Buffelgrass (*Pennisetum ciliare*) Invades Lands Surrounding Cultivated Pastures in Sonora, Mexico

Jacob C. Brenner and L. Leann Kanda*

We examined relationships between land disturbance and the extent and abundance of exotic buffelgrass (*Pennisetum ciliare*) at the interface of cultivated pastures and native desert lands in Sonora, Mexico. Plot and transect surveys of lands inside and outside pasture fences and general linear mixed models revealed complex relationships among buffelgrass, native vegetation, distance from pasture fences, and three categories of land disturbance (undisturbed, moderate, and severe). Results illustrate that buffelgrass invasion is extensive in lands surrounding pastures, and that buffelgrass abundance declines steeply with distance from pasture fences. The role of disturbance is weak but significant in its interaction with distance from the fence. Buffelgrass is more successful at colonizing severely disturbed lands than native vegetation, and its decline in abundance on severely disturbed lands is relatively more gradual than on other disturbance regimes, so landscapes where severely disturbed lands are interspersed with buffelgrass pastures could become centers of extensive buffelgrass invasion. In light of its potential to transform the Sonoran Desert, buffelgrass outside pastures warrants attention in a region-wide control scheme, as well as in future research, which ideally would involve remote sensing.

Nomenclature: Buffelgrass, *Pennisetum ciliare* (L.) Link.

Key words: Arid/semiarid lands, cattle ranching, invasive alien species, pasture cultivation, Sonoran Desert conservation.

The Sonoran Desert of southwestern North America is among the most diverse arid ecological systems in the world (Nabhan and Plotkin 1994; Turner and Brown 1982), hosting an extraordinary native flora and uncommon ecological richness (Dimmit 2000). It is among 200 global ecoregions warranting special attention from conservationists (Olson and Dinerstein 1998), and it is valued locally by a variety of stakeholders (Pima County Government 2006). Today, the Sonoran Desert is experiencing the greatest land transformation and demographic change in its human history (Brusca and Bryner 2004), owing in large part to a 20th-century boom in commercial cattle ranching (Brenner 2011). Furthermore, it is a hotspot of land-use conflict (Sayre 2002; Sheridan 2007) that presents significant conservation challenges (Búrquez and Martínez-Yrizar 2006; Nabhan and Holdsworth 1998). Nevertheless, despite a long history of human impact (Bahre 1991), rapid recent changes, and a contentious land-use situation, the Sonoran Desert remains largely intact, and thus it offers great conservation opportunities (Mittermeier et al. 2003).

One of the most widespread and serious threats to the Sonoran Desert ecoregion is buffelgrass [*Pennisetum ciliare* (L.) Link], an invasive exotic forage introduced on ranches throughout northern Mexico starting in the 1950s (Van Devender et al. 2009). Buffelgrass pastures are expanding especially quickly across the desert rangelands of Mexico's northwestern state of Sonora. Here, since the early 1970s, nearly one million hectares of desert scrub have been cleared, tilled, and sown with buffelgrass to create cattle pastures (Franklin et al. 2006). The pasture conversion process entails profoundly negative consequences for native Sonoran vegetation (Lyons et al. 2009; Morales-Romero et al. 2012; Morales-Romero and Molina-Freaner 2008), particularly through the introduction of a grass-fire cycle in a fire-intolerant ecosystem (Brooks et al. 2004; McDonald and McPherson 2011). Although wildfire triggers a rapid transformation of Sonoran Desert ecosystems, the threat emerges slowly as buffelgrass naturalizes on Sonoran Desert lands (Cox et al. 1988; Ibarra-F. et al. 1995) via drought tolerance, vegetative reproduction, and prolific seed production (Burgess et al. 1991; Mack 2002; Van Devender and

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* First author: Assistant Professor, Department of Environmental Studies and Sciences, Ithaca College, 953 Danby Rd., Ithaca, NY 14850 USA; second author: Assistant Professor, Department of Biology, Ithaca College, 953 Danby Rd., Ithaca, NY 14850 USA; Corresponding author's E-mail: jbrenner@ithaca.edu

