranges of either Montana, United States (MT) or La Pampa, Argentina (LP). Different cohorts of invaders were added to plots in Montana versus La Pampa to represent exotic species in each introduced range that were native to Turkey, and these same cohorts were added to corresponding plots in Turkey. Treatments were applied to separate plots in each of 2 years, and results represent the collective response across years. Inset shows background recruitment of focal invaders in unseeded plots. Asterisk above bars indicate significant disturbance effects ($p < 0.05$) based on post hoc comparisons evaluating the disturbance × range × invader cohort interaction.

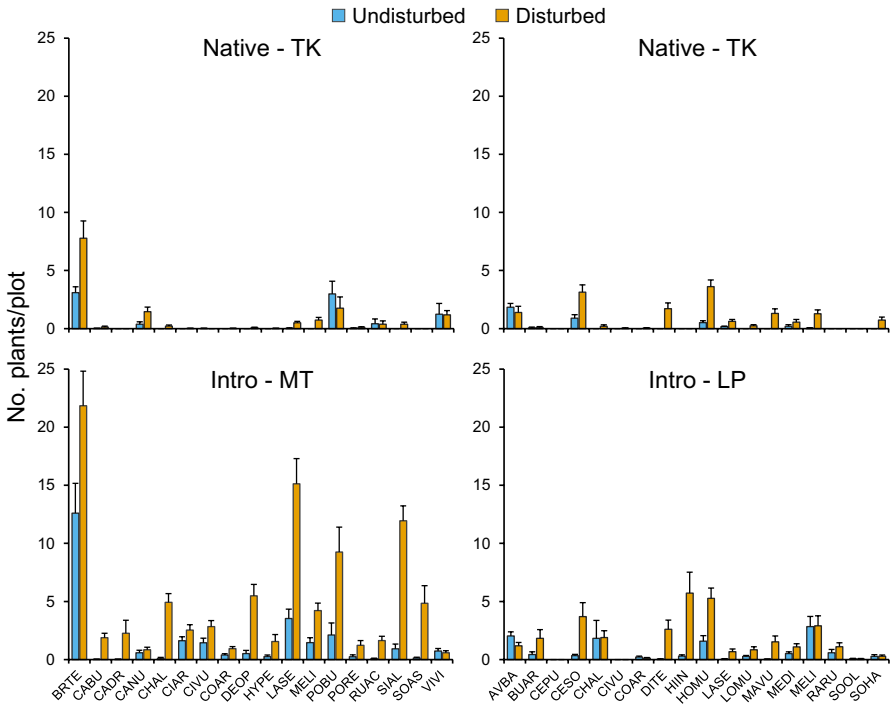

FIGURE 2 Mean (+SE) recruitment of individual species of focal invaders in disturbed versus undisturbed plots in their native range of Turkey and introduced ranges of either Montana, United States (MT) or La Pampa, Argentina (LP). Different cohorts of invaders were added to plots in Montana versus La Pampa to represent exotic species in each introduced range that were native to Turkey, and these same cohorts were added to corresponding plots in Turkey. Treatments were applied to separate plots in each of 2 years, and results represent the collective response across years. MANOVA revealed consistent responses of individual focal species to disturbance as compared between the native and introduced range for each cohort of invaders (Appendix S3; Table S7). AVBA, *Avena barbata*; BRTE, *Bromus tectorum*; BUAR, *Buglossoides arvense*; CABU, *Capsella bursa-pastoris*; CADRA, *Cardaria draba*; CANU, *Carduus nutans*; CEPU, *Centaurium pulchellum*, CESO, *Centaurea solstitialis*; CHAL, *Chenopodium album*; CIAR, *Cirsium arvense*; CIVU, *Cirsium vulgare*; COAR, *Convolvulus arvensis*; DESO, *Descurainia sophia*; DITE, *Diplotaxis tenuifolia*; HIIN, *Hirschfeldia incana*; HOMU, *Hordeum murinum*; HYPE, *Hypericum perforatum*; LASE, *Lactuca serriola*; LOMU, *Lolium multiflorum*; MAVU, *Marrubium vulgare*; MEDI, *Medicago lupulina*, *M. minima*, and *M. minima*; MELI, *Melilotus albus* and *M. officinalis*; POBU, *Poa bulbosa*; PORE, *Potentilla recta*; RARU, *Rapistrum rugosum*; RUAC, *Rumex acetosella*; SIAL, *Sisymbrium altissimum*; SOAS, *Sonchus asper*; SOHA, *Sorghum halepense*; SOOL, *Sonchus oleraceus*; and VIVI, *Vicia villosa*.

