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Are exotic plants more abundant in the introduced versus native range?

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Abstract

1. Many invasion hypotheses postulate that introducing species to novel environments allows some organisms to escape population controls within the native range to attain higher abundance in the introduced range. However, introductions may also allow inherently successful species access to new regions where they may flourish without increasing in abundance.
2. To examine these hypotheses, we randomly surveyed semi-arid grasslands in the native and two introduced ranges (12,000–21,000 km^2 per range) to quantify local abundance (mean cover per occupied plot) and occurrence (percentage of 1-m^2 plots occupied) for 20 plant introductions that included pest and non-pest species. For each of these metrics, we evaluated relationships between abundance in the introduced vs. native range (1) across all species and (2) according to designated pest status in the introduced range. We predicted that if escape from population controls primarily explained invader success, then these species would be more abundant in the introduced range; while if invader success was driven primarily by intrinsic species attributes, then their abundance would be correlated between ranges.
3. Across all 20 invaders, we found that neither cover nor occurrence metrics were correlated between ranges. While cover was significantly higher in the introduced range, this result was driven by pest species. When the four pest species were excluded, cover but not occurrence was correlated between ranges. Interestingly, whereas cover of pest and non-pest species was comparably low in the native range, pest species cover increased sevenfold in the introduced range.
4. *Synthesis*. Our results confirm previous findings that local abundance in the native range predicts local abundance in the introduced range for many introduced plants, suggesting that intrinsic species' attributes may determine most invasion outcomes. However, we also found that some species increased in local abundance in the

introduced range, suggesting that changes in biogeographic context may also play an important role. While these latter species were pests, the small sample size precluded strong inferences. Determining what underlies the success of invasive pests remains elusive due to their low representation among introduced species.

KEYWORDS
biogeography, invasion, local abundance, occurrence, performance, pests, population release, weeds

1 | INTRODUCTION

Introduced plants sometimes achieve numerical dominance within native plant communities (Pyšek et al., 2012; Vilà et al., 2011), but why this occurs is not fully understood. Many prominent invasion hypotheses invoke biogeographic context by postulating that translocations may free introduced species from population controls, facilitate evolutionary changes, and/or establish novel interactions that allow invaders to increase in abundance and dominate over native species in the recipient range (e.g. Blossey & Notzold, 1995; Callaway & Aschehoug, 2000; Callaway et al., 2011; Darwin, 1859; Elton, 1958; Gaskin & Schaal, 2002; Hierro, Maron, & Callaway, 2005; Keane & Crawley, 2002; Keller & Taylor, 2010; Kolbe et al., 2004). Alternatively, some species may possess functional traits or attributes that facilitate higher abundance independent of community context, and translocating such species may simply allow them access to new ranges where they may dominate over natives without increasing in abundance or relative community stature (e.g. Baker, 1965; see Colautti et al., 2014). Determining the relative influence of these pathways on the abundance of introduced species is central to understanding the role that provenance plays in invasions (Davis et al., 2011; Kuebbing & Simberloff, 2015; Rejmánek & Simberloff, 2016; Simberloff, 2011; Simberloff & Vitule, 2014; Valéry, Fritz, & Lefeuvre, 2013; Van der Wal, Fischer, Selge, & Larson, 2015).

Elucidating the mechanisms underlying the success of introduced species requires comparing their performance between their native and introduced ranges. If species perform better in the introduced range, this would suggest that they benefit from changes linked to shifts in biogeographic context; if species perform similarly between ranges, this would suggest that intrinsic species attributes determine success independent of biogeographic context (Colautti et al., 2014; Firn et al., 2011; Hufbauer & Torchin, 2008; Parker et al., 1999, 2013). Invader performance has been measured in terms of organism size, fecundity and abundance (e.g. Colautti et al., 2014; Parker et al., 2013). However, abundance is arguably the most definitive metric, as changes in individual plant performance such as size and fecundity do not necessarily translate to corresponding changes in population outcomes (e.g. Crawley, 1989; Maron & Crone, 2006; Pearson, Ortega & Maron 2017). Moreover, a species' abundance, as measured by its frequency of occurrence and local abundance, can be directly linked to invader impacts (*sensu* Parker et al., 1999). Unfortunately, due to the tremendous logistical challenges associated with comparing abundance of multiple species between their native and introduced ranges, very few studies have formally examined the role of biogeography in influencing invader abundance (Colautti et al., 2014; Firn et al., 2011; Parker et al., 2013).

