

The fluctuating resource hypothesis explains invasibility, but not exotic advantage following disturbance

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Abstract. Invasibility is a key indicator of community susceptibility to changes in structure and function. The fluctuating resource hypothesis (FRH) postulates that invasibility is an emergent community property, a manifestation of multiple processes that cannot be reliably predicted by individual community attributes like diversity or productivity. Yet, research has emphasized the role of these individual attributes, with the expectation that diversity should deter invasibility and productivity enhance it. In an effort to explore how these and other factors may influence invasibility, we evaluated the relationship between invasibility and species richness, productivity, resource availability, and resilience in experiments crossing disturbance with exotic seed addition in 1-m² plots replicated over large expanses of grasslands in Montana, USA and La Pampa, Argentina. Disturbance increased invasibility as predicted by FRH, but grasslands were more invulnerable in Montana than La Pampa whether disturbed or not, despite Montana's higher species richness and lower productivity. Moreover, invasibility correlated positively with nitrogen availability and negatively with native plant cover. These patterns suggested that resource availability and the ability of the community to recover from disturbance (resilience) better predicted invasibility than either species richness or productivity, consistent with predictions from FRH. However, in ambient, unseeded plots in Montana, disturbance reduced native cover by >50% while increasing exotic cover >200%. This provenance bias could not be explained by FRH, which predicts that colonization processes act on species' traits independent of origins. The high invasibility of Montana grasslands following disturbance was associated with a strong shift from perennial to annual species, as predicted by succession theory. However, this shift was driven primarily by exotic annuals, which were more strongly represented than perennials in local exotic vs. native species pools. We attribute this provenance bias to extrinsic biogeographic factors such as disparate evolutionary histories and/or introduction filters selecting for traits that favor exotics following disturbance. Our results suggest that (1) invasibility is an emergent property best explained by a community's efficiency in utilizing resources, as predicted by FRH but (2) understanding provenance biases in biological invasions requires moving beyond FRH to incorporate extrinsic biogeographic factors that may favor exotics in community assembly.

Key words: community assembly; diversity; fluctuating resource hypothesis; invasibility; invasion; productivity; resilience; resource availability.

INTRODUCTION

Invasibility, the susceptibility of a community to colonization by outside species, is an emergent community property, a manifestation of multiple processes that can be influenced by factors such as resident species diversity, productivity, resource availability, disturbance, and system resilience (Lonsdale 1999, Davis et al. 2000). Yet, most research has focused on isolating the role that diversity plays in affecting invasibility (Fridley et al. 2007), based on the notion that higher diversity is a key factor reducing the susceptibility of native communities to exotic plant invasions (Elton 1958). Experimental work has demonstrated that higher diversity can reduce invasibility at local scales (1 m²), when all other

factors are held constant (Tilman 1997, Knops et al. 1999, Naeem et al. 2000, Maron and Marler 2007). In contrast, observational studies, particularly at larger spatial scales (>30 m²), have shown positive relationships between native diversity and invasibility (Levine and D'Antonio 1999, Lonsdale 1999, Stohlgren et al. 1999, Fridley et al. 2007). These divergent patterns have been attributed to scaling effects, with positive correlations at larger scales attributed to factors such as productivity, resource availability, and heterogeneity affecting natives and exotics similarly, and negative relationships at local scales attributed to competition (Stohlgren et al. 1999, Shea and Chesson 2002, Fridley et al. 2007). However, observational studies have also shown positive relationships at local scales across community types (Stohlgren et al. 1999, Sax 2002, Keeley et al. 2003, Cleland et al. 2004, Ortega and Pearson 2005). Moreover, experimental work has demonstrated that this relationship can shift between negative and positive at local scales due to

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variation in productivity or resource availability (Davies et al. 2007, Sandel and Corbin 2010), and that resource availability or natural enemies can drive invasibility with no effects of diversity (Heckman et al. 2017). Hence, the role that diversity plays in influencing invasibility appears to be dependent on other factors, factors that can covary with diversity and even override diversity's effects on invasibility. Understanding invasibility and the role that diversity plays in influencing overall invasion outcomes requires accounting for the fact that invasibility is an emergent community property influenced by numerous biotic and abiotic processes.

Mechanistically, invasibility reflects the community-level economics of resource availability. The idea that resource availability is the key determinant of community invasibility was encapsulated by Davis et al. (2000) when they introduced the fluctuating resource hypothesis (FRH). These authors argued that resource availability, driven either by changes in resource input rates (extrinsic) or changes in controls over resource uptake rates (intrinsic), could explain community invasibility more directly than variation in specific community attributes such as diversity or productivity. The reasoning behind these conclusions is that resource availability can vary across a range of specific community attributes due to the complex ways that these and other environmental factors interact to determine net resource balances. Accordingly, FRH predicts that individual community attributes such as diversity or productivity should not consistently predict differences in community invasibility (Predictions 6 and 7; Davis et al. 2000). Rather, resource availability should predict invasion outcomes as a function of how the combined effects of community attributes merge to influence resource budgets. Importantly, FRH recognizes that resource availability can fluctuate within a community as a function of disturbances that release resources from community control, with the expectation that the degree of disturbance and the rate at which the community recovers from disturbance, its engineering resilience (sensu Holling 1996), should influence invasion outcomes (Predictions 1–4; Davis et al. 2000).