Resilience to disturbance measured as recovery of native cover and richness in unseeded plots in the 2 years following treatment varied markedly by range and functional group. Disturbance depressed native plant cover in the first post-treatment year (disturbance: $p < 0.001$), with strong effects in Turkey and MT and relatively weak effects in LP (disturbance × range: $p = 0.035$; Figure 3a; Table S3). Two years after treatment, native plant cover in disturbed plots remained depressed in Turkey and MT but had recovered to undisturbed levels in LP (disturbance × range: $p = 0.021$; Figure 3b; Table S3), indicating very high resilience to disturbance in this community. These patterns were driven primarily by native perennial species (Figure 3a,b; Table S3), which dominated cover in all communities in the absence of disturbance. In contrast, cover of native ruderals (annuals and biennials) was a minor component of intact communities. While this group responded positively to disturbance in all ranges, native ruderal cover remained low except in Turkey, where this group became dominant under disturbed conditions (Figure 3a,b; Table S3).

Disturbance depressed native species richness in unseeded plots only in MT, specifically in the first post-treatment year as driven by the loss of perennials (disturbance × range: $p = 0.004$; Figure S2; Table S4). Although Turkey also lost native perennials to disturbance, this decrement was buffered by the large number of ruderal species, which dominated richness metrics in this range regardless of disturbance (Figure S2; Table S4). In LP, native species richness was dominated by perennials that rapidly recovered from disturbance unlike in the other ranges (Figure S2; Table S4).

In unseeded plots, disturbance increased exotic species cover in post-treatment years 1 and 2, but only in MT (disturbance × range: $p \leq 0.005$) as driven by ruderal invaders (Figure 3c,d; Table S5). Exotic species cover comprised a minor component of communities except in MT under disturbed conditions, where native species lost their cover advantage (Figure 3c,d).

Disturbance increased nitrogen availability (NO_3^-) and reduced potassium (K), but these effects did not differ significantly among ranges (disturbance × range: $p > 0.58$; Figure S3). Overall, levels of NO_3^- were highest in Turkey and lowest in LP ($p < 0.001$), while K showed the opposite pattern ($p < 0.001$; Figure S3). Phosphorus did not vary significantly with disturbance or range ($p > 0.11$; Figure S3).

While the above results suggested that the relatively strong recruitment of exotics in MT following disturbance was linked to low resilience rather than soil nutrient responses, we wanted to more