Management Implications

Buffelgrass (*Pennisetum ciliare*) is widely understood to be a threat to the Sonoran Desert because of its ability to outcompete native vegetation and introduce a new wildfire regime. Conservationists and land managers tend to focus on buffelgrass as it impinges on protected and urbanized areas, neglecting unprotected rural lands such as ranches. In Sonora, Mexico, ranchers aggressively cultivate buffelgrass, and the resulting pastures serve as large seed sources. Furthermore, buffelgrass pastures in Sonora tend to be surrounded by mixed-use landscapes, with soils disturbed in different ways and to different degrees. This research demonstrates that buffelgrass extends far beyond pasture boundaries, and its invasion of the Sonoran landscape is associated with disturbed (particularly severely disturbed) lands. These findings suggest that an integrated region-wide buffelgrass control scheme must take seriously the existing widespread invasion from Sonoran pastures, as well as the great potential for further invasion facilitated by disturbance in Sonora's heterogeneous and dynamic landscapes. Land managers should not continue to neglect the important role of pastures and their interactions with their surrounding lands in promoting buffelgrass invasion in Sonora, Mexico.

Dimmitt 2000) (Figure 1). Habitat suitability models project that buffelgrass could invade most of southern Arizona USA (Olsson 2006) and Sonora Mexico (Arriaga et al. 2004) in the coming decades. Although research for many years has warned in general terms that pasture conversion poses a threat to Sonoran Desert ecosystems (Búrquez-Montijo et al. 2002; Yetman and Búrquez 1994), until now the link between pastures and surrounding desert lands vis-à-vis buffelgrass invasion has remained unexamined.

While different land-use impacts play varied and complex roles in plant invasions (Decker et al. 2012), there is broad agreement on the potential of soil or land disturbance to increase a landscape's ''invasibility'' (Davis et al. 2000; Levine et al. 2003; Lonsdale 1999; Rejmanek 1989; Thompson and Grime 2005). Research has shown that buffelgrass invasion is facilitated by disturbances, both historical (Burgess et al. 1991) and contemporary (Búrquez-Montijo et al. 2002). For example, roadsides (Figure 1) appear to serve as pathways for invasion into undisturbed desert scrub (Van Devender and Dimmitt 2006), as do land clearings for residential development (De la Barrera 2008). Hypothetically, pastures serve as origins of buffelgrass invasion (Stevens and Falk 2009), with land disturbance facilitating the colonization of surrounding undisturbed areas. However, empirical research has yet to establish this particularly important invasion pathway. The objective of this study was to characterize disturbances in the band of land surrounding pastures, the ''environmental envelope'' (Stohlgren and Schnase 2006) where buffelgrass invasion in this region starts. What do patterns of buffelgrass distribution and abundance at the pasture–desert interface reveal about land disturbance and its relationship with buffelgrass invasion?

Materials and Methods

Study Site. This study took place on a 10,687 km^2 (4126 m^2) section of arid rangeland surrounding Caborca, Sonora, Mexico, a center of pasture conversion (Brenner 2010) where large ranches are bordered by native Arizona Upland Sonoran desert scrub under various degrees of physical land disturbance. We documented evidence of buffelgrass expansion by: (1) recording and categorizing disturbance on lands surrounding buffelgrass pastures; (2) measuring the extent of buffelgrass outside pasture boundaries; (3) measuring the abundance of buffelgrass and native vegetation on lands surrounding pastures; and (4) statistically analyzing associations of land disturbance with buffelgrass and native vegetation.

Sampling. Vegetation sampling began with field mapping of buffelgrass pastures using a handheld Global Positioning System (GPS) receiver. We used high-spatial-resolution digital imagery to guide a census of active buffelgrass pastures throughout the study area, resulting in a 61-pasture spatial dataset. From this we selected a random sample of seven pastures for plot and transect surveys.