The FRH was introduced as a general theory of invasibility intended to explain plant invasions independent of species' origins (Davis et al. 2000). These authors explicitly stated that, "Invasions by exotic species are often studied and discussed as if they were a distinct ecological phenomenon (citations omitted). However, we concur with Huston (1994) that the basic processes that admit exotic plant species are essentially the same as those that facilitate colonizations by native species or allow repeated regeneration at the same site." In essence, Davis et al. (2000) argued that colonization processes act on species traits independent of provenance, and hence the FRH should predict invasion outcomes equally for native and exotic species. Yet, empirical studies demonstrate that exotics commonly benefit more than natives following disturbances (MacDougall and Turkington 2005, MacDougall et al. 2014, Jauni et al. 2015, Seabloom et al. 2015), suggesting that native and exotic species may respond differently to resource fluxes (Hierro et al. 2005). This provenance bias suggests that FRH is insufficient to fully explain invasion outcomes. Such an exotic advantage could, however, be explained by accounting for the effects of species source pools and introduction filtering

processes in the context of community assembly theory (sensu Pearson et al., 2018). For example, disturbance could favor exotics over natives if local exotic species pools were disproportionately represented by species bearing ruderal or competitive strategies that are better adapted to exploiting resource pulses (sensu Grime 1977, Van Kleunen et al. 2010). This could occur if (1) exotic donor pools are disproportionately biased toward ruderal strategies relative to native species pools due to differences in evolutionary or ecological histories (Kalusová et al. 2017), (2) if introduction pathways or initial establishment filters for exotics favor species bearing ruderal traits (Mack and Lonsdale 2001), or (3) if introductions include species bred by humans for such traits (Mack 1989, Williams and Baruch 2000). In this context, an additional prediction can be generated from FRH to test for provenance effects: invasion outcomes following increased resource availability should reflect the native-exotic representation in local species pools. If increased resource availability shifts communities toward exotics, this would suggest that one of the above or related processes generated a provenance bias.

Here, we used the fluctuating resource hypothesis as a framework for evaluating the relative roles of diversity, productivity, resource availability, and engineering resilience (resilience hereafter) in affecting the invasibility of two disparate grassland systems that differed in these community attributes and their susceptibility to invasion. By crossing disturbance (\pm) and exotic seed addition (\pm) treatments at the 1-m² plot scale within 19 grasslands distributed over large regions of western Montana, USA and La Pampa, Argentina, we were able to test general predictions posed by FRH regarding how disturbance, species richness, productivity, and resource availability affected community invasibility while controlling for invader propagule pressure. Additionally, by following unseeded plots for 4 yr after disturbance, we were able to evaluate the roles of resilience and provenance on invasion outcomes under ambient conditions.

METHODS

If invasibility is an emergent system property, then experimentally determining the relative influence of multiple factors on invasibility (each of which may vary greatly across natural systems) can rapidly become logistically infeasible and potentially unrealistic using common garden experiments. Hence, we conducted in situ experiments in two natural systems that represented similar community types that appeared to differ in invasibility in order to explore how natural variation in prospective drivers of invasibility might influence invasion outcomes. The study sites were located within the Intermountain region of western Montana, USA (latitude 46.8° N and longitude 114.0° W for centroid) and the Caldenal of La Pampa, Argentina (latitude 37.3° S and longitude 64.6° W for centroid). Both communities are semiarid grasslands dominated by native, perennial, caespitose grasses (Montana: *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Poa secunda*; La Pampa: *Piptochaetium napotaense*, *Nassella tenuissima*, *N. clarazii*, and *Poa ligularis*), with native forbs comprising >50% of species richness, and both communities have similar species abundance

distributions (Pearson et al. 2017: Fig. 3). Cattle grazing is the primary land use in each system. Growing seasons occur during each system's respective spring and summer, but abiotic conditions differ in that Montana grasslands experience harsher conditions with freezing winters, hot, dry summers, and only 32 cm of annual precipitation occurring primarily as snow during winter and rain in late spring to early summer; while La Pampa grasslands experience mild winters and hot, wetter summers, with 63 cm annual precipitation occurring as rain primarily during spring and summer. Importantly, extensive surveys (400 1-m² plots from 20 locations in each system) indicated that the proportion of total plant cover represented by exotics was 14 times higher in Montana (0.27 ± 0.26 [mean \pm SE]) vs. La Pampa (0.02 ± 0.009 ; D. E. Pearson, Y. K. Ortega, Ö. Eren & J. L. Hierro, *unpublished data*), suggesting that Montana might be more invasible. Hence, the two systems were ecologically similar but appeared to differ in invasibility as well as factors that might influence invasibility.

Our experiments were replicated at nine sites in Montana and 10 sites in La Pampa spread over 15,000 and 4,000 km², respectively. At each site, in areas of minimal invasion, we established three blocks, each consisting of four 1-m² 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 removing plant biomass from the plots. Seed addition involved adding seeds of 19 (Montana) or 20 (La Pampa) exotic plant species to each seed addition plot. The species added reflected those occurring within each system and so differed between systems with the exception of six overlapping species (Appendix S1: Table S1). To reflect the fact that larger-seeded plants produce fewer seeds (Westoby et al. 1996), we varied the number of seeds added according to seed size (Appendix S1: Table S1). Seeds were collected locally from ≥ 3 populations in each system. Experimental treatments were applied at the end of the respective growing seasons in Montana in 2011 and in La Pampa in 2012. Treatments were repeated the following year 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. All plots were read during peak growing season the year following treatment by counting the number of seedlings of each added species. Cover (%) was estimated in each plot prior to initial treatments and in the first post-treatment year. We visually estimated cover by species to the nearest 5%, except species under 10% cover were estimated to the nearest 1% and species <1% were recorded as 0.1% cover (see Pearson et al. 2017). For non-seed addition plots initiated in year one of the study, cover per species was also estimated in post-treatment years two and four. Seeded exotics were not allowed to reproduce and were eliminated after sampling in Montana.