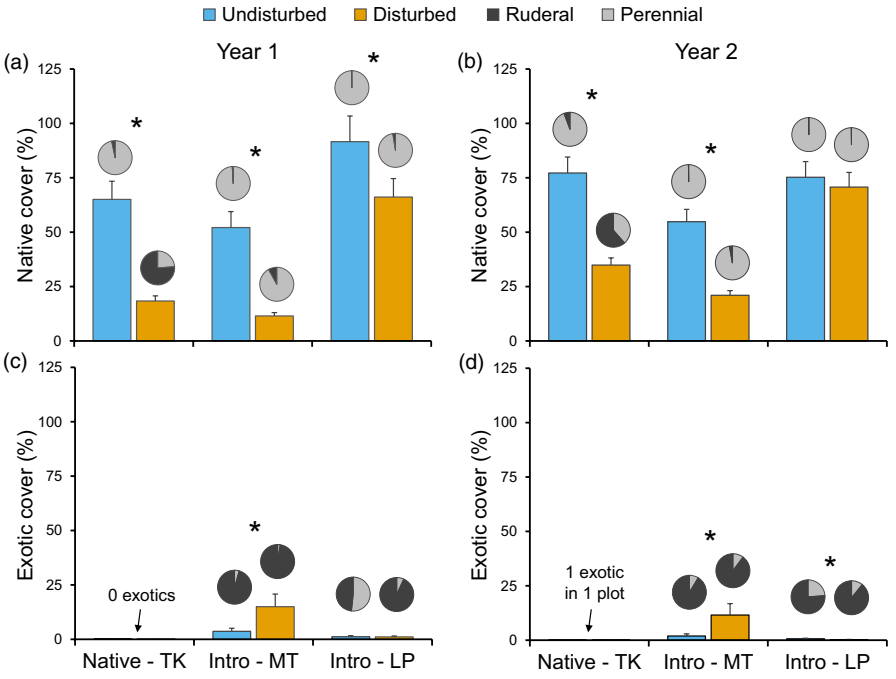

FIGURE 3 Native (a, b) and exotic (c, d) cover ($\bar{x}+SE$) in undisturbed versus disturbed plots with no seeds added in the native range of Turkey (TK) and the introduced ranges of Montana, United States (MT) and La Pampa, Argentina (LP), assessed in the first (Year 1) and second (Year 2) post-treatment years. Pie charts show the proportional representation of ruderal (annual and biennial) versus perennial functional groups derived from mean cover estimates. Asterisk above bars indicate significant disturbance effects ($p<0.05$), as assessed via post hoc comparisons evaluating the interaction between disturbance and range. See Table S4 for full model results for total cover and split by functional group.

explicitly evaluate how invasion patterns in seeded plots related to community (native cover and richness, split by functional group) and soil nutrient covariates. To do so, we ran a series of models treating focal invader recruitment as the response, with covariates included either singly or together (see Appendix S4 for details). Cover of native perennial species was the strongest explanatory factor in this analysis, showing a negative association with recruitment that was consistent across invader cohorts, disturbance treatments and ranges. In contrast, soil nutrients showed weaker more variable correlations with focal invader recruitment that did not align with range differences.

Representation of ruderals (annuals and biennials) versus perennials in local native species pools was much greater in the native range relative to introduced ranges (Figure 4). In Turkey, 52% of 309 native species were ruderal compared to only 22% of 96 native species in MT ($\chi^2=31.0$, $p<0.001$) and 34% of 67 native species in LP ($\chi^2=7.0$, $p=0.008$). Representation of ruderals in exotic species pools of the introduced ranges was higher than in native pools in both MT (76% [of 29] vs. 22%; $\chi^2=31.8$, $p<0.001$) and LP (79% [of 24] vs. 34%; $\chi^2=14.3$, $p<0.001$; Figure 4). Notably, 79% of MT exotics were species native to Turkey as were 83% of LP exotics. Moreover, the proportion of these Turkey natives that were ruderal (MT: 78% of 23 species; LP: 89% of 20 species) was much higher than in the native pool of Turkey (52%; $\chi^2=5.9$, $p=0.015$ and $\chi^2=8.2$, $p=0.004$ respectively).