Surveys. Pastures were all irregular polygons defined by 4 to 14 boundary segments. Each segment separated the pasture interior from the exterior landscape, which we categorized for disturbance in one of three ways (Table 1). Undisturbed lands had intact native vegetation and showed no signs of perturbation in vegetation or soils. Moderately disturbed lands had intact native vegetation but showed signs of moderate grazing and animal or vehicular traffic. Severely disturbed lands had been disrupted by either heavy grazing, heavy traffic, or in some cases tilling. These sites exhibited compromised (or removed) native vegetation, as well as heavily impacted soil. For example, we would characterize a grazed native rangeland as moderately disturbed because of the presence of clipped vegetation, tracks, and scat. We would characterize an abandoned agricultural parcel as severely disturbed, because it was apparent that native vegetation had been cleared and tilled for cultivation.

We positioned 61 200 m (656 f)-long transects across the sampled pastures' boundary segments, avoiding indentations (concavities) where transects might overlap (Figure 2). We oriented each transect perpendicular the fence line at the boundary segment midpoint, with 100 m inside and 100 m outside the fence. Starting at the fence, we recorded the linear distance of buffelgrass occurrence (colonization) outside the pasture boundary, which in some cases continued beyond the transect's 100 m endpoint.

Next, we placed 2 m by 2 m vegetation plots at 10 m transect intervals, including a plot at the fence (0 m) on