We defined invasibility as the number of seeded exotic plants establishing per seed addition plot. Richness of native species per plot and year served as our metric of diversity. Cover per plot and year was summed by species by provenance category (i.e., native vs. exotic). Productivity was estimated as average native plant cover in undisturbed, unseeded plots per site. We quantified engineering resilience as the degree of recovery of native cover and

richness in unseeded disturbed vs. unseeded undisturbed plots up to 4 yr after treatment. Soils were sampled coincident with vegetation sampling in the first growing season after treatment year one by collecting two soil cores (5 cm diameter \times 10 cm deep) from each of the unseeded disturbed and undisturbed plots per site and then pooling the samples by disturbance treatment for each site. Soils were sent to Ward Laboratories (Kearney, Nebraska, USA) for standard nutrient analyses. We focused on available nitrogen (NO₃[–]), phosphorus (P, Mehlich 3), and potassium (K) as key limiting nutrients for plants (per Davis et al. 2000).

Statistical analyses

All analyses were conducted using generalized linear mixed models (GLMMs) in SAS (version 9.4, PROC GLIMMIX; SAS Institute 2013) unless otherwise stated. Site, block within site, site within year, and block within site and year were included in models as random factors. 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 exotics and native species richness; log-normal distribution for native cover, NO₃[–], P, and K). We present least squares means and SEs back-transformed from the scale used in analysis.

Our first two questions were, do (1) invasibility and (2) ecological covariates (native richness, native cover/productivity, NO₃[–], P, and K) differ between study systems under disturbed and/or undisturbed conditions? To address the first question, we treated invasibility as the response variable, measured by the number of seeded exotics recruiting in each seed addition plot one year after treatments in each of 2 yr, with counts adjusted for ambient levels of seeded species by subtracting the number of plants recruiting in non-seed addition plots (0.8 ± 0.04 plants/plot [mean \pm SE]) from the same block, disturbance treatment, and year. System (Montana vs. La Pampa), disturbance (\pm), and their interaction were treated as fixed factors in the model. To evaluate whether differences in exotic species composition between systems affected invasibility results, we repeated this analysis for the six exotics seeded in both systems (Appendix S1: Table S1). To address the second question, we evaluated each ecological covariate as a response variable independently. Models included system and disturbance as fixed factors per the model structure described above. Models for soil nutrients excluded random effects associated with block and year given that soil was only sampled at the level of site \times disturbance treatment in one year.

Next, we wanted to evaluate which covariates might best predict invasibility, given the observed differences in invasibility and ecological covariates between systems. To do this, we took two complementary approaches, both of which used models treating invasibility as the response variable. Ecological covariates were treated as fixed factors, but model structure varied between the two approaches. In the first approach, we examined correlations between invasibility and ecological covariates while excluding system and disturbance from models to understand the overall relationships

between ecological covariates and invasibility. Covariates were tested individually and also together in a multivariable model. Interactions among covariates were not included in the multivariable model for simplicity. While P values tested for significant relationships, we also wanted a means of comparing the relative contribution of each covariate to overall variation in invasibility (akin to an r^2 value, which is difficult to compute for GLMMs with negative binomial distributions). For this purpose, we calculated Akaike's Information Criterion corrected for small sample sizes (AIC_c), a measure of expected predictive power weighted by the number of model parameters (Bolker et al. 2009), for each individual covariate model using maximum likelihood estimation (package *glmmADMB*, R version 3.2; R Core Team 2016). To assess the relative contribution of covariates in the multivariable model, we dropped each covariate in turn from the full model to determine the effect on AIC_c . In the second modeling approach, we accounted for system and disturbance factors and their potential interactions with ecological covariates. This allowed us to test (1) whether variation in invasibility within systems or disturbance treatments correlated significantly with individual ecological covariates and (2) whether these relationships differed by system or disturbance treatment. To do so, each covariate was tested individually in models that included system and disturbance. In initial models, we included all interactions between the covariate and experimental factors. We then successively dropped non-significant interactions ($P > 0.05$) to arrive at the reduced model.

Finally, we wished to evaluate how resilience to disturbance related to invasion of exotics under ambient conditions while testing whether disturbance responses differed by provenance. To do so, we used data from unseeded plots collected through post-treatment year four. The response per provenance category was measured by cover and species richness, respectively, with each year tested separately. Fixed factors in all models were system, disturbance, provenance, and their interactions, and random factors included plot within block and site. Additionally, in an effort to understand how life history strategies might have influenced responses to disturbance, we conducted a similar analysis that compared outcomes between annual vs. perennial/biennial species, under the assumption that annuals represent more ruderal strategies (*sensu* Grime 1977). Cover per plot and year was summed for each provenance by life history category and treated as the response. Each system and year was tested separately in a model that included disturbance, provenance, life history strategy, and their interactions as fixed factors. To examine how the proportional representation of life history strategies within local species pools for exotics vs. natives might influence responses to disturbance in each system, we used the species list derived from unseeded plots across all years of sampling to test for differences in the proportion of annual vs. perennial species by provenance category using a χ^2 test for homogeneity of variance.