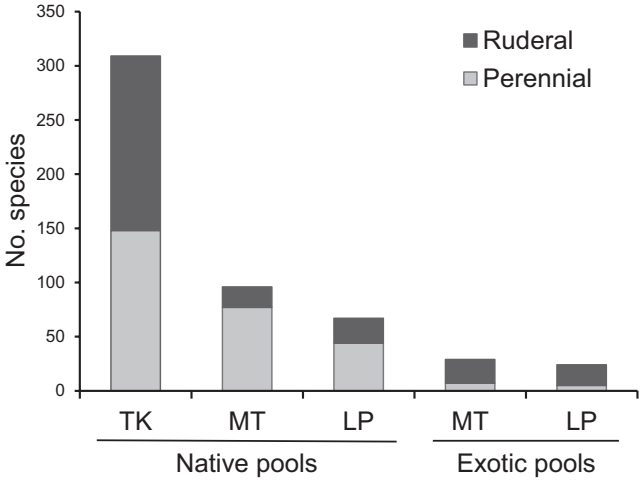

FIGURE 4 Number of plant species in local native and exotic pools split by functional group into ruderal (annual and biennial) versus perennial taxa, in the native range of Turkey (TK) and the introduced ranges of Montana, United States (MT) and La Pampa, Argentina (LP). Note that the exotic pool in Turkey consisted of only three species and is not shown.

4 | DISCUSSION

Disturbance plays a prominent role in invasions, but why disturbance commonly favours exotic over native species is unclear. By conducting biogeographic disturbance and seed sowing experiments that contrasted the native range with two introduced ranges differing in invasibility, we provide valuable insights regarding when and how disturbance facilitates plant invasions. We found that sown focal invaders recruited better following disturbance in both their native and introduced ranges, but this disturbance effect was greatly exaggerated in the more invasible introduced range. In the less invasible introduced range, invader recruitment was largely suppressed as rapidly recovering native perennials quickly filled the disturbance gap, demonstrating strong community resilience. In contrast, in the more invasible introduced range, community resilience and hence resistance to

invasion was undermined by sluggish recovery of the native community linked to slow-growing perennials. Importantly, we found that a higher proportional representation of ruderals in the donor species pools, enhanced by introduction filters that also appeared to favour ruderals, strongly bolstered representation of exotics in ruderal species pools of the introduced ranges. This bias towards ruderal traits in exotic species pools, combined with the low representation of native ruderals, promoted the shift towards exotics following disturbance in the more invasible range, as exotic ruderals exploited open resource space. Our results reveal that exotic success following disturbance can be explained by weak native resilience in the recipient community combined with extrinsic processes that bias exotic species pools towards ruderal species, highlighting the roles of biogeography and context dependence in plant invasions.

Our experiment provides valuable information regarding the consistency versus conditionality of disturbance effects on abiotic and biotic processes. Disturbance elevated available nitrogen and reduced plant competitors in each system. Hence, it was not surprising that disturbed plots experienced higher recruitment of sown species than undisturbed plots across systems, particularly since most sown species were ruderals (Table S1). Nonetheless, disturbance had the greatest effect in elevating recruitment in the more invasible introduced range, even though nutrient pulses associated with disturbance were comparable among ranges. This outcome was linked to variability in community resilience to disturbance among systems, with the more resilient community closing the resource gap and elevating competitive resistance more quickly. Community recovery was strongest in the invasion resistant LP, where native perennial cover rapidly rebounded to >70% of undisturbed levels in the first year and essentially 100% in the second year following disturbance, thereby strongly suppressing sown invaders, despite a poor representation of native ruderals. In the more invasible range of MT where stress-tolerant perennials were slow to recover and native ruderals were uncommon, ecological resilience was low, and sown species readily exploited the opportunity created by disturbance. Importantly, both introduced ranges are dominated by bunch-forming grasses that reproduce only by seed. Hence, differences in resilience between these ranges appeared to be driven by differences in fecundity and growth rates of these community dominants. These results provide experimental support for extensive surveys demonstrating the high invasibility of MT and low invasibility of LP (Pearson, Ortega, Villarreal, et al., 2018), while revealing the underlying mechanisms driving invasibility. In sum, ecological resilience, the rate and extent of recovery of the native community, played a strong role in determining invader success, with differences in resilience between invaded systems linked to differences in functional composition of native communities.