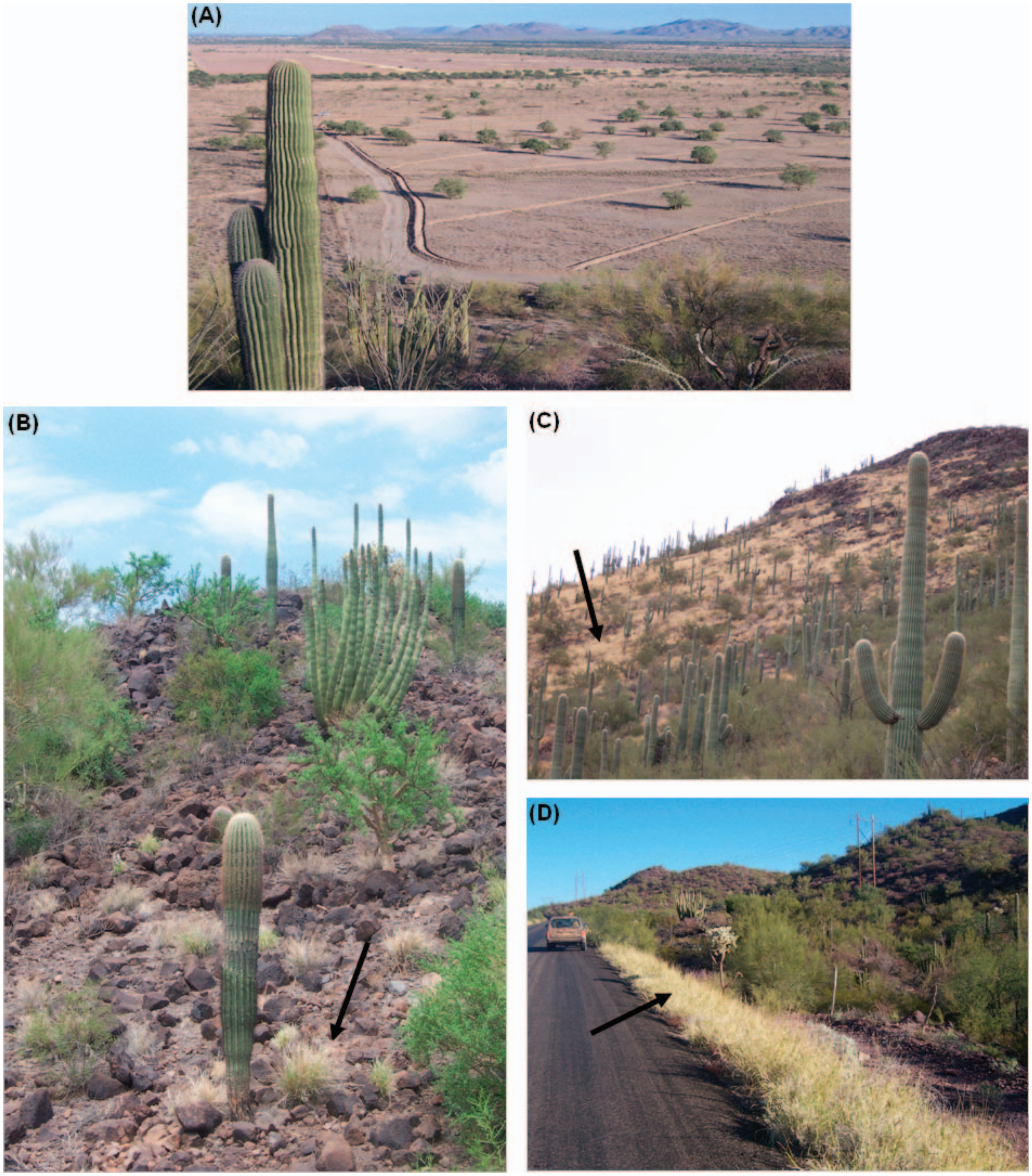

Figure 1. Buffelgrass pasture and invasion in Sonoran desert scrub vegetation. Arrows show buffelgrass among native vegetation. Pastures are cultivated in a patchwork of variably disturbed lands (A), with invasible abandoned agricultural lands (A, background left) interspersed with cultivated pastures (A, midground) and undisturbed desert scrub (A, foreground). Incipient invasion (B), with buffelgrass individuals sparsely distributed among native plants, quickly advances to a point where there is sufficient buffelgrass cover to propagate wildfire (C). Anecdotal observations show disturbed areas, such as roadways (D), linking large seed sources, such as pastures, with surrounding invasible lands, a pathway for plant invasions observed in other locales (Meunier and Lavoie 2012). (Color for this figure is available in the online version of this paper.)

Table 1. Criteria for characterizing physical land disturbance in transects outside pasture boundaries.

Undisturbed

- Intact native vegetation (Arizona Upland desert scrub)
- No sign of grazing or traffic
- No change in land-cover type

Moderately disturbed

- Intact native vegetation (Arizona Upland desert scrub)
- Light grazing (scat, clipped vegetation, trampled soil)
- Moderate animal or vehicular traffic
- No change in land-cover type

Severely disturbed

- Compromised or removed native vegetation
- Heavy grazing (scat, clipped vegetation, trampled soil)
- Heavy animal or vehicular traffic
- Tilling
- Change in land-cover type

either side. With each transect having 22 plots (11 inside and 11 outside), the plot total for all 61 transects was 1,342 (671 inside and 671 outside) (Figure 2). We used these plots for measuring buffelgrass and native vegetation abundance.