RESULTS

Mean invasibility in seeded plots was >200% higher in Montana relative to La Pampa ($F_{1,17} = 17.3$, $P = 0.0007$;

Fig. 1a). Disturbance significantly increased invasibility in both systems ($F_{1,177} = 94.0$, $P < 0.0001$), and this effect was marginally stronger in Montana vs. La Pampa (system \times disturbance: $F_{1,177} = 2.7$, $P < 0.1$). Given the combined effects of system and disturbance, invasibility was greatest in disturbed plots of Montana, with mean levels >300% higher than in other treatments. Results were parallel when we repeated this analysis using only species seeded in both systems, with invasibility significantly higher in Montana ($F_{1,16} = 8.4$, $P = 0.011$), in disturbed plots ($F_{1,155} = 59.0$, $P < 0.0001$), and particularly when these factors were combined (system \times disturbance: $F_{1,155} = 10.0$, $P = 0.002$; Fig. 1a).

Richness of native species was significantly higher in Montana than La Pampa ($F_{1,17} = 12.3$, $P = 0.003$) and was reduced by disturbance ($F_{1,215} = 7.9$, $P = 0.005$; Fig. 1b). However, disturbance had a bigger effect on richness in Montana (system \times disturbance: $F_{1,177} = 2.7$, $P < 0.1$) such that Montana's richness advantage over La Pampa weakened under disturbed conditions (system \times disturbance: $F_{1,177} = 2.7$, $P < 0.1$), with a difference in mean species richness of 90% in undisturbed plots vs. 24% when disturbed. Native cover was lower in Montana ($F_{1,17} = 28.0$, $P < 0.0001$), and was reduced by disturbance ($F_{1,180} = 243.8$, $P < 0.0001$; Fig. 1c), but the disturbance effect was stronger in Montana (system \times disturbance: $F_{1,180} = 21.8$, $P < 0.0001$), reducing mean native cover by 80% vs. 56%, respectively. Therefore, while mean native cover in undisturbed plots, i.e., productivity, was 30% lower in Montana vs. La Pampa, cover differences grew to 68% under disturbed conditions. Overall, native cover was lowest in disturbed plots of Montana, where invasibility was highest.

Nitrogen availability (NO_3^-) was higher in Montana than La Pampa ($F_{1,17} = 6.8$, $P = 0.019$; Fig. 1d), with mean levels differing by 120%. Disturbance increased NO_3^- ($F_{1,17} = 53.5$, $P < 0.0001$), with an increase of 180% in mean values attributable to this factor and no interaction with system (system \times disturbance: $F_{1,17} < 0.1$, $P = 0.95$). Given these additive effects, NO_3^- was highest in disturbed plots of Montana, where invasibility was highest. Phosphorous (P) availability did not differ significantly between systems ($F_{1,17} = 2.7$, $P = 0.12$) or by disturbance treatment ($F_{1,17} = 0.4$, $P = 0.52$; Appendix S1: Fig. S1a). However, these factors interacted, with disturbance tending to reduce P in Montana vs. increase it in La Pampa ($F_{1,17} = 9.6$, $P = 0.007$). Even so, disturbance effects on P were small in both systems. Potassium (K) availability was lower in Montana ($F_{1,17} = 32.5$, $P < 0.0001$), but was unaffected by disturbance in either system (disturbance: $F_{1,17} = 0.1$, $P = 0.76$; system \times disturbance: $F_{1,17} = 0.1$, $P = 0.82$; Appendix S1: Fig. S1b).

In models evaluating overall relationships between invasibility and individual ecological covariates (i.e., excluding experimental factors from models; see Appendix S1: Table S2 for all test statistics and model details), invasibility varied negatively with both native cover ($P < 0.0001$) and K ($P = 0.048$) vs. positively with NO_3^- ($P < 0.0001$; Fig. 2). Invasibility did not vary significantly with either native richness or P ($P > 0.17$). Across individual covariate models, native cover accounted for the most variation in invasibility (ΔAIC_c