Placing our results in the context of community assembly theory (Pearson, Ortega, Eren, & Hierro, 2018) reveals the crucial roles that donor community composition and invasion filters can play in establishing invader traits within local species pools. While we recognize that Turkey is not the sole donor pool or even necessarily the specific source population for all our study species, we believe that Turkey provides a reasonable representation of the donor community for our invaders because most New World invaders come from Asia, Europe or Africa (van Kleunen et al., 2015) and Turkey's flora is reflective of its phytogeographic conflux for these regions (Davis, 1971; Şekercioğlu et al., 2011). Moreover, sampling across the entire native ranges for 34 species would be infeasible, so identifying a reasonably representative subset of the native range is necessary. As empirical support for Turkey's representative status, we show that ≈80% of all the introduced species in our plots were native to Turkey (79% of MT species 83% of LP's). In order to compare these donor and recipient species pools, we simplified community composition into ruderals (annuals and biennials) versus perennials and found that the proportion of natives that are ruderal species was far greater in Turkey (52%) than in MT (22%) or LP (34%). Furthermore, within the introduced ranges, the proportion of Turkish species (i.e. exotics native to Turkey) that were ruderal versus perennial increased substantially (78% and 89% in MT and LP, respectively) relative to the donor range (52%), suggesting that introduction filters favour the arrival of ruderal species (filters may apply within the native range, in transit, and/or upon arrival; see Colautti et al., 2006). These findings suggest that ruderal species pools in the introduced ranges may become biased towards exotics due to a higher proportion of ruderals in donor pools and/or introduction filters that select for ruderal species. Of course, sampling effects may result in some particularly aggressive ruderals being introduced from such a large donor species pool—species like *B. tectorum*, which is the most aggressive invasive plant in Montana grasslands (Pearson et al., 2016, 2022; Pearson, Eren, Ortega, et al., 2018). Yet, despite the fact that *B. tectorum* was the dominant recruiter in Montana, it did not drive overall results, as other species showed similar disturbance responses (see Figure 2). Other biogeographic factors such as release from natural enemies or novel weapons could exaggerate effects of donor pools and translocation filters, but these were not measured in this study. Importantly, the final effect of the observed donor pools and filtering processes, which were evident in both introduced ranges, played a much stronger role in the less resilient Montana grasslands relative to the more resilient La Pampa grasslands, emphasizing the role of context dependence in invasion outcomes.

Propagule pressure has the potential to strongly influence invasion outcomes from continental to local scales (Colautti et al., 2006; Lockwood et al., 2005; Rouget & Richardson, 2003). While it is very difficult to explicitly quantify propagule pressure and decipher intrinsic from extrinsic sources, we found little evidence that background propagule pressure played a substantive role in our experiments. Ambient recruitment of target species in unseeded plots was low across our study systems. Hence, we conclude that propagule pressure did not drive overall outcomes. Nonetheless, background propagule pressure could have played a minor role in Montana where natural recruitment of target species was significantly higher in the unseeded disturbed versus undisturbed plots relative to the native range where it was comparable in both treatments. This result is

consistent with studies showing an interaction between disturbance and propagule pressure (Britton-Simmons & Abbott, 2008; Eschtruth & Battles, 2009). Of course, if the anthropogenic propagule faucet were turned up, this result could be exaggerated, and if it were turned up high enough, propagule pressure could overwhelm biotic resistance (e.g. Colautti et al., 2006; Lockwood et al., 2005). Seed addition studies have shown that (1) many plants are naturally seed limited (Clark et al., 2007), which can result in low seed rain as observed in our unseeded plots, and (2) seed addition can overcome strong biotic resistance sources like competition and seed predation (Maron et al., 2019; Seabloom et al., 2003). Hence, while propagule pressure was not determinant in our results, we expect its potential role in driving invader responses to disturbance is a function of variation in the strength of inputs across the landscape (see Cassey et al., 2018).