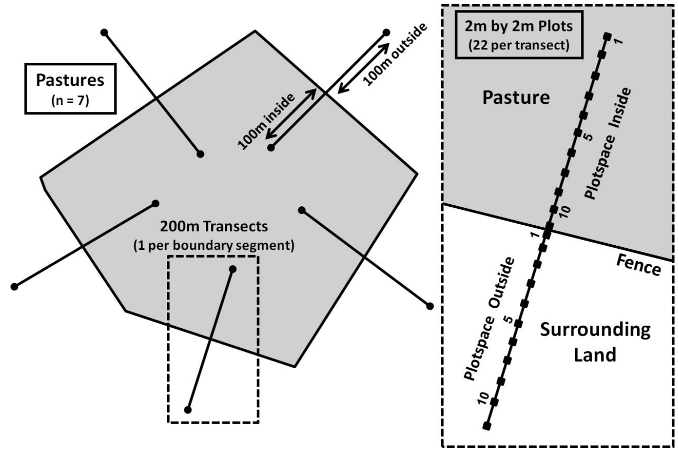

Figure 2. Vegetation sampling methods included randomly selecting seven pastures from among the 61 pastures mapped across the study area. Transects 200 m in length were placed across the pasture boundaries so that 100 m were inside and 100 m were outside the pasture. Plots 4 m^2 in size were then placed at 10 m intervals along each transect, including on either side of the fence intercept, for a total of 22 plots per transect, 11 inside and 11 outside pasture boundaries (in total, 671 inside and 671 outside). Disturbance categories (un-, moderately, and severely disturbed) varied by transect, and were recorded only for outside plots.

Analysis. *Spatial Distribution of Vegetation.* We used generalized linear mixed models with Poisson distribution (glmer in R package lme4) (Bates et al. 2011; R Development Core Team 2011) to examine the effects of plot position on the number of buffelgrass individuals per plot in two ways: (a) along the transect gradient (plotspace); and (b) inside versus outside the pasture fence (in–out). Pasture and transect nested in pasture were included as random variables. Individual plot was also included as a random variable to account for overdispersion in the buffelgrass counts (Elston et al. 2001). Since a nonlinear distribution seemed likely (particularly for buffelgrass), we examined models that included not only plotspace and in–out, but also the nonlinear term, plotspace^2, as fixed factors. We built a series of nested models including these terms individually, additively, and with interaction. We used analysis of variance (ANOVA) to compare these nested models and identify when additional terms significantly improved model fit. We used a similar procedure to analyze native vegetation abundance. We checked the residual plot of each model to assure that it met multivariate assumptions.

Disturbance outside Pastures. As a result of the pasture cultivation process (Brenner 2010) all lands inside pasture fences met our criteria for severe disturbance. Outside pasture boundaries on adjacent parcels, the land disturbances we observed and categorized varied according to past and current land use. Pastures could be surrounded on different sides across different boundary segments by land parcels under different categories of disturbance. We therefore measured and analyzed the relationships between abundance of buffelgrass or native vegetation and disturbance at the transect level. We first considered generalized linear mixed models (Poisson distribution) with disturbance as a fixed factor, with pasture and transect as random factors. Again, individual plots were included as an extra random factor to account for overdispersion. Effects among undisturbed, moderately disturbed, and severely disturbed categories were compared with Tukey multiple comparisons of means. We also examined models that included plotspace and nonlinear plotspace effects. As before, we compared nested models with ANOVA to locate those with factors that significantly improved model fit.

To examine whether transect-level disturbance related to the distance buffelgrass extended outside pasture boundaries, we used a linear mixed model including disturbance as a fixed factor (with plots here serving as replicates clustered by transect) and pasture as a random factor. Significance of disturbance as a factor was determined by ANOVA comparing this model to a model without disturbance. Buffelgrass extent was log-transformed to meet normality assumptions.

Results and Discussion

Spatial Distribution of Vegetation. The mixed model that best fits buffelgrass abundance across all transects

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Table 2. Mixed model fixed effects predicting buffelgrass abundance across all plots. Pasture and transect were included as nested random effects. Significant p-values are in bold.

	Estimate	SE	z	p
Intercept	2.35	0.13	17.82	**< 0.0001**
Plotspace*	−0.09	0.05	−1.99	**0.047**
In–Out (Outside)	−0.70	0.19	−3.59	**< 0.001**
Plotspace^2	0.01	0.00	1.62	0.105
Plotspace × In–Out (Outside)	−0.50	0.08	−6.19	**< 0.0001**
Plotspace^2 × In–Out (Outside)	0.03	0.01	4.87	**< 0.0001**

* Plotspace runs from 1–11; inside the fence plotspace 1 is central to the pasture (101 m inside fence), outside the fence plotspace 1 is adjacent to the fence (0m).

includes plotspace (transect gradient), plot position inside or outside the fence (in–out), and both linear and nonlinear interactions among these terms (Table 2). As expected, the abundance of buffelgrass is considerably higher inside pastures than on surrounding lands (Figure 3A). However, while buffelgrass is not as dense even immediately outside the fence as inside, its distribution on surrounding lands is extensive (with a site-wide extent maximum of 500m). Outside pastures there is a significant nonlinear decline in buffelgrass abundance with distance from the fence. A smaller but significant linear decline in buffelgrass occurs within the pasture as transect plots approach the fence.