While a number of studies have compared abundance of individual invaders between the native and introduced ranges (Bossdorf et al., 2005; González-Moreno, Diez, Richardson, & Vilà, 2015; Grigulis, Sheppard, Ash, & Groves, 2001; Vilà, Maron, & Marco, 2005; Williams, Auge, & Maron, 2010), only three studies, to our knowledge, have done so for multiple invaders (Colautti et al., 2014; Firn et al., 2011; Parker et al., 2013). Firn et al. (2011) compared local abundance and species occurrence data between the native and introduced ranges for 26 plant species and concluded that "abundance of introduced species at home predicts abundance away," emphasizing the overall importance of intrinsic species attributes over biogeographic factors. However, they also noted that 12% of their species increased in occurrence and 23%–50% showed higher measures of local abundance in the introduced range. Colautti et al. (2014) evaluated databases containing coarse-scale occurrence data for 1416 plant species from their native and introduced ranges and found that most exotics were less common in the introduced range (lower occurrence values) but that the subset of exotics which were most common (described as "invasive") demonstrated higher occurrence values in the introduced vs. native range. Their results suggest that biogeographic factors were influential in that they reduced the occurrence of most introduced plants but elevated occurrence of the most invasive ones. Parker et al. (2013) applied meta-analyses to individual studies that examined performance in the native and/or introduced ranges for invaders specifically identified as pests. Their examination of 26 plant species suggested that some plant pests were larger or more fecund in the introduced ranges, but they found little evidence for differences in abundance between ranges.

These pioneering studies suggest that biogeographic factors may contribute to some invasion outcomes, but not others. They also hint that biogeographic factors may be linked to pest status in some cases, but this pattern is not clear. The mixed findings from these studies may be attributed to several causes, including (1) the differing approaches taken to overcome the logistical challenges associated with tackling this question, (2) differences in the performance metrics used and/

or (3) differences among invaders included in the studies, i.e. pest vs. non-pest species, in how they respond to translocation. Given the importance of context dependence in ecology (e.g. Agrawal et al., 2007; Bronstein, 1994), it seems likely that at least some introduced species would behave differently in the recipient vs. native ranges (see Pearson et al. in review). Moreover, general invasion patterns as depicted by the "Ten's Rule" predict that most introduced species will be suppressed with a subset of invaders experiencing little change or perhaps benefitting from translocation (Williamson & Fitter, 1996), suggesting that only a subset of species may benefit from introduction. However, which species benefit, for what reasons, and how this may relate to pest status in the introduced range remains unclear.

In this study, we quantified abundances for 20 introductions of 17 plant species in their native and two introduced ranges (three species occurred in both invaded ranges) by randomly sampling over large regions of semi-arid, perennial grasslands in each range (sampling was independent of species abundances). The invaders sampled ranged from innocuous, naturalized species to "pests" designated as invasive or noxious within the introduced regions studied. While abundance may be measured in a variety of ways, we focused on metrics of local abundance (mean percent cover for each species in occupied plots) and occurrence (the proportion of 1-m^2 plots occupied by a species). For each metric, we tested (1) whether abundance was correlated between the introduced and native ranges across all invaders, and (2) whether abundance differed between ranges (i.e. was generally higher or lower) across all invaders. If abundance across the suite of species was correlated between ranges but not generally higher or lower in the introduced range, this would provide evidence that invader success was driven by intrinsic species attributes, with little biogeographic influence. However, if abundance was uncorrelated between ranges but generally higher or lower in the introduced range, this would suggest that biogeographic factors influenced invader success. Finally, we examined whether the above abundance patterns differed for pest compared to non-pest species.

2 | MATERIALS AND METHODS

We examined 20 introductions of 17 herbaceous plant species within semi-arid grasslands of their native range in southwestern Turkey and two introduced ranges in central Argentina and northwestern USA. As the intersection of key phytogeographical regions notorious for contributing invasive species to the New World (European, Asian, Mediterranean and North African regions), Turkey provided a central region within the native range where random sampling was expected to generate abundance data for numerous invaders (Table S1). The two introduced ranges were selected because they represent disparate recipient ranges with similar habitats to the native range. We focused on semi-arid, perennial grasslands to control for community context, i.e. we examined how grassland species from the native range behaved in similar grassland types in the introduced ranges. The Turkey and USA systems occur within the montane zone where dryer conditions create grassland openings or where grasslands occur below lower timberline. These systems are subject to long, cold winters with snow and freezing temperatures, wet springs and hot, dry summers. The Argentina grasslands occur on the dry pampas plains as openings within the Caldenal savanna habitat type or adjacent to these habitats. These grasslands rarely experience freezing conditions, with most precipitation coming during the growing season. The mean annual precipitation is 69, 32 and 63 cm for the study areas in Turkey, Montana and Argentina, respectively. The primary source of disturbance in all three systems is domestic grazing.

In each range, we randomly surveyed 16–20 grasslands dispersed over 12,000–21,000 km^2 (Figure S1; southwestern Turkey: latitude = 37.7° and longitude = 29.3° for centroid; elevation 1,100–2,000 m; Montana, northwestern USA: latitude = 46.8° and longitude = −114.0° for centroid; elevation 900–1,500 m; La Pampa, central Argentina: latitude = −36.7° and longitude = −64.6° for centroid; elevation 150–350 m). We selected grasslands for surveys in the native and introduced ranges independent of local species distributions using the following criteria: they (1) conformed to the focal semi-arid grassland type in the region as indicated by native perennial vegetation, (2) had not been transformed from their natural state by severe disturbances such as ploughing, planting or extreme grazing; and (3) were a minimum of 1 ha in area, >5 km apart and proximal to invader propagule sources such as roads. Prospective survey areas (grassland patches ≥1 ha) were initially screened for these criteria and stratified to maximize dispersion across the study area using GIS, after which observers established a survey site at the first location encountered within a prospective area that fit the above criteria.