A notable finding from our seed sowing experiments was that invaders generally recruited better in both introduced ranges relative to the native range, an outcome supported by other biogeographic studies focused on individual plant invaders (e.g. Hierro et al., 2006; Maron et al., 2013; Williams et al., 2010). This result supports the hypothesis that introducing species to new ranges may generally free them from population controls in the native range (e.g. Mitchell & Power, 2003). Moreover, it suggests an important role of release effects on early life stages linked to recruitment and establishment. While many studies have evaluated potential effects of enemy release on adult invaders (Colautti et al., 2004), research evaluating such effects on seeds or seedlings is less common (DeWalt et al., 2004; Maron et al., 2013; Williams et al., 2010). Studies of adults may inform outcomes for seedlings if pathogens and herbivores attacking adults have similar effects on seedlings (DeWalt et al., 2004; Maron et al., 2013; Williams et al., 2010), but the generality of such patterns are not clear. However, some seed predators differ from the natural enemies attacking adult plants. For example, some rodent and ant seed predators, which do not directly attack adult plants, can strongly influence invader establishment (Lucero et al., 2019; Maron et al., 2012; Pearson, Hierro, et al., 2014; Pearson, Icasatti, et al., 2014). Biogeographic or provenance-related differences in seed predator and seed pathogen attack rates (Connolly et al., 2018; Pearson et al., 2022) may help to explain some exotic recruitment advantages, which could be exacerbated by disturbance, but more research is needed, especially for pathogens. While natural enemy attack via seed predators or pathogens or other processes like rapid evolution might help to explain greater recruitment in the introduced ranges, they do not explain why the patterns would differ between the two introduced ranges we studied. Rather, the interplay between native community resilience and the functional traits of the invaders seems to offer the most parsimonious explanation for the overall patterns we observed, although these other factors may play important contributing roles.

Our focus on small-scale soil disturbances is relevant for grassland systems where ungulate grazing and trampling, rodent disturbances and mesocarnivore disturbances predominate. Moreover, the same processes likely scale to broader anthropogenic disturbances like overgrazing and mechanical disturbance. However, processes affecting invasion outcomes following other disturbances like fire and flooding may differ, as these disturbances may selectively kill plants as a function of fire- or flood-specific adaptations, and they can introduce as well as release resources following disturbances (e.g. Gerard et al., 2008; Reinhart et al., 2016; Zedler et al., 2007).

Invasions have been described as idiosyncratic and unpredictable (Moles et al., 2008; Moyle & Light, 1996). However, conceptual breakthroughs have helped thin this veil of idiosyncrasy by revealing how deterministic processes like propagule pressure can inform or confound (if ignored) understandings of invasion outcomes (e.g. Lockwood et al., 2005). Community assembly theory provides a means for integrating these and other key invasion processes to understand invasion outcomes and account for context dependence and the apparent idiosyncrasy it produces when ignored (Pearson, Ortega, Eren, & Hierro, 2018). Placing our results in this framework reveals how extrinsic factors like donor species pools and introduction filters (sensu Colautti et al., 2006) can influence the trait composition of local exotic species pools to affect invasion outcomes. However, it also illustrates how these outcomes are conditioned by the recipient community. We found that following disturbance, invader success arises from the interplay between invader traits and recipient community resilience, which itself is determined by the traits of the local species pool and their interactions with biotic and abiotic processes. Accounting for both invader traits and community resilience illustrates how powerfully disturbance can shift native communities towards exotic species composition in certain systems while also underscoring the conditionality of these processes. This study helps to explain when and why exotic plants can gain advantage over native plants following disturbance.