The strong discrepancy between the distance outside the fence at which buffelgrass is common (< 20 m) and the greatest extent at which buffelgrass was detected (500 m) suggests that invasion begins as a sparse, widespread dispersal that later fills in, perhaps fueled by propagule pressure in the pasture. Two implications of this pattern of colonization present challenges for buffelgrass control. First, the real edge of invasion may occur far from pastures or other large seed sources and be difficult to detect (Moody and Mack 1988). Second, the pattern suggests a process of saltation, whereby invasion proceeds in extensive jumps taken by a few colonizers, rather than as a steady, frontal advance (Davis and Thompson 2000). The limitations of this study (short-term duration, transect length, plot placement, etc.) prohibited a robust characterization of particular invasion dynamics, but future work should focus on this topic.

Across all transects, native vegetation abundance changes with plotspace and in–out, as well as a linear interaction between these terms (Table 3). As anticipated, natives are much more abundant in plots outside pastures. On plots inside pastures, natives are rare but become slightly more common closer to the fence (Figure 3B).

Disturbance outside Pastures. Ignoring the spatial position of plots along transects, the level of disturbance

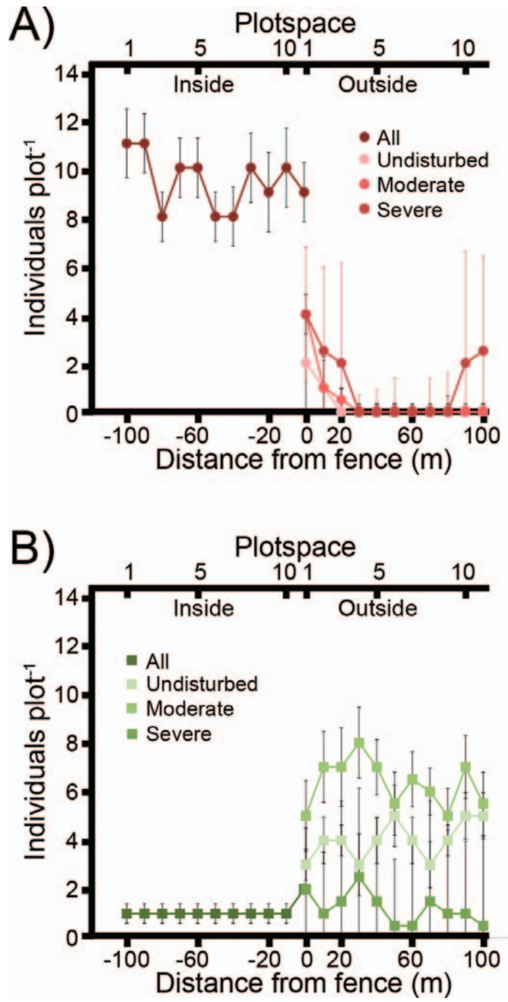

Figure 3. Median buffelgrass abundance (A) and native vegetation abundance (B) per plot along transects. Transects are labeled by meters from the fence, with positive distance outside and negative distance inside. Error bars represent 95% confidence intervals. (Color for this figure is available in the online version of this paper.)

outside pastures weakly influences the prediction of buffelgrass abundance. Severe disturbance tends to support higher buffelgrass abundance than no disturbance, but in multiple comparison this difference is nonsignificant ($p = 0.081$). However, the model fit is improved if it includes both linear and nonlinear plotspace terms and the interaction of disturbance with the nonlinear plotspace term (Table 4). As seen in the larger spatial distribution model, buffelgrass abundance declines steeply with distance from the pasture fence. However, the decline is significantly more gradual in severely disturbed areas (Figure 3), where buffelgrass abundance is relatively greater throughout the 20 m band immediately surrounding the pasture fence. There is also evidence that buffelgrass increases again beyond 90 m in severely disturbed areas, although this was highly variable.