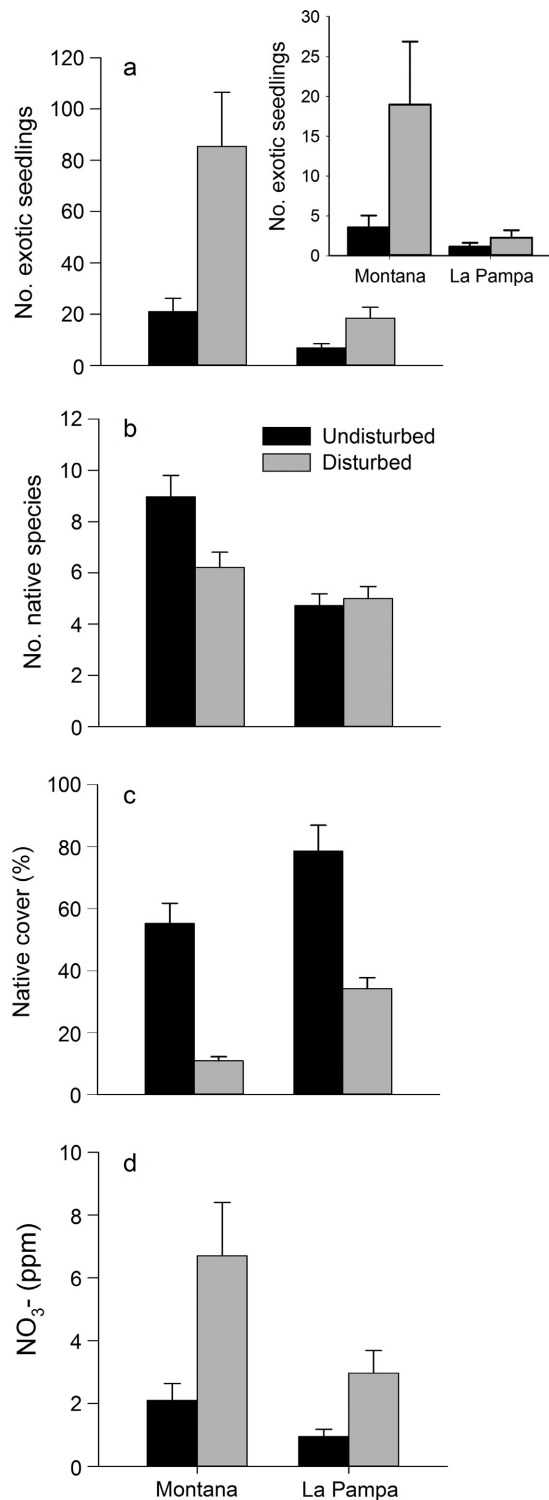


FIG. 1. (a) Invasibility as measured by the number of seeded exotic plants (inset shows data for the subset of six exotics sown in both ranges), (b) native species richness, (c) native cover, and (d) nitrogen availability in disturbed and undisturbed plots in Montana, USA and La Pampa, Argentina. Values are means \pm SE.

for remaining models = 40–90) and was the only covariate performing better than the model containing experimental factors alone ($\Delta AIC_c = -18$). In the multivariable

model containing all ecological covariates, invasibility again showed a negative relationship with native cover ($P < 0.0001$) and a positive relationship with NO_3^- ($P = 0.0005$). However, invasibility also correlated positively with native richness in the multivariable model ($P = 0.015$), while neither P nor K showed significant relationships ($P > 0.7$). Removal of native cover from the multivariable model caused the largest decrement in model quality ($\Delta AIC_c = 49$), with removal of NO_3^- and native richness causing relatively small decrements ($\Delta AIC_c = 7$ and 3, respectively) and remaining covariates having little effect ($\Delta AIC_c = -2$). Despite weak contributions of covariates other than native cover, the multivariable model performed better than individual covariate models ($\Delta AIC_c < -3$).

In models evaluating relationships between invasibility and individual ecological covariates while accounting for system and disturbance treatments (see Appendix S1: Table S3 for all test statistics and model details), invasibility varied negatively with native cover ($P < 0.0001$), and this relationship did not vary significantly by system or disturbance ($P < 0.05$). However, invasibility varied positively with native species richness in La Pampa but not in Montana (richness \times system: $P = 0.008$). In addition, relationships between invasibility and productivity varied by both system and disturbance treatment (productivity \times system \times disturbance: $P = 0.006$); in disturbed plots, positive relationships were evident in both systems, while in undisturbed plots, this relationship became steeper in Montana vs. negative in La Pampa. Invasibility was also positively associated with NO_3^- in disturbed but not undisturbed plots ($NO_3^- \times$ disturbance: $P = 0.013$). Neither P nor K varied significantly with invasibility ($P > 0.1$).

Resilience to disturbance was strongly linked to provenance shifts in naturally invaded, unseeded plots. Prior to treatment, plant cover was strongly biased toward native vs. exotic species ($P < 0.0001$), although the native advantage was less pronounced in Montana than La Pampa (system \times provenance: $P < 0.0001$; Appendix S1: Table S4; Fig. 3). These patterns did not differ between disturbed and undisturbed plots prior to treatment ($P > 0.4$ for all disturbance effects). However, in the first year after treatment, the advantage of natives over exotics diminished in disturbed vs. undisturbed plots (disturbance \times provenance: $P < 0.0001$), particularly in Montana (system \times disturbance \times provenance: $P < 0.0001$; Appendix S1: Table S4; Fig. 3). Indeed, only in disturbed plots of Montana did native species lose their strong cover advantage over exotic species, as evident through the fourth post-treatment year (Appendix S1: Table S4; Fig. 3). Native cover in disturbed plots was still depressed 4 yr after treatment in Montana vs. reaching undisturbed levels by post-treatment year two in La Pampa. Conversely, exotic cover remained elevated by disturbance through post-treatment year four in Montana, while not varying by disturbance in any year in La Pampa. Evaluation of responses in terms of species richness produced similar results (Appendix S1: Fig. S2, Table S4). Examination of patterns by life history strategy (Appendix S1: Table S5, Fig. S3) showed that native perennial species consisting primarily of bunchgrasses represented