Sampling of plant communities was conducted during the peak months of the growing season in each range during each of 2 years (Argentina 2010–2011, USA 2011–2012, Turkey 2011 and 2013). At each survey site, we established a 100 m × 100 m grid parallel to and as close to the road as possible but beyond the immediate disturbance zone of the road (usually 10–30 m from the road edge). We randomly selected n = 20 1-m^2 plots in herbaceous vegetation within the established grid, with a minimum of 10 m separating plots (total plots = 1,120; 16 grasslands and 320 plots in Turkey; 20 grasslands and 400 plots each in the USA and Argentina). At each plot, we visually estimated cover of each plant species within a frame demarcated to indicate 1% cover units. Cover <10% was estimated to the nearest 1%, and cover ≥10% was estimated to the nearest 5%. Species that occupied <1% of a plot were recorded as 0.5% cover. Methods were standardized across regions by the principal investigator (DEP).

We focused on two metrics of abundance for each species, local abundance and occurrence, following methods used in a previous study examining how invader abundance is linked to impact (Pearson, Ortega, Eren, & Hierro, 2016). We approximated local abundance as mean percent cover per plot occupied across the sampled range, focusing on an absolute rather than relative metric because most invasion hypotheses speak to absolute changes in abundance of species between ranges. For example, Elton (1958) likened invasions to "ecological explosions" described as "the enormous increase in numbers" resulting from species introductions. However, in order to evaluate our results in the context of other work, we also conducted analyses

using a relativized measure of local abundance (e.g. Colautti et al., 2014; Firn et al., 2011), specifically mean cover per occupied plot divided by mean total cover (sum cover across species) across all plots in the range. Similarly, we examined maximum cover as a metric of localized dominance for comparison with Firn et al. (2011). However, given that maximum and mean cover were highly correlated across species (r^2 = 0.80, p < .0001) and produced parallel results, we did not present data for the latter metric. Occurrence was measured by the percentage of plots in which a species was found across sampled grasslands in each range. The percentage of plots a species occupied was highly correlated with the percentage of grasslands occupied (r^2 = 0.90, p < .0001), but we chose the plot-level measure for concordance with the scale used for cover estimation (after Pearson et al., 2016).

All analyses were conducted with SAS, version 9.4 (SAS Institute, 2013). Most analyses used simple abundance metrics calculated per species and range according to the description above to examine patterns across all 20 sampled invaders (i.e. 20 introductions of 17 species). Note that we use the term "invader" to indicate all established introduced species regardless of their pest status or potential impacts per Pearson et al. (2016). This approach allowed inclusion of all species introductions in analyses of local abundance regardless of the number of plots occupied in each range. In 80% of cases, species were found in at least 1% of the 320 or 400 plots/range (minimum of n = 4 plots), occurring in an average of 15% of plots (±*SE* of 3%) per range and distributed over an average of 8 (±1) grasslands, with low variation around mean cover values (*SE* ≤ 1%; Table S1). Abundance metrics were analysed on the natural log scale to meet assumptions of normality and homoscedasticity. Each metric was evaluated separately. To determine whether each abundance metric was linearly correlated between the introduced and native range, we used Pearson's correlation coefficient. To test whether species invaders differed in abundance between the introduced and native ranges (i.e. deviated from the 1:1 line of equal abundance between ranges), we treated each abundance metric as the response in a GLLM (PROC GLIMMIX, SAS Institute, 2013) that included range as a fixed factor and invader as a random factor.

To examine the potential linkage between abundance metrics and pest status, we categorized invaders as pests vs. non-pests based on pest classifications that were specific to the regions that we sampled because invaders may behave differently in different communities or regions (e.g. Zenni & Nuñez, 2013; see also Section 4). For USA, we designated species included on the Montana Noxious Weed List as of 2017 (http://agr.mt.gov/weeds) as pests. For Argentina, we designated species defined as invasive in Argentina by Herrera, Goncalves, Pauchard, and Bustamante (2016) as pests. In both classification systems, listed exotics are deemed to pose significant ecological threats to flora, fauna or system productivity (per Montana state law MCA 7-22-2101 [http://leg.mt.gov/bills/mca/7/22/7-22-2101.htm] and Herrera et al., 2016). This approach resulted in the assignment of three USA and one Argentina invaders as pests, with the remaining 16 invaders assigned to non-pest status (Table S1). To examine whether correlations between abundance in the introduced relative to native range might be sensitive to pest status, we omitted invaders classified as pests and repeated correlation tests using abundance metrics for non-pests only. To evaluate whether between-range differences in abundance were consistent for invaders identified as pests vs. non-pests, we added pest status and the range × pest status interaction to the GLMM for each abundance metric (PROC GLIMMIX, SAS Institute, 2013). To examine interactions between range and pest status, we used the Bonferroni method to conduct post hoc comparisons (adjusted for the number of comparisons) that specifically tested (1) whether the abundance metric differed between the introduced and native range for each pest group, and (2) whether the abundance metric differed between pests and non-pests within each range. To allow calculation of the relativized cover metric, we determined total cover across all plots per range as follows. Mean total cover across all plots per grassland was treated as the response variable in a GLM with a log-normal distribution and range as a fixed factor (PROC GLIMMIX, SAS Institute, 2013).