AUTHOR CONTRIBUTIONS

Dean E. Pearson and José Hierro conceptualized the project, working with Yvette K. Ortega, Özkan Eren and Diego Villarreal to refine and implement experiments. Ylva Lekberg conducted soil sampling. Özkan Eren, José Hierro and Dean E. Pearson oversaw experiments in Turkey. Diego Villarreal, José Hierro and Dean E. Pearson oversaw experiments in Argentina. Yvette K. Ortega and Dean E. Pearson oversaw experiments in Montana. Yvette K. Ortega conducted data analysis with input from Dean E. Pearson. Dean E. Pearson coordinated the project and drafted the manuscript. All authors contributed to the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.12jm63z3x (Pearson et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Evaluation of fencing effect for experimental plots in La Pampa, Argentina.

Appendix S2. Comparing the incidence of natural disturbance among ranges.

Appendix S3. Experimental effects on recruitment of individual focal invader species.

Appendix S4. Relationships between focal invader recruitment and measured covariates.

Table S1. Focal plant species added to experimental plots in their native range of Turkey and introduced ranges of either Montana, USA (MT); La Pampa, Argentina (LP); or both. Seeds were added to separate plots in each of two years (Turkey and MT: 2011 and 2012; LP: 2012 and 2013). Given for each species is the functional group based on life history strategy, with annuals and biennials defined as ruderal (R) and distinguished from perennials (P). These designations are relevant in all ranges where a species was sown with one exception noted below. The number of seeds added per plot varied among seed size classes as shown. See Section 2 for details.

Table S2. Variation in available nitrogen (NO_3^-), phosphorus (P, Mehlich 3), and potassium (K) by study site as measured in soils from experimentally undisturbed (−D) and disturbed (+D) plots in the native range of Turkey and the introduced ranges of Montana, USA and La Pampa, Argentina. Soils were sampled in each of three experimental blocks per site in the first post-treatment growing season (Turkey and Montana 2012, La Pampa 2013) and then pooled by disturbance treatment for each site. See Section 2 for details.

Table S3. Summary statistics from generalized linear mixed models evaluating the response of native plant species to disturbance (±), as measured by cover (total and split by perennial vs. ruderal [annual and biennial]) in unseeded plots compared among the native range of Turkey and the introduced ranges of Montana, USA and La Pampa, Argentina. Separate models were run for the year prior to treatment and each of two post-treatment years. Given are denominator dfs (numerator df = 1 for disturbance and df = 2 for range effects).

Table S4. Summary statistics from generalized linear mixed models evaluating the response of native plant species to disturbance (±), as measured by richness (total and split by perennial vs. ruderal [annual and biennial]) in unseeded plots compared among the native range of Turkey and the introduced ranges of Montana, USA and La Pampa, Argentina. Separate models were run for the year prior to treatment and each of two post-treatment years. Given are denominator dfs (numerator df = 1 for disturbance and df = 2 for range effects).

Table S5. Summary statistics from generalized linear mixed models evaluating the response of exotic plant species to disturbance (±), as measured by cover (total and split by perennial vs. ruderal [annual and biennial]) in unseeded plots compared among the native range of Turkey and the introduced ranges of Montana, USA and La Pampa, Argentina. Separate models were run for the year prior to treatment and each of two post-treatment years. Given are denominator dfs (numerator df = 1 for disturbance and df = 2 for range effects).

Table S6. Summary statistics from generalized linear mixed models evaluating focal invader recruitment in response to disturbance (±) as compared between the native range of Turkey and the introduced ranges of either Montana, USA or La Pampa, Argentina. Different cohorts of invaders were added to experimental plots in the native range and in each introduced range to represent either Montana or La Pampa exotics. Focal invader recruitment was also assessed in adjacent unseeded plots and analyzed in a separate model. Given are denominator dfs (numerator df = 1 for all effects).