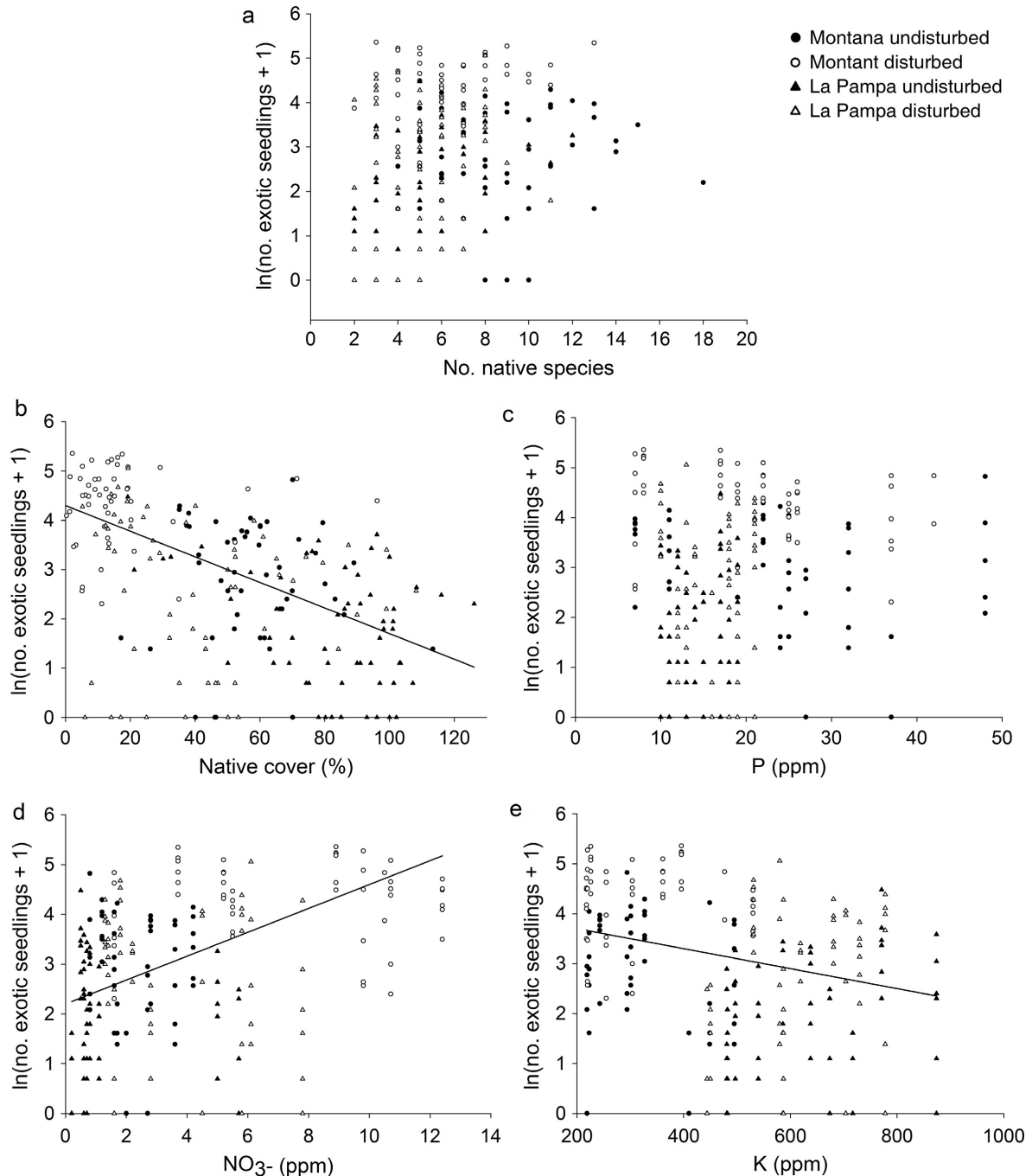


FIG. 2. Invasibility (number of seeded exotic plants) vs. (a) native species richness, (b) native cover, and soil (c) NO_3^- , (d) P, and (e) K, as measured in disturbed and undisturbed plots in Montana, USA and La Pampa, Argentina. Lines depict significant relationships ($P < 0.05$) in single-covariate generalized linear mixed models that omitted experimental factors.

the majority of cover in both systems prior to treatment. In Montana, disturbance depressed this group while promoting exotic annuals. In contrast, disturbance had relatively weak and fleeting effects in La Pampa, with native perennial species retaining their cover advantage over other groups. In both Montana and La Pampa, annual vs. perennial life history strategies were much more strongly represented in the exotic ($\geq 70\%$ of species) than the native species pool ($< 40\%$ of species; $\chi^2 > 11.0$, $P < 0.001$; $n = 133$ and $n = 97$, respectively; Appendix S1: Fig. S3).