We also conducted a more detailed analysis of local abundance that tested for variation in range effects by invader using data for 13 invaders found in ≥1% of plots per range. Cover per species and plot was the response variable in a GLMM (PROC GLIMMIX, SAS Institute, 2013) that included range, invader and their interaction as fixed factors; and grassland within range, invader within grassland and plot within grassland as random factors. Post hoc comparisons were conducted as described above to test for differences between the introduced and native range for each invader.

3 | RESULTS

Across the 20 plant introductions examined, mean cover per invader was not significantly correlated between the introduced and native ranges (r^2 = 0.12, p = .13; Figure 1a,b). However, when the four invaders classified as pests were omitted from this analysis, mean cover did correlate significantly between ranges (r^2 = 0.4, p = .008). Comparisons of cover estimates between the introduced and native ranges helped to explain this result. Overall, mean cover was significantly higher in the introduced range across the 20 invaders, indicating deviation from the 1:1 line ($F_{1,19}$ = 4.5, p = .048; Figure 1a,b). However, in the model accounting for pest status, between-range differences in mean cover varied by pest status (range × pest status: $F_{1,18}$ = 23.8, p < .001; Table S2). Specifically, mean cover was significantly higher in the introduced vs. native range for pests (post hoc test: t_{18} = 5.8, p < .001) but not for non-pests (post hoc test: t_{18} = 0.6, p > .99; Figure 2a). Additionally, pests had significantly higher mean cover than non-pests in the introduced range (post hoc test: t_{18} = 3.8, p = .004) but not in the native range (post hoc test: post hoc test: t_{18} = −0.6, p > .99). These differences in local abundance by range and pest status were not sensitive to exclusion of the pest species with the highest mean cover in the introduced range, *Bromus tectorum* (range × pest status: $F_{1,17}$ = 15.8, p = .001), as the group of three remaining pests followed the same pattern, with significantly higher mean cover in the introduced compared to native range (post hoc test: t_{17} = 4.6, p = .002) and significantly higher mean cover