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Table 3. Mixed model fixed effects predicting native vegetation abundance across all plots. Pasture and transect were included as nested random effects. Significant p-values are in bold.

	Estimate	SE	z	p
Intercept	−0.05	0.12	−0.47	0.639
Plotspace*	0.04	0.01	3.27	**0.001**
In–Out (Outside)	1.51	0.09	15.94	**< 0.0001**
Plotspace: In–Out (Outside)	−0.03	0.01	−2.50	**0.012**

* Plotspace runs from 1–11; inside the fence plotspace 1 is central to the pasture (101 m inside fence), outside the fence plotspace 1 is adjacent to the fence (0m).

A similar pattern emerges when examining the extent of buffelgrass along transects outside pastures (Figure 4). The median extent was higher in severely disturbed areas (195 m in severely disturbed areas vs 88 m in moderately disturbed areas and 120 m in undisturbed areas), but because of high variability among transects within each disturbance regime, a mixed model with disturbance as a factor was no better at predicting log (extent) than a model with random effects alone.

Outside the pasture fence, plotspace does not significantly contribute to a mixed model predicting native vegetation abundance, leaving only disturbance as a fixed effect. Severely disturbed areas host significantly reduced native abundance as compared to both undisturbed (Tukey contrasts; $z = -3.00$, $p = 0.007$) and moderately disturbed areas ($z = -5.45$, $p < 0.001$) (Figure 5). Moderately disturbed areas tend toward higher native abundance than undisturbed areas, but this is nonsignificant after correction for multiple comparisons ($z = 1.97$, $p = 0.118$).

Table 4. Mixed model fixed effects predicting buffelgrass abundance per plot outside of pastures. Pasture and transect were included as nested random effects. Significant p-values are in bold.

	Estimate	SE	z	p
Intercept	1.48	0.33	4.43	**< 0.0001**
Plotspace*	−0.75	0.08	−9.05	**< 0.0001**
Plotspace^2	0.04	0.01	5.39	**< 0.0001**
Disturbance (Moderate)	−0.02	0.42	−0.04	0.971
Disturbance (Severe)	0.30	0.51	0.60	0.547
Plotspace^2 × Disturbance (Moderate)	0.01	0.00	1.48	0.140
Plotspace^2 × Disturbance (Severe)	0.02	0.00	4.48	**< 0.0001**

* Plotspace runs from 1–11; outside the fence plotspace 1 is adjacent to the fence (0 m) and plotspace 11 is 100 m outside.

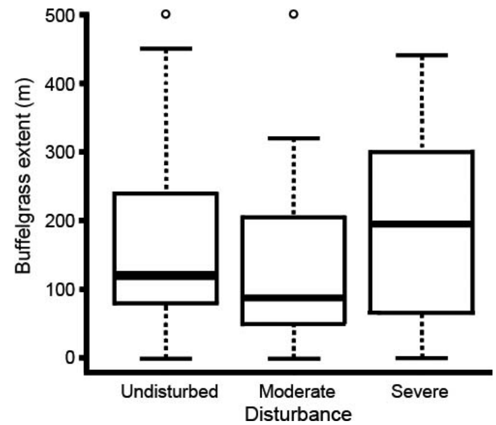

Figure 4. Furthest buffelgrass extent in meters outside the pasture fence for each disturbance regime.