DISCUSSION

Research focused on diversity as a primary driver of invasibility has failed to produce general understandings of community invasibility (Fridley et al. 2007). However, results from these studies have accrued evidence that invasibility is an emergent property influenced by multiple processes, as proposed by Lonsdale (1999). Here, we applied the fluctuating resource hypothesis (FRH), which encapsulates the emergent nature of invasibility in terms of resource

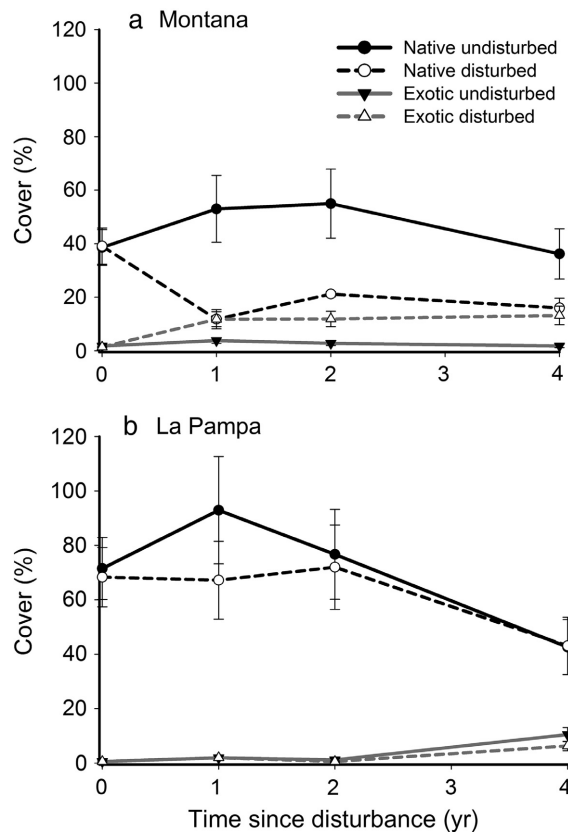


FIG. 3. Changes in native and exotic cover (mean \pm SE) over time in undisturbed and disturbed plots experiencing ambient seed rain (no seeds added) in (a) Montana, USA and (b) La Pampa, Argentina, as determined via generalized linear mixed models.

availability, as a framework to evaluate how diversity, productivity, soil nutrient availability, and resilience related to invasibility in the context of experiments that crossed disturbances with exotic seed addition in two grassland systems. We found that disturbance increased invasibility in both systems, as expected. However, Montana grasslands were over three times more susceptible to invasion than La Pampa grasslands, particularly when disturbed, despite having 90% higher species richness and 30% lower productivity when undisturbed. Soil nutrient availability varied between systems, but only nitrogen availability correlated with invasibility. Overall, native plant cover appeared to best explain variation in invasion outcomes within and between systems. La Pampa's low-diversity, high-productivity grasslands had high native cover and low nitrogen availability associated with low invasibility in undisturbed conditions. Native cover in these communities also rapidly recovered from disturbance to minimize resource availability and exotic invasion. In contrast, in Montana's high-diversity, low-productivity grasslands, native plant cover was substantially lower and nitrogen availability higher in undisturbed communities that were readily invaded. Moreover, relatively sluggish native responses to disturbance resulted in weak initial recovery of native cover, while exotics rapidly exploited the resource pulse under ambient seed rain. These results suggest that baseline resource capture rates and recovery of resource capture by native plants following disturbance may drive

community invasibility more than diversity or productivity, as predicted by FRH. However, they also demonstrate a provenance bias wherein exotics benefitted more than natives following disturbance in Montana. This provenance bias cannot be explained by FRH. However, we suggest that it can be explained by considering potential biogeographic influences on the balance of exotic vs. native traits represented in local species pools.

Our results supported several predictions of FRH. We found that invasibility increased following disturbance coincident with higher soil nutrient availability, presumably due to reduced nutrient uptake by resident natives. These results are consistent with many disturbance studies (e.g., Gross et al. 2005) and support Predictions 2 and 3 of FRH. Our finding that the more invulnerable system exhibited higher species richness and lower productivity was inconsistent with the notions that invasibility should be reduced by high diversity (Elton 1958) and low productivity (e.g., Stohlgren et al. 1999), even at 1-m² plots scales. However, these results supported Predictions 6 and 7 of FRH, which postulate that neither diversity nor productivity should necessarily predict invasibility. In fact, diversity–invasibility and productivity–invasibility relationships varied between systems and by disturbance treatment. While species richness contributed to the multivariable model explaining invasibility, positive richness effects were strongly overshadowed by negative effects of native cover. Fewer studies have examined the effect of resilience on invasions (e.g., Hierro et al. 2016), but our results demonstrated that the more resilient system, the one that recovered to its pre-disturbance cover state more quickly, was more resistant to invasion, consistent with Prediction 4 of FRH. Collectively, these findings support the premise that invasibility is an emergent community property, not well predicted by diversity or productivity alone in natural systems (Stohlgren et al. 1999, Davis et al. 2000). However, we found that resident species cover and its resilience to disturbance predicted variation in invasibility within and between systems, likely reflecting the role of resident natives in capturing available resources to impede invasion. In support, native cover and nitrogen availability were negatively correlated across the treatments ($F_{1,35} = 46.9$, $P < 0.0001$; Fig. 1c, d).

Our results suggest that plant cover (or biomass) may provide a tractable index of invasibility as a reciprocal metric of resource availability. This finding is heartening given the difficulty associated with directly estimating resource availability, likely the key determinant of invasibility. However, we caution that cover metrics may best predict variation in invasibility within communities, where resource inputs, diversity, productivity, and other factors are conditioned by community context. In our case, cover predicted differences in invasibility between systems reasonably well, but this was likely because differences in cover between the systems aligned with differences in resource uptake. While cover should generally vary negatively with resource availability within systems, the specific relationship may differ among systems because communities can differ substantially in their capacities and efficiencies for resource uptake. In such cases, cover alone may not predict differences in invasibility among systems. However, resilience to disturbance, as measured by the recovery of plant cover to ambient levels following disturbance, may provide an integrative metric of

resource use efficiency that better reflects differences in invasibility across systems, as demonstrated in our case study (see also Chambers et al. 2014). In short, resilience, which is an emergent community property, may provide a better metric of invasibility than individual community attributes such as diversity or productivity, in part because it integrates cover–resource-use relationships.