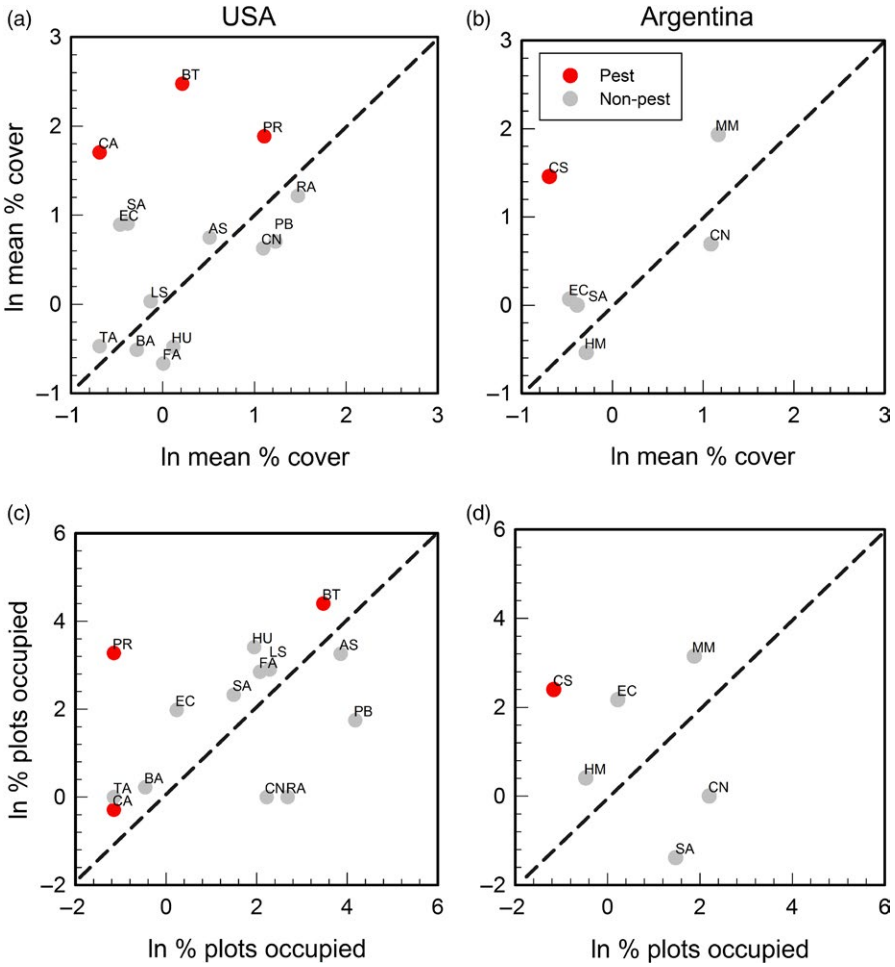

FIGURE 1 Abundance as measured by mean percent cover (per occupied plot) (a) and (b), and occurrence (percentage of plots occupied) (c) and (d) for 20 introductions of 17 species of plants within semi-arid grasslands in their native range of Turkey and introduced ranges of USA or Argentina. The 1:1 line indicates the expectation of no difference in abundance between ranges. Species codes are: AS, *Arenaria serpyllifolia*; BA, *Buglossoides arvense*; BT, *Bromus tectorum*; CA, *Cirsium arvense*; CN, *Carduus nutans*; CS, *Centaurea solstitialis*; EC, *Erodium cicutarium*; FA, *Filago arvensis*; HM, *Hordeum murinum*; HU, *Holosteum umbellatum*; LS, *Lactuca serriola*; MM, *Medicago minima*; PB, *Poa bulbosa*; PR, *Potentilla recta*; RA, *Rumex acetosella*; SA, *Sisymbrium altissimum* and TA, *Thlaspi arvense*

compared to non-pests in the introduced range (t_{17} = 2.9, p = .04) but not native range (post hoc test: t_{17} = −0.7, p > .99).

More detailed analysis of cover estimates showed significant variation in the range effect among the 13 invaders tested (p < .001; range × invader: $F_{12,152}$ = 3.0, p < .001; Table S3). The one pest species included in this analysis, *B. tectorum*, had significantly higher cover in the introduced relative to native range (post hoc test: t_{152} = 6.9, p < .001), while remaining invaders, all non-pests, did not differ in cover between ranges (post hoc tests: t_{1152} < 0.9, p > .99; Table S3). When *B. tectorum* was removed from the analysis, the range effect no longer varied by invader (range x invader: $F_{11,119}$ = 0.3, p = .97). As such, across the 12 non-pests, cover averaged comparably low in the introduced (M = 1.8 ± SE = 0.5%) and native ranges (M = 1.9 ± 0.5%).

When cover was calculated in relative terms to account for total cover of all species in each range, results were parallel to those seen for absolute cover. This was the case despite significant differences in total cover among ranges ($F_{2,53}$ = 14.3, p < .0001; M = 47.5 ± 3.7% USA, 47.4 ± 3.7% Argentina, 82.9 ± 7.3% Turkey). As seen for absolute cover, relative cover per invader was not correlated between ranges when tested across the 20 invaders (r^2 = 0.12, p = .13), but was correlated when pest species were omitted (r^2 = 0.4, p = .008). Relative cover across all invaders was significantly higher in the introduced vs. native range ($F_{1,19}$ = 21.8, p < .001). However, once again, between-range differences in abundance were driven by invaders classified as pests rather than non-pests (range × pest status interaction: $F_{1,18}$ = 23.8, p < .001; Figure S2). Similarly, more detailed analysis indicated that the range effect varied significantly among the 13 invaders tested (range x invader: $F_{12,152}$ = 3.4, p < .001), with the pest *B. tectorum* increasing in relative cover in the introduced compared to native range (post hoc test: t_{152} = 7.6, p < .001), and non-pest species showing no significant differences (post hoc tests: t_{152} < 0.4, p > .99).

Occurrence, as measured by the percentage of plots occupied per invader, was not correlated between the introduced and native range across the 20 invaders (r^2 = 0.08, p = .22; Figure 1c,d), and this result held when the four invaders classified as pests were omitted (r^2 = 0.11, p = .21). Occurrence also did not differ significantly between ranges when pest status was ignored ($F_{1,19}$ = 0.9, p = .36; Figure 1c,d). However, as seen for cover metrics, there was significant variation in the range effect with pest status (range × pest status interaction: $F_{1,18}$ = 6.7, p = .02; Table S2). Specifically, occurrence increased in the introduced compared to native range for pests (post hoc test: t_{18} = 2.8, p = .048) but not for non-pests (post hoc test: t_{18} = −0.2, p > .99; Figure 2b). Within-range differences in occurrence between pests and non-pests were not significant (post hoc test: t_{18} < 1.2, p > .4). As seen with cover metrics, these results held when the pest *B. tectorum*, the invader with the highest frequency of occurrence, was excluded from