An interesting interpretation arises from consideration of the coincidence of buffelgrass with native plants and its relationship with variable disturbance regimes (Figure 3A, B). Native vegetation is as abundant close to the pasture fence, where it coexists with dense buffelgrass, as it is 100 m away, where buffelgrass substantially declines. Native vegetation thus appears to be impacted by disturbance directly, not necessarily by competition with buffelgrass. Interactions between buffelgrass and native vegetation were not systematically assessed in this study, so inferences about competition here are limited. Studies elsewhere have established that significant competition occurs between buffelgrass and other native plant species (Lyons et al. 2009; McIvor 2003; Olsson et al. 2012). Clearly, more research is needed on this topic, particularly as concerns lands surrounding pastures.

This research shows clearly that buffelgrass is extensive and prevalent on desert lands surrounding cultivated pastures, and further that buffelgrass is disproportionately prevalent on disturbed (particularly severely disturbed) lands. Thus, there is obvious buffelgrass invasion risk in Sonora's mixed-use landscapes, where largely intact native plant communities are crisscrossed by arroyos, livestock and wildlife trails, ranch roads, and other small-scale disturbances. More troubling still is the large-scale land disturbance legacy of destructive trial-and-error land uses, including extensive heavy grazing (Bahre 1991), livestock intensification (Búrquez and Martínez-Yrizar 2000), and agricultural intensification (West 1993) followed by land abandonment. The most recent chapter in this land-use history, a decades-long boom in intensive, groundwater-irrigated agriculture (Almada Bay 2000) has faded in recent years because of falling crop prices, rising electric pumping costs, receding aquifers, and increasing drought conditions (Vásquez-León et al. 2003). When agricultural plots interspersed with pastures fail and are abandoned, they

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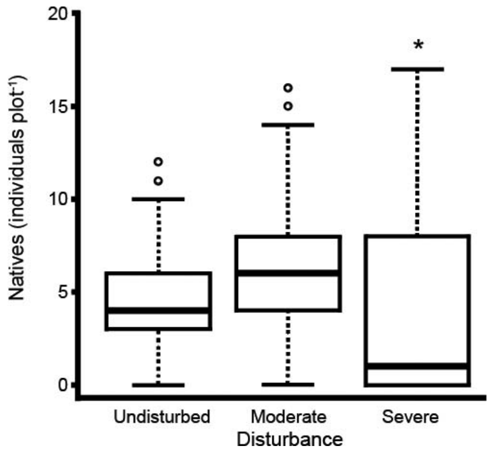

Figure 5. Native vegetation abundance per plot for each disturbance regime. * indicates severe disturbance has significantly lower abundance.

become susceptible to buffelgrass invasion given the fact that buffelgrass is the most successful local colonizer of severely degraded land.

Despite the fact that buffelgrass pastures occur throughout the state of Sonora (including southern thornscrub environments as well as Arizona Upland), pastures continue to be overlooked by many conservationists and dismissed as an ecological threat by Sonoran landowners and government officials (Brenner 2011). Their potential as origins of invasion in Sonora continues to be neglected while buffelgrass control and eradication efforts focus elsewhere in the Sonoran Desert on urban and protected natural areas (Stevens and Falk 2009). This dangerous oversight leaves Sonora's unprotected, but largely intact, desert landscapes at great risk, and it stands in the way of an integrated region-wide buffelgrass control program.

Field surveys of buffelgrass invasion on intact desert landscapes such as this are laborious, resource-intensive, and impossible in many cases given the remote location, hostile climate, and rugged terrain of many Sonoran ranches. Great benefits could accrue from investment in data and methods for remote sensing of buffelgrass as it invades Sonoran desert scrub. Some advances have been made on this front, but at present small colonies of buffelgrass within intact Sonoran Desert remain undetectable (Brenner et al. 2012; Franklin et al. 2006; Nagler et al. 2009). More research is needed on the relationships between pasture cultivation, land abandonment, and buffelgrass invasion, but from this study it appears that the simultaneous intensification of pasture management for livestock and abandonment of risky desert agriculture are turning rural Sonora's agricultural centers into crucibles for a new kind of landscape change driven by buffelgrass invasion.

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