In contrast to our above findings supporting predictions of FRH, our results did not support the prediction that invasion outcomes following disturbance should be blind to provenance. Rather, we found strong conditional effects of provenance on these outcomes. We predicted that if invasion was indifferent to provenance, then under ambient conditions, the representation of natives vs. exotics should not differ in disturbed relative to undisturbed plots. In La Pampa, communities rapidly recovered from disturbance to retain high representation of natives. However, in Montana, the weak recovery of natives following disturbance resulted in a shift in composition from 93% to only 50% native cover, with a reciprocal increase in exotics (Appendix S1: Fig. S3). Importantly, the community appeared to equilibrate to this new invaded state, as this pattern persisted 4 yr after treatment (Fig. 3) reflecting the high susceptibility of Montana's Intermountain grasslands to transformation by exotic plant invasions (Pearson et al. 2016).

These results provide important context for understanding how provenance influences invasions. Numerous authors have argued that the process of invasion is indifferent to species origins (Huston 1994, Davis et al. 2000, 2011), while others have countered that the ubiquitous success of exotic invaders indicates an important role of provenance in invasion outcomes (Hierro et al. 2005, Simberloff 2011). According to succession theory, disturbed conditions associated with high resource availability and low competition should favor species that exhibit more ruderal life history strategies over more competitive or stress-tolerant strategies (Grime 1977, Glenn-Lewin et al. 1992, Prach et al. 1997). Hence, theory predicts that disturbance should shift community composition according to these strategies and associated traits (Grime 1977) regardless of species' origins (*sensu* Davis et al. 2000). Understanding how provenance can influence invasions in this context requires consideration of extrinsic community assembly processes unique to biological invasions (Pearson et al., 2018). In the context of community assembly theory, disturbance could favor exotics over natives if (1) exotic donor pools are disproportionately biased toward ruderal species relative to native species pools (due to inherent biogeographic differences in species composition [Kalusová et al. 2017] or due to introduction pathways or establishment filters favoring exotic species bearing such traits [Mack and Lonsdale 2001]), (2) exotics express ruderal/competitive traits more strongly than the natives (due to stronger selection on those traits in the native range or introductions of species bred by humans for such traits [Mack 1989, Williams and Baruch 2000, Kalusová et al. 2017]), or (3) humans elevate propagule pressure of exotics over that of the natives (Lockwood et al. 2005).

In our study, we did not quantify ambient propagule pressure, but in evaluating local species pools relative to annual vs. perennial life history strategies, we found evidence that

these first two extrinsic processes likely conditionally facilitated the provenance bias that we observed following disturbance in unseeded plots. Annual strategies were more strongly represented than perennial strategies in the exotic vs. native species pools in both systems (Appendix S1: Fig. S3). In Montana, this difference appeared to contribute to the shift in the balance of life history strategies by provenance from native perennials prior to disturbance toward exotic annuals after. Additionally, the stronger response of exotic vs. native annuals held after controlling for the number of species responding, suggesting that the species-level performance also differed by provenance, with exotic annuals expressing ruderal traits more strongly than their native counterparts. In contrast, in La Pampa both pre- and post-disturbance communities were dominated by native perennials. Although annuals increased following disturbance in this system, the shift was small, short-lived, and not biased by provenance. We attribute the differential provenance effects by system to the fact that in the harsher Montana environment, native perennials are largely stress-tolerators that are slow to respond to disturbances and resource influxes (see Maron et al. 2012, Pearson et al. 2017, but see Taylor et al. 2017), whereas in the more hospitable and productive La Pampa system, many native perennials are highly competitive species that are quick to recover from disturbance, allowing them to preempt both native and exotic annuals. These results illustrate how extrinsic community assembly processes that may bias local species pools in favor of certain exotic traits may play out very differently depending on the traits of resident species and their efficiency in responding to resource fluctuations.

Overall, we found that FRH provides a more complete framework for understanding invasibility than approaches emphasizing single factors like diversity because it considers invasibility as an emergent property linked to community resource economics. In this light, our results suggest that plant cover/biomass may provide a tractable metric of invasibility within communities by reflecting resource capture levels. However, FRH cannot explain why exotic plant invaders commonly outperform natives following disturbances. This provenance bias can only be understood by placing FRH within a broader community assembly framework that integrates extrinsic factors influencing exotic invasions such as donor pools, introduction filters, and propagule pressure (Pearson et al., 2018). FRH also ignores the effects that processes other than plant competition have on invasibility such as seed predation (e.g., Maron et al. 2012, Pearson et al. 2014a,b). Placing FRH in the context of community assembly theory allows for the incorporation of both extrinsic and intrinsic processes and expands our ability to explain invasion outcomes.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2235/supinfo>

DATA AVAILABILITY

Data associated with this study are available from the Dryad Data Repository: <https://doi.org/10.5061/dryad.cn0q14t>