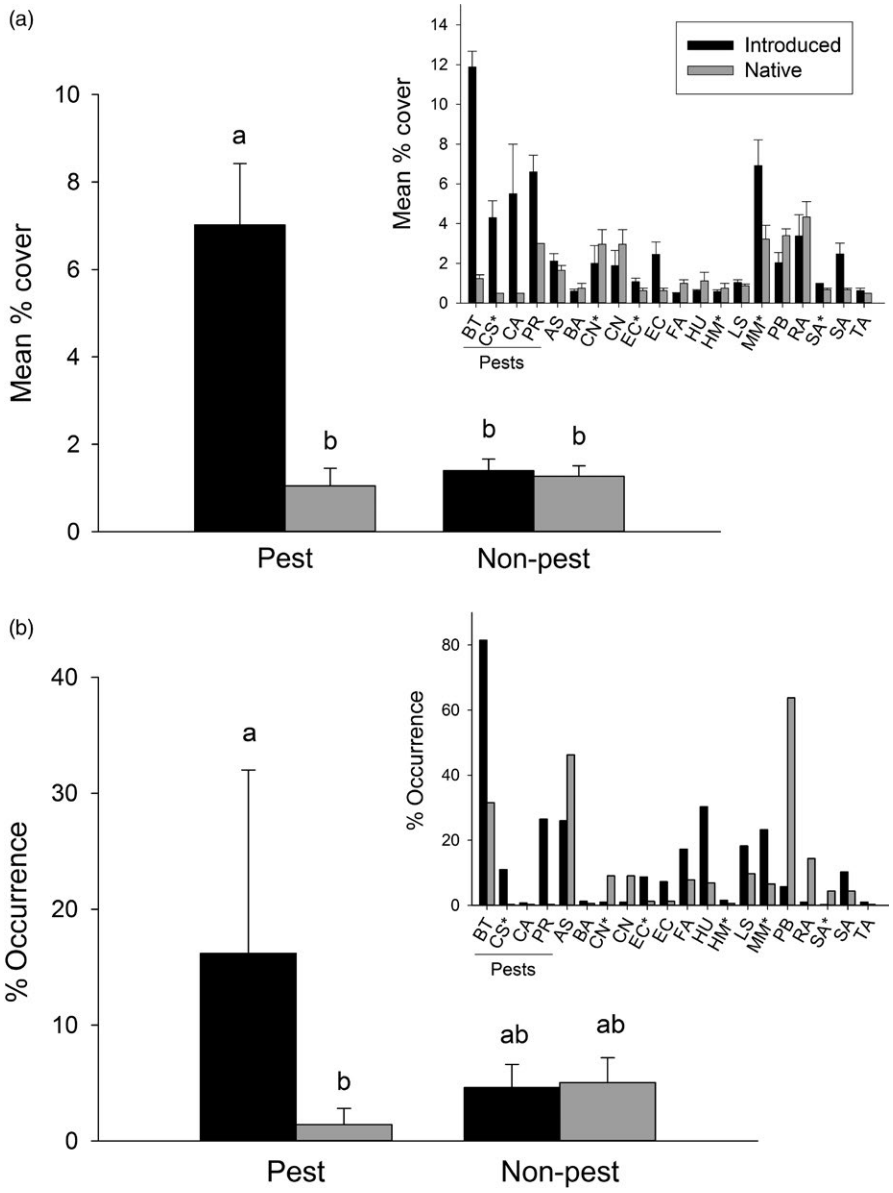

FIGURE 2 Abundance (*M* + *SE*) as measured by mean percent cover (per occupied plot) (a) and occurrence (percentage of plots occupied) (b) for 20 plant invaders categorized as pests (n = 4) vs. non-pests (n = 16) in their introduced ranges of the USA and Argentina compared to their native range of Turkey. Different letters indicate significant differences (p < .05) between ranges and pest categories determined by post hoc comparisons of the range × pest status interaction term in GLMMs. Insets show the data broken out by invader (species codes are as indicated in Figure 1, *indicates Argentina invader), with the four pests grouped on the left

analysis. The range effect again varied with pest status (range × pest status: $F_{1,17}$ = 7.6, p = .01), as occurrence increased for pests in the introduced vs. native range (post hoc test: t_{17} = 2.9, p = .04). Occurrence did not differ between pests and non-pests in the introduced range (t_{17} = 0.4, p > .99), but in the native range there was significantly lower occurrence of pests relative to non-pests (t_{17} = 2.9, p = .043).

4 | DISCUSSION

A fundamental question in invasion ecology is whether the notable success of some introduced species is driven by changes in biogeographic context, or whether such introductions simply extend the ranges of organisms that are inherently successful. Answering this question requires comparison of invader abundance between the native and introduced ranges for many introduced species—a logistical feat that has rarely been accomplished. In comparing abundance for 20 introductions of 17 species between their native and two introduced ranges, we found that both mean cover (local abundance) and occurrence metrics were uncorrelated between ranges. However, the four pest species as a group differed from the non-pests in that they exhibited higher mean cover and occurrence in the introduced range (although the latter pattern was more variable among species). After these pest species were excluded from analyses, mean cover but not occurrence was strongly correlated between ranges for the remaining 16 invaders. These results suggest that intrinsic species attributes may predict the local abundance of many introduced species in their new ranges independent of biogeographic context. However, we also found evidence that changes in biogeographic context may facilitate an increase in local abundance for some introduced species. Understanding how species attributes or changes in biogeographic context influence the local abundance of introduced plants is important in the light of recent findings linking invader local abundance to their impacts in recipient communities (Pearson et al., 2016).