Table S7. Summary of MANOVA evaluating recruitment of individual species of focal invaders in response to disturbance (±) as compared between the native range of Turkey and the introduced ranges of either Montana, USA or La Pampa, Argentina. Different cohorts of invaders were added to experimental plots in the native range and in each introduced range to represent either Montana or La Pampa exotics. Asterisk indicate a significant ($p < 0.05$) increase in recruitment due to disturbance, in the introduced versus native range, or in response to the multiplicative combination of these two factors (disturbance × range interaction). Note that one La Pampa invader, *Centaurium pulchellum*, could not be tested due to a lack of recruitment in both ranges and is omitted below.

Table S8. Overall relationships between recruitment of focal invaders and ecological covariates measured in seeded plots in the native range of Turkey and the introduced range of Montana, USA, as analyzed via generalized linear mixed models that excluded experimental factors (disturbance and range). Covariates were tested individually and in a multivariable model containing all covariates. Individual covariate models were compared via AICc scores. To assess the relative contribution of covariates to the multivariable model (AICc = 1794), each covariate was dropped from the model to determine the associated change in AICc score. In all models, denominator dfs were allowed to fluctuate (numerator df = 1 in all cases) according to the influence of random factors via the Satterthwaite method (PROC GLIMMIX, SAS version 9.4).

Table S9. Overall relationships between recruitment of focal invaders and ecological covariates measured in seeded plots in the native range of Turkey and the introduced range of La Pampa, Argentina, as analyzed via generalized linear mixed models that excluded experimental factors (disturbance and range). Covariates were tested individually and in a multivariable model containing all covariates. Individual covariate models were compared via AICc scores. To assess the relative contribution of covariates to the multivariable model (AICc = 1592), each covariate was dropped from the model to determine the associated change in AICc score. In all models, denominator dfs were allowed to fluctuate (numerator df = 1 in all cases) according to the influence of random factors via the Satterthwaite method (PROC GLIMMIX, SAS version 9.4).

Table S10. Relationships between recruitment of focal invaders and ecological covariates measured in seeded plots in the native range of Turkey and the introduced range of Montana, USA, as analyzed via generalized linear mixed models that accounted for the experimental factors, disturbance (±D) and range (Turkey = TK vs. Montana = MT). Shown are slope estimates for the highest-order factors that were significant ($p < 0.05$). Denominator dfs were allowed to fluctuate (numerator df = 1 in all cases) according to the influence of random factors via the Satterthwaite method (PROC GLIMMIX, SAS version 9.4).

Table S11. Relationships between recruitment of focal invaders and ecological covariates measured in seeded plots in the native range of Turkey and the introduced range of La Pampa, Argentina, as analyzed via generalized linear mixed models that accounted for the experimental factors, disturbance (±D) and range (Turkey = TK vs. La Pampa = LP). Shown are slope estimates for the highest-order factors that were significant ($p < 0.05$). Denominator dfs were allowed to fluctuate (numerator df = 1 in all cases) according to the influence of random factors via the Satterthwaite method (PROC GLIMMIX, SAS version 9.4).

Figure S1. Sites (green circles) used for experimental disturbance and seed addition of 34 plant species in the native range of southwestern Turkey and two introduced ranges of Montana, USA and La Pampa, Argentina. Not all symbols are visible due to overlap. Insets all use the same scale.

Figure S2. Native richness ($\bar{x}$ + SE) in undisturbed versus disturbed plots with no seeds added in the native range of Turkey (TK) and the introduced ranges of Montana, USA (MT) and La Pampa, Argentina (LP), assessed in the first (Year 1) and second (Year 2) post-treatment years. Pie charts show the proportional representation of ruderal (annual and biennial) versus perennial functional groups derived from mean richness estimates. Asterisk above bars indicate significant disturbance effects ($p < 0.05$), as assessed via post-hoc comparisons evaluating the interaction between disturbance and range. See Table S6 for full model results.

Figure S3. Mean (+SE) available nitrogen (NO_3^-), phosphorus (P), and potassium (K) in disturbed and undisturbed plots in the native range of Turkey (TK) and the introduced ranges of Montana, USA (MT) and La Pampa, Argentina (LP).

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