Placing our results in the context of previous work, the only prior study to use standardized data collection protocols to compare local abundance and occurrence data between ranges for multiple plant introductions was conducted by Firn et al. (2011). Consistent with our results, these authors found that invader abundance was correlated between the native and introduced ranges for most species, suggesting an important role of intrinsic species attributes, but they also found that some species were significantly more abundant in the introduced range, suggesting that biogeographic factors may be important for some introduced species. Although Firn et al. did not evaluate whether the deviant invader responses they observed were linked to pest status, they did pose the question, "Do species that are more abundant away represent unusual, but important, anomalies?" Studies that have explored the relationship between changes in biogeographic context and invader pest status provide evidence of a conditional link between biogeographic increases in abundance and pest status. Colautti et al.'s (2014) evaluation of occurrence data indicated that most species were less common (lower occurrence values) in the introduced range, but that the most "invasive" species exhibited increased occurrence in the introduced range. In their meta-analysis examining whether pest species performed better in the introduced range, Parker et al. (2013) found mixed results for plant invaders. Overall, they found that pest species were generally larger and more fecund but not more abundant in the introduced range. However, six of 17 pests (35%) in their analysis did show significant increases in abundance. This result suggests that increased abundance may help to transform some plant species into pests, but many may achieve pest status without increased abundance, presumably as a function of intrinsic species attributes.

Our results for the 16 non-pests provided fairly robust evidence that mean cover in the native range predicted mean cover in the introduced range for this group. The finding that pests were more abundant than the non-pests in the introduced range was particularly interesting, but these results are somewhat tenuous given that the pest group consisted of only four species. The small sample of pests is representative of typical invasion patterns, particularly given our approach of randomly sampling with respect to individual species occurrences. The Ten's Rule (Williamson & Fitter, 1996) predicts two pests from a random sample of 20 established introductions, so four pests was a generous result. Yet, despite the small sample of pests, this group had significantly higher mean cover than non-pests in the introduced range, in part due to the consistency of the pattern among pests. Notably, this result held after excluding *B. tectorum*, the species attaining the highest mean cover in the introduced range. A similar finding of pests having higher mean cover than non-pests was demonstrated for a larger sample of introduced species studied in the same USA system (Pearson et al., 2016).

The pattern of pests having higher mean cover than non-pests in the introduced ranges was linked to a shift in mean cover for pests from quite low in the native range to relatively high in the introduced range—a consistent pattern among pests that was not exhibited by the non-pest group, which had low mean cover in both ranges (Figure 2a, Table S3). This shift in local abundance of pests suggests that the success of these species in the introduced ranges was driven more by changes in biogeographic context than inherent performance advantages. While these results are robust for *B. tectorum*, the general pattern across the four pest species is more tenuous given that the cover estimates for the other pests in the native range were based on few plots (Table S1; Figure 2). Nonetheless, we believe the low sample returns for these species are indicative of their inherently low abundance and sporadic distribution in grasslands of their native range (in contrast to comparable habitats in the introduced ranges). Genetic data suggest that Asia Minor (Turkey) is the region of highest genetic diversity and hence the likely region of origin for *B. tectorum* (Lindon, 2007; Kelly, 2012; Richard Mack pers. comm.) and also for *Centaurea solstitialis* (Eriksen et al., 2014), and distribution records indicate that this region is central to *Potentilla recta*'s native range (Werner & Soule, 1976) and well within the core of *Cirsium arvense*'s native range (Holm, Pancho, Herberger, & Plucknett, 1979; Holm, Plucknett, Pancho, & Herberger, 1977; Moore, 1975). Furthermore, we observed that these latter three species in and adjacent to our sample grids where they went undetected in sampled plots due to their sporadic distribution. Obtaining robust samples for comparing abundance of pest species that are uncommon or spotty in their distribution in the native range presents an added challenge to study the biogeography of invasions, beyond the challenge of obtaining samples with sufficient pest species relative to non-pests.

Bromus tectorum was sufficiently well sampled in both the introduced and native ranges to provide a robust example on its own, and this species exemplified the general pattern seen for pests for changes in abundance between ranges. *Bromus tectorum*, other pests, and non-pests each averaged about 1% cover in the native range, but pests as a group increased to 7% mean cover and *B. tectorum* increased to nearly 12% mean cover in the introduced ranges. *Bromus tectorum* and other pests also increased substantially in occurrence in the introduced ranges, but this pattern was highly variable across species. Although the increases in local abundance may seem low in absolute terms, it is important to note that these are mean cover estimates based on random sampling across a wide range of abundances for each species. Placing

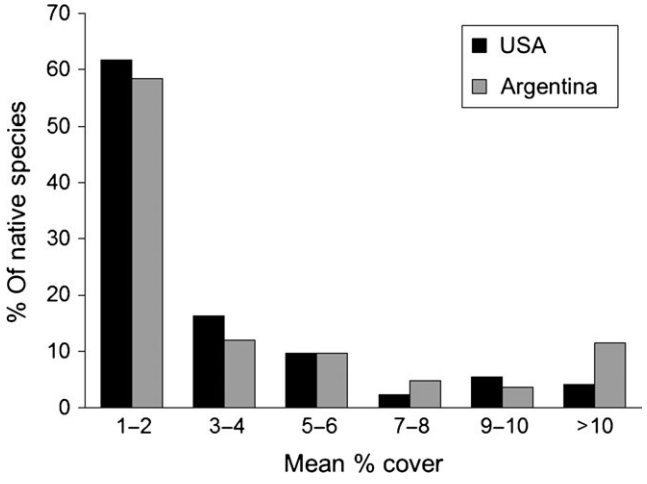

FIGURE 3 Frequency distribution of mean percent cover per occupied plot for native species in the introduced ranges of USA and Argentina (n = 165 and 166 total native species, respectively)

these metrics in the context of native species cover patterns provides important context. Calculating mean cover per native species in each introduced range using the same plot data illustrates that about 60% of the natives occurred at only 1%–2% mean cover, with <20% of natives, the dominants, having mean cover ≥7% in either introduced range (Figure 3). These patterns reflect classic species abundance distributions with most species in a community occurring at low abundance and relatively few species dominating (McGill et al., 2007; Whittaker, 1965). These patterns also illustrate how remaining at 1% mean cover in the introduced relative to native range, as the non-pests did, vs. increasing from 1% to 7% or 12% mean cover, as did the pests as a group and *B. tectorum* individually, can greatly elevate an invader's standing in the recipient community. High local abundance of introduced plants has been linked to their impacts on native plants, with *B. tectorum* identified as the highest impact invader in the USA grasslands sampled in this study (Pearson et al., 2016). In fact, this species is one of the most notorious invaders in the western USA (DiTomaso, 2000; Mack, 1981), where it achieves densities high enough to alter fire regimes and transform native systems (Whisenant, 1990).

One critical factor that importantly influences the conclusions of any study attempting to evaluate introduced pests is how pest status is determined. In line with our community-specific approach, we defined pest status using classifications as specific as possible to the introduced ranges sampled (see Section 2). This precluded designating pests based on compilations of multiple classification sources (e.g. Mitchell & Power, 2003) because few sources are available at local to regional scales. However, this approach ensures that pest designations reflect local conditions as closely as possible. This is important because introduced species may behave differently, or their impacts may be perceived differently, across introduced ranges. For example, 24 of the 26 plant species examined by Firn et al. were identified as pests ("declared weed species") in at least one introduced range considered, with nearly one-third of species identified as both a pest and a non-pest ("not a listed weed species") depending on the particular introduced range (see Table 1 in Firn et al., 2011). In short, invader success is likely context dependent (Moles, Gruber, & Bonser, 2008; Zenni & Nuñez, 2013), and pest designations can vary among recipient ranges (Table 1 in Firn et al., 2011). Although pest classifications may be subjective (Pearson et al., 2016; Quinn, Barney, McCubbins, & Endres, 2013), the pest designations we applied to the USA invaders based on Montana Noxious Weed List aligned well with independent empirical analyses of invader impacts on native plants for the species we examined in this system (Pearson et al., 2016).

Our findings add resolution to prior studies comparing invader abundance between the native and introduced ranges. Consistent with Firn et al. (2011), we found evidence that intrinsic species' attributes may determine the abundance of most invaders. Of course, in this light, it is important to acknowledge that such attributes may sometimes be the result of anthropogenic selection (Driscoll et al., 2014; Lolicato & Rumball, 1994; Mack & Lonsdale, 2001). However, a subset of invaders appear to benefit from translocation into new ranges where they can become more locally abundant and/or widely dispersed than in the native range (Colautti et al., 2014; Firn et al., 2011; Parker et al., 2013; the current study), presumably due to novel interactions arising from changes in biogeographic context. These studies suggest that provenance does influence some invasion outcomes, perhaps some of the more important invasion outcomes. Hence, the question in invasion ecology should not be whether provenance matters (Davis et al., 2011; Simberloff, 2011), but rather when and how. To answer these questions, additional studies are needed that compare invader abundance between ranges while controlling for community context and accounting for invader impacts or pest status in the recipient ranges.

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AUTHORS' CONTRIBUTIONS

D.E.P., J.H., Ö.E., and Y.K.O. initiated the project and designed survey and experimental protocols. All authors contributed to data collection. Y.K.O. conducted data analyses. D.E.P wrote the first draft of the manuscript, and Y.K.O., J.H. and Ö.E., edited and contributed to writing.

DATA ACCESSIBILITY

Data from this paper are available from Table S1 and the Dryad Digital Repository https://doi.org/10.5061/dryad.r7v91 (Pearson et al., 2017